UNIVERSIDADE FEDERAL DE SÃO CARLOS
CENTRO DE CIÊNCIAS E TECNOLOGIAS PARA A SUSTENTABILIDADE
CAMPUS DE SOROCABA

PROGRAMA DE PÓS-GRADUAÇÃO EM
DIVERSIDADE BIOLÓGICA E CONSERVAÇÃO

O papel da limitação de sementes e da limitação no estabelecimