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Seed limitation of woody plants in Neotropical savannas

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Abstract The failure of seeds to arrive at all suitable sites (seed limitation) greatly affects plant distribution and abundance. In contrast to tropical forests, the degree of seed limitation in Neotropical savannas is unclear because empirical studies at the community level are scarce. We estimated seed limitation of 23 woody species from annual seed rain measurements along a tree density gradient in the savannas of Central Brazil. These savannas differ in tree density and canopy cover, from closed to open savannas, and are located along shallow topographic gradients. We also studied post-dispersal seed predation and removal of 17 representative woody species, and seed viability loss over time of 12 common woody species under

dry-storage conditions. Annual seed rain was lower in open (410 seeds/m²) than in closed savannas (773 seeds/m²). Average seed limitation across woody species was higher than 80% along the tree density gradient. More than 60% of seeds of the studied woody species were predated or removed within 30–45 days in all savannah types. Seeds of most common woody species (66%) lost their viability in less than 12 months of dry storage. This study shows that Neotropical savannah woody plants are strongly seed-limited because of low and poor distribution of seeds among sites, post-dispersal seed removal, and short seed longevity. The high seed limitation of tree species in Neotropical savannas, particularly in open savannas, also may contribute to maintain their relatively low tree densities and help to explain the spatial variation of tree abundance along topographic gradients.

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Introduction

Spatial patterns of seed dispersal are crucial for determining the structure and dynamics of plant populations (Nathan and Muller-Landau 2000). Seed dispersal is an important source of new individuals and provides a means for reaching potential sites of plant recruitment (Harper 1977). Although vegetative reproduction may be important for plant persistence,

sprouts are less likely than seedlings to colonize unoccupied sites relatively far from parent plants (Bond and Midgley 2001). Thus, experimental studies and theoretical models have been used to study the impact of seed dispersal on patterns of species distribution and diversity at local and landscape levels (Nathan and Muller-Landau 2000; Muller-Landau et al. 2002; Poulsen et al. 2007). The results of these studies suggest that many plant communities are seed-limited, meaning that micro-sites where seeds could arrive and germinate remain vacant (Hubbell et al. 1999). Indeed, approximately 50% of all plant species investigated in various seed addition experiments have found evidence of seed limitation (Turnbull et al. 2000).

Seed limitation can arise from limited seed numbers and/or limited dispersal of available seeds among sites (Clark et al. 1998). Post-dispersal events of seed predation may critically reduce seedling recruitment in populations that are limited by the availability of seeds rather than by micro-sites (Denham 2008). Seed predators are likely to have substantial effects on recruitment by reducing seed supply (Campbell and Clarke 2006) and consequently, the number of established seedlings often increases when seeds are protected from predators (Terborgh and Wright 1994; Asquith et al. 1997; Perez et al. 2006). Likewise, seed viability loss over time may constrain plant recruitment by preventing the formation of persistent seed-banks if seeds remain alive for short periods. Thus, seed dispersal limitation along with post-dispersal processes of seed predation, removal, and seed viability loss can critically affect plant reproductive success and ultimately shape patterns of species distribution across the landscape.

In contrast to temperate herbaceous communities and tropical forests, the role of seed limitation in Neotropical savannas is unclear because empirical studies at the community level are very scarce. The savannas of central Brazil (cerrado), the largest tropical ecosystem after the Amazonian rain forest, cover approximately 2 million km², nearly 23% of the country. More than 500 species of trees and shrubs grow in the cerrado, and individual sites may contain up to 70 or more woody species per hectare (Haridasan 2008). These savannas are characterized by a strong seasonality of precipitation and by well-drained, deep, nutrient-poor soils (Furley 1999). Vegetation exhibits consistent changes in tree canopy cover, tree density,

and tree size along shallow topographic gradients of several meters in elevation (~50 m) and a few kilometers in length. Vegetation structure varies from closed savannas with a relatively high density of tall trees (up to 12 m) in the upper-most portions of the gradient to open savannas with relatively few small trees in the lowest portions of the topographic gradient. Herbaceous plant abundance follows the opposite trend, with higher abundance in open than in closed savannas (Eiten 2001).

Determinants of tree density variations along topographic gradients in Neotropical savannas have long been discussed and several hypotheses have been suggested to explain such patterns. Most of these hypotheses emphasize the effects that environmental factors such as fire, soil nutrient content, soil aluminum concentration, and water table depth have on adult trees, as major determinants of tree density variations (Goodland and Pollard 1973; Furley 1999) but have ignored early life-history stages of woody plants. Whether or not seed dynamics of woody species are consistent with variations in tree canopy cover across the cerrado landscape has not been determined, but certainly seed dynamics could potentially influence the distribution and abundance of tree species along topographic gradients in tropical savannas.

The aim of this study was to investigate critical aspects of seed dynamics of woody plants such as seed rain and post-dispersal seed loss at different temporal and spatial scales in Neotropical savannas. We addressed the following questions: (1) Does seed rain of woody plants (richness, abundance, and species composition) differ among savannah types? (2) To what extent are savannah woody plants seed-limited? (3) What is the level of post-dispersal seed loss due to predation, removal, and seed viability loss?

Methods

Study site

This study was conducted from June 2005 until November 2007 at the Instituto Brasileiro de Geografia e Estatística (IBGE) reserve, a 1300 ha field station located 35 km south of Brasília, 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 rainless. Relative humidity during the rainy season is about 80% and drops to 55% during the dry season when daily minimum relative humidity may reach values as low as 10% at midday and maximum wind speed may reach up to 5 m/s. Mean monthly temperatures range from 19 to 23°C. The soils are very deep, well-drained oxisols, and nutrient poor. The IBGE reserve contains all major vegetation types from very open to closed savannas: Closed savannas (cerrado denso) are semi-closed woodlands (40–60% tree crown cover) with a moderately tall (7–12 m) tree canopy. Intermediate savannas (cerrado sensu stricto) are savannas dominated by trees and shrubs (canopy generally less than 7-m tall) with 10 to less than 40% tree crown cover. Open savannas (campo sujo) have few short trees and scattered shrubs over a near continuous herbaceous layer (the woody layer usually covers less than 10% of the ground).

In June 2005, we established three transects of approximately 1000 m in length, spanning the three major vegetation types (closed, intermediate, and open savannas) in different places of the IBGE reserve. We placed the transects along continuous topographic gradients, each with a different elevation, ranging from 1117 to 1153 m, in areas 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 (Hoffmann 2000) and to eliminate potential effects of different fire frequencies in each study site. We established randomly nine plots of 20 × 20 m along each transect (three per vegetation type), for a total of 27 permanent plots. A total of 90, 70, and 85 species of woody species were found in closed, intermediate, and open savannas, respectively. Figure 1 shows the relative abundance of the most common woody species in each vegetation type.

Seed rain

To estimate seed rain at the study sites, four seed traps were located within each of the 20 × 20 m plots, ~5 m away from each corner, for a total of 108 traps (36 per vegetation type). We determined the size and the number of seed traps from results of previous studies performed in similar study sites (Souza 1993) and following Chabrerie and Alard (2005). Seed traps consisted of a plastic funnel (22 cm in diameter;

