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Soil seed bank during succession at an abandoned pasture in the upper Paraná river-floodplain, Brazil

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ABSTRACT. We evaluated density and species composition of the soil seed bank in active pasture and in secondary forest on a 10 year-old abandoned pasture to identify changes in density, richness, diversity and species composition during secondary succession of abandoned pastures. The implications of those changes for the forest recovery process were also considered. Soil samples were collected at Porto Rico island, state of Paraná, in 2007. The seedling emergence method was used. Data on active pasture collected in 1996, published by Campos and Souza (2003) were used for comparative analysis. No evidence was found of a pattern of changes in density of the soil seed bank during succession of abandoned pastures. We observed increases in richness and diversity, in the contribution of tree and shrub species and dominance of herb species for the seed bank during the first 10 years of abandonment of pastures in riparian forests. At the end of succession, the soil used as pasture can result in systems that are different from the original environment, due to seed bank impoverishment and presence of exotic species.

Key words: riparian vegetation, invasive exotic species, environmental conservation areas, *Psidium guajava*.

RESUMO. Banco de sementes do solo durante sucessão em pastagem abandonada na planície de inundação do alto rio Paraná, Brasil. Foi avaliada a densidade e composição de espécies do banco de sementes em pastagem ativa e floresta secundária sobre pastagem abandonada (dez anos), visando entender as variações na densidade, riqueza, diversidade e composição de espécies durante sucessão de pastagens abandonadas, e as implicações dessas mudanças para o processo de recuperação da floresta. Foram coletadas amostras de solo na ilha Porto Rico, Porto Rico Estado do Paraná, em 2007, sendo utilizado o método de emergência de plântulas. Para uma análise comparativa foram utilizados dados de 1996 (condição de pastagem ativa) publicados por Campos e Souza (2003). Não há evidências sobre alterações na densidade do banco de sementes do solo durante a sucessão de pastagens abandonadas. Por outro lado, ocorreu acréscimo na riqueza e diversidade, com o predomínio de espécies herbáceas e acréscimo na contribuição de espécies arbustivo-arbóreas no banco de sementes durante os primeiros dez anos de abandono de pastagens em florestas ripárias. O uso do solo como pastagem pode, portanto, resultar em ambientes distintos do original no final da sucessão, pelo empobrecimento do banco de sementes e presença de espécies exóticas.

Palavras-chave: floresta ripária, espécies exóticas invasoras, unidades de conservação, *Psidium guajava*.

Introduction

A soil seed bank is formed by all viable seeds on or in the soil (SIMPSON et al., 1989), as a dynamic input and output system (FENNER, 1985; GARWOOD, 1989). The bank is a source of genetic variability for plant communities (HARPER, 1977; FENNER, 1985; SIMPSON et al., 1989). It is also the main seed provider for the regeneration of natural gaps (BAIDER et al., 1999; DALLING et al., 1997; GARWOOD, 1989; SAULEI; SWAINE, 1988) and for areas in early stages of secondary succession (BAIDER et al., 1999; FENNER, 1985). Therefore, when an area is disturbed by natural or anthropic events, the structure of its secondary vegetation is determined primarily by the seeds already in the soil (CAMPOS; SOUZA, 2003; GARWOOD, 1989; UHL; CLARK, 1983).

Tropical forests are frequently destroyed for conversion to agriculture and cattle raising (AIDE et al., 1995, 1996, 2000; UHL et al., 1988; ZAHAWI; AUGSPURGER, 1999). After being used for several years, pastures undergo significant soil degradation and frequent fires, usually in highly fragmented landscapes (AIDE et al., 2000). Cattle raising leads to soil compaction (REINERS et al., 1994), thus inhibiting or rendering difficult vegetation recovery and lowering the quantity and quality of seed banks (CAMPOS, 1999a). These conditions inhibit the recovery of native forest and can result in different ecosystems (AIDE et al., 1996).

Knowledge of the early stages of succession can significantly improve the understanding of ecological processes that relate abandoned pastures and forests in advanced stages of succession (DUPUY; CHAZDON, 1998). Several studies on the regeneration process of forests in abandoned pastures have been conducted (AIDE et al., 1995, 1996, 2000; CAMPOS; DICKINSON, 2005; HOLL, 1999; REINERS et al., 1994; UHL et al., 1988; ZAHAWI; AUGSPURGER, 1999; ZIMMERMAN et al., 2000). Few of them, however, have been on changes occurring in the seed bank during pasture succession (CUBIÑA; AIDE, 2001; QUINTANA-ASCÊNCIO et al., 1996; ZAHAWI; AUGSPURGER, 1999), particularly in riparian forests associated with floodplains. Furthermore, very few studies have been repeated on the same site (BEKKER et al., 2000).

This is a study of density and composition of species found in the seed bank of a secondary forest on pasture abandoned for 10 years, to observe (1) changes in density, richness, diversity, and composition of species during secondary succession of abandoned pastures, and (2) implications of such changes for the forest recovery process.

