SOIL SEED BANK VARIATION PATTERNS ACCORDING TO ENVIRONMENTAL FACTORS IN A NATURAL GRASSLAND[1]

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ABSTRACT - This research aimed to determine the soil seed bank and its relationship with environmental factors that have an influence in the distribution of the vegetation above the ground in an excluded area of natural grassland in the South of Brazil. Most of the 122 identified species in the seed bank were perennials. Data analysis indicated three distinct community groups, according to the size and composition of the soil seed bank in lowlands with permanent wet soils, in lowlands and in other areas. In general, lowlands were characterized by low-fertility soils, high moisture and aluminum contents, being spatially homogeneous habitats and, therefore, more restricted to vegetation heterogeneity than other parts of the relief. Environmental factors most associated with soil seed bank size and composition were relief position and their co-related soil variables such as: soil moisture content, potassium content, organic matter, basic saturation of cation exchange soil capacity, exchangeable basics sum of the soil and clay soil content. According to that, relief position, associated with combined effects of soil chemical properties related to it, determines the observed variation pattern of the soil seed bank, as a reflection of the vegetation above the area.

Index terms: buried seeds, moisture, grassland ecosystem.

PADRÕES DE VARIAÇÃO DO BANCO DE SEMENTES DO SOLO DE UM CAMPO NATURAL EM FUNÇÃO DE FATORES DE AMBIENTE

RESUMO - O trabalho objetivou determinar o banco de sementes presente em uma área excluída de campo natural localizado na região sul do Brasil e sua correspondência com fatores abióticos que possuem influência no desenvolvimento e distribuição da vegetação presente. Foram identificadas 122 espécies, sendo a maioria perenes. Observou-se uma nítida separação entre o banco de sementes dos campos uliginosos, o banco de sementes de áreas baixas não alagáveis do relevo e o banco de sementes das outras porções do relevo. Os extremo inferiores alagáveis do relevo (campos uliginosos) apresentaram solos menos férteis, com maiores graus de umidade e de alumínio, constituindo habitat espacialmente homogêneo e, portanto, mais restritivo à heterogeneidade da vegetação em relação às demais áreas. Os fatores do ambiente mais associados à composição e tamanho do banco de sementes do solo foram a posição do relevo e variáveis correlacionadas como: grau de umidade, teor de potássio, matéria orgânica, saturação da capacidade de troca catiônica por bases, soma de bases trocáveis e teor de argila do solo. Desta forma, a posição do relevo, associada aos efeitos combinados das propriedades químicas do solo dele decorrentes, determinaram o padrão de variação observado no banco de sementes do solo, através da influência na vegetação da área.

Termos para indexação: sementes enterradas, umidade, ecossistema campestre.

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INTRODUCTION

The Southern region of Brazil has an area around 10.5 million hectares of natural grasslands, which corresponds to 37% of total surface of Rio Grande do Sul state, with almost 400 species of Poaceae and 150 species of Fabaceae (Boldrini, 1997) contributing with 90% of food used for almost 14 million cattle and 5 million sheep (UCPEL/ITEPA, 2001). Besides sheep and cattle, the natural grassland feeds other domestic herbivores and wild fauna, all of which influence the natural vegetation present in the area. However, these natural grassland ecosystems are in a permanent state of degradation due to overgrazing, intensive burn and tillage practices. Wealth and heterogeneity are declining due to a drastic frequency reduction observed in the most palatable winter C3 Poaceae and Fabaceae species. An expressive number of these elements are considered endangered species. Successful guidelines for the recovery of these plants require the best scientific information concerning the ecological factors affecting the directional dynamic of this natural grassland ecosystem.

Generally the perenniality of most species can rely on vegetation propagation in a natural grassland ecosystem. However, Milberg (1992) claimed that soil seed bank (SSB) reflects the past local vegetation and absent species from vegetation that can sometimes stay buried in the soil for decades, and represents the most important regeneration strategy that occurs in terrestrial vegetation (Grime, 1989). Bekker et al. (1998) emphasized that where plant species have disappeared, due to catastrophic events such as burning, long dry spells and others, buried seeds can play an important role in the conservation and restoration of the plant community. The effect of SSB in maintaining a natural reserve of genetic biodiversity is also becoming more apparent in the context of declining biodiversity (Fenner, 1955).

Soil seed bank composition relies basically on past and present community vegetation production and composition, as well as on the seed longevity of each species (López-Mariño et al., 2000). Studies on seed bank composition have revealed considerable differences between soil seed banks under grassland communities (Bekker et al., 1997). According to the authors, the effects of fertilization or abandonment on the vegetation and soil seed bank were similar in the beginning, but then diverge in time, and in the case of fertilization this divergence occurs more rapidly, showing that soil fertility can affect differently both vegetation and the soil seed bank. It is also well-known that fluctuations in light, temperature, and moisture content of the soil are the main environmental factors that can affect seed dormancy and viability (Cook, 1980; Samimy & Khan, 1983; Egley, 1986; Hilhorst & Karssen, 1990; Karssen & Hilhorst, 1993; Baskin & Baskin, 1989, 1992), modifying soil seed bank size and composition.

Therefore, it is important to develop knowledge that contributes to a better comprehension of natural grassland ecosystem dynamics. The aim of this study was to determine the size and composition of soil seed banks present in these ecosystems and identify associations between the seed bank and different environmental factors of the study area, thereby establishing their effects on buried seeds.

MATERIAL AND METHODS

Site Description

The study was developed in an area of 100 hectares at the Agronomic Experimental Station of the Federal University of Rio Grande do Sul (UFRGS), in Eldorado do Sul-RS, South of Brazil (aproximately 30º05´27´´S and 51º40´18´´W). This area has been grazed in the last 30 years by cattle, sheep and occasionally by horses. There is no registration of fertilizer utilization or soil cropping disturbances.

The region's climate is humid subtropical Cfa, with average temperatures of 14ºC in the coldest months and 24ºC in the hottest months (SARS, 1979), and average annual precipitation of 1440 mm (Bergamaschi & Guadagnin, 1990).

Soil type is typical Dystrophic Red Argissoil (Embrapa 1999) in higher places and Gley in lower places (Mello *et al.,* 1966). There are patches of granitic outcrops on the banks of the Corticeiras river, which crosses the study area and in some places, in the nearby field close to a gallery forest (Focht, 2001).

Most of the vegetation present in that region is formed by dry short grasslands and gallery forest around streams and lowlands (Moreno, 1961). The physiognomy is very homogeneous and it is formed mostly by the Poaceae, Asteraceae, Fabaceae, Cyperaceae, Rubiaceae and Apiaceae species (Escosteguy, 1990; Boldrini, 1993). In a vegetation study by Focht (2001) in the same area, the most frequent species were *Paspalum notatum* Fl., *Andropogon lateralis* Nees, *Piptochaetium montevidense* (Spreng.) Parodi, *Oxalis* sp., *Rhynchospora microcarpa* Baldw. ex Gray, *Baccharis trimera* (Less.) DC. and *Eryngium horridum* Malme.

Soil Seed Bank Sampling

Twenty soil cores of 7.3cm in diameter (Roberts & Neilson, 1982; Medeiros & Steiner, 2002) were taken to a depth of 7cm, all of which were systematically distributed around each one of the 46 permanent squares of 0.75m^2 (1.5 x 0.5m) arranged in 18 transects located preferentially on relief gradients in upper area, intermediate and lower relief positions, with some of the last ones located in permanent wet areas (Focht, 2001). A total of 1854.15cm^3 were sampled in the site in March 2000, when most spring/summer species had finished seed dispersion. Each set of 20 soil cores from the same squares were pooled to provide one sample. Pooled samples were dried for three days, at 30 to 35ºC and stored in a refrigerator at 5ºC. After that, samples were broken in a pin mill (Tecnal), homogenized and weighed, thereby defining the work samples (1/20 of sample weight) (Medeiros & Steiner, 2002).

Work samples were spread out in aluminum trays (12 x 20cm), in a 3cm layer with equal volume of vermiculite (Favreto *et al.,* 2000; Medeiros & Steiner, 2002). The trays were then placed in a greenhouse to allow germination to occur (Gross, 1990), and kept moistened by surface irrigation. Air temperatures inside the greenhouse were monitored daily. Three germination cycles were done to promote germination of most seeds. To remove seed dormancy, trays were kept dry, between each germination cycle for a period of seven days. Seedlings were identified, counted and removed, at least once a week, when possible. Non-identified seedlings were transplanted to larger pots and grown to maturity for identification (Medeiros & Steiner, 2002).

Environmental Variables Analysis

As far as the other soil samples go, chemical analyses were also carried out. The following analyses were conducted: clay (%), pH (H_2O), P (mg.L^{-1}), organic matter (%), Al (cmol$_c$.L^{-1}), Ca (cmol$_c$. L^{-1}), Mg (cmol$_c$.L^{-1}), Al + H (cmol$_c$.L^{-1}), cation exchange capacity (cmol$_c$.L^{-1}), basic saturation of the cation exchange capacity (%), saturation of the cation exchange capacity with Al (%), proportion Ca/Mg, Ca/K and Mg/K, S (mg.L^{-1}), Zn (mg.L^{-1}), Cu (mg.L^{-1}), B (mg.L^{-1}) and Mn (mg.L^{-1}). With these analyses, the exchangeable basics sum (cmol.L^{-1}) was calculated by the following formula: S = (Ca + Mg) + K + Na (meg.100ml^{-1} or cmol$_c$.L^{-1}); Na (meg.100ml^{-1}) = ppm Na/230; K (meg.100ml^{-1}) = ppm K/ 390.

Soil was classified in classes of texture and fertility, according to Casalinho (1997). Data were interpreted and other variables were also sorted in classes (Comissão de Fertilidade do Solo-RS/SC, 1995).

Relief position (upland-1, intermediate sites-2, lowland-3) and soil moisture (moist only after rain-1, periodically wet-2, permanently wet-3) were determined in each square, the last one by tactile and visual estimate. However, the few transects (10,13,15 and 17) classified as upland (ES) are at the top of the hill. Furthermore, a few relief positions classified as lowland (EI) are in wet lowlands areas, while all intermediate positions (I) are in the middle part of the hill (Focht, 2001).

These variables were chosen due to their influence in the soil fertility and, consequently, in the vegetation growth and reproduction.

Statistics

Multivariate analyses were done using software MULTIV 2.0.3 (Pillar, 1997, 1994-2001) aiming at the detection of variation patterns of the SSB and its relation with environmental factors.

Cluster analysis of sample units, groups' significance tests, ordination, ordination axis significance tests and randomization tests were done using square root transformed data.

