Timing of seed dispersal and dormancy, rather than persistent soil seed-banks, control seedling recruitment of woody plants in Neotropical savannas

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Abstract

A large fraction of tree species forming persistent soil seed-banks and with dormant seeds are expected to be found in strongly seasonal ecosystems such as Neotropical savannas, where seedling recruitment could be highly variable. In the savannas of Central Brazil, we studied seed characteristics (type of dormancy, longevity and moisture content) of 14 representative woody species differing in seed dispersal season. We also studied the dynamics of soil seed-banks and similarity patterns in woody species composition among seed rain, soil seed-bank, seedling bank and standing vegetation along shallow topographic gradients that differ in canopy cover. Woody species composition of the soil seed-bank largely differed from the standing vegetation, the seed rain and the seedling bank species composition, suggesting low recruitment of woody species from the soil seed-bank. Seeds of the 14 woody species remained viable for less than 16 months in laboratory dry-storage conditions. Of those, most seeds dispersed in the dry season were dormant and exhibited low moisture content, while most seeds dispersed in the wet season were non-dormant and exhibited high moisture content. Longevity of these seeds dispersed in the dry and the wet seasons did not differ significantly. This study shows that both timing of seed dispersal and dormancy appear to control timing of seed germination and seedling recruitment of most Neotropical savanna woody species, which did not form persistent soil seed-banks. This study contributes to the understanding of tree/grass coexistence and tree density variations along topographic gradients in tropical savannas.

Introduction

The coexistence of woody and herbaceous species (mainly grasses) is a fundamental feature of savanna ecosystems (Sarmiento, 1984). Recent studies (Jackson *et al.*, 1999; Higgins *et al.*, 2000; Goldstein *et al.*, 2008) have emphasized the importance of environmental variability and stochasticity in tropical savanna ecosystems to explain the coexistence of woody and herbaceous species. These studies recognize that savannas may not represent a stable (equilibrium) mixture of these life forms as has been suggested in other studies (Walker *et al.*, 1981; Langevelde *et al.*, 2003), but an unstable (non-equilibrium) mixture which persists as a result of complex, non-linear interactions between climate, soil and disturbances such as fire, herbivory and fluctuating annual rainfall (Goodland, 1971; Goodland and Pollard, 1973; Furley and Ratter, 1988; Ratter *et al.*, 1997; Scholes and Archer, 1997; Furley, 1999; Gardner, 2006).

Studies on the early life history stages of woody species have often been ignored in the discussion of tree and grass coexistence and equilibrium models of tropical savannas. These early stages may affect not only the relative abundance of trees and grasses but may also determine the spatial distribution of these

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contrasting life forms (Hurtt and Pacala, 1995), which in Neotropical savannas consistently changes along shallow topographic gradients. Thus, understanding tree/grass coexistence in tropical savannas, as well as the factors that control the spatial distribution of trees along topographic gradients, requires studies of early life history stage such as seed dispersal, seed germination, soil seed-bank and seedling dynamics of woody species.

Soil seed-banks play an important role in the long-term survival of individual species and plant communities (Simpson *et al.*, 1989; Baskin and Baskin, 1998) because they constitute a source of propagules for recruitment after disturbances (Dalling and Hubbell, 2002; Williams *et al.*, 2005), and an alternative source of propagules when seed production of species fails for long periods. Soil seed-banks are known to be highly heterogeneous (Uhl *et al.*, 1981; Garwood, 1989). Some factors resulting in high spatial heterogeneity of soil seed-bank densities are the seed dispersal patterns of the different species (Hall and Swaine, 1980; Uhl *et al.*, 1981; Swaine and Hall, 1983), physical and chemical soil characteristics (Garwood, 1989), the proximity of a seed source (Hartshorn, 1980; Geritz *et al.*, 1984) and the spatial and temporal pattern of disturbances (i.e. opening of canopy gaps). Intrinsic rates of loss in seed viability following dispersal and variation in the timing and duration of fruit production also influence soil seed-bank densities (Dalling *et al.*, 1997; Dalling, 2004; Fornara and Dalling, 2005).

Soil seed-bank characteristics are well known for ecosystems such as temperate forest (Thompson and Grime, 1979) and tropical rainforests, which contain abundant seeds of pioneer species that recruit in response to canopy openings (Whitmore, 1983; Dalling *et al.*, 1997). While tropical rainforests have soils with high water content most of the year, most Neotropical savannas are strongly seasonal with about 4 or 5 months that are practically rainless. Even though soil water can be available throughout the year at depth for mature trees with deep roots, upper soil layers have very negative soil water potentials during the dry season. Negative water potentials in upper soil layers may impair seed germination or decrease the rate of growth and establishment of new seedlings (Goldstein *et al.*, 2008).

Strongly seasonal conditions may result in highly variable seedling recruitment success, which should result in selective pressures favouring seed dormancy in tropical savanna species. High frequencies of species with dormant seeds have been particularly associated with unpredictable environments and climates with variable rainfall trends, such as seasonal tropical dry forests (Khunara and Singh, 2001). In addition to the highly variable precipitation, competition with grasses and fire highly constrain seedling emergence and establishment of tropical savanna woody species. Thus, a relatively large fraction of woody species forming persistent soil seed-banks is expected to be found in savanna ecosystems compared to more humid tropical forests. Differences in the kind of dormancy are also expected between seeds dispersed in the dry and wet seasons and therefore dormancy may be an important mechanism controlling the time of germination of savanna trees.

In the savannas of central Brazil (*cerrado*), the largest tropical ecosystem after the Amazonian rainforest, the relative dominance of herbaceous and woody species varies along shallow topographic gradients of 50 m in elevation and a few hundred metres in length. The uppermost portions of the gradients are characterized by relatively closed savannas with a nearly continuous layer of trees up to 12 m tall and a low abundance of herbaceous plants, while the low portions of the gradient are characterized by open savannas with few isolated small trees or shrubs and a continuous layer of herbaceous plants (Eiten, 2001). Fire frequency, water-table depth and nutrient availability have been suggested to be major factors that determine the abundance of trees along the topographic gradients (Oliveira-Filho and Ratter, 2002). Whether or not soil seed-bank dynamics of woody species are consistent with variations in tree canopy cover across the *cerrado* landscape has not been determined, but could potentially influence such spatial patterns of tree density and canopy cover, which ultimately could affect tree–grass coexistence in tropical savannas.

In this study we investigated temporal processes of seed production and dynamics of seeds in the soil, related to the strong seasonality in precipitation, as well as spatial patterns of seed production and dynamics of seeds in the soil along a topographic gradient. We addressed the following questions: (1) What fraction of woody species form persistent soil seed-banks? (2) Do seed characteristics (dormancy type, longevity and moisture content) of common woody plants differ between seeds dispersed during dry and wet seasons? (3) Do soil seed-bank densities of woody and herbaceous species differ temporally (between seasons) and/or spatially (along topographic gradients)? (4) Is the woody species composition among the soil seed-bank, seed rain, seedling banks and the standing vegetation similar along topographic gradients and similar to each other?