Material and methods

Study area

The study was conducted in Porto Rico Island, Porto Rico, Paraná State (Figure 1), in the upper Paraná river-floodplain, the only remaining free-flowing portion of Paraná river in Brazil (AGOSTINHO et al., 2004).

The area vegetation is classified as alluvial semidecidual seasonal forest (CAMPOS; SOUZA, 1997; IBGE, 1992). According to the Köeppen system, the climate is Cfa – tropical-subtropical with hot summers (mean annual temperature of 22°C) with mean annual precipitation of 1500 mm. Some years have a Cwa climate, with dry winters (MAACK, 2002). The altitude is close to 230 m (CAMPOS; COSTA-FILHO, 1994).

Porto Rico Island was originally covered by dense vegetation, but more than half of the island was deforested between 1952 and 1965. In 1996, only three forest fragments remained and covered 5.98% of the territory, the rest was in pasture (CAMPOS, 1999b).

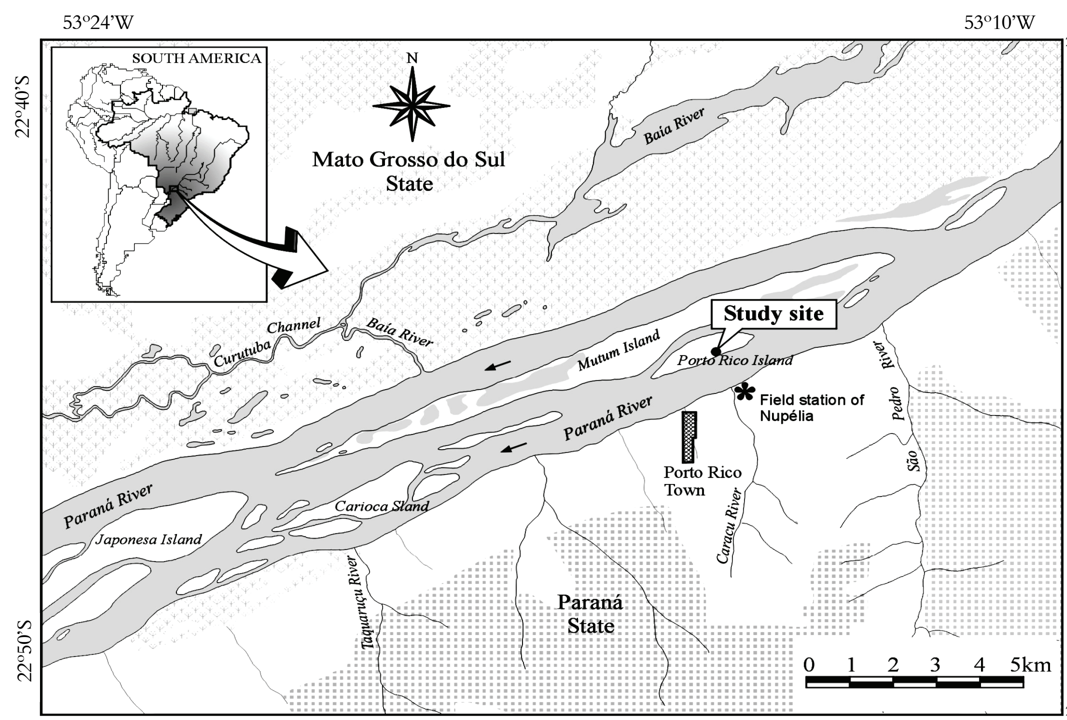

Figure 1. Map of the study area, the upper Paraná river floodplain, Brazil (by Jaime Luis Lopes Pereira).

The ecological importance of the region (AGOSTINHO et al., 2004) led to the creation of the Environmental Protection Area of the Islands and Floodplains of Paraná River (Área de Proteção Ambiental das Ilhas e Várzeas do Rio Paraná, APA - IVRP) in 1997, a federal conservation unit for sustainable use (CAMPOS; DICKINSON, 2005). The creation of APA - IVRP resulted in several actions sponsored by the state and environmental organizations to forbid the use of island soil for crop or livestock production. It also led to the beginning of the secondary succession process in the region.

Seed bank

Forty soil samples, including litter, were collected randomly from a previously delimited area that had been abandoned for 10 years. The samples were collected in September 2007. The sampling device was made of metal and the samples were collected from soil patches measuring 20 x 20 and 5 cm-deep. The total area sampled equaled 1.6 m^2.

The samples were kept in dark plastic bags and placed in a greenhouse covered with transparent PVC and sides covered with sunscreen, located at the Forest Nursery of the Instituto Ambiental do Paraná (IAP), in Mandaguari, Paraná, State. The samples were spread on 20 x 40 cm trays with inert vermiculite substrate. Four trays did not receive the soil samples to observe potential contamination (BROWN, 1992). The trays were watered 3 times a day; 5 months later the ground was revolved. The experiment was conducted during 10 months.