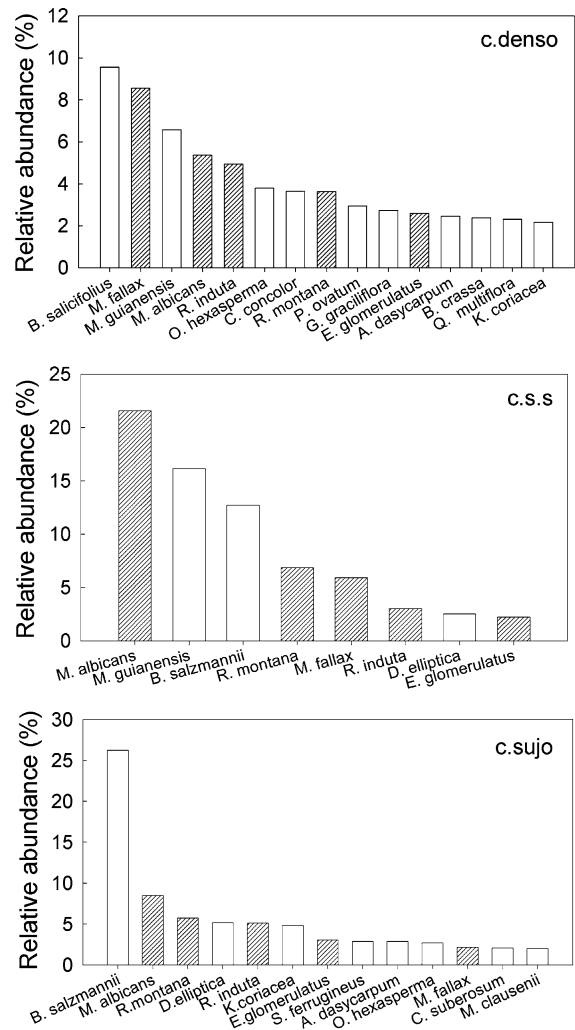


Fig. 1 Relative abundance of individuals taller than 1 m from woody species with relative abundance >2% in each vegetation type: cerrado denso (c.denso), cerrado sensu stricto (c.s.s), and campo sujo (c. sujo). Values for each species combine the abundance of the three transects. Bars with shading represent species present in all three vegetation types

0.038 m² collection area) that was inserted into a PVC tube (5-cm diameter) that held the funnel neck in place. Funnel traps provide a measure of the auto-regeneration capacity of the vegetation through its local seed production (Chabrerie and Alard 2005), prevent seed predation, and are easy to check (Kollmann and Goetze 1998). The height of the funnel opening was elevated 50 cm above the ground. A nylon mesh bag (0.1 mm) was attached at the funnel base to collect the diaspores because a preliminary inventory in the plots showed that 90%

of the woody plants exhibited fruit and seed diameters between 0.2 and 45 mm. Our design could have prevented the collection of diaspores smaller than 0.1 mm and larger than 50 mm, but species with such seed sizes represent less than 10% of the standing woody vegetation. PVC tubes had several 5-mm diameter holes for drainage. All diaspores (seeds, fruits, and fruit parts) were collected once a month over a 13 month period, from November 2005 until February 2007. The mesh bags were replaced when necessary. Whole, apparently intact diaspores were separated according to their morphologies as wind-dispersed or not wind-dispersed, then identified to species (or at least to family), and dried to constant mass. Identification was based on published literature, by comparison with herbarium collections, and by comparison with reference specimens collected from reproductive plants outside the plots.

Annual and monthly estimations of total number of species of diaspores (richness), the total number of diaspores (abundance), and the Shannon diversity index (H') of diaspores were performed in each vegetation type. (H') was calculated as $-\sum p_i \ln p_i$, where p_i is the proportion of diaspores of species i relative to the total number of species diaspores (Ricklefs 2001).

Seed limitation

From the annual seed rain measurements, seed limitation was calculated for 23 woody species in each transect of the three vegetation types according to Clark et al. (1998) and Muller-Landau et al. (2002). Fundamental seed limitation (SL_F) is the proportion of sites or traps not receiving seeds. $SL_F = 1 - (a/n)$ where a is the number of traps receiving seeds of a particular species and n is the number of traps (i.e., 12 traps per transect in each vegetation type). SL_F ranges from 0 to 1. A value of 1 indicates maximum limitation because seeds of a particular species are not captured in any trap. Because seed limitation can arise from limited seed numbers and/or limited distribution of available seeds among sites, seed limitation can be decomposed into source limitation and dispersal limitation (Clark et al. 1998). Source limitation (SL_S) is the failure of seeds to reach sites because of insufficient seed number assuming a uniform random distribution of seeds among traps given the random distribution patterns of the woody plant communities.

Uniform distribution is defined stochastically as a Poisson distribution with equal expectation of seeds everywhere. The proportion of traps at which no seeds arrive under such a distribution is the Poisson probability of zero events given an expectation of s/n seeds. Thus, source limitation can be calculated as $SL_S = e^{(-s/n)}$ where s is the number of seeds of a particular species and n is the number of traps. The influence of restricted dispersal (Dispersal limitation) can be assessed by comparing the actual proportion of traps reached by seeds with the proportion of traps that would be reached by seeds if dispersal were uniform. Thus, dispersal limitation (SL_D) which is seed limitation because of non-uniform distribution of seeds among sites can be calculated as $SL_D = 1 - [(a/n)/(1 - SL_S)]$. SL_D ranges from 0 to 1. A value of 1 indicates maximum dispersal limitation.

Seed predation, removal, and viability

To quantify seed predation and seed removal, we performed field experiments with diaspores collected from 17 woody species. These species are widely distributed throughout the cerrado region (Silva Júnior 2005) and belong to a wide range of plant families: *Brosimum gaudichaudii* (Moraceae), *Eriotheca pubescences* (Malvaceae), *Erythroxylum suberosum* (Erythroxylaceae), *Guapira graciliflora* (Nyctagynaceae), *Guapira noxia* (Nyctagynaceae), *Heteropterys byrsonimifolia* (Malpigiaceae), *Miconia ferruginata* (Melastomataceae), *Mimosa clausenii* (Fabaceae), *Ouratea hexasperma* (Ochnaceae), *Palicourea rigida* (Rubiaceae), *Piptocarpha rotundifolia* (Astereaceae), *Protium ovatum* (Bursereaceae), *Pterodon pubescens* (Fabaceae), *Rourea induta* (Connaraceae), *Schefflera macrocarpa* (Araliaceae), *Stryphnodendron adstringens* (Fabaceae), and *Styrax ferrugineus* (Styracaceae). Seeds or dispersal units (For simplicity we will refer as “seeds” to both true seeds and dispersal units) from at least three individuals were collected in the field and mixed to form a bulked sample. During the fruiting period of each species, seed removal from the ground was studied in all vegetation types.

Within each 20 × 20 m plot, seeds were scattered on four randomly selected sites within circular frames of 15-cm diameter. Each frame received 10 seeds of a single-plant species. We recorded the number of missing seeds, as well as seeds predated upon every day for 30 or 45 days (depending on the species). The

experiments were performed during late wet season (February 2007), middle dry season (July 2007), and early wet season (November 2007). Because seeds dispersed in dry and wet seasons may experience differential periods of drought in the field, we evaluated the rate of seed viability loss during 4–5 months under laboratory dry-storage conditions. Seeds from 12 common woody species were collected at the study site: *Acosmium dasycarpum* (Fabaceae), *E. pubescences*, *E. suberosum*, *G. graciliflora*, *G. noxia*, *Kielmeyera coriacea* (Guttiferae), *M. ferruginata*, *O. Hexasperma*, *P. rigida*, *P. rotundifolia* *Solanum lycocarpum* (Solanaceae), and *S. Ferrugineus*. Fruits and seeds from at least three individuals were collected in the field and mixed to form a bulked sample. Seed viability was estimated using a 1% Tetrazolium[®] solution (2,3,5-triphenyltetrazolium chloride). Three samples of 50 seeds, previously stored in dry conditions (i.e., inside paper bags at room temperature) were used for each species every month for a period of 4–5 months. Seeds were soaked in the Tetrazolium solution in flasks totally wrapped with aluminum foil, which were placed in an oven at 40°C. Embryo coloration patterns were evaluated under a dissecting scope every hour until embryos were completely stained within 24 h. Seeds were recorded as viable when embryos were homogeneously stained (i.e., both radicle and cotyledons).