Materials and methods

Study site

This study was conducted from June 2005 until July 2008 at the Instituto Brasileiro de Geografia

e Estatística (IBGE) reserve, a field experimental station located 35 km south of Brasilia, Brazil (15°56′S, 47°63′W, altitude 1100 m). Average annual precipitation is about 1500 mm with a pronounced dry season from May to September. The months of June, July and August are often completely rainless. Average relative humidity during the rainy season is about 80% and decreases to 55% during the dry season, when daily minimum relative humidity may reach values as low as 10%. Mean monthly temperatures range from 19°C to 23°C. The soils are clay-rich oxisols, very deep, well-drained, red or yellow, and nutrient poor. The IBGE reserve contains all the major *cerrado* vegetation types: *cerrado denso*, *cerrado sensu stricto* and *campo sujo*. *Cerrado denso* is a semi-closed woodland (40–60% tree crown cover) with a moderately tall (usually 7–12 m) tree canopy. Because of the shade created by the canopy trees, the herbaceous and semi-woody ground vegetation has a lower cover than in relatively open *cerrado* vegetation. *Cerrado sensu stricto* is a savanna dominated by trees and shrubs (canopy generally less than 7 m tall) with 10 to less than 40% tree crown cover. *Campo sujo* has few short trees and scattered shrubs over a nearly continuous grass layer (the woody layer usually covers less than 10% of the ground).

In June 2005, we established three transects (of approximately 1000 m) in the reserve, and each spanned the three major vegetation types. The transects were placed along continuous topographic gradients, each with a different elevation, ranging from 1117 to 1153 m, in vegetation that had been protected from fire for at least 30 years, to rule out the confounding effect of fire on sexual reproduction on most *cerrado* woody species (Hoffman, 2000) and to eliminate possible different fire frequencies in each study site. We performed preliminary species–area curves in *cerrado denso* and *campo sujo* areas, which indicated that about 85% of the maximum richness of woody plants (>1 m tall) was attained at 1024 m². Hence, nine plots of 400 m² (20 × 20 m) were established in each transect (three in each vegetation type), for a total of 27 permanent plots.

Canopy cover and species diversity of woody plants

During the dry season of 2005 we estimated canopy cover by measuring leaf area index (LAI: area of leaves per unit area of soil surface) of the standing vegetation with a Decagon® AccuPAR model LP-80 PAR/LAI Ceptometer (Decagon Devices Inc., Pullman, Washington, USA). This instrument calculates LAI based on the above- and below-canopy photosynthetic photon flux density (PPFD: the flux of photons between 400 and 700 nm wavelength per unit area) measurements. LAI measurements were taken

1 m above the soil surface, at midday (on clear days) at eight random points within each plot.

Species composition and abundance in each plot was assessed by identifying and counting all woody individuals taller than 1 m. For each plot, within each vegetation type we calculated Shannon diversity index (H′): $H' = -\Sigma p_i \, lnp_i$. p_i is the proportion of species i relative to the total number of species.

Soil seed-bank

Seed-bank composition and density were assessed through seedling emergence and thus this study examines the germinable soil seed-bank. To assess soil seed-bank composition and density we collected soil samples in each of the 27 plots during late wet seasons (March 2006 and February 2007) and middle dry seasons (June 2006 and June 2007). During each collection period, soil samples were taken from 81 points (three random points per plot) to a depth of 5 cm. This depth was chosen because preliminary studies found that 90% of the seeds were concentrated between 0.5 cm and 2 cm (Andrade, 2002). At each point, a total volume of 3125 cm³ of soil was extracted by using an iron square (25 × 25 × 5 cm) pushed into the soil. Within 24 h of collection, the soil was passed through a sieve (5 mm) and large pieces of rock, roots and litter were discarded. Each sample was then spread in plastic trays (25 × 30 × 4 cm) which had several 0.5 mm holes to allow drainage. Trays were placed in a neutral shade greenhouse under prevailing mean temperature conditions of 25–28°C, 30% full sunlight, and 12 h/12 h photoperiod. Trays were watered daily (three times a day for 2 min) with overhead sprinklers for the duration of the experiment. Seed germination was checked every 4 d and seedlings were identified, counted and removed from the trays. Each tray was observed for 12 weeks. Individuals too small to identify at the end of 12 weeks were transplanted and grown to a larger size until they could be identified. To estimate the number of species that entered, left or persisted in the soil seed-bank in each vegetation type, we counted the number of new, absent and persisting (re-occurring) species, as compared to the previous soil sampling season.

Seed characteristics of woody species

Fourteen woody species were used to test if seed moisture content, dormancy and longevity differed between seeds dispersed during dry and wet seasons. These species are common and widely distributed throughout much of the *cerrado* (Silva Júnior, 2005). They differ in their dispersal season and belong to a wide range of plant families: *Acosmium dasycarpum* (Fabaceae), *Brosimum gaudichaudii* (Moraceae), *Eriotheca*

pubescens (Malvaceae), *Eremanthus glomerulatus* (Asteraceae), *Erythroxylum suberosum* (Erythroxylaceae), *Guapira graciliflora* (Nyctaginaceae), *Guapira noxia* (Nyctaginaceae), *Kielmeyera coriaceae* (Clusiaceae), *Miconia ferruginata* (Melastomataceae), *Ouratea hexasperma* (Ochnaceae), *Palicourea rigida* (Rubiaceae), *Rourea induta* (Connaraceae), *Solanum lycocarpum* (Solanaceae) and *Styrax ferrugineus* (Styracaceae).

During dry and wet seasons, available mature seeds from several individuals of the above species were collected directly from parent trees or from the ground if they were in good condition. After mixing and cleaning, three groups of 50 seeds were weighed to calculate the average number of seeds per gram and also to determine fresh moisture content. To determine fresh seed moisture content the seeds were weighed, then dried at 70°C for at least 72 h, and then re-weighed until they attained a constant dry mass.

To evaluate natural seed dormancy we performed germination tests without any seed pre-treatment under greenhouse conditions. Five replicates of 20 seeds per species were sown in plastic trays (25 × 30 × 4 cm) filled with an artificial substrate (mix of 70% peat moss and 30% vermiculite). The trays were randomly distributed on the greenhouse benches, under prevailing mean temperature conditions of 25–28°C, 30% full sunlight, 12 h/12 h photoperiod, and watered every day (three times a day for 2 min) with an automated sprinkler system. Germination, defined as radicle emergence, was monitored every 3 d for 8–12 weeks. We recorded the dates of the first and last seeds to germinate and calculated the median length of germination (pooling germinated seeds of each species from the four replicates) from the germination times of all seeds that germinated (Blakesley *et al.*, 2002). A species was considered to have dormant seeds if the median length germination time (MLG) was 30 d or longer (Sautu *et al.*, 2007).

Five different classes of dormancy were considered following the classification of Baskin and Baskin (2004): (1) physical dormancy (PY), species with a water-impermeable seed (or fruit) coat; (2) morphological dormancy (MD), species with an underdeveloped embryo and MLG ≤ 30 d; (3) morphophysiological dormancy (MPD), those with an undeveloped embryo and MLG > 30 d; (4) physiological dormancy (PD), those that have a permeable seed coat, fully developed embryo and MLG > 30 d; and (5) combinational dormancy (PY + PD), species with an impermeable seed coat and a physiologically dormant embryo.