Species that identified each group (differential species) were sorted by randomization tests for each species individually, according to the cluster analysis. The test was similar as the one done by Wildi & Orlóci (1990) and Jancey (1979). Species were classified according to the calculated probability of the test, adding the information of percentage of presence and mean value of abundance when present (Mp), calculated by the formula: Mp = (total species number in the group x number of squares with the species)/total number of squares in the group.

RESULTS AND DISCUSSION

Apparently, three different vegetation physiognomies were identified in the study area environment. *Aristida* sp. and *Eryingium horridum* were physiognomically predominant in the upland vegetation communities. Intermediate sites were also dominated by these species. They were, however, more spread out and with lot of open soil gaps, while the other part of the vegetation was comprised of short height species. The Lowlands also had relatively short height species, formed by the most frequent species of the area (*Paspalum notatum, Andropogon lateralis*) and, in the permanently wet spots, by many short height species of Cyperaceae. The latter is a distinct and very homogeneous habitat. *Eleocharis* sp. is a very dominant species, which is an indication of a more restricted habitat for vegetation heterogeneity than other sites.

According to the seeds that germinated from the soil core samples in the greenhouse, 122 species were identified in the seed bank, most of them perennial (Table 1). This kind

TABLE 1. Percentage of presence and dominance (abundance average when present) of each species in the sample units of the studied ecosystem, calculated by the software SYNCSA 2.0.2.

Species	Family	% Presence	Average when present
Oxalis corniculata L.	Oxalidaceae	73,3	2,1
Hypoxis decumbens L.	Hypoxidaceae	55,6	3,8
Fimbristylis autumnalis (L.) Roem. & Schult.	Cyperaceae	46,7	7,1
Gamochaeta spicata (Lam.) Cabrera	Asteraceae	46,7	1,9
Sisyrinchium micranthum Cav.	Iridaceae	44,4	3,8
Fimbristylis dichotoma (L.) Vahl	Cyperaceae	44,4	2,6
Erechtites valerianaefolia (Wolf) DC.	Asteraceae	42,2	1,4
Rhynchospora tenuis Link	Cyperaceae	40,0	10,5
Piptochaetium montevidense (Spreng.) Parodi	Poaceae	40,0	1,9
Gamochaeta americana (Mill.) Wedd.	Asteraceae	37,8	6,3
Cyperus sesquiflorus (Torrey) Mattf. *et* Kük	Cyperaceae	37,8	2,5
Eleocharis sp.	Cyperaceae	35,6	61,4
Hydrocotyle exigua (Urb.) Malme	Apiaceae	35,6	4,8
Galium uruguayense Bacig.	Rubiaceae	35,6	1,8
Sporobolus indicus (L.) R. Br.	Poaceae	33,3	1,9
Juncus capillaceus Lam.	Juncaceae	31,1	3,4
Rhynchospora sp.	Cyperaceae	28,9	19,3
Bulbostylis capillaris (L.) C.B. Clarke	Cyperaceae	28,9	6,2
Cyperus lanceolatus Poir.	Cyperaceae	28,9	3,1
Centella asiatica (L.) Urb.	Apiaceae	26,7	2,0
Luzula cf. *campestris* (L.) DC.	Juncaceae	26,7	1,7
Eragrostis lugens Nees	Poaceae	26,7	1,6
Panicum hians Elliott	Poaceae	26,7	1,3
Gamochaeta sp.	Asteraceae	24,4	5,5
Gamochaeta filaginea (DC.) Cabrera	Asteraceae	24,4	2,3
Mecardonia tenella (Cham. *et* Schlecht.) Pennell	Scrophulareaceae	24,4	2,1
Axonopus affinis Chase	Poaceae	22,2	1,4
Eragrostis neesii Trin.	Poaceae	22,2	1,3
Rhynchospora uleana Boeck.	Cyperaceae	17,8	5,4
Cyperus meyenianus Kunth	Cyperaceae	17,8	2,1
Baccharis trimera (Less.) DC.	Asteraceae	17,8	1,4
Dichondra sericea Sw.	Convolvulaceae	17,8	1,1
Juncus dichotomus Elliott	Juncaceae	15,6	22,6
Setaria geniculata (Lam.) Beauv.	Poaceae	15,6	1,7
Cyperus brevifolius (Rottb.) Hassk.	Cyperaceae	15,6	1,3
Relbunium humile (Cham. *et* Schlecht.) K. Schum.	Rubiaceae	13,3	1,8
Chevreulia acuminata Less.	Asteraceae	13,3	1,0
Bacopa tweedii (Benth.) Parodi	Scrophulareaceae	11,1	7,2
Gratiola peruviana L.	Scrophulareaceae	11,1	2,2
Rhynchospora rugosa (Vahl) Gale	Cyperaceae	11,1	2,0
Briza rufa (Presl) Steud.	Poaceae	11,1	2,0
Briza poaemorpha (Presl) Henrard	Poaceae	11,1	1,6
Baccharis dracunculifolia DC.	Asteraceae	11,1	1,2
Paspalum pumilum Nees	Poaceae	11,1	1,2
Agrostis montevidensis Spreng. *ex* Nees	Poaceae	8,9	2,3
Cardamine chenopodiifolia Pers.	Brassicaceae	8,9	2,0
Eryngium horridum Malme	Apiaceae	8,9	1,8
Evolvulus sericeus Sw.	Convolvulaceae	8,9	1,8
Juncus bufonius L.	Juncaceae	8,9	1,8
Carex cf. *phalaroides* Kunth	Cyperaceae	8,9	1,8
Pratia hederaceae (Cham.) G. Don.	Primulaceae	8,9	1,3