Data analysis

Pearson correlations were used to examine the relationship between seed rain patterns and precipitation in each vegetation type. Kruskal–Wallis tests were used to test for differences in species diversity (Shannon index) among vegetation types. ANOSIM test was used to test the similarity in species composition of the seed rain among vegetation types using the program PRIMER v5 (Clarke and Warwick 2001). Values on a scale of 0 to 1 reflect multiple pairwise comparisons with sites highly similar ($R > 0.75$), sites overlapping but differing ($R > 0.5$) or sites highly dissimilar ($R < 0.25$). Differences in fundamental seed limitation, source limitation, and dispersal limitation among vegetation types were examined using one-way ANOVAs using the program JMP 7 (SAS Cary, NC). To fulfill the assumptions of normality, the data were transformed by calculating the arcsine of the square root of each original value. Tukey's HSD post-

hoc test was used for multiple comparisons of means. Differences of these variables at the species level were examined using one-way ANOVAs for every species in each vegetation type. Speed of seed loss (R^{50}) was calculated as the number of days until 50% of the seeds had been lost (either preyed upon or removed). Differences in the final percentage of seed predation, seed removal, total seed loss, and R^{50} among vegetation types were examined with two-way ANOVAs, where vegetation type was treated as fixed factor and species as random factor. Tukey HSD post-hoc tests were used for multiple comparisons of means. Negative exponential and linear functions were fitted to the data of percentage seed viability loss as a function of time. The functions with the highest coefficients of determination (R^2) and lowest significant levels (P) were selected as the best fitted equations. The percentage of potential viability for each species after 12 months of storage was calculated based on the best fitted equations.

Results

Seed rain

During the study period, the dry season extended from April to September and the months of June, July, and August received on average less than 10 mm of rain per month (Fig. 2). Seed rain exhibited a strong seasonal pattern across vegetation types. Diaspores of most species were dispersed during the late dry season and early wet season in all three vegetation types (Fig. 3). Seasonal patterns of richness and abundance of diaspores were similar for the three vegetation types; however, diaspores were more abundant in closed than in open savannas during the dry season (Fig. 3). Although annual diversity of diaspores throughout the study period was slightly higher in open savannas (2.72) than in closed (2.50) or intermediate savannas (2.40), no significant differences in the mean monthly diversity of diaspores were found among vegetation types (Kruskal–Wallis test, $\chi^2 = 0.99$, $P = 0.60$). In the three vegetation types, wind-dispersed (anemochoric) diaspores exhibited stronger seasonal variations (Pearson correlations, $R > 0.73$; $P < 0.05$) than animal-dispersed (zoochoric) diaspores ($R < 0.39$; $P > 0.05$; Fig. 4). Seasonal variations in the abundance of anemochoric and zoochoric

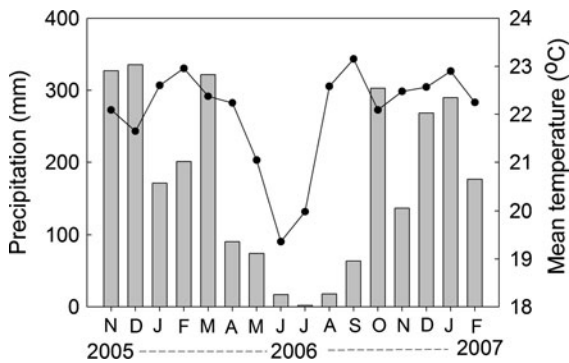


Fig. 2 Total monthly precipitation (bars) and mean monthly temperature (line and solid symbols) from November 2005 until February 2007 obtained from the IBGE meteorological station located near the study sites

diaspores followed a similar pattern as species richness (Fig. 5).

Throughout the period of study, a total of 3156 diaspores (724 seeds m⁻²) belonging to 38 species, 27 genera, and 17 families were trapped (Table 1). The species of trapped diaspores represented 20, 29, and 19% of the woody species found in closed,

intermediate, and open savannas, respectively. Neither the mean number of species/m² (diaspore richness) (One-way anova; $F_{2,6} = 0.27$; $P = 0.77$), nor the mean number of diaspores/m² (One-way ANOVA: $F_{2,6} = 1.49$; $P = 0.77$) differed significantly among the three vegetation types; however, the total number of diaspores trapped during the period of this study was lower in open savannas (593) than in closed (1121) or intermediate (1440) savannas. Species composition of diaspores differed among the vegetation types (ANOSIM; $R = 0.49$, $P = 0.014$). For example, Asteraceae species were more abundant in open than in closed savannas while Bignoniaceae species were more abundant in closed than in open savannas (Table 1).

The relative abundance of the trapped diaspores, characterized according to their dispersal modes, was consistent with the relative abundance of the dispersal syndromes of the species found in open and in intermediate savannas (Table 2). The relative abundance of the diaspores according to their dispersal syndromes in closed savannas, however, did not match those of the vegetation because of the high abundance

Fig. 3 Number of species per m² (a, b, c) and number of diaspores per m² (d, e, f) from November 2005 until February 2007 in the three vegetation types: cerrado denso (black bars), cerrado sensu stricto (gray bars), and campo sujo (white bars) (closed, intermediate, and open savannas, respectively). Bars are total number of diaspores of woody species trapped in each vegetation type and therefore do not have standard errors. Shaded boxes indicate months without measurements

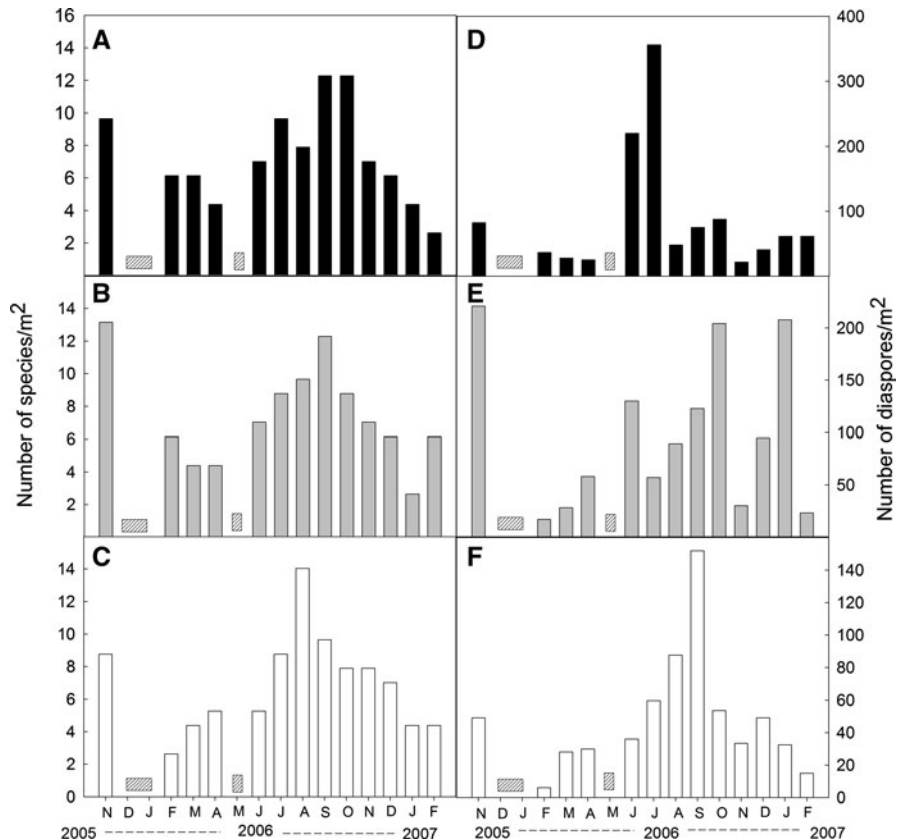
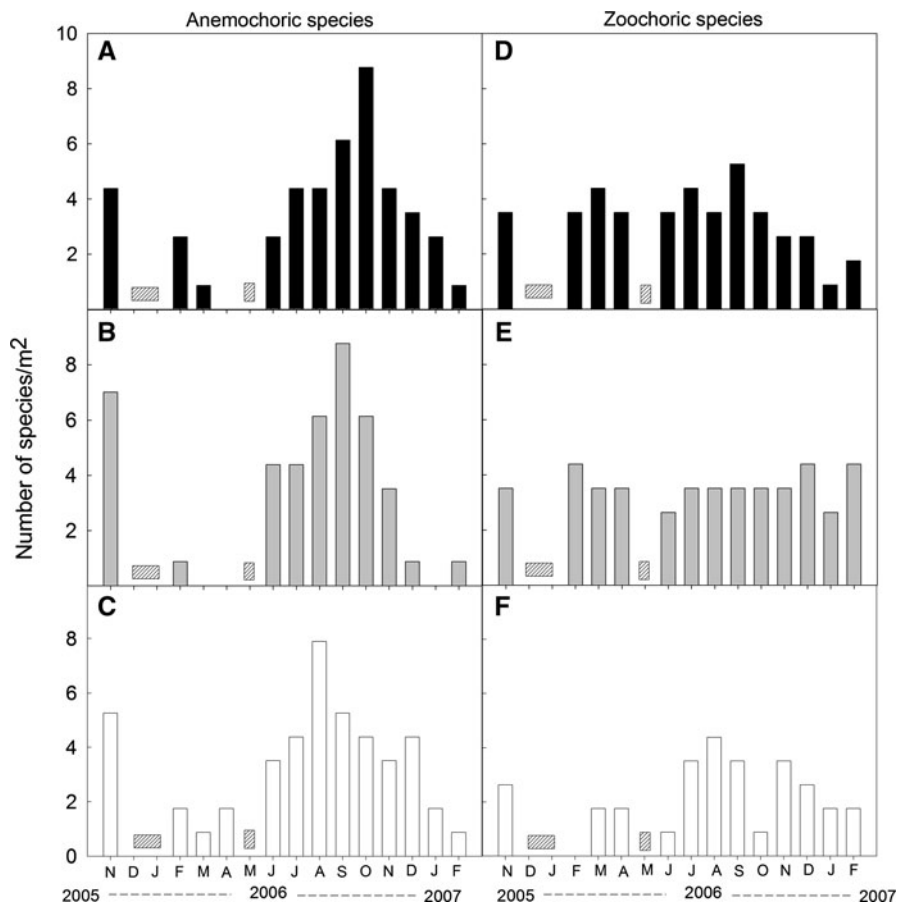


Fig. 4 Number of anemochoric (a, b, c) and zoochoric (d, e, f) species per m² from November 2005 until February 2007 in the three vegetation types: cerrado denso (black bars), cerrado sensu stricto (gray bars), and campo sujo (white bars) (closed, intermediate, and open savannas, respectively). Bars are total number of woody species trapped in three vegetation types and therefore do not have standard errors. Shaded boxes indicate months without measurements



of diaspores from a wind-dispersed species trapped during June and July 2006 of the Bignoniaceae family.

Seed limitation

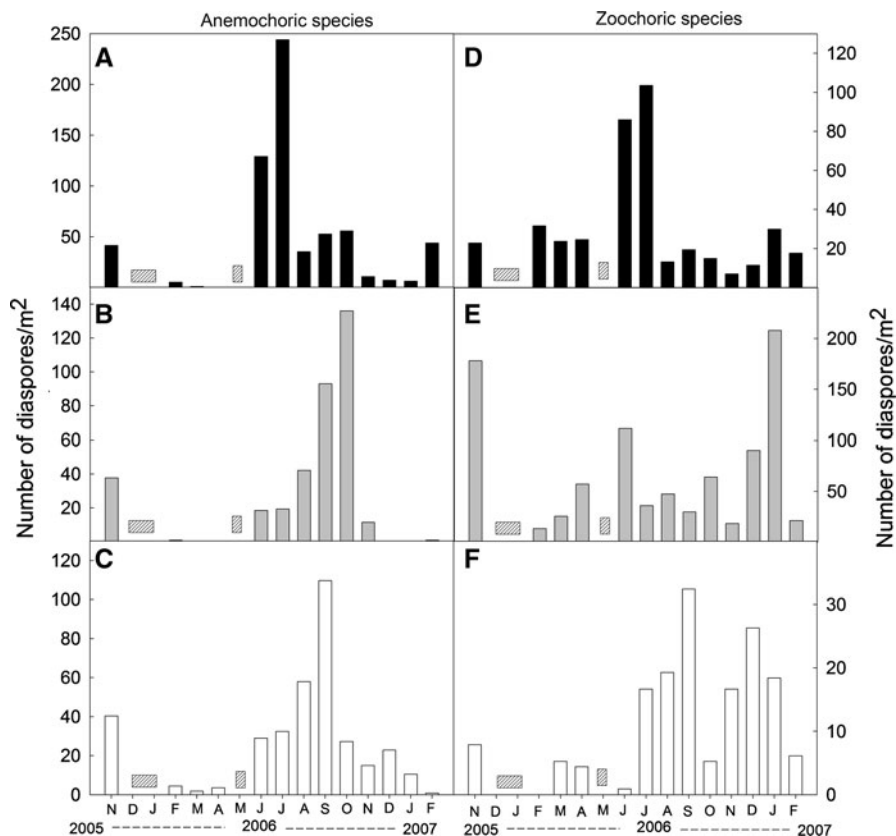
Mean fundamental seed limitation across woody plants was higher than 80% in all three vegetation types (Table 3). Significant differences among the three vegetation types ($P < 0.05$) were found for five species: *Baccharis salzmanii* ($F = 7.79$; $P = 0.02$), *Bignoniaceae* sp. ($F = 15.72$; $P = 0.004$), *Byrsonima cf. crassa* ($F = 7.00$; $P = 0.03$), *Miconia* sp1 ($F = 12.30$; $P = 0.008$), and *Myrsine guianensis* ($F = 6.64$; $P = 0.03$). Four of these five species had substantially higher seed limitation in open than in closed or intermediate savannas. Source limitation of woody species in the three vegetation types also was higher than 60% with only three species differing significantly ($P < 0.05$) among vegetation types (Table 4). Likewise, dispersal limitation was high

for most woody species (Table 5). All species, except *Miconia* sp1, did not differ significantly ($P > 0.05$) across the three vegetation types.

Seed predation, removal, and viability

Seed predation differed among species, but not among vegetation types (Two-way ANOVA $F_{\text{species } 16,555} = 15.37$; $P < 0.0001$; $F_{\text{vegetation } 2,555} = 0.91$; $P = 0.40$; $F_{\text{species} \times \text{vegetation } 32,555} = 2.47$; $P < 0.0001$). Seed predation ranged from 0 to 64% while seed removal ranged from 0 to 100% (Table 6). Seed removal differed among species and among vegetation types (Two-way ANOVA $F_{\text{species } 16,555} = 59.45$; $P < 0.0001$; $F_{\text{vegetation } 2,555} = 13.45$; $P < 0.0001$; $F_{\text{species} \times \text{vegetation } 32,555} = 3.31$; $P < 0.0001$) (Table 6). Seed loss because of both predation and removal also differed among species and vegetation types (Two-way ANOVA $F_{\text{species } 16,555} = 59.47$; $P < 0.0001$; $F_{\text{vegetation } 2,555} = 9.53$; $P < 0.0001$;

Fig. 5 Number of anemochoric (a, b, c) and zoochoric (d, e, f) diaspores per m² from November 2005 until February 2007 in the three vegetation types: cerrado denso (black bars), cerrado sensu stricto (gray bars), and campo sujo (white bars) (closed, intermediate, and open savannas, respectively). Bars are total number of diaspores of woody species trapped in three vegetation types and therefore do not have standard errors. Shaded boxes indicate months without measurements



$F_{\text{species} \times \text{vegetation}} 32,555 = 2.53$; $P < 0.0001$). Seed loss was significantly higher in intermediate (70.78%) than in open savannas (60.83%). Neither intermediate nor open savannas, however, differ significantly from closed savannas (67.17%) in their total seed loss (Table 6).

The speed of seed loss (R^{50}) differed among species and among vegetation types (Two-way ANOVA, $F_{\text{species}} 12,370 = 30.17$; $P < 0.0001$; $F_{\text{vegetation}} 2,370 = 5.18$; $P = 0.006$; $F_{\text{species} \times \text{vegetation}} 24,370 = 3.14$; $P < 0.0001$) ranging from 1.66 ± 0.19 to 36.00 ± 9.00 days (Table 7). The mean R^{50} across species was significantly lower in intermediate than in open or closed savannas (Table 7).