A seed was considered to have physical dormancy if it did not imbibe water. The method described by Bansal *et al.* (1980) was used for imbibition tests. Briefly, seeds were weighed and then placed in water at room temperature (*c.* 22°C). At hourly intervals for 8–24 h, seeds were removed from the water, blotted dry and reweighed. An increase in seed mass indicates that seeds (or fruits) have water-permeable coats, whereas no increase in mass indicates that they have water-impermeable coats. To determine whether seeds had a fully developed or underdeveloped embryo, we examined the embryos under a dissecting microscope after being removed from previously imbibed seeds. Seed longevity was calculated using information on monthly viability loss by seeds kept stored in paper bags at room temperature and 40% relative humidity. Because seeds may experience drought periods of different length in the field, we evaluated the rate of seed viability loss under laboratory dry storage conditions. Every month, for 4–5 months, seed viability percentage of each species was estimated by using 1% tetrazolium red solution (2,3,5-triphenyl-tetrazolium chloride). Three samples of 50 seeds were used for each species every month. Cut seeds were soaked in the tetrazolium solution in flasks totally wrapped with aluminium foil, which were placed in an oven and kept at 40°C. Embryo coloration patterns were evaluated under a dissecting microscope every hour until embryos were completely stained. For the species in this study, staining required 12–24 h. Seeds were recorded as viable when embryos were homogeneously stained (i.e. both radicle and cotyledons). Exponential and linear functions, fitted to the decrease in viability loss as a function of time, were used to estimate the longevity of each species under dry-storage conditions.

Seed rain and seedling bank

Species composition, abundance and diversity of annual seed rain at the study sites were estimated using seed traps located at the corners of each of the permanent plots (four per plot). Seed traps consisted of a plastic funnel, 20 cm in diameter, with a collection area of $0.0314 \, m^2$ that was inserted into a PVC tube (5 cm diameter) that held the funnels in place. A small nylon mesh bag was attached at the funnel base to collect seeds and dispersal units. All seeds, fruits and fruit parts were collected once a month for a 13-month period, from November 2005 until February 2007. Whole, apparently intact seeds/diaspores were identified to species (or at least to family when it was not possible to identify the species) and dried to constant weight. Identification was based on published literature and by comparison with herbarium specimens and specimens collected from mature plants.

To determine seedling bank composition, in July 2005 eight $1\text{-}m^2$ subplots were randomly established within each of the 27 permanent plots for a total of 216 subplots. According to preliminary curves of seedling species richness versus number of $1\text{-}m^2$ subplots performed in *cerrado denso* and *campo sujo* areas, about 90% of the seedling richness was attained with a total

of eight 1-m² subplots per plot. In July 2006, all seedlings of woody species up to 30 cm tall within the subplots were counted and identified. Identification was made by comparison with herbarium specimens and with reference specimens collected from outside the subplots and with help from local botanists. Sixteen per cent of seedlings could not be identified.

Data analysis

Differences in species abundance, diversity and leaf area index among vegetation types were examined with one-way ANOVAs using the program JMP 7 (SAS Institute Inc., Cary, North Carolina, USA). The data from the nine plots of each vegetation type were pooled. Tukey HSD *post hoc* tests were used for multiple comparisons of means.

Differences in the number of species/m² and seed density of the germinable soil-bank among vegetation types and collection periods (season) were examined with two-way ANOVAs with vegetation type and season as main factors. To fulfil the assumption of normality, the data of seed density were square-root transformed. Tukey HSD *post hoc* tests were used for multiple comparisons of means. Non-parametric Kruskal–Wallis tests were used to test differences in the proportion of woody/herbaceous species among vegetation types and among seasons, as well as differences in species diversity (Shannon index) among vegetation types. Negative exponential and linear functions were fitted to the data of percentage seed viability loss as a function of time. Differences in moisture content and longevity between seeds dispersed in dry and wet seasons were examined with Student's *t*-test.

Non-metric multi-dimensional scaling (NMDS) ordination was used to examine patterns in species composition. Ordinations for the vegetation, seed rain, soil seed-bank and seedling bank of woody species were performed with PRIMER v5 (Clarke and Warwick, 2001) combining all taxa found during the sampling periods (in the case of seed rain and seed bank). The purpose of the ordinations is to represent the sites as points in a two-dimensional space such that the relative distances among points reflect the relative dissimilarities of the sites. Similarities between every pair of the nine sites were calculated using Bray–Curtis coefficients, after square-root transforming species abundances of every entry in the similarity matrix. Analyses of similarities in species composition among vegetation types were examined with an analogue of the one-way ANOVA (ANOSIM) under the null hypothesis that there are no species assemblage differences among vegetation types. ANOSIM routines are permutation/randomization tests that assess differences between average ranks between and within groups. Values on a scale of 0 (indistinguishable) to 1 (all similarities within vegetation types are less than any similarity between vegetation types) reflect multiple pairwise comparisons with sites well separated ($R > 0.75$), sites overlapping but differing ($R > 0.5$) or barely separated at all ($R < 0.25$). To determine the extent of agreement between pairs of ordinations (agreement in the high-dimensional multivariate data underlying this low-dimensional plot), Spearman rank correlation coefficients (ρ) between all the elements of any two similarity matrices were calculated under the null hypothesis that there is no relation whatsoever between any two similarity matrices ($\rho = 0$).

Results

LAI and species diversity of woody plants

The major difference in vegetation structure among the vegetation types was in leaf area index (LAI), which ranged from about 1.5 in *cerrado denso* to about 0.6 in *campo sujo* (Fig. 1a). Woody species diversity was significantly higher in *cerrado denso* than in *cerrado sensu stricto* (Kruskal–Wallis test, $H = 12.17$; $P = 0.0005$) or *campo sujo* (Krukal–Wallis; $H = 5.47$; $P = 0.02$) (Fig. 1b). Species diversity did not differ between *cerrado sensu stricto* and *campo sujo* (Kruskal–Wallis test $H = 0.56$; $P = 0.45$) (Fig. 1b). Mean abundance (number of 1-m tall individuals in 400 m²) did not differ significantly among vegetation types (Fig. 1c) [the total number of woody species found in each vegetation type (3600 m² each) can be seen in Table 3].

Soil seed-bank density

The germinable soil seed-bank collected in all study sites between March 2006 and July 2007 contained a total of 35 species belonging to 25 genera and 10 families (Table 1). Twenty-one species were herbs, ten were woody species (trees and shrubs) and six were undetermined. Seeds of shrubs and herbs of Asteraceae, Poaceae, Rubiaceae, Cyperaceae and Melastomataceae were the most abundant and comprised 88% of the total number of seeds that were found (Table 1).

Vegetation type (two-way ANOVA; $F_{2,312} = 0.17$; $P = 0.84$), season ($F_{3,312} = 2.20$; $P = 0.08$) and their interaction ($F_{6,312} = 1.61$; $P = 0.14$), did not have a significant effect on the number of species per m² found in the germinable soil seed-bank (Fig. 2a). Vegetation type (two-way ANOVA; $F_{2,312} = 3.38$; $P = 0.03$) and season ($F_{3,312} = 4.39$; $P = 0.005$), but not their interaction ($F_{6,312} = 1.21$; $P = 0.30$), had a statistically significant effect on soil seed density
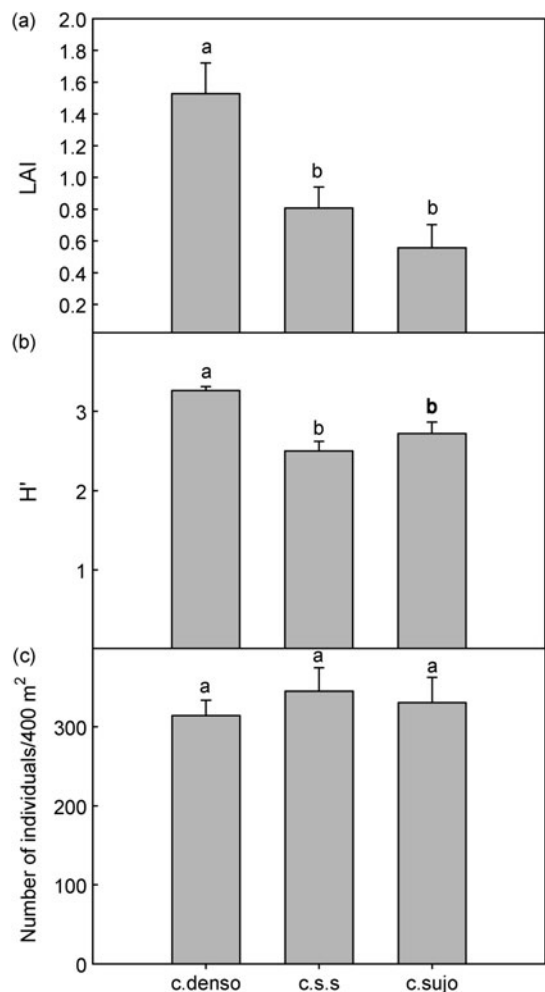
Figure 1. (a) Leaf area index (LAI), (b) Shannon species diversity index (H′), and (c) number of individuals of woody species taller than 1 m in each vegetation type: *cerrado denso* (c.denso, high tree canopy cover), *cerrado sensu stricto* (c.s.s, intermediate tree canopy cover) and *campo sujo* (c.sujo, low tree canopy cover). Bars are means + SE ($n = 9$). Means with the same letters do not differ significantly ($P > 0.05$) according to Tukey HSD *post hoc* test (a, c) or according to Kruskal–Wallis (b) pairwise tests.

(Fig. 2b), indicating that seasonal changes in soil seed-bank density did not depend on vegetation type. Mean seed density across seasons was significantly higher in *cerrado denso* (144.30 ± 24.13 seeds m^{-2}) than *cerrado sensu stricto* (70.20 ± 10.91 seeds m^{-2}). Seed density in *campo sujo* (98.22 ± 21.66 seeds m^{-2}) did not differ from that in *cerrado denso* or *cerrado sensu stricto*. Seasonal differences in seed density were the result of a significantly higher seed density in the dry season of June 2006 in comparison to the wet season of 2007, but no other seasonal differences in seed density were detected. The proportion of woody/herbaceous species did not differ significantly among vegetation types (Kruskal–Wallis; $H = 0.4351$; $P = 0.804$) but differed significantly among seasons (Kruskal–Wallis

$H = 9.264$; $P = 0.026$), with a higher proportion of woody/herbaceous species during the wet season of 2006 than during other sampled seasons (Fig. 2c).

Soil seed-bank persistence

Less than 16% of all the herbaceous and woody species found in the soil were present in the four sampling seasons, suggesting that they were among the few species potentially forming persistent seed-banks (seeds living in the soil for a period longer than 1 year). Only *Baccharis salzmannii*, *Echinolaena inflexa* and *Miconia albicans* were consistently present in all vegetation types. *Spermacoce* cf. *verticilata* and *Cassitha filiformis* were also found in all four sampling periods but only in *cerrado sensu stricto* and *campo sujo*. More than 48% of the species were present in only one of the four sampling dates.

Similar trends in the number of species entering, exiting and persisting in the soil seed-bank were observed in each vegetation type over the period of study (Fig. 3) with more species leaving the soil bank during the wet season of 2007 than during the dry seasons of 2006 and 2007. In the wet season of 2007, the number of species leaving the soil bank was higher than both the number of species entering into the bank and the number of species persisting in the bank, in all three vegetation types. The number of species persisting in the soil bank was higher during the dry seasons than during the wet season of 2007 (Fig. 3).

Seed characteristics of woody plants

The number of seeds per gram of woody species ranged from 3.31 to 654.04 (Table 2). Seed moisture content ranged from 8.91 to 81.62%. Nine of the 14 species had moisture content higher than 28% (moist seeds), and five species had less than 28% moisture content (dry seeds). Dispersal season had a significant effect on seed moisture content ($t_{1,34} = 5.38$; $P < 0.001$); species dispersed in the dry season had lower moisture content ($22.49\% \pm 4.98$) than those dispersed in the wet season ($59.36\% \pm 4.62$) (Table 2).

We assigned seed dormancy types based on median length germination time (MLG), permeability of the seed coat to water and type of embryo. Seeds of *Eremanthus glomerulatus* did not germinate, probably because of extremely low initial viability (2.47%). Six species (42.86%) were non-dormant (MLG $\leq$ 30 d) and seven species (57.14%) were dormant (Table 2). Seventy-five per cent of the species dispersed during the dry season had dormant seeds whereas 43% of the species dispersed during the wet season had dormant seeds (Table 2). *Acosmium dasycarpum* was the only species exhibiting physical dormancy (PY) because of

Table 1. Mean seed density (number of seeds m^{-2}) of herbaceous and woody species found in the soil seed-bank of each vegetation type (*cerrado denso*, *cerrado sensu stricto* and *campo sujo*; high, intermediate and low tree canopy cover, respectively) over four sampling periods. Soil samples were collected during two consecutive wet seasons (March 2006 and February 2007) and two consecutive dry seasons (June 2006 and June 2007)