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Species	Family	% Presence	Average when present
Panicum sabulorum Lam.	Poaceae	8,9	1,0
Bacopa monnieri (L.) Penn.	Scrophulareaceae	6,7	4,3
Stipa nutans Hack.	Poaceae	6,7	2,7
Chevreulia sarmentosa (Pers.) Blake	Asteraceae	6,7	2,0
Eragrostis bahiensis Schrad. *ex* Schult.	Poaceae	6,7	1,7
Oxalis lasiopetala Zucc.	Oxalidaceae	6,7	1,3
Sisyrinchium vaginatum Spreng.	Iridaceae	6,7	1,3
Cyperus aggregatus (Willd.) Endl.	Cyperaceae	6,7	1,0
Briza macrostachya (Presl) Steud.	Poaceae	6,7	1,0
Scleria hirtella (L.) Urb.	Cyperaceae	6,7	1,0
Fimbristylis diphylla (Retz.) Vahl	Cyperaceae	4,4	8,5
Bulbostylis sp.	Cyperaceae	4,4	4,5
Briza uniolae (Nees) Nees *ex* Steud.	Poaceae	4,4	3,5
Micropsis spathulata (Pers.) Cabrera	Asteraceae	4,4	3,5
Cyclospermum leptophyllum (Pers.) Sprague *ex* Britton *et* P. Nilson.	Apiaceae	4,4	2,5
Sisyrinchium cf. *laxum* Otto *ex* Sims	Iridaceae	4,4	2,5
Conyza bonariensis (L.) Cronquist	Asteraceae	4,4	2,0
Kyllinga vaginata Lam.	Cyperaceae	4,4	2,0
Spermacoce verticillata L.	Rubiaceae	4,4	1,5
Plantago tomentosa Lam.	Plantaginaceae	4,4	1,5
Andropogon lateralis Nees	Poaceae	4,4	1,5
Oxalis corymbosa DC.	Oxalidaceae	4,4	1,5
Mitracarpus hirtus (L.) DC.	Rubiaceae	4,4	1,5
Richardia brasiliensis Gomes	Rubiaceae	4,4	1,0
Lotus subbiflorus Lag.	Fabaceae	4,4	1,0
Relbunium richardianum (Gill. *ex* Hook. *et* Arn.) Hicken	Rubiaceae	4,4	1,0
Gamochaeta simplicicaulis (Will.) Cabrera	Asteraceae	4,4	1,0
Andropogon selloanus (Hack.) Hack.	Poaceae	4,4	1,0
Richardia humistrata (Cham. *et* Schlecht.) Steud.	Rubiaceae	4,4	1,0
Soliva pterosperma (Juss.) Less.	Asteraceae	4,4	1,0
Tibouchina sp.	Melastomataceae	4,4	1,0
Stipa filiculmis Delile	Poaceae	4,4	1,0
Pterocaulon sp.	Asteraceae	2,2	4,0
Stemodia cf. *hyptoides* Cham. & Schltdl.	Scrophulareaceae	2,2	4,0
Pseudognaphalium cf. *cheiranthifolium* (Lam.) Hilliard & Burt	Asteraceae	2,2	3,0
Wahlenbergia linarioides (Lam.) DC.	Campanulaceae	2,2	3,0
cf. *Cyperus* sp.	Cyperaceae	2,2	2,0
Gamochaeta calviceps (Fernald) Cabrera	Asteraceae	2,2	1,0
Cyperus reflexus Vahl	Cyperaceae	2,2	1,0
Hypochoeris sp.	Asteraceae	2,2	1,0
Conyza sp.	Asteraceae	2,2	1,0
Spermacoce capitata Ruiz *et* Pav.	Rubiaceae	2,2	1,0
Mikania sp.	Asteraceae	2,2	1,0
Facelis retusa (Lam.) Sch. Bip.	Asteraceae	2,2	1,0
Schizachyrium tenerum Nees	Poaceae	2,2	1,0
Hyptis sp.	Lamiaceae	2,2	1,0
Paspalum sp.	Poaceae	2,2	1,0

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Species	Family	% Presence	Average when present
Panicum decipiens Nees *ex* Trin.	Poaceae	2,2	1,0
Rhynchospora cf. *rufa* (Nees) Boeck.	Cyperaceae	2,2	1,0
Paspalum plicatulum Michx.	Poaceae	2,2	1,0
Senecio selloi (Spreng.) DC.	Asteraceae	2,2	1,0
Luzula sp.	Juncaceae	2,2	1,0
Mollugo verticillata L.	Aizoaceae	2,2	1,0
Verbena litoralis Kunth	Verbenaceae	2,2	1,0
Cyperus sp.	Cyperaceae	2,2	1,0
Cuphea cf. *lindmaniana* Koehne *ex* Bacig.	Lythraceae	2,2	1,0
Cuphea cf. *carthagenensis* (Jacq.) J. F. Macbr.	Lythraceae	2,2	1,0
Hypericum silenoides Juss.	Clusiaceae	2,2	1,0
Eragrostis sp.	Poaceae	2,2	1,0
Paspalum urvillei Steud.	Poaceae	2,2	1,0
Cerastium sp.	Cariophyllaceae	2,2	1,0
Briza subaristata Lam.	Poaceae	2,2	1,0
Cliococca selaginoides (Lam.) C.M. Rogers & Mildner	Linaceae	2,2	1,0
Trifolium vesiculosum Savi	Fabaceae	2,2	1,0
Elyonurus cf. *candidus* (Trin.) Hack.	Poaceae	2,2	1,0
Baccharis cf. *conyzoides* DC.	Asteraceae	2,2	1,0
Desmanthus virgatus (L.) Willd.	Fabaceae	2,2	1,0
Pterocaulon cf. *rugosum* (Vahl) Malme	Asteraceae	2,2	1,0
Panicum bergii Arechav.	Poaceae	2,2	1,0
Pluchia laxiflora Vell.	Styracaceae	2,2	1,0
Glandularia sp.	Verbenaceae	2,2	1,0