Initial viability percentage and rate of viability loss differed among the species (results not shown). The percentage of seed viability after 4 months of storage across the 12 studied species ranged from 2.48 to 66.97%. All species, except *Acosmium dasycarpum* exhibited seed viability percentages lower than 50% after 4 months of dry storage. Negative exponential and linear functions were fitted to the data for

percentage viability loss as a function of time. The coefficient of determination (R^2) of the functions ranged from 0.75 to 0.99 and they were significant at $P \leq 0.02$. With these functional relationships, we predicted the potential viability for each species after 1 year of storage (Even though seeds in the field would experience less than 12 months of drought). Out of the 12 species, *Acosmium dasycarpum*, *Palicourea rigida*, *Erythroxylum suberosum*, and *Guapira graciliflora* were the only species that maintained their viability after 12 months of storage, but at levels lower than 15%.

Discussion

Seed rain of woody species in the three vegetation types exhibited seasonal variations with most species being dispersed during the mid-late dry season (August and September) and early wet season (October and November). These variations in the seed rain of woody species are consistent with previous studies

Table 1 Total number of diaspores of woody species found in seed traps located in three vegetation types: cerrado denso, cerrado sensu stricto, and campo sujo (closed, intermediate, and open savannas, respectively) during 13 months of observations

| Syndrome | Species | Family | Cerrado denso | Cerrado sensu stricto | Campo sujo |
|------------|------------------------------------|-----------------|---------------|-----------------------|------------|
| Zoochory | <i>Byrsonima cf crassa</i> | Malpighiaceae | 5 | 1 | 0 |
| | <i>Byrsonima</i> sp. | Malpighiaceae | 63 | 5 | 3 |
| | <i>Cordia</i> sp. | Rubiaceae | 16 | 0 | 0 |
| | <i>Davilla elliptica</i> | Dilleniaceae | 28 | 109 | 25 |
| | <i>Guapira graciliflora</i> | Nyctagenaceae | 0 | 5 | 0 |
| | <i>Miconia albicans</i> | Melastomataceae | 0 | 42 | 0 |
| | <i>Miconia fallax</i> | Melastomataceae | 48 | 119 | 46 |
| | <i>Miconia ferruginata</i> | Melastomataceae | 0 | 3 | 0 |
| | <i>Miconia</i> sp1 | Melastomataceae | 47 | 107 | 19 |
| | <i>Miconia</i> sp2 | Melastomataceae | 18 | 22 | 8 |
| | <i>Miconia</i> sp3 | Melastomataceae | 0 | 13 | 0 |
| | <i>Myrsine guianensis</i> | Myrsinaceae | 35 | 549 | 4 |
| | <i>Ouratea hexasperma</i> | Ochnaceae | 1 | 15 | 10 |
| | <i>Rourea induta</i> | Connaraceae | 17 | 17 | 10 |
| | <i>Styrax ferrugineus</i> | Styracaceae | 5 | 15 | 21 |
| | <i>Stryphnodendron adstringens</i> | Fabaceae | 0 | 4 | 11 |
| | Subtotal | | | 283 | 1026 |
| Anemochory | <i>A. dasy carpum</i> | Leguminosae | 0 | 0 | 3 |
| | <i>A. macrocarpa</i> | Apocynaceae | 9 | 23 | 0 |
| | Asteraceae sp1 | Asteraceae | 0 | 0 | 22 |
| | Asteraceae sp2 | Asteraceae | 1 | 121 | 0 |
| | Asteraceae sp3 | Asteraceae | 16 | 2 | 8 |
| | <i>Baccharis salzmännii</i> | Asteraceae | 30 | 78 | 181 |
| | <i>Dalbergia miscolobium</i> | Fabaceae | 4 | 20 | 0 |
| | <i>Eremanthus glomerulatus</i> | Asteraceae | 78 | 68 | 90 |
| | <i>Eremanthus goyazensis</i> | Asteraceae | 10 | 12 | 5 |
| | <i>Eremanthus</i> spp. | Asteraceae | 6 | 4 | 7 |
| | <i>Eriotheca pubescens</i> | Bombacaceae | 12 | 2 | 0 |
| | <i>Heteropterys</i> sp1 | Malpighiaceae | 22 | 3 | 0 |
| | <i>Heteropterys</i> sp2 | Malpighiaceae | 6 | 9 | 0 |
| | <i>Jacaranda ulei</i> | Bignoniaceae | 0 | 0 | 6 |
| | <i>Kielmeyera coriacea</i> | Clusiaceae | 0 | 6 | 15 |
| | Bignoniaceae sp. | Bignoniaceae | 434 | 0 | 0 |
| | <i>Pera glabrata</i> | Euphorbiaceae | 180 | 0 | 8 |
| | <i>Piptocarpha rotundifolia</i> | Asteraceae | 4 | 40 | 8 |
| | <i>Qualea</i> sp. | Vochysiaceae | 0 | 0 | 4 |
| | <i>Vernonia fruticulosa</i> | Asteraceae | 26 | 25 | 48 |
| | Vochysiaceae sp. | Vochysiaceae | 0 | 1 | 2 |
| Subtotal | | | 838 | 414 | 416 |
| Autochoric | <i>Mimosa clausenii</i> | Fabaceae | 0 | 0 | 14 |
| Total | | | 1121 | 1440 | 595 |

Species are grouped according to their dispersal syndromes: zoochory (animal), anemochory (wind), and autochory (self)

Table 2 Abundance (%) of woody species (Plants) classified according to their dispersal syndrome (animal, wind, self) across three vegetation types: cerrado denso, cerrado sensu stricto, and campo sujo (closed, intermediate, and open savannas, respectively), and relative abundance (%) of diaspores (seeds) of woody species collected from seed traps located in each of the above sites that were animal, wind, and self-dispersed

| Dispersal syndrome | | Cerrado denso | Cerrado sensu stricto | Campo sujo |
|--------------------|--------|---------------|-----------------------|------------|
| Animal | Plants | 71.06 | 67.69 | 44.07 |
| | Seeds | 22.30 | 77.85 | 27.85 |
| Wind | Plants | 25.11 | 28.35 | 49.58 |
| | Seeds | 66.04 | 22.15 | 64.60 |
| Self | Plants | 0.50 | 0.42 | 3.66 |
| | Seeds | 0.00 | 0.00 | 2.35 |

in cerrado plant communities (Batalha and Mantovani 2000; Munhoz and Felfili 2007) and tropical dry forests (Cecon and Hernandez 2009). Wind-dispersed diaspores, however, exhibited a stronger

seasonal variation than animal-dispersed diaspores. Because wind-dispersed diaspores tend to be drier than animal-dispersed ones, drought, wind, and leaf fall may all facilitate seed releasing mechanisms such as dehydration of fruit pericarps (Batalha and Martins 2004). The more stable seed rain of animal-dispersed seeds throughout the year suggests that animal-dispersed seeds could increase their chances of being dispersed by remaining available for long periods of time during the year (Mantovani and Martins 1988).

Our data indicate that almost 70% of the species found in both closed and intermediate savannas rely on animals for seed dispersal whereas most woody species in open savannas rely on wind for seed dispersal. Wind dispersal has been generally associated with open vegetation like campo sujo, whereas a more even distribution of animal and wind dispersal syndromes has been associated with closed vegetation like cerrado denso (Munhoz and Felfili 2007). Studies have found that the proportion of animal to wind-dispersed species increases as the proportion of

Table 3 Fundamental seed limitation \pm standard deviation ($n = 3$) for 23 woody species in three cerrado vegetation types: cerrado denso, cerrado sensu stricto, and campo sujo (closed, intermediate, and open savannas, respectively)

A value of 1 indicates maximum limitation because seeds of that particular species were not found in seed traps during the study. (See methods for details). Bold rows indicate species that differ significantly according to Tukey HSD post-hoc test. For those species, means with the same letter do not differ significantly among vegetation types

| Species | Cerrado denso | Cerrado sensu stricto | Campo sujo |
|------------------------------------|-------------------------------------|-------------------------------------|------------------------------------|
| <i>Baccharis salzmannii</i> | 0.83 \pm 0.08a | 0.89 \pm 0.13a | 0.50 \pm 0.17b |
| Bignoniaceae sp. | 0.89 \pm 0.05b | 1.00 \pm 0.00a | 1.00 \pm 0.00a |
| <i>Byrsonima cf crassa</i> | 0.92 \pm 0.00b | 0.97 \pm 0.05ab | 1.00 \pm 0.00a |
| <i>Byrsonima</i> sp. | 0.78 \pm 0.13 | 0.94 \pm 0.05 | 0.94 \pm 0.05 |
| <i>Dalbergia miscolobium</i> | 0.94 \pm 0.05 | 0.97 \pm 0.05 | 1.00 \pm 0.00 |
| <i>Davilla elliptica</i> | 0.70 \pm 0.52 | 0.86 \pm 0.05 | 0.94 \pm 0.05 |
| <i>E. glomeratus</i> | 0.67 \pm 0.30 | 0.56 \pm 0.26 | 0.47 \pm 0.34 |
| <i>Eremanthus</i> sp. | 0.92 \pm 0.00 | 0.92 \pm 0.14 | 0.92 \pm 0.08 |
| <i>Heteropterys</i> sp1 | 0.89 \pm 0.13 | 0.95 \pm 0.05 | 0.94 \pm 0.05 |
| <i>Heteropterys</i> sp2 | 0.89 \pm 0.19 | 0.94 \pm 0.05 | 1.00 \pm 0.00 |
| <i>Kielmeyera coriacea</i> | 1.00 \pm 0.00 | 0.97 \pm 0.05 | 0.86 \pm 0.24 |
| <i>Miconia albicans</i> | 1.00 \pm 0.00 | 0.97 \pm 0.05 | 1.00 \pm 0.00 |
| <i>Miconia fallax</i> | 0.78 \pm 0.17 | 0.53 \pm 0.19 | 0.81 \pm 0.17 |
| <i>Miconia</i> sp1 | 0.78 \pm 0.13a | 0.42 \pm 0.17b | 0.94 \pm 0.10a |
| <i>Miconia</i> sp2 | 0.72 \pm 0.05 | 0.83 \pm 0.17 | 0.94 \pm 0.10 |
| <i>Myrsine guianensis</i> | 0.75 \pm 0.29ab | 0.33 \pm 0.17b | 0.89 \pm 0.05a |
| <i>Ouratea hexasperma</i> | 0.97 \pm 0.05 | 0.97 \pm 0.14 | 0.94 \pm 0.10 |
| <i>Pera glabrata</i> | 0.89 \pm 0.13 | 1.00 \pm 0.00 | 0.91 \pm 0.08 |
| <i>Piptocarpha rotundifolia</i> | 0.92 \pm 0.08 | 0.86 \pm 0.13 | 0.88 \pm 0.09 |
| <i>Rourea induta</i> | 0.94 \pm 0.05 | 0.89 \pm 0.13 | 0.89 \pm 0.19 |
| <i>Stryphnodendron adstringens</i> | 1.00 \pm 0.00 | 0.97 \pm 0.05 | 0.94 \pm 0.10 |
| <i>Styrax ferrugineous</i> | 0.87 \pm 0.10 | 0.92 \pm 0.00 | 0.92 \pm 0.00 |
| <i>Vernonia fruticulosa</i> | 0.92 \pm 0.08 | 0.83 \pm .014 | 0.72 \pm 0.21 |
| Mean | 0.88 \pm 0.02 | 0.85 \pm 0.03 | 0.89 \pm 0.02 |

Table 4 Source limitation \pm standard deviation ($n = 3$) for 23 woody species in the three vegetation types studied: cerrado denso, cerrado sensu stricto, and campo sujo (closed, intermediate, and open savannas, respectively)

| Species | Cerrado denso | Cerrado sensu stricto | Campo sujo |
|------------------------------------|-------------------------------------|---------------------------------------|------------------------------------|
| <i>Baccharis salzmannii</i> | 0.51 \pm 0.21 | 0.38 \pm 0.31 | 0.10 \pm 0.10 |
| Bignoniaceae sp. | 0.30 \pm 0.30b | 1.00 \pm 0.00a | 1.00 \pm 0.00a |
| <i>Byrsonima cf crassa</i> | 0.87 \pm 0.02b | 0.97 \pm 0.03a | 1.00 \pm 0.00a |
| <i>Byrsonima</i> sp. | 0.40 \pm 0.27 | 0.88 \pm 0.14 | 0.92 \pm 0.04 |
| <i>Dalbergia miscolobium</i> | 0.90 \pm 0.06 | 0.72 \pm 0.27 | 1.00 \pm 0.00 |
| <i>Davilla elliptica</i> | 0.70 \pm 0.30 | 0.36 \pm 0.30 | 0.69 \pm 0.27 |
| <i>E. glomerulatus</i> | 0.30 \pm 0.15 | 0.25 \pm 0.18 | 0.29 \pm 0.22 |
| <i>Eremanthus</i> sp. | 0.84 \pm 0.04 | 0.91 \pm 0.09 | 0.84 \pm 0.10 |
| <i>Heteropterys</i> sp1 | 0.63 \pm 0.22 | 0.92 \pm 0.04 | 0.80 \pm 0.11 |
| <i>Heteropterys</i> sp2 | 0.88 \pm 0.13 | 0.79 \pm 0.11 | 1.00 \pm 0.00 |
| <i>Kielmeyera coriaceae</i> | 1.00 \pm 0.00 | 0.87 \pm 0.13 | 0.76 \pm 0.24 |
| <i>Miconia albicans</i> | 1.00 \pm 0.00 | 0.68 \pm 0.32 | 1.00 \pm 0.00 |
| <i>Miconia fallax</i> | 0.37 \pm 0.21 | 0.09 \pm 0.07 | 0.43 \pm 0.28 |
| <i>Miconia</i> sp1 | 0.36 \pm 0.17 | 0.11 \pm 0.05 | 0.74 \pm 0.27 |
| <i>Miconia</i> sp2 | 0.61 \pm 0.06 | 0.66 \pm 0.24 | 0.84 \pm 0.16 |
| <i>Myrsine guianensis</i> | 0.57 \pm 0.25ab | 0.001 \pm 0.0008b | 0.90 \pm 0.02a |
| <i>Ouratea hexasperma</i> | 0.97 \pm 0.03 | 0.76 \pm 0.24 | 0.81 \pm 0.19 |
| <i>Pera glabrata</i> | 0.64 \pm 0.32 | 1.00 \pm 0.00 | 0.81 \pm 0.10 |
| <i>Piptocarpha rotundifolia</i> | 0.78 \pm 0.13 | 0.62 \pm 0.25 | 0.91 \pm 0.09 |
| <i>Rourea induta</i> | 0.66 \pm 0.17 | 0.73 \pm 0.23 | 0.81 \pm 0.19 |
| <i>Stryphnodendron adstringens</i> | 1.00 \pm 0.00 | 0.91 \pm 0.09 | 0.80 \pm 0.20 |
| <i>Styrax ferrugineous</i> | 0.87 \pm 0.05 | 0.71 \pm 0.09 | 0.92 \pm 0.00 |
| <i>Vernonia fruticulosa</i> | 0.66 \pm 0.27 | 0.63 \pm .024 | 0.38 \pm 0.21 |
| Mean | 0.69 \pm 0.04 | 0.65 \pm 0.05 | 0.76 \pm 0.04 |

A value of 1 indicates maximum limitation because seeds of that particular species were not found in seed traps during the study. Bold rows indicate species that differ significantly according to Tukey HSD post-hoc test. For those species, means with the same letter do not differ significantly among vegetation types

woody/herbaceous species increases along the cerrado tree density gradient (Oliveira and Moreira 1992; Gottsberger and Silberbauer-Gottsberger 2006).