Family	Species	Growth form	Cerrado denso	Cerrado sensu stricto	Campo sujo	Average
Asteraceae	*Achyrocline satureoides*[nn]	Herb-P	0.30	0.59	0.15	0.35
	Ageratum conyzoides[nn]	Herb-A	0.15	0	0.15	0.10
	Morphospecies 1	*	0.30	0.15	0.15	0.20
	Morphospecies 2	*	1.19	0.15	0	0.44
	Baccharis salzmannii	Shrub-D	26.81	17.78	17.49	20.69
	Bidens pilosa	Herb-A	0.30	0.30	0.44	0.35
	Eremanthus glomerulatus	Tree-E	0	1.04	0.30	0.44
	Eremanthus goyazensis	Tree-E	0.30	1.04	0.74	0.69
	Eremanthus sp.	Tree-E	0.15	0	0	0.05
Cyperaceae	*Bulbostylis capilaris*	Herb-P	0.89	0.59	0	0.49
	Bulbostylis sp.	Herb-P	3.58	0.30	0.89	2.42
	Rhynchospora sp.	Herb-P	1.04	1.93	1.54	1.50
	Rhynchospora exaltata	Herb-P	2.52	1.19	4.00	2.57
Lamiaceae	*Hyptis* cf. *lophanta*	Herb-A	0.30	0.15	0.15	0.20
Lauraceae	*Cassitha filiformis*	Herb-P	7.70	11.41	11.75	10.29
Fabaceae	*Chamaecrista* cf. *orbiculata*	Shrub-D	0.74	0.61	0.89	0.75
	Leguminosae 1	*	0.15	0.15	0	0.10
	Leguminosae 2	*	0.15	0	0	0.05
	Mimosa sp.	Tree-D	0.44	0	0.15	0.20
Malvaceae	*Sida rhombifolia*	Herb-P	0.44	0	0	0.15
Melastomataceae	*Miconia albicans*	Shrub-E	17.48	2.96	6.98	9.14
	Ossaea congestiflora	Shrub-E	0.59	0.15	0.16	0.30
Oxalidaceae	*Oxalis densifolia*	Herb-A	0.74	0.89	0.30	0.64
Poaceae	*Axonopus* sp.	Herb-P	0.15	0.30	0	0.15
	Echinolaena inflexa	Herb-P	76.09	23.26	43.20	58.65
	Ichnanthus camporum	Herb-P	0.15	0.44	0.15	0.25
	Morphospecies 1	Herb-*	0	0	0.15	0.05
	Morphospecies 2	Herb-*	0	0.15	0	0.05
	Paspalum cf. *gardnerianum*	Herb-P	1.63	0.89	1.27	1.26
	Schizachyrium tenerum	Herb-P	0.07	0.15	0.30	0.17
	Trachypogon sp.	Herb-*	0.15	0	0	0.05
Rubiaceae	*Coccocypselum aureum*	Herb-*	0.30	0	0	0.10
	Cordiera sp.	Tree	1.04	0	0	0.35
	Sabicea brasiliensis	Shrub	0.30	0	1.33	0.54
	Spermacoce cf. *verticilata*[nn]	Herb-P	3.26	2.67	4.04	3.32
Total			144.30	70.20	98.22	104.38

Herbs were classified as perennials (P) and annuals (A) and trees and shrubs as evergreen (E) and deciduous (D). *, Not determined; [nn], non-native species.

impermeable seed coats (data not shown). Four species (28.57%) had permeable coats and MLG > 30 d, and thus were classified as having physiological dormancy (PD). Finally, two species (14.29%) were assigned to have morphophysiological dormancy (MPD) because they exhibited permeable coats, underdeveloped embryos and MLG > 30 d (Table 2). No species were found to have either morphological dormancy (MD) or combinational dormancy (PY + PD).

Seed viability at 4–5 months ranged from 2.77 to 44.83% (Table 2). Estimated seed longevity (i.e. viability in storage) ranged from 5.81 to 26.48 months; however, only four species remained viable longer than 12 months (Table 2). Dispersal season did not have a significant effect on seed longevity ($t_{1,34} = 0.55$; $P = 0.29$).

Seed rain and seedling bank

The total number of woody species found in the annual seed rain ranged from 23 in *campo sujo* to 28 in *cerrado sensu stricto* while the total number of woody species in the seedling bank ranged from 36 in *cerrado sensu stricto* to 45 in *cerrado denso* (Table 3). In the three vegetation types, the species diversity of the seed rain was lower than the species diversity of the seedling bank and the standing vegetation (Table 3).
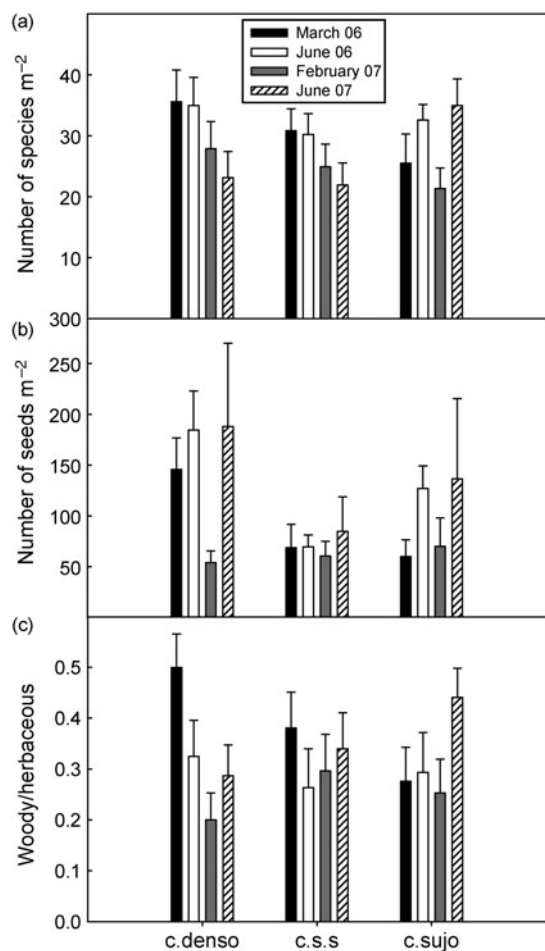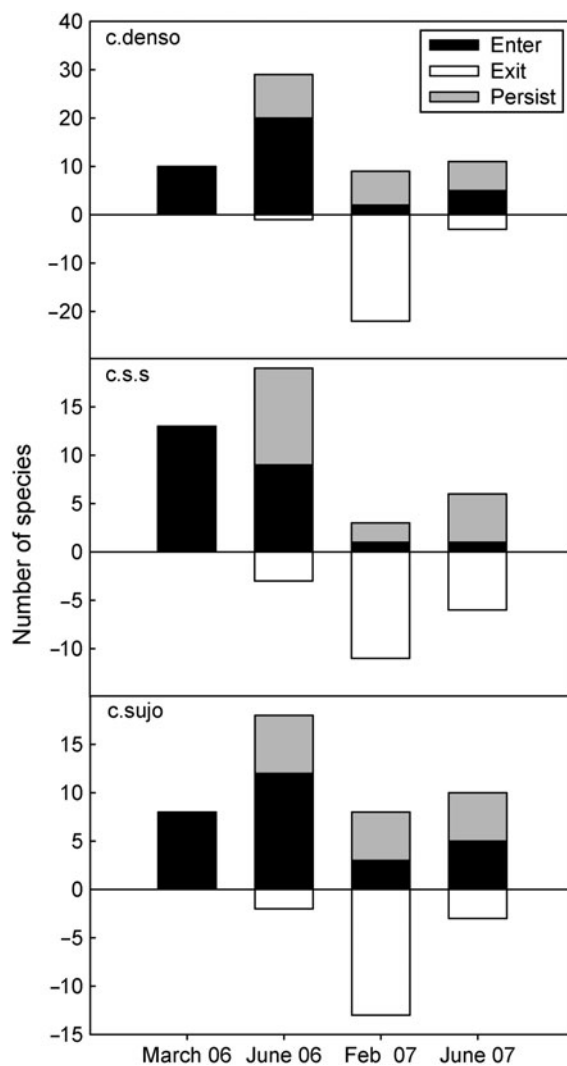
Figure 2. (a) Number of species m^{-2}, (b) number of seeds m^{-2} (density), and (c) proportion of woody/herbaceous species in the germinable soil seed-bank collected during wet (March 2006, February 2007) and dry (June 2006, June 2007) seasons. Species richness and number of seeds include both herbaceous and woody species. Soil samples are from *cerrado denso* (c.denso, high tree canopy cover), *cerrado sensu stricto* (c.s.s, intermediate tree canopy cover) and *campo sujo* (c.sujo, low tree canopy cover). Bars are means + SE ($n = 27$).

Figure 3. Number of species that enter (black), number of species that exit (white) and number of species that persist (grey) in the soil seed-bank with respect to the previous collection period in each vegetation type from March 2006 until June 2007: *cerrado denso* (c.denso, high tree canopy cover), *cerrado sensu stricto* (c.s.s, intermediate tree canopy cover) and *campo sujo* (c.sujo, low tree canopy cover). Bars are the total number of species and therefore do not have standard errors. The bar of March 2006 indicates the number of species found in the soil bank at the beginning of the study. Soil samples were collected during two consecutive wet seasons (March 2006 and February 2006) and two consecutive dry seasons (June 2006 and June 2007).

Similarity in species composition among seed bank, seed rain, seedling bank and standing vegetation

Species composition of woody plants in the nine study sites differed among vegetation types (Fig. 4a). Sites from each of the three vegetation types partially overlapped in their species composition but were statistically distinguishable in the two-dimensional ordination space (ANOSIM; $R = 0.66$, $P = 0.007$). On average, *cerrado denso* sites were more similar to each other (shorter distances in the ordination space) than *cerrado sensu stricto* sites or *campo sujo* sites. The average similarity of the three sites of *cerrado denso* (average of the three pairwise comparisons) was 66.40%; of *cerrado sensu stricto*, 62.06%; and of *campo*

sujo, 59.98%. On the other hand, the soil seed-bank composition of woody species did not differ significantly among the vegetation types (Fig. 4b). Consequently, the soil seed-bank composition of the three vegetation types did not ($P = 0.268$) separate well in the two-dimensional plot. The average similarity in species composition of the seed-bank composition of *campo sujo* sites was 61.39%; *cerrado sensu stricto* sites, 48.72%; and *cerrado denso* sites, 46.68%.

Table 2. Seed characteristics of 14 woody species from the Brazilian *cerrado*. Dispersal season: dry (D), wet (W), dry and wet (DW). Seeds g^{-1}, number of seeds (or diaspore) g^{-1}; seed MC, mean fresh moisture content $\pm$ SD. Dormancy type (abbreviations from Baskin and Baskin, 2004): non-dormant (ND), physical dormancy (PY), physiological dormancy (PD), morphophysiological dormancy (MPD)*. Estimated longevity: number of months that seeds remain viable (% viability > 1%) in dry storage conditions at 20℃. Exponential and linear functions, fitted to the decrease in viability loss as a function of time, were used to estimate the longevity of each species

Species	Dispersal season	Seeds g^{-1}	Seed MC (%)	Dormancy	Viability at one 4–5 months (%)	Estimated longevity months
Acosmium dasycarpum	D	25.08	9.78 $\pm$ 3.44	PY	66.97	13.43
Brosimum gaudichaudii	W	17.06	47.19 $\pm$ 4.96	ND	–	–
Eremanthus glomerulatus	D	654.04	9.44 $\pm$ 1.96	–	–	–
Eriotheca pubescens	D	3.31	9.96 $\pm$ 0.46	ND	16.66	5.81
Erythroxylum suberosum	D	5.85	66.14 $\pm$ 1.01	MPD	44.83	26.48
Guapira graciliflora	W	8.88	64.41 $\pm$ 0.29	ND	44.68	16.34
Guapira noxia	W	27.86	54.82 $\pm$ 0.91	ND	0.00	3.80
Kielmeyera coriaceae	D	9.01	24.36 $\pm$ 4.12	PD	23.53	5.18
Miconia ferruginata	W	18.61	71.22 $\pm$ 0.01	PD	3.76	7.56
Ouratea hexasperma	W	28.74	37.51 $\pm$ 1.35	ND	27.97	9.01
Palicourea rigida	W	17.32	72.92 $\pm$ 0.77	PD	35.99	14.92
Rourea induta	W	5.31	67.47 $\pm$ 0.98	PD	–	–
Styrax ferrugineus	DW	4.59	81.62 $\pm$ 0.04	MPD	2.77	7.56
Solanum lycocarpum	DW	6.00	8.91 $\pm$ 1.44	ND	35.55	7.72

–, Not determined.
*No species showed morphological (MD) nor combinational dormancy (PY + PD).

Composition of woody species in the seed rain differed among vegetation types (Fig. 4c) (ANOSIM; $R = 0.49$, $P = 0.014$). Seed rain composition of *cerrado sensu stricto* sites was more similar to each other than seed rain composition of *cerrado denso* and *campo sujo* sites. The average similarity of *cerrado sensu stricto* sites was 49.31% versus 45.76% for *cerrado denso* sites and 42.96% for *campo sujo* sites.
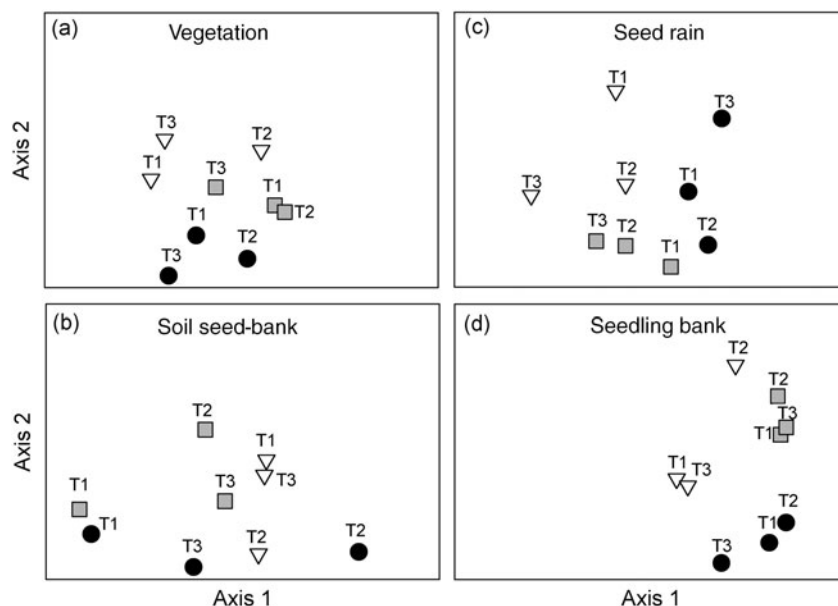
Species composition of the woody seedling bank differed significantly among vegetation types (ANOSIM; $R = 0.753$, $P = 0.0004$) and the sites separated well from each other in the ordination space (Fig. 4d). Seedling composition of *cerrado sensu stricto* sites was more similar to each other than to that of *cerrado denso* and *campo sujo* sites. The average similarity of the three sites of *cerrado sensu stricto* was 73.38% versus 71.99% for *cerrado denso* sites and 69.36% for *campo sujo* sites.

Seed rain and vegetation composition across sites were more similar to each other than either was to the seed bank and seedling bank composition of woody species (Table 4). The correlation between the vegetation and the seed rain was 0.52. Seedling bank composition was more similar to the vegetation composition than to the seed bank or seed rain (Table 4). The correlation between the seedling bank

Table 3. Total number of species, density (vegetation, number of individuals m^{-2}; seed rain, number of diaspores m^{-2}; seedling, number of seedlings m^{-2}), and Shannon diversity indices of woody species found in the standing vegetation, seed rain and seedling bank in three vegetation types: *cerrado denso*, *cerrado sensu stricto* and *campo sujo* (high, intermediate and low tree canopy cover, respectively)

	Vegetation type	Number of species	Density	Shannon diversity index
Vegetation	*cerrado denso*	90	0.78	3.69
	cerrado sensu stricto	76	0.86	2.93
	campo sujo	86	0.83	3.18
Seed rain	*cerrado denso*	24	976.65	2.23
	cerrado sensu stricto	28	1165.04	2.24
	campo sujo	23	484.78	2.37
Seedling	*cerrado denso*	45	4.64	3.26
	cerrado sensu stricto	36	4.40	3.10
	campo sujo	45	4.15	3.32

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of (a) composition of woody species in each vegetation type, (b) soil seed-bank of woody species, (c) seed rain of woody species, and (d) seedling bank of woody species, in *cerrado denso* (high tree canopy cover, black circles), *cerrado sensu stricto* (intermediate tree canopy cover, grey squares) and *campo sujo* (low tree canopy cover, open triangles). T1, T2 and T3 correspond to Transect 1, Transect 2 and Transect 3 sites, respectively. Points that are close together represent sites with similar species composition; points that are far apart correspond to sites with very different species composition.

and the vegetation was 0.29; between seedling bank and seed bank 0.12; and between seedling bank and seed rain, 0.03.

Discussion

Soil seed-bank density

Soil seed-banks in the three vegetation types were mostly composed by herbaceous species and very few woody species. The relatively high abundance of herbaceous species found in the seed bank has been reported previously for the Brazilian *cerrado* (Andrade, 2002) and for other tropical savannas (McIvor and Gardener, 1991; Perez and Santiago, 2001).

Table 4. Spearman rank correlation coefficients (ρ) between pairs of similarity matrices indicates how closely related a set of multivariate data are. In this case, the data are the abundance of each species present in the vegetation, seed rain, seed bank and seedling bank. ρ = 1 if similarity matrices are identical; ρ = 0 if there is no relation between similarity matrices. *P* values are indicated in parentheses

	Vegetation	Seed rain	Seed bank
Seed rain	0.52 (*P* = 0.0001)		
Seed bank	0.08 (*P* = 0.654)	0.03 (*P* = 0.559)	
Seedling bank	0.29 (*P* = 0.054)	0.03 (*P* = 0.451)	0.12 (*P* = 0.24)

In our study, mean density of seeds in the soil ranged from 144 seeds m^{-2} in *cerrado denso*, to 70 seeds m^{-2} in *cerrado sensu stricto*. Because of the soil depth (4 cm) we used in the germination trays, it is possible that our study underestimates seed density (Dalling *et al.*, 1995). However, our mean density values are within the range of 25–3350 seeds m^{-2} reported for tropical forests (Garwood, 1989), and it is also within densities reported in other *cerrado* studies (i.e. 757 seeds m^{-2}, Sassaki *et al.*, 1999; 143 seeds m^{-2}, Andrade, 2002) for soil samples obtained from the first 5 cm depth of soil. The average soil seed-density of the three vegetation types (104 seeds m^{-2}) in this study, were much higher than seed densities observed in tropical savannas of Venezuela (1.70 seeds m^{-2}, Perez and Santiago, 2001; 52.50 seeds m^{-2}, Flores and Dezzeo, 2005). Seed-bank densities in the three vegetation types studied were, however, lower than seed densities found in burned and tilled soils, and in areas planted with pasture that were covered by *cerrado* vegetation in the past (Andrade, 2002; Ikeda *et al.*, 2008); in these areas, seeds of non-native species formed larger seed-banks than seeds of native species. In our study, we found few non-native species, such as *Ageratum conyzoides*, *Achyrocline satureoides* and *Spermacoce* cf. *verticilata*, in the soil, probably because of the lack of recent major disturbances (i.e. fire).

The mean number of species m^{-2} in the soil bank did not differ among vegetation types. Vegetation type and season, on the other hand, had a significant effect

on soil seed-density, suggesting that seasonal changes in soil seed-bank density occurred independently of vegetation type effects. Soil seed-density was higher during dry seasons than during wet seasons for all three vegetation types. This pattern also was consistent with the high number of species persisting in the soil during dry seasons. Seeds could persist better in the soil during the dry season because clay-rich soils tend to develop prominent cracks, of varying depth and width, where seeds can easily become buried (Garwood, 1989; Espinar *et al.*, 2005). In contrast, during the wet season heavy rains can fill the spaces between soil aggregates, limiting opportunities for small seeds to be incorporated into the soil (Pearson *et al.*, 2003; Dalling, 2004).

Differences in soil seed-density between dry and wet seasons could also be the result of the phenology of seed dispersal and germination in the *cerrado*. In another study (Salazar, 2010) we found that, in all three vegetation types, more seeds were dispersed during the mid and late dry season and early wet season, particularly of wind-dispersed species. Seeds of many *cerrado* woody species germinate early in the wet season (Oliveira and Silva, 1993; Gottsberger and Silberbauer-Gottsberger, 2006). Thus, soil collected during mid dry season (June 2006 and June 2007) could have a higher number of seeds (that were dispersed in the previous season) than the soil collected during late wet season (March 2006 and February 2007), after the germination season was over.

The differences in seed density found between the two dry seasons and between the two wet seasons also could be attributed to differences in annual seed rain and/or differences in mean annual precipitation (4.6 mm in 2006 versus 3.2 mm in 2007; IBGE-Recor meteorological data:http://www.recor.org.br).

Soil seed-bank persistence

More than 50% of the herbaceous and woody species found in the soil seed-bank in each vegetation type were present only during one of the four consecutive sampling periods, which suggests that most species form short-lived, transient banks. Sixteen per cent of woody and herbaceous species found in the soil at each vegetation type were observed in all four seasons, suggesting that these species, which represent a small percentage of all reproductive plants in the area, might form persistent banks. Among the ten woody species found in the soil seed-bank, only *Baccharis salzmannii* and *Miconia albicans* were well represented in all four collection periods (seasons). *B. salzmannii* fruits during the dry season while *M. albicans* fruits in the wet season. Both species produce large numbers of small seeds (diameter of 0.5 mm and 0.1 mm, respectively) which germinate

under light exposure (Gomes and Fernandez, 2002; Carreira and Penteado Zaidan, 2007). Thus, in the absence of light, large amounts of seeds of these species could remain in the soil for relatively long periods of time, which could explain why they form persistent soil seed-banks. With the exception of these two species, we found that most *cerrado* woody species did not form persistent soil seed-banks. The small fraction of persistent soil seed-banks of woody species could be explained by their short seed longevity. Among the 14 woody species studied, only four species maintain their viability in storage for periods longer than 12 months (at levels lower than 15%). Our results agree with those observed in tropical rain-forests where most seeds remain alive for a short time in the soil (Vásquez-Yanes and Orozco-Segovia, 1993) and where there is a persistent soil seed-bank dominated by the dormant seeds of a small fraction of the species present in the community (Garwood, 1989). That a small fraction of savanna trees form persistent soil seed-banks is also consistent with studies done in seasonal dry tropical forests, which show that only a few pioneer tree species form persistent seed-banks (Putz, 1983; Marod *et al.*, 2002) while most species form seasonal-transient seed-banks (Vieira and Scariot, 2006).

Seed characteristics of woody species

We found that seed moisture content and seed dormancy, but not seed longevity, of *cerrado* woody species were consistent with dispersal season. The consistency between these seed characteristics and dispersal season suggests that timing of seed dispersal is highly involved in controlling timing of germination in *cerrado* species, so that germination occurs when environmental conditions are suitable for seedling establishment (Fenner and Thompson, 2005). Previous studies in the *cerrado* have shown that non-dormant seeds and seeds coming out of dormancy at the beginning of the wet season can germinate immediately after the first heavy rains once soil moisture becomes a non-limiting factor in the upper soil layers (Gottsberger and Silberbauer-Gottsberger, 2006). In this study, the proportion of species with dormant versus non-dormant seeds was relatively higher during the dry season than during the wet season. Thus, it seems that, in addition to timing of dispersal, dormancy also is involved in controlling timing of germination of savanna woody species. Although we have data for only a few species, our results suggest that, similar to seasonal moist tropical forests (Garwood, 1983; Sautu *et al.*, 2006), the germination time of *cerrado* species could be controlled by both seed dormancy and timing of seed dispersal.

Similarity in species composition among seed bank, seed rain, seedling bank and standing vegetation

Although tree density of woody species taller than 1 m did not differ significantly among the vegetation types, species diversity, composition and canopy cover (measured as leaf area index) of woody species differed significantly among the three vegetation types. *Cerrado denso* was more species diverse and exhibited higher canopy cover than *cerrado sensu stricto* and *campo sujo*, which were dominated by relatively few woody species. We found that vegetation and seed rain were moderately similar to one another in their woody species composition. In contrast, the species composition of the germinable seed-bank differed greatly from that of both the vegetation and the seed rain. The relatively high similarity between the seed rain and the vegetation composition (Table 4) suggests that seeds of a large number of species fall near parental trees, and that long-distance dispersal contributed few seeds of species not growing nearby.

The composition of the germinable seed-bank differed from that of the vegetation and the seed rain largely because very few woody species were found in the soil seed-bank. The low similarity between the seed rain and the seed bank composition, between the seed bank and the vegetation composition, and between the woody seedling bank and the seed bank composition, suggest that recruitment of woody species from the soil seed-bank is extremely low in all three vegetation types.

Often, in tropical forests, there is little correspondence between the species composition of the vegetation and the seed bank (Hall and Swaine, 1980; Young *et al.*, 1987; Saulei and Swaine, 1988; Hopfensperger, 2007), or between the annual seed rain and the seed bank (Saulei and Swaine, 1988). The same patterns have been found in temperate forests (Fenner and Thompson, 2005) and grasslands (Peco *et al.*, 1998). These dissimilarities have been explained by the minor contribution of long-lived species to the seed bank, and because, in general, pioneer species contribute much more to the soil seed-bank than do secondary species (Harper, 1977). We think that most *cerrado* woody species do not form persistent soil seed-banks (seeds living longer than 1 year in the soil) because germination of most woody species occurs at the beginning of the rainy season soon after dispersal, making possible the subsequent survival and establishment of seedlings throughout the 7-month period (October–March) of the wet season and thus reducing the period of time seeds are exposed to predators (Vieira and Scariot, 2006).

That timing of seed dispersal and dormancy, rather than persistent soil seed-banks, control seed germination of most *cerrado* woody species is consistent with some assumptions of non-equilibrium/demographic-bottleneck models that explain tree–grass coexistence in savannas (Higgins *et al.*, 2000; Sankaran *et al.*, 2004; Meyer *et al.*, 2007). These models represent a departure from traditional equilibrium models of savannas (e.g. trees and grasses have different rooting depth to avoid competitive exclusion) in that the emphasis is on demographic rather than physiological mechanisms of water and nutrient exploitation. For example, in arid savannas, the primary demographic bottleneck for trees is thought to be the germination and seedling establishment stage (Jeltsch *et al.*, 1998). In mesic savannas, the death of saplings, because of frequent fires, is assumed to be the main demographic mechanism that prevents recruitment to adulthood (Higgins *et al.*, 2000). In the savannas of Brazil, Gardner (2006) identified the differences in tree reproductive response to fire as the main determinant of tree–grass ratios across vegetation types. Our study indicates that, even in the absence of fire, the recruitment stage is also a significant demographic bottleneck for woody species because recruitment of savanna woody seedlings occurs only when seed dispersal coincides with appropriate environmental conditions that allow rapid germination.

Overall, this study shows that during periods favourable for sexual reproduction, when major disturbance factors such as fire are excluded from the Brazilian savannas: (1) the soil seed-bank along topographic gradients (closed, intermediate and open savannas) is mostly composed of herbaceous species and very few woody species, which form seasonal-transient seed-banks; (2) soil seed-density of woody and herbaceous species differs temporally between dry and wet seasons and spatially along the topographic gradient; (3) most of the seeds of common woody species dispersed during the dry season have low moisture content and are dormant, but, in contrast, most of the seeds of common woody species dispersed during the wet season have high moisture content and are non-dormant, allowing them to germinate with the first heavy rains; (4) along the topographic gradients woody species composition of the soil seed-bank and seedling bank largely differ from the vegetation and the seed rain species composition, suggesting low recruitment of woody species from the soil seed-bank; therefore (6) seedling recruitment of tropical savanna woody species is from recently dispersed seeds in the rainy season which can take advantage of the high moisture content of the soils. Early life-history stages of woody species appear to play a more significant role in maintaining tree density variations along topographic gradients in Neotropical savannas than previously recognized.

Acknowledgements

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