of environment, with low disturbance, is associated with a high abundance of perennial species (Harper, 1977). This fact determines an increase in the longevity of the vegetation species (Cook, 1980) and, a decrease in the vegetation spaces for regeneration. This community condition determines a reduction in the soil seed bank size, mainly for annual species.

The result of ordination analysis of soil seed bank data is the dispersion diagram of sample units in Figure 1, considering axis I and II. This diagram allows visualization of three distinct groups or clusters of sample units, distributed according to environmental gradients of moisture and relief position: the first group is characterized by sample units from permanently wet grassland (permanently wet lowland areas-EI); the second group is comprised by other sample units from the lowlands (periodically wet soils in lowland areas-EI); and the third group is characterized by sample units from the uplands (ES) and intermediate sites (I), with three sample units of periodically wet lowland (6EI, 13EI and 17EI) areas included.

The significance test of the axis determined that only axis I is deemed significant (P=0.02), for a=0.05. Axis I represented 40% of data total variation. Axis II and III have probabilities of 0.246 and 0.17, respectively. Axis 1 most correlated species were: *Eleocharis* sp. (-0.97), *Bulbostylis capillaris* (-0.79)*, Centella asiatica* (-0.67)*, Rhynchospora tenuis* (-0.60)*, Elyonurus* cf. *candidus* (-0.58)*, Hyptis* sp. (-0.58), *Paspalum plicatulum* (-0.58)*, Stemodia* cf. *hyptoides* (-0.58)*, Rhynchospora* sp. (-0.53), *Cuphea* cf. *lindmaniana* (-0.53)*, Cyperus* sp. (-0.53), *Hypericum silenoides* (-0.53), *Panicum decipiens* (-0.53), *Gratiola peruviana* (-0.51), *Cyperus lanceolatus* (-0.49), *Bacopa monnieri* (-0.49), *Oxalis lasiopetala* (-0.41), *Galium uruguayense* (0.39), *Relbunium humile* (-0.36), *Briza poaemorpha* (-0.35), *Paspalum pumilum* (-0.34), *Hypoxis decumbens* (0.34) and *Piptochaetium montevidense* (0.31). Species that showed high negative correlation with this axis characterize sample units on the left part of the diagram (wet grasslands), while species with high positive correlation characterize sample units more on the right.

Therefore, as well as in the vegetation, seed banks of the *Eleocharis* sp., *Bulbostylis capillaris* and *Centella asiatica* species are associated with wetter habitats (permanently wet areas) and lowlands, represented by sample units on the left part of the diagram (Group 1); *Rhynchospora* sp., *Cyperus lanceolatus*, *Cuphea* cf. *lindmaniana, Panicum decipiens,*

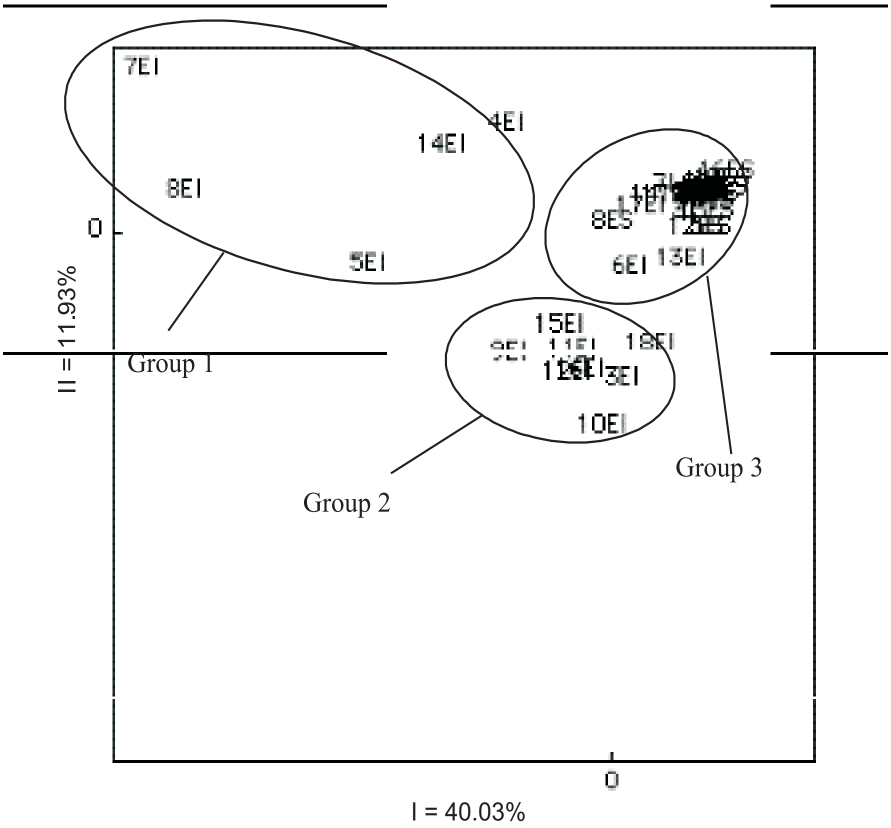

FIGURE 1. Ordination diagram of 45 sample units in the axis I and II, according to principal coordinate analysis, based on euclidian distance of soil seed bank data, EEA/UFRGS, Eldorado do Sul, Brazil, 2000.

Paspalum plicatulum, Paspalum pumilum and *Briza poaemorpha* also have seed banks associated with wet habitats and lowlands in transition with intermediate sites (Group 2); soil seed banks of *Galium uruguayense, Hypoxis decumbens* and *Piptochaetium montevidense* are associated with less wet habitats and uplands and intermediate sites, represented by sample units on the right part of the diagram (Group 3).

Cluster analysis of soil seed bank data confirmed these three groups shown in the ordination diagram (Figure 1). The cluster significance test was done for 2, 3 and 4 groups, resulting in probabilities of 0.19, 0.129 and 0.098, respectively. So, the null hypothesis that groups are stable, for a=0.05 must be accepted, which agrees with the hypothesis on the three distinct groups of sample units shown before.

Focht (2001) described two distinct groups in the vegetation communities of the study area: the first one comprised of sample units in lowlands and the second one constituted by sample units in uplands and intermediate sites, which differs from the three distinct soil seed banks groups observed in the area. In regards to size and composition of the soil seed bank, separation between upland and intermediate sites was not observed. However, the third group registered by soil seed bank data analysis is due to the distinction of permanently wet and non-wet areas in the lowlands, probably because of the great accumulation of *Eleocharis* sp. seeds in wet areas, pointed out by the resemblance measure used for data analysis. It was possible to observe that *Eleocharis* sp. is a species with great potential to accumulate seeds in the soil, around 40958 seeds.m^{-2}, even when present in only in 35.6% of the sample units, thus showing then an aggregated distribution. The species was responsible for the biggest quantity of buried seeds from the permanently wet soils in lowland areas (more details about soil seed bank size in Maia *et al.*, 2003). In this way, it is possible to say that the soil seed bank variation pattern was very similar to the vegetation variation pattern observed by Focht (2001) in the same study area.

The typical arc or shoe horse pattern formation of a gradual substitution of the species through an environmental gradient, which is very frequent in floristic vegetation studies such as the one registered in this area and year by Focht (2001) was not observed for soil seed bank data. However, in the present study, soil seed bank composition and size characteristic of each sample unit in the diagram promoted a close distribution with clear distinction according to the moisture gradient and relief position.

Secondarily, the combined effects of superficial water run off moving seeds from the upper to the lower parts of the relief and a high frequency of gaps in intermediate parts of the relief can reduce soil seed bank size and contribute to this close distribution of the soil seed bank.

The ordination analysis of soil seed bank data done using euclidian distance measure, that considers the size or quantity of seeds in the soil, showed differences in seed bank size and composition between permanently wet areas in lower parts of the relief and less wet areas in upper parts of the relief were emphasized, showed a more abrupt transition than the one observed by Focht (2001) to the aboveground flora, using chord distance, that emphasizes just species wealth.

Based on the three groups identified in the soil seed bank, randomization tests were done according to the presence of each species, individually, trying to identify the species that could differentiate these three groups. Table 2 shows the rank of each differential species by its presence or absence, according to the probability in each contrast, besides species abundance average when present and percentage of presence in the squares of the group. Some of these species were the ones that showed the highest correlation with axis I of the ordination diagram (Figure 1) and that characterized the seed banks of the groups, in accordance with this analysis.

Group 1, constituted by sample units in permanently wet areas in low parts of the relief, was characterized by seed banks of *Eleocharis* sp., *Cyperus lanceolatus, Centella asiatica, Bulbostylis capillaris* and *Gratiola peruviana*. *Eleocharis* sp. and *C. asiatica* were present in all sample units of this group, with an average of 922 and 13 per square, respectively (Table 2), showing that *Eleocharis* sp. was the most abundant. *B. capillaris* and *C. lanceolatus* were also

TABLE 2. Rank of differential species, according to probabilities in each contrast (-2 +1 +1 and 0 –1 +1, e.g., difference between group 1 and the others, and groups 2 and 3), abundance average of the species when present in the square of 1.5 x 0.5 m (Mp) and percentage of the species in each squares of the group (%Pr).

Species	Probability	Group 1		Group 2		Group 3	
		Mp	%Pr	Mp	%Pr	Mp	%Pr
Contrast -2 +1 +1							
Eleocharis spp.	0.001	922	100	27.5	62.5	69.78	18.75
Cyperus lanceolatus	0.001	18.4	80	3.75	37.5	1.31	18.75
Centella asiatica	0.002	13	100	2.5	50	1.12	9.37
Bulbostylis capillaris	0.004	44	80	10.5	50	2.25	15.62
Hypoxis decumbens	0.020	0	0	7	50	52.5	65.62
Gratiola peruviana	0.030	2	40	0.5	25	0.125	3.12
Contrast 0 –1 +1							
Fimbristylis autumnalis	0.001	-	-	101	100	11.56	31.25
Rhynchospora rugosa	0.001	-	-	4	50	0.06	3.12
Rhynchospora sp.	0.001	-	-	190	100	2.34	6.25
Rhynchospora tenuis	0.001	-	-	110	100	15.31	18.75
Rhynchospora uleana	0.001	-	-	35	87.5	0	0
Paspalum pumilum	0.005	-	-	1.5	37.5	0.03	3.12
Oxalis lasiopetala	0.007	-	-	0.75	25	0	0
Sisyrinchium vaginatum	0.010	-	-	0.75	25	0	0
Briza poaemorpha	0.010	-	-	1.87	37.5	0.03	3.12
Galium uruguayense	0.018	-	-	0	0	14	50
Hydrocotyle exigua	0.022	-	-	0	0	34.69	46.87
Relbunium humile	0.026	-	-	1.87	37.5	0.09	3.12
Andropogon lateralis	0.028	-	-	0.75	25	0	0

abundant (44 and 18.4 per square, respectively), but present in only 80% of the sample units (Table 2). Boldrini (1993), in a survey carried out at the same Experimental Station, also observed that plants of *Eleocharis* sp. and *C. asiatica* constituted a typical wet area community, and *C. asiatica* shows a growing and well distinct increase along bad drained soils. The absence of *Hypoxis decumbens* also characterized this group.

Group 2, formed by sample units in low and not permanently wet parts of the relief, was characterized by the presence of *Fimbristylis autumnalis, Rhynchopora rugosa, Rhynchopora* sp., *Rhynchospora tenuis, Rhynchopora uleana, Paspalum pumilum, Oxalis lasiopetala, Sisyrinchium vaginatum, Briza poaemorpha, Relbunium humile* and *Andropogon lateralis* soil seed banks. Table 2 shows that *F. autumnalis* and *R. rugosa* were identified in all sample units of the group, and were also the most abundant of the differential species (101 and 110 per square, respectively). Plants of *A. lateralis, P. pumilum* and *C. lanceolatus* are associated with poorly-drained soils, characterizing habitats in low parts of the relief (Boldrini, 1993). *Briza poaemorpha*, encountered in the Group 1, also occurs preferentially in low topographical zones of the relief as reported in the literature (Girardi-Deiro & Gonçalves, 1987; Boldrini, 1993). The absence of *Galium uruguayense* and *Hydrocotyle exigua* promoted a difference in the composition of groups 2 and 3.

Group 3, constituted by other sample units, was characterized by the presence of *Galium uruguayense* and *Hydrocotyle exigua* soil seed banks and the absence of *Rhynchospora uleana, Oxalis lasiopetala, Sisyrinchium vaginatum* and *Andropogon lateralis* species. *H. exigua* was the most abundant of the differential species of this group (34.69 per square), being present in 46.87% of the sample units of the group.

Jancey (1979) used a procedure similar to the one carried out in this study, ranking species with great diagnostic value in the differentiation between relief positions and finding groups of species able to reproduce successfully a group structure correlated with relief position. The methodological difference was that the author used the F Test for probabilities distribution.

Regarding the ranking of the differential species, in some cases, the presence of some variables that do not contribute to groups structure can, instead, obscure them (Wishart, 1969), so we cannot consider them as differential or diagnostic species even if they are those with high frequency in the group.

Variables that have shown deemed significant differences ($P<0.1$) in soil seed bank size and composition were relief position of the squares and soil factors correlated to moisture content, K, Al, organic matter, clay, basic saturation of the cation exchange capacity and exchangeable basics sum. These variables related to soil fertility determine the habitat conditions that permit the growth and reproduction of some species better adapted to it. In this way, it is important to emphasize that the relation between the environmental similarity and the soil seed bank variation pattern observed is indirect, as the environmental influence of soil fertility is in the distribution pattern of the vegetation above the ground.

In order to make it more visible, the variation pattern of the seed bank and the environmental factors that have influenced significant differences in soil seed bank size and composition, the ordination diagram of sample units according to the size and composition of the seed bank was done (Figure 2) by changing sample units´ names by the state of the variables. To draw a cluster analysis, sample units represented only by these eight variables were used. The result showed groups equivalent to the same pattern of the variable relief position that by itself can demonstrate the behavior of all the others.

According to these groups, sample units of groups 1 and 2, placed in lowlands, are in wet areas and, in some cases, permanently wet ones, with the highest organic matter content, lowest K content, lowest basic saturation of the cation exchange capacity, lowest exchangeable basics sum, and highest Al content, sometimes in levels toxic to the vegetation, characterizing habitats with medium and, mainly, low fertility.

Species such as *Eleocharis* sp., *Bulbostylis capillaris, Centella asiatica, Rhynchospora tenuis, Elyonurus* cf. *candidus, Hyptis* sp., *Paspalum plicatulum, Stemodia* cf. *hyptoides, Cuphea* cf. *lindmaniana, Cyperus* sp. and *Hypericum silenoides* have a great correlation with these habitats, that can also be shown by their buried seeds.

According to McNaughton (1983), vegetation patterns are related to soil patterns influenced by water availability. It also happened in the pattern of the seed bank of the present study, as well as in other studies done in natural grasslands at the same Agronomic Experimental Station (Boldrini, 1993; Favreto *et al.*, 2000). The study by Franceschi & Paro (1998), *apud* Boldrini (1993), showed that the relations observed among vegetation community groups demonstrate that some environmental factors are greatly associated with topographical gradients, in which species and communities regulate their distribution. The soil seed bank, in this case, shows similar behavior, where the relief position, which is related mainly to soil moisture, and other soil variables, promotes differences in its size and composition.

So, although the relief position may apparently be the main

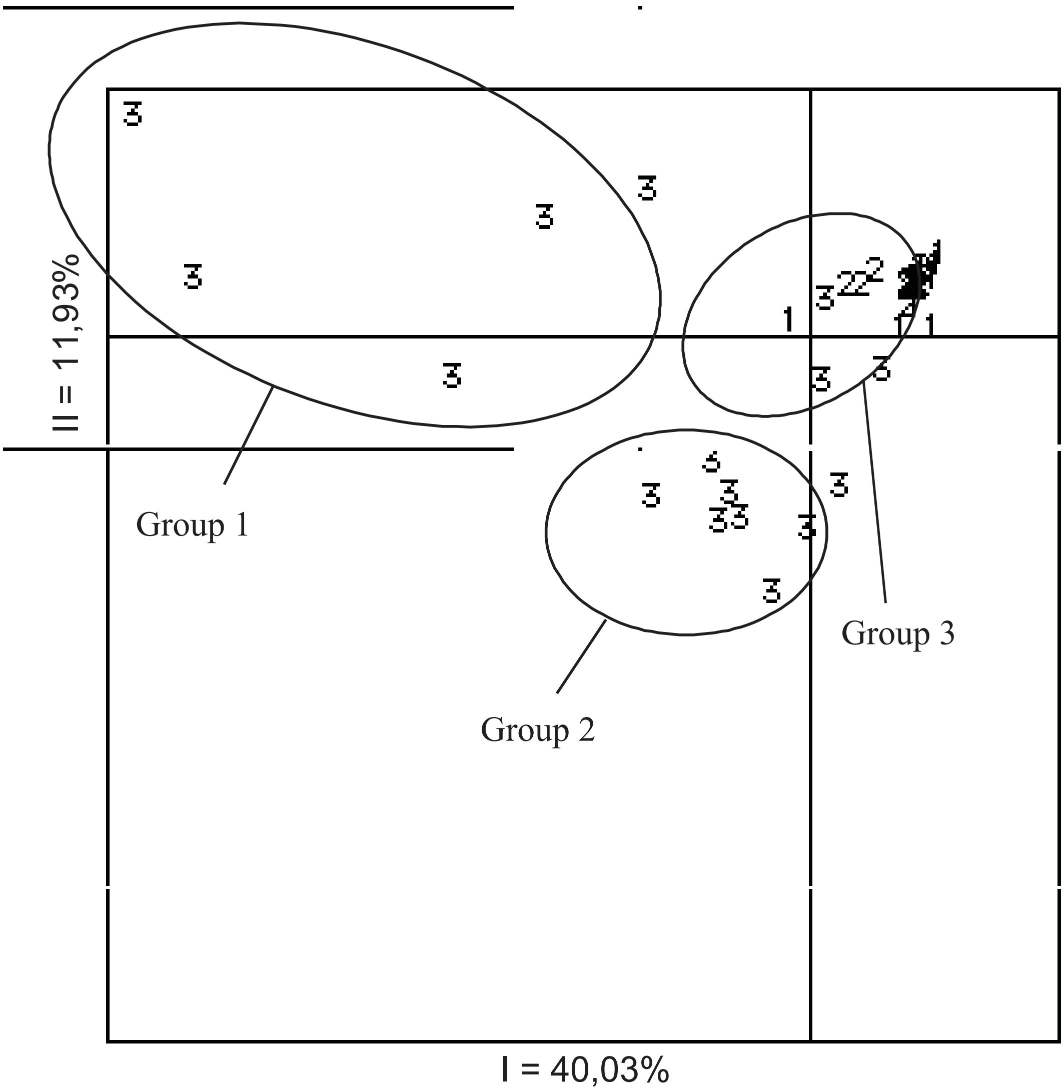

FIGURE 2. Ordination diagram of 45 sample units in the axis I and II, according to principal coordinate analysis, based on euclidian distance of soil seed bank data, EEA/UFRGS, Eldorado do Sul, Brazil, 2000. Numbers 1 to 3 are related to the groups from cluster analysis of the sample units according to moisture content of the soil, relief position, basic saturation of the cation exchange capacity of the soil and exchangeable basics sum of the soil, K, Al, organic matter and clay. Axis I most correlated species were *E.* spp. (-0.97), *B. capillaris* (-0.79), *C. asiatica* (-0.67), *R. tenuis* (-0.60), *E.* cf. *candidus* (-0.58), *H.* sp. (-0.58), *P. plicatulum* (-0.58), *S.* cf. *hyptoides* (-0.58), *R.* sp. (-0.53), *C.* cf. *lindmaniana* (-0.53), *C.* sp. (-0.53), *H. silenoides* (-0.53).

factor that can explain the variation in the seed bank size and composition in the study area, the cluster analysis of the sample units done with only eight significant environmental variables showed that some soil properties, such as moisture content, K, Al, organic matter, clay, basic saturation of the cation exchange capacity and exchangeable basics sum, associated with the relief, promote the variation pattern observed in the soil seed bank, which agrees with the distribution pattern of the vegetation above the ground observed by Focht (2001).

CONCLUSIONS

Most of the species identified in the soil seed bank were perennial, due to the low disturbed environment.

Relief position, associated with the combined effects of some soil properties related to it such as moisture content, K, Al, organic matter, clay, basic saturation of the cation exchange capacity and exchangeable basics sum, determines the observed variation pattern of the soil seed bank, as a reflection of the vegetation above the area.

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