Seedlings were counted weekly, using the emergence or germination method (BROWN, 1992). After collection and identification, seedlings were preserved in alcohol solution at 40%. Unidentifiable seedlings were considered control specimens and collected with reproductive material for later identification.

For the comparative analysis between seed banks of active pasture and secondary forest on abandoned pasture for 10 years, we used the pasture seed bank data collected on the same site, by Campos and Souza (2003), in a 1996 study comparing seed banks from pasture and three forest remnants in Porto Rico Island.

Data analysis

The species were classified according to life form (tree, shrub, herb and liana), following Font Quer (1989). Tree species were classified according to the vegetation succession stages, as follows: pioneer, secondary, climax and invasive (BUDOWSKI, 1963, 1965, 1966; KAGEYAMA, 1992). Classification was also based on personal observations on the field.

The absolute and relative density (MÜELLER-DOMBOIS; ELLENBERG, 1974), the Shannon-Weaver index of diversity (*H'*) and equitability (*J'*) (KREBS, 1989) were obtained.

The non-parametric Mann-Whitney test (U-Test) (ZAR, 1999) was used for the independent samples to determine the difference in total density of viable seeds. Significant differences in richness, diversity, and equitability were assessed by using the *t* test for independent samples at 5% significance level (ZAR, 1999). The rarefaction curve (KREBS, 1989) was designed to compare richness without the density effect. The differences in equitability were determined by the dominance/diversity curve or Whittaker plot (MAGURRAN, 2004).

We used the χ^2 test for contingency table (ZAR, 1999) at 5% significance to determine whether the proportions among species of different life forms depended on the vegetation succession stage, by comparing densities and richness. The statistical tests were processed using BioDiversity Pro (MCALEECE et al., 1997), BioEstat v4.0 (AYRES et al., 2005), and STATISTICA for Windows (STASOFT, 2005).

Results and discussion

Density

The total density of viable seeds in the soil decreased from 6312 ± 1233 seeds m-2 (viable seeds per square meter ± standard error) in 1996, to 3792 ± 428 in 2007. The decrease that was not statistically different (Z(U) = 1.16; p = 0.25), probably due to data variability (350-36575 seeds m^{-2} in 1996 and 875-13600 seeds m^{-2} in 2007); such variability is widely observed in seed banks due to their high spatial heterogeneity (BIGWOOD; INOUYE, 1988; BUTLER; CHAZDON, 1998; GARWOOD, 1989).

Most research on tropical forests show that seed bank size reaches its biggest size early in the succession process and gradually decreases (ARAÚJO et al., 2001; BAIDER et al., 1999, 2001; DALLING; DENSLOW, 1998; DUPUY; CHAZDON, 1998; GARWOOD, 1989; YOUNG, 1985; YOUNG et al., 1987). We counted between 48 and 18900 seeds m^{-2}, which are within the expected range for pastures and secondary tropical forests according to the literature review undertaken by Garwood (1989) and Young (1985).

Campos and Souza (2003) found seed bank densities of 1574, 1338, 2513 seeds m^{-2} in forest remnants of Porto Rico Island. Grombone-Guaratini and Rodrigues (2002) found much lower densities (32, 50 and 44 seeds m^{-2}) in a semidecidual seasonal fragment, whereas Grombone-Guaratini et al. (2004) found densities of 243 and 499 seeds m^{-2} in a semidecidual seasonal riparian forest.

Difference in densities within a phytophysiognomic dominium can be due to differences in the history of soil and landscape use (ARAÚJO et al., 2004; DUPUY; CHAZDON, 1998), or due to different methodologies used during the study.

Richness and diversity

In 1996, 68 taxa were identified (active pasture); in 2007, taxa increased to 81 (secondary forest on abandoned pasture) (Table 1), a significant difference ($t = -2.16$; $p = 0.03$). The rarefaction curve also revealed a higher estimated number of species in secondary forest on abandoned pasture (2007) than in active pasture (1996) (Figure 2A).

The index of diversity for active pasture (1996) (H' = 1.198) differed significantly ($t = -3.61$; $p < 0.01$) from the index for secondary forest (2007) (H' = 1.3). The index of equitability was also significantly higher ($t = -2.63$; $p = 0.01$) in secondary forest (J' = 0.677) than in active pasture (J' = 0.654).

The Wittaker plot (Figure 2B) showed a tendency for high equitability in active pasture and secondary forest.

Richness can be considered high because the number of species exceeds the limit of 8 to 67 species in pasture and secondary forest, as reported by Garwood (1989). There was also a tendency to increase richness and diversity during succession and a decrease in dominance.

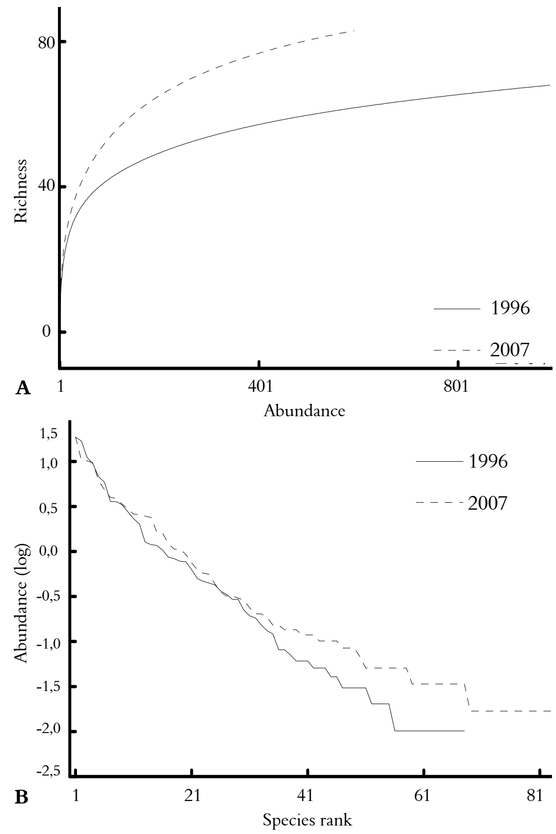

Figure 2. Rarefaction curve for estimated richness of species (A) and Wittaker plot (B) in active pasture (1996) and secondary forest on abandoned pasture (2007), Porto Rico Island, Paraná, Sate, Brazil.

Table 1. Density (seeds m^{-2} ± standard error), life form (LF) (T = tree; S = shrub; H = herb; L = liana), and ecological category (C) (P = pioneer; I = invasive; S = secondary) of species collected from the soil seed bank in Porto Rico Island in active pasture (1996) and secondary forest on 10-year abandoned pasture (2007).

Specie	Family	LF	C	Density	
				1996	2007
Cecropia pachystachya Trécul	Urticaceae	T	P	$28^{\pm 7}$	$94^{\pm 21}$
Croton urucurana Baill.	Euphorbiaceae	T	P	$5^{\pm 3}$	$90^{\pm 13}$
Machaonia brasiliensis Cham. & Schltdl.	Rubiaceae	T	S		$40^{\pm 19}$
Psidium guajava L.	Myrtaceae	T	I		$35^{\pm 21}$
Tabernaemontana catharinensis A. DC.	Apocynaceae	T	I		$1^{\pm 1}$
Asteraceae sp.1	Asteraceae	S			$1^{\pm 1}$
Conyza canadensis (L.) Cronquist	Asteraceae	S		$19^{\pm 6}$	$185^{\pm 88}$
Diodia brasiliensis Spreng.	Rubiaceae	S		$76^{\pm 36}$	$231^{\pm 71}$
Eupatorium maximiliani Schrad. ex DC.	Asteraceae	S			$63^{\pm 46}$
Lippia alba (Mill.) N. E. Br.	Verbenaceae	S		$10^{\pm 4}$	$3^{\pm 2}$
Malvaceae	Malvaceae	S			$4^{\pm 2}$
Miconia prasina (Sw.) DC.	Melastomataceae	S			$113^{\pm 37}$
Mimosa pudica L.	Fabaceae	S			$3^{\pm 2}$
Pfaffia glomerata (Spreng.) Pedersen	Amaranthaceae	S		$1^{\pm 1}$	
Senna obtusifolia (L.) H. S. Irwin & Barneby	Fabaceae	S			$1^{\pm 1}$
Triumfetta bartramia L.	Malvaceae	S			$1^{\pm 1}$
Vernonia chamaedrys Less.	Asteraceae	S			$4^{\pm 3}$
Vernonia incana Less.	Asteraceae	S		$27^{\pm 10}$	
Vernonia westiniana Less.	Asteraceae	S			$7^{\pm 4}$
Ageratum conyzoides L.	Asteraceae	H			$17^{\pm 4}$
Amaranthus lividus L.	Amaranthaceae	H		$4^{\pm 3}$	
Ambrosia elatior L.	Asteraceae	H		$8^{\pm 5}$	

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Specie	Family	LF	Density	
			1996	2007
Apium leptophyllum F. Muell. ex Benth.	Apiaceae	H	$1^{\pm1}$	
Asteraceae sp.2	Asteraceae	H		$45^{\pm45}$
Asteraceae sp.3	Asteraceae	H	$65^{\pm41}$	
Caperonia palustris A. St. -Hil.	Euphorbiaceae	H	$1^{\pm1}$	
Chamaesyce hyssopifolia (L.) Small	Euphorbiaceae	H	$1^{\pm1}$	
Conyza bonariensis (L.) Cronquist	Asteraceae	H		$2^{\pm2}$
Croton glandulosus L.	Euphorbiaceae	H	$49^{\pm20}$	$11^{\pm11}$
Cuphea carthagenensis (Jacq.) J. F. Macbr.	Lythraceae	H	$703^{\pm538}$	$98^{\pm21}$
Cuphea sp.	Lythraceae	H		$1^{\pm1}$
Cyperaceae sp.1	Cyperaceae	H	$8^{\pm8}$	
Cyperaceae sp.2	Cyperaceae	H	$14^{\pm14}$	
Cyperus ferax (L.) Rich.	Cyperaceae	H	$1179^{\pm678}$	
Cyperus spp.	Cyperaceae	H		$395^{\pm120}$
Dichondra microcalyx (Hallier f.) Fabris	Convolvulaceae	H		$1^{\pm1}$
Digitaria ciliaris (Retz.) Koeler	Poaceae	H	$1^{\pm1}$	
Digitaria sp.1	Poaceae	H	$128^{\pm64}$	
Digitaria sp.2	Poaceae	H	$1^{\pm1}$	
Digitaria violascens Link	Poaceae	H	$371^{\pm99}$	
Eclipta alba L. ex B.D.Jacks.	Asteraceae	H	$3^{\pm2}$	$1^{\pm1}$
Eleusine tristachya (Lam.) Lam.	Poaceae	H	$3^{\pm2}$	
Erechtites hieraciifolius (L.) Raf. ex DC.	Asteraceae	H		$3^{\pm2}$
Erechtites sp.	Asteraceae	H		$1^{\pm1}$
Euphorbia heterophylla L.	Euphorbiaceae	H	$1^{\pm1}$	
Euphorbiaceae sp.1	Euphorbiaceae	H	$5^{\pm3}$	
Euphorbiaceae sp.2	Euphorbiaceae	H	$19^{\pm6}$	
Gnaphalium pensylvanicum Willd.	Asteraceae	H	$3^{\pm2}$	$2^{\pm2}$
Gnaphalium spicatum Lam.	Asteraceae	H	$226^{\pm105}$	$99^{\pm28}$
Heliotropium indicum L.	Boraginaceae	H	$12^{\pm12}$	$5^{\pm3}$
Heliotropium procumbens Mill.	Boraginaceae	H	$594^{\pm299}$	$387^{\pm100}$
Hybanthus communis (A.St.-Hil.) Taub.	Violaceae	H		$4^{\pm2}$
Hyptis brevipes Poit.	Lamiaceae	H		$4^{\pm2}$
Hyptis sp	Lamiaceae	H	$29^{\pm19}$	
Ipomoea cairica (L.) Sweet	Convolvulaceae	H		$4^{\pm2}$
Ipomoea grandifolia (Dammer) O'Donell	Convolvulaceae	H		$1^{\pm1}$
Ipomoea sp.	Convolvulaceae	H		$1^{\pm1}$
Lamiaceae	Lamiaceae	H	$4^{\pm3}$	
Ludwigia spp.	Onagraceae	H		$6^{\pm4}$
Ludwigia suffruticosa Walter	Onagraceae	H	$1^{\pm1}$	
Lynaceae	Lynaceae	H	$2^{\pm2}$	
Marsypianthes chamaedrys Kuntze	Lamiaceae	H	$21^{\pm10}$	$1^{\pm1}$
Melanthera latifolia (Gardn.) Cabrera	Asteraceae	H	$1^{\pm1}$	$1^{\pm1}$
Unidentified 1	Unidentified	H	$2^{\pm2}$	
Unidentified 2	Unidentified	H		$1^{\pm1}$
Unidentified 3	Unidentified	H		$1^{\pm1}$
Unidentified 4	Unidentified	H		$1^{\pm1}$
Unidentified 5	Unidentified	H		$21^{\pm21}$
Unidentified 6	Unidentified	H		$4^{\pm3}$
Unidentified 7	Unidentified	H		$1^{\pm1}$
Unidentified 8	Unidentified	H		$1^{\pm1}$
Unidentified 9	Unidentified	H		$40^{\pm35}$
Unidentified 10	Unidentified	H		$3^{\pm3}$
Murdannia nudiflora (L.) Brenan	Commelinaceae	H	$1^{\pm1}$	
Nicotiana bonariensis Lehm.	Solanaceae	H	$2^{\pm1}$	
Nicotiana sp.	Solanaceae	H		$4^{\pm2}$
Panicum sp.1	Poaceae	H	$80^{\pm21}$	
Panicum sp.2	Poaceae	H	$210^{\pm72}$	
Panicum sp.3	Poaceae	H		$128^{\pm24}$
Paspalum conjugatum P.J.Bergius	Poaceae	H	$426^{\pm125}$	
Paspalum sp.	Poaceae	H		$151^{\pm47}$
Phytolacca americana L.	Phytolaccaceae	H	$1^{\pm1}$	
Phyllanthus carolinensis Walther	Phyllanthaceae	H	$31^{\pm19}$	
Phyllanthus niruri L.	Phyllanthaceae	H		$35^{\pm10}$
Phyllanthus tenellus Roxb.	Phyllanthaceae	H		$8^{\pm3}$
Phyllanthus sp.1	Phyllanthaceae	H	$74^{\pm30}$	
Phyllanthus sp.2	Phyllanthaceae	H	$1^{\pm1}$	
Phyllanthus sp.3	Phyllanthaceae	H	$3^{\pm2}$	
Physalis angulata L.	Solanaceae	H	$1^{\pm1}$	
Plantago tomentosa Lam.	Plantaginaceae	H		$1^{\pm1}$
Pluchea sagittalis (Lam.) Cabrera	Asteraceae	H	$1^{\pm1}$	$9^{\pm3}$
Poaceae sp.1	Poaceae	H	$146^{\pm36}$	
Poaceae sp.2	Poaceae	H	$1064^{\pm192}$	
Poaceae sp.3	Poaceae	H	$3^{\pm2}$	
Poaceae sp.4	Poaceae	H		$365^{\pm60}$
Poaceae sp.5	Poaceae	H		$12^{\pm10}$