We found that the local vegetation is an important source of seeds, particularly in, open and intermediate savannas (Table 2) where the relative abundance of the seeds, (according to the dispersal syndromes) reflected the relative abundance of local woody species characterized by their dispersal syndromes. The relative abundance of the seeds according to their dispersal syndromes in closed savannas, on the other hand, did not reflect the dispersal syndromes of the species found there. This disparity could be explained by the high abundance of seeds of a wind-dispersed Bignoniaceae species that was over-represented in these sites during June and July 2006 (dry season). The low percentage of animal-dispersed seeds found in closed savannas also could be the result of a large proportion of endozoochoric species (dispersal inside the animal) rather than epizoochoric (dispersal outside the animal), which would impede seeds from being

collected by traps. Indeed, in a cerrado area of Sao Paulo State in Brazil, Gottsberger and Silberbauer-Gottsberger (2006) found that the relative abundance of endozoochoric species was significantly higher in closed than in intermediate savannas.

The annual seed rain in our study sites ranged from 773 seeds/m² in closed savannas to 410 seeds/m² in open savannas. These values are higher than seed rain densities in the savannas of Venezuela (122 seeds/m²/year, Flores and Dezzio 2005) but lower than in tropical forests (965 seeds/m²/year, Svenning and Wright 2005). We found that seeds from a low fraction of the standing vegetation were present in the traps (i.e., 20, 29, and 19% in closed, intermediate, and open savannas, respectively) and that most savannah woody species in our study sites exhibited seed limitation values higher than 80%. Strong seed limitation at the community level also has been found in temperate savannas (Foster and Tilman 2003), tropical semi-deciduous forest (Svenning and Wright 2005), and tropical moist forests (Terborgh et al. 2011). In our

Table 5 Dispersal limitation \pm standard deviation ($n = 3$) for 23 woody species in the three vegetation types: cerrado denso, cerrado sensu stricto, and campo sujo (closed, intermediate, and open savannas, respectively)

| Species | Cerrado denso | Cerrado sensu stricto | Campo sujo |
|------------------------------------|-------------------------------------|------------------------------------|------------------------------------|
| <i>Baccharis salzmännii</i> | 0.47 \pm 0.41 | 0.88 \pm 0.15 | 0.45 \pm 0.10 |
| Bignoniaceae sp. | 0.57 \pm 0.53 | 1.00 \pm 0.00 | 1.00 \pm 0.00 |
| <i>Byrsonima cf. crassa</i> | 0.30 \pm 0.26 | 0.67 \pm 0.58 | 1.00 \pm 0.00 |
| <i>Byrsonima</i> sp. | 0.43 \pm 0.39 | 0.57 \pm 0.51 | 0.49 \pm 0.50 |
| <i>Dalbergia miscolobium</i> | 0.54 \pm 0.51 | 0.97 \pm 0.06 | 1.00 \pm 0.00 |
| <i>Davilla elliptica</i> | 0.88 \pm 0.21 | 0.53 \pm 0.50 | 0.62 \pm 0.58 |
| <i>E. glomerulatus</i> | 0.57 \pm 0.26 | 0.44 \pm 0.14 | 0.29 \pm 0.28 |
| <i>Eremanthus</i> sp. | 0.36 \pm 0.32 | 0.71 \pm 0.51 | 0.66 \pm 0.30 |
| <i>Heteropterys</i> sp1 | 0.76 \pm 0.42 | 0.49 \pm 0.50 | 0.80 \pm 0.19 |
| <i>Heteropterys</i> sp2 | 0.72 \pm 0.50 | 0.82 \pm 0.16 | 1.00 \pm 0.00 |
| <i>Kielmeyera coriaceae</i> | 1.00 \pm 0.00 | 0.93 \pm 0.12 | 0.80 \pm 0.34 |
| <i>Miconia albicans</i> | 1.00 \pm 0.00 | 0.97 \pm 0.05 | 1.00 \pm 0.00 |
| <i>Miconia fallax</i> | 0.64 \pm 0.17 | 0.50 \pm 0.15 | 0.77 \pm 0.20 |
| <i>Miconia</i> sp1 | 0.67 \pm 0.07ab | 0.34 \pm 0.20b | 0.93 \pm 0.12a |
| <i>Miconia</i> sp2 | 0.25 \pm 0.20 | 0.61 \pm 0.38 | 0.89 \pm 0.20 |
| <i>Myrsine guianensis</i> | 0.36 \pm 0.35 | 0.33 \pm 0.17 | 0.03 \pm 0.05 |
| <i>Ouratea hexasperma</i> | 0.67 \pm 0.57 | 0.88 \pm 0.20 | 0.75 \pm 0.43 |
| <i>Pera glabrata</i> | 0.58 \pm 0.52 | 1.00 \pm 0.0 | 0.67 \pm 0.38 |
| <i>Piptocarpha rotundifolia</i> | 0.75 \pm 0.44 | 0.78 \pm 0.20 | 0.61 \pm 0.34 |
| <i>Rourea induta</i> | 0.89 \pm 0.10 | 0.55 \pm 0.34 | 0.80 \pm 0.34 |
| <i>Stryphnodendron adstringens</i> | 1.00 \pm 0.00 | 0.90 \pm 0.17 | 0.91 \pm 0.16 |
| <i>Styrax ferrugineous</i> | 0.38 \pm 0.54 | 0.44 \pm 0.43 | 0.30 \pm 0.52 |
| <i>Vernonia fruticulosa</i> | 0.94 \pm 0.11 | 0.61 \pm 0.50 | 0.48 \pm 0.21 |
| Mean | 0.61 \pm 0.04 | 0.70 \pm 0.04 | 0.72 \pm 0.04 |

A value of 1 indicates maximum limitation because seeds of that particular species were not found in seed traps during the study. Bold rows indicate species that differ significantly according to Tukey HSD post-hoc test. For those species, means with the same letter do not differ significantly among vegetation types

study, mean fundamental seed limitation, source limitation, and dispersal limitation across species were consistently higher in open than in closed savannas suggesting that open savannas are more limited in seeds of woody species than closed savannas. This high seed limitation in open savannas might help to maintain their relatively low tree densities because tree abundance could not increase as quickly if seeds do not reach all suitable sites (Muller-Landau et al. 2002). Likewise, seed limitation of savannah woody plants might contribute to maintain species richness and tree-grass coexistence in Neotropical savannah ecosystems by slowing competitive dynamics of dominant species as in tropical deciduous forests (Hubbell et al. 1999).

In our study, more than 60% of seeds of the studied woody species were predated or removed within 30–45 days in all savannah types suggesting that post-dispersal events of seed predation and removal may

critically reduce seed availability in Neotropical savannas. These rates of seed loss are comparable to those found for species in tropical semi-deciduous forests (Forget et al. 2002), tropical temperate woodlands in Australia (Campbell and Clarke 2006), and in fire-prone ecosystems of South-eastern Australia (Denham 2008). Although seed removal cannot be considered a proxy for seed predation because some seeds could be transported intact by ants, scatterhoarding animals, or abiotic agents to safe micro-sites (Vander Wall et al. 2005), the relatively high and fast seed removal suggests that secondary dispersal might play a more significant role in seed dynamics of Neotropical savannah woody species than previously recognized. Secondary seed dispersal by ants has been found to reduce predation by rodents, reduce parent-offspring conflict and sibling competition, and may facilitate the location of favorable micro-sites (Parr et al. 2007). Experiments following seed fates could

Table 6 Percent (%) of seed predation and seed removal for 17 woody species in cerrado denso, cerrado sensu stricto, and campo sujo: (closed, intermediate, and open savannas, respectively)

| Species | Predation | | | Removal | | |
|--------------------------|-----------------------|-----------------------|----------------------|------------------------|-----------------------|-----------------------|
| | Cerrado denso | Cerrado sensu stricto | Campo sujo | Cerrado denso | Cerrado sensu stricto | Campo sujo |
| <i>B. gaudichaudii</i> | 5.00 ± 1.95 | 7.50 ± 2.18 | 17.50 ± 6.98 | 1.67 ± 1.12b | 29.17 ± 9.24a | 1.67 ± 1.12b |
| <i>E. pubescens</i> | 0.83 ± 0.83 | 0 ± 0 | 1.67 ± 1.12 | 95.83 ± 3.36 | 95.00 ± 5.00 | 90.00 ± 4.08 |
| <i>E. suberosum</i> | 13.33 ± 8.34 | 20.00 ± 9.92 | 25.00 ± 10.11 | 69.17 ± 11.51ab | 75.83 ± 11.11a | 40.83 ± 11.45b |
| <i>G. graciliflora</i> | 0.00 | 0.00 | 0.00 | 90.00 ± 6.10 | 97.50 ± 1.30 | 99.17 ± 0.83 |
| <i>G. noxia</i> | 39.17 ± 7.01ab | 44.17 ± 5.43a | 21.67 ± 6.0b | 55.00 ± 5.97ab | 47.50 ± 5.10b | 70.83 ± 6.80a |
| <i>H. byrsonimifolia</i> | 24.17 ± 8.30 | 30.83 ± 8.21 | 27.50 ± 5.80 | 43.33 ± 10.40 | 58.33 ± 8.60 | 50.00 ± 9.21 |
| <i>M. ferruginata</i> | 8.33 ± 2.97 | 13.33 ± 5.12 | 13.08 ± 5.11 | 15.00 ± 4.35 | 25.83 ± 6.33 | 25.00 ± 4.75 |
| <i>M. claussenii</i> | 55.00 ± 12.73a | 25.83 ± 6.57ab | 21.67 ± 5.23b | 12.50 ± 7.40 | 12.50 ± 8.97 | 0.83 ± 0.83 |
| <i>O. hexasperma</i> | 0.00 | 0.00 | 0.00 | 97.50 ± 1.95a | 100 ± 0.00a | 88.33 ± 4.41b |
| <i>P. rigida</i> | 27.50 ± 5.62 | 22.50 ± 4.94 | 25.00 ± 5.15 | 68.33 ± 4.91ab | 76.67 ± 4.66a | 58.33 ± 3.66b |
| <i>P. rotundifolia</i> | 0.00 | 0.00 | 0.00 | 59.17 ± 5.96b | 87.50 ± 3.29a | 91.67 ± 4.74a |
| <i>P. ovatum</i> | 11.67 ± 8.24 | 23.33 ± 10.40 | 45.83 ± 11.31 | 62.50 ± 12.56a | 60.83 ± 13.56a | 14.17 ± 7.93b |
| <i>P. pubescens</i> | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>R. induta</i> | 9.17 ± 4.68 | 8.33 ± 4.41 | 18.33 ± 7.16 | 56.67 ± 13.00 | 75.00 ± 8.83 | 60.00 ± 10.59 |
| <i>S. macrocarpa</i> | 24.17 ± 10.11b | 39.17 ± 9.33b | 64.17 ± 5.70a | 72.50 ± 10.45a | 47.50 ± 12.32a | 6.67 ± 1.88b |
| <i>S. adstringens</i> | 35.00 ± 8.66 | 20.83 ± 7.01 | 16.67 ± 4.82 | 0.83 ± 0.83 | 3.33 ± 1.88 | 0.83 ± 0.83 |
| <i>S. ferrugineus</i> | 35.00 ± 10.26 | 12.50 ± 4.94 | 22.50 ± 5.38 | 28.33 ± 9.11 | 42.50 ± 11.55 | 19.17 ± 6.79 |
| Mean | 17.47 ± 2.00 | 15.78 ± 1.67 | 18.62 ± 1.78 | 49.70 ± 2.90ab | 55.00 ± 2.88a | 42.21 ± 2.84b |

Values are means ± SE (n = 12). A total of 360 seeds were used for each species. Bold numbers indicate species that differ significantly in predation or removal among vegetation types according to Tukey HSD post-hoc test. For those species, means with the same letter do not differ significantly among vegetation types

reveal the effect of secondary dispersal on recruitment rates of savannah woody species along tree density gradients. Seeds of only 33% of the woody species studied had the potential to remain viable for longer than 12 months, but at very low percentages (less than 15%). Seed viability loss may further reduce seed supply of woody plants by preventing the formation of persistent soil seed-banks (seeds living in the soil for periods longer than 1 year) from which seedlings recruit. In Neotropical savannas, seeds of most common woody species do not form persistent but seasonal transient soil seed-banks (Salazar et al. 2011). Short-lived soil seed-banks further increase the magnitude of seed limitation because viable seeds do not accumulate in the soil over time and cannot recruit into the population even during a productive seed year for that species (Deveny and Fox 2006; Clark et al. 2007; Zobel et al. 2000; Moles and Westoby 2002). Although seed limitation does not

necessary reduce seedling recruitment (Orrock et al. 2006), it is highly likely that the combination of poor seed dispersal among sites, post-dispersal seed loss, and short-lived soil seed-banks enhance seed limitation reducing the potential seedling recruitment of woody species in tropical savannas. Although many of the studied cerrado woody plants resprout vigorously following fires (Hoffmann 1998), the contribution of vegetative reproduction relative to sexual reproduction to population growth in fire-protected savannas, where this study was done, is still unknown. Therefore, seed addition experiments should be conducted to examine the degree at which seedling establishment is affected by seed versus micro-site limitations, as well as studies that examine the relative importance of sexual versus vegetative reproduction on tree recruitment rates, particularly in unburned tropical savannas.

In conclusion, our study shows that Neotropical savannah woody plants are seed-limited because of

Table 7 Speed of seed loss because of predation and removal calculated as the number of days at which 50% of the seeds are predated or removed (R^{50}) for 13 woody species that exhibited a final seed loss higher than 50%

| Species | R^{50} (days) | | |
|--------------------------|----------------------|-----------------------|----------------------|
| | Cerrado denso | Cerrado sensu stricto | Campo sujo |
| <i>E. pubescens</i> | 6.58 ± 0.72a | 3.91 ± 1.51b | 5.41 ± 2.84ab |
| <i>E. suberosum</i> | 14.90 ± 4.07 | 9.33 ± 1.57 | 12.63 ± 1.87 |
| <i>G. graciliflora</i> | 2.64 ± 0.58 | 2.42 ± 0.50 | 3.58 ± 0.51 |
| <i>G. noxia</i> | 1.75 ± 0.22b | 1.66 ± 0.19b | 5.00 ± 0.74a |
| <i>H. byrsonimifolia</i> | 7.30 ± 1.90 | 5.83 ± 1.26 | 5.25 ± 0.91 |
| <i>M. clausenii</i> | 18.33 ± 2.46b | 33.00 ± 3.80a | 36.00 ± 9.00a |
| <i>O. hexasperma</i> | 2.91 ± 0.34 | 2.66 ± 0.33 | 3.00 ± 0.56 |
| <i>P. rigida</i> | 6.17 ± 1.11b | 4.57 ± 0.70b | 9.55 ± 1.01a |
| <i>P. rotundifolia</i> | 5.22 ± 0.70 | 5.33 ± 0.94 | 7.17 ± 0.63 |
| <i>P. ovatum</i> | 24.89 ± 5.29 | 13.00 ± 2.96 | 26.00 ± 6.96 |
| <i>R. induta</i> | 8.64 ± 2.44 | 4.42 ± 1.23 | 5.80 ± 1.62 |
| <i>S. macrocarpa</i> | 16.67 ± 3.46a | 6.82 ± 0.95b | 3.21 ± 1.12b |
| <i>S. ferrugineus</i> | 15.50 ± 2.53 | 16.56 ± 4.73 | 17.57 ± 5.88 |
| Mean | 9.96 ± 0.87a | 7.26 ± 0.72b | 8.18 ± 0.78a |

Experiments were done in cerrado denso, cerrado sensu stricto, and campo sujo (closed, intermediate, and open savannas, respectively). Values are means ± SE ($n = 12$). A total of 360 seeds were used for each species. Bold rows indicate species that differ significantly according to Tukey HSD post-hoc test. For those species, means with the same letter do not differ significantly among vegetation types

low and poor distribution of seeds among sites, post-dispersal seed removal and predation, and short seed longevity. The high seed limitation of tree species in Neotropical savannas, particularly in open savannas, also may contribute to maintain their relatively low tree densities and help to explain the spatial variation of tree abundance along cerrado topographic gradients.

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