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Specie	Family	LF	Density	
			1996	2007
Poaceae sp.6	Poaceae	H		$61^{\pm 22}$
Polygonum punctatum Elliott	Polygonaceae	H		$5^{\pm 4}$
Porophyllum ruderale (Jacq.) Cass.	Asteraceae	H	$1^{\pm 1}$	$1^{\pm 1}$
Richardia brasiliensis Gomez	Rubiaceae	H	$23^{\pm 15}$	$2^{\pm 1}$
Scleria pterota Presl	Cyperaceae	H	$12^{\pm 4}$	$24^{\pm 5}$
Scoparia montevidensis R.E.Fr.	Plantaginaceae	H	$2^{\pm 1}$	
Scrophulariaceae	Scrophulariaceae	H	$227^{\pm 123}$	
Sida rhombifolia L.	Malvaceae	H	$54^{\pm 27}$	$6^{\pm 2}$
Solanum americanum Mill.	Solanaceae	H	$4^{\pm 2}$	$2^{\pm 1}$
Solanum sisymbrifolium Lam.	Solanaceae	H	$53^{\pm 18}$	$8^{\pm 3}$
Solanum viarum Dunal	Solanaceae	H	$4^{\pm 2}$	$2^{\pm 1}$
Soliva anthemifolia (A. Juss.) Sweet	Asteraceae	H	$49^{\pm 23}$	$2^{\pm 1}$
Spermacoce capitata Ruiz & Pav.	Rubiaceae	H	$40^{\pm 16}$	$11^{\pm 4}$
Stemodia humilis (Sol.) G. Dawson	Plantaginaceae	H	$174^{\pm 82}$	
Stemodia trifoliata Rchb.	Plantaginaceae	H		$715^{\pm 219}$
Synedrellopsis grisebachii Hieron. & Kuntze	Asteraceae	H		$28^{\pm 22}$
Triumfetta lappula L.	Malvaceae	H		$12^{\pm 7}$
Verbena bonariensis L.	Verbenaceae	H		$1^{\pm 1}$
Verbena litoralis Kunth	Verbenaceae	H		$1^{\pm 1}$
Verbenaceae sp.1	Verbenaceae	H		$148^{\pm 85}$
Verbenaceae sp.2	Verbenaceae	H		$1^{\pm 1}$
Aristolochia sp.	Aristolochiaceae	L		$1^{\pm 1}$
Dalechampia scandens L.	Euphorbiaceae	L		$2^{\pm 1}$
Dalechampia sp.	Euphorbiaceae	L	$2^{\pm 1}$	
Fabaceae	Fabaceae	L		$1^{\pm 1}$
Mikania cordifolia Willd.	Asteraceae	L	$1^{\pm 1}$	$1^{\pm 1}$
Passiflora misera Kunth	Passifloraceae	L	$1^{\pm 1}$	
Smilax brasiliensis Spreng.	Smilacaceae	L		$5^{\pm 3}$
Total density			$6312^{\pm 1233}$	$3792^{\pm 428}$
Total richness			68	81

Campos and Souza (2003) registered richness of 64, 47, and 52 in three remnants of the Island. We obtained higher values for richness in pasture and much higher in secondary forest. Araújo et al. (2001) found the highest richness and diversity in the early stage of succession, when a 6-year-old forest had 72 species (H' = 2.23), and a 17-year-old (H' = 1.9) and a 30-year-old (H' = 1, 12) forest had 62 and 59 species, respectively.

Scherer and Jarenkow (2006) found what they considered low diversity for a seasonal forest in Southern Brazil (H' = 1.639 and H' = 1.717). These, however, were higher than the values we found.

Quintana-Ascêncio et al. (1996) found that species richness increases in communities open to sites abandoned for 4 to 12 years, and decreases in communities at more advanced succession stages. Data from our study, in addition to those reported by Campos and Souza (2003) and by other cited authors provide support for the pattern found by Quintana-Ascêncio et al. (1996).

Dalling and Denslow (1998), and Wills and Read (2007), however, found no significant correlation between species richness and time after disturbance. There seems to be a significant increase in species richness as pasture approaches forest borders (CUBIÑA; AIDE, 2001; ZIMMERMAN et al., 2000). According to the review by Garwood (1989), the number of species found in seed banks of mature forests and in tropical secondary forests/pastures is similar.

The results above point to a difficulty in establishing a pattern of richness and diversity for seed banks in succession processes of abandoned pastures. This is probably due to the aggregated distribution pattern of the seed bank (BIGWOOD; INOUYE, 1988; BUTLER; CHAZDON, 1998; GARWOOD, 1989), and consequently, to problems in defining a representative sample. Another reason is the lack of a well-defined methodology for the study of seed banks, including criteria for sample size and number of samples.

According to Garwood (1989) review, seed-banks of tropical forests have high dominance. The high equitability obtained in our study in addition to those obtained by Araújo et al. (2001) suggest that equitability follows the richness pattern, thus increasing at the early stages of succession and gradually decreasing thereafter. Araújo et al. (2001) found the highest equitability in a 6-year-old forest (J' = 0.52), and lower values in older sites, a 17-year (J' = 0.46) and a 30-year (J' = 0. 26) forest.

Species composition – Herb species had the highest number of seeds per square meter both in active pasture (1996) and in secondary forest on abandoned pasture (2007), followed by the shrub, tree, and liana species (Table 2). As far as richness, herb species were also first, followed by the shrub, liana, and tree species in active pasture; in secondary forest, shrub species were followed by both liana and tree species at equal levels (Table 3). The χ^2 test shows that the relation between density and life form depends on vegetation succession stage ($\chi^2 = 1116$; $p < 0.01$), whereas richness does not ($\chi^2 = 3.92$; $p = 0.27$).

Table 2. Absolute density (seeds m^{-2}) and standard error, and relative density (in parenthesis) for each species life form in the seed bank of Porto Rico Island, in active pasture (1996) and in secondary forest on 10-year abandoned pasture (2007).

Year	Tree	Shrub	Herb	Liana
1996	$33^{\pm 7}$ (0.53)	$131^{\pm 37}$ (2.08)	$6144^{\pm 1227}$ (97.33)	$3^{\pm 2}$ (0.05)
2007	$261^{\pm 39}$ (6.88)	$628^{\pm 146}$ (16.55)	$2895^{\pm 398}$ (76.32)	$10^{\pm 4}$ (0.26)

The dominance of herb species in seed banks supports previous studies that show seed banks of tropical forests as made primarily of herb pioneer species and shrub-tree species of short life cycles (ARAÚJO et al., 2004; BAIDER et al., 2001; DUPUY; CHAZDON, 1998; GASPARINO et al., 2006; LOPES et al., 2006; MELO et al., 2007; QUINTANA-ASCÊNCIO et al., 1996; RAMIREZ-MARCIAL et al., 1992; SAULEI; SWAINE, 1988; ZAHAWI; AUGSPURGER, 1999; YOUNG et al., 1987).

Table 3. Richness and percentage (in parenthesis) for each species life form in the seed bank of Porto Rico Island, in active pasture (1996) and in secondary forest on 10-year abandoned pasture (2007).

Year	Tree	Shrub	Herb	Liana
1996	2 (2.9)	5 (7.4)	58 (85.3)	3 (4.4)
2007	5 (6.2)	13 (16)	58 (71.6)	5 (6.2)

In the study by Wills and Read (2007), herbaceous species were the main cause of dissimilarity in succession stages. The high number of pioneer herb species in seed banks is due to their facultative dormancy and efficient dispersion mechanisms (GASPARINO et al., 2006).

The results above show a decrease in density of herb species and an increase in density and richness of shrub-tree species in seed banks during recovery of abandoned pastures. Also in Porto Rico Island, Campos and Souza (2003) found tree dominance in all three forest remnants studied. Grombone-Guaratini and Rodrigues (2002) found similar results in a semidecidual seasonal forest fragment. However, Grombone-Guaratini et al. (2004) observed the predominance of herb species in a semidecidual seasonal riparian forest, probably due to its high level of degradation (ARAÚJO et al., 2004; DUPUY; CHAZDON, 1998).

The increase in shrub-tree species in more advanced succession stages, also reported extensively (BAIDER et al., 2001; GASPARINO et al., 2006; QUINTANA-ASCÊNCIO et al., 1996; SAULEI; SWAINE, 1988), shows that the seed bank seems to recover considering that banks of mature forests contain tree species (GARWOOD, 1989) with pioneer traits (GARWOOD, 1989; GASPARINO et al., 2006; WHITMORE, 1983, 1992).

Campos and Dickinson (2005) assessed forest succession at the same site, after five years of abandonment. They found dominance of pioneer species in the arboreal stratum, and secondary and climax species in the sub-forest. This might have caused the increase in density and richness of trees in the soil seed bank due to the high levels of seed production by pioneer species (WHITMORE, 1983; VÁZQUEZ-YANES; OROZCO-SEGOVIA, 1987).

In 2007, during the phytosociological survey conducted at the same pasture land after 10 years of abandonment, 12 tree species were found in the arboreal stratum (unpublished data), only five of them were found in the seed bank (Table 3). The pioneer tree species typical of hydromorphic soils found in seed banks (LORENZI, 1992) were also found in other seed bank studies (ARAÚJO et al., 2001; CAMPOS; SOUZA, 2003; GASPARINO et al., 2006; GROMBONE-GUARATINI et al., 2004).

The species *Cecropia pachystachya* and *Croton urucurana* were found in all phytosociological studies conducted in the upper Paraná river floodplain (CAMPOS et al., 2000; CAMPOS; SOUZA, 2002, 2003; CAMPOS; DICKINSON, 2005; KITA; SOUZA, 2003; SOUZA; MONTEIRO, 2005). Pioneer species in seed banks are important for the regeneration of tropical forests after natural or anthropic disturbances.

The presence of the two main pioneer species and one secondary species in the seed bank, the more than seven-time increase in tree density and over four-time increase in shrub species (Table 1) shows that the seed bank is ready to establish the ecological groups such as the pioneer species group, and the richness of shrub-tree species (BAIDER et al., 1999).

However, the presence of invasive exotic species in the seed bank, mainly *Psidium guajava*, is worrisome. The invasive species found in our study were also reported by Gasparino et al. (2006) in a riparian forest seed bank under the dominium of a semidecidual seasonal forest. Both results show the potential formation of seed banks with the species *Psidium guajava* and *Tabernaemontana catharinensis*.

The *P. guajava* has been registered as an invasive species of secondary forests on abandoned pasture in the upper Paraná river Floodplain (CAMPOS; DICKINSON, 2005). Understories dominated by *P. guajava* are poorer in species and specimens than areas dominated by native species, showing an invasion process in the recovery area of Porto Rico island (CHAPLA et al., 2008). Plant invasion is a threat to biodiversity and the stability of native ecosystems, and can affect the functioning and processes of ecosystems (EHRENFELD, 2003; GORDON, 1998; MACK et al., 2000; VITOUSEK et al., 1997).

The succession model proposed for the study area (CAMPOS; DICKINSON, 2005) shows that anthropic disturbances can lead to the establishment and dominance of the invasive species *Psidium guajava* and *Tabernaemontana catharinensis*, and render difficult or impossible the establishment of pioneer or secondary species in the area, thus modifying the succession process and allowing for the dominance of *Psidium guajava*.

Psidium guajava has been reported as an invasive species in pastures (SOMARRIBA, 1985; SOMARRIBA; BEER, 1985) and as an important pioneer in the recovery process of abandoned pastures (AIDE et al., 1996, 2000; BERENS et al., 2008; CUBIÑA; AIDE, 2001; ZAHAWI; AUGSPURGER, 1999), although found only in young secondary forests (AIDE et al., 2000). *Psidium guajava* success in occupying pastures is due to its re-growth capacity and easy dispersion by birds and cattle (BERENS et al., 2008; SOMARRIBA, 1985; SOMARRIBA; BEER, 1985).

Forest recovery in abandoned pastures is slow compared with recovery due to several kinds of natural disturbances such as land clearing caused by storms or fall of branches, as well as by anthropic disturbances such as slash-and-burn agriculture (UHL, 1987; UHL et al., 1988; AIDE et al., 1995; CUBIÑA; AIDE, 2001).

Seed banks change drastically under pasture and lose their natural traits. These changes can alter the secondary succession process (QUINTANA-ASCÊNCIO et al., 1996).

Finally, the replacement of forests by pasture leads to changes in vegetation, including invasion of exotic species and decrease of most tree species (RAMIREZ-MARCIAL et al., 1992; QUINTANA-ASCÊNCIO et al., 1996).

Therefore, further intervention in Porto Rico Island will be necessary if the goals for creating the Environmental Protection Area (Área de Proteção Ambiental - APA) go beyond the recovery of the island vegetation and increased Carbon sequestration, aiming also at the restoration of species composition.

Conclusion

Density changes in the soil seed bank during succession of abandoned pastures did not follow a pattern. Richness and diversity increased, herb species were dominant and the number of tree species in the seed bank increased during the first 10 years of abandonment of pastures in riparian forests.

Soil use as pasture can result in a different environment at the end of succession due to seed bank deterioration and establishment of invasive exotic species, which can dominate the phytophysiognomy of the new ecosystem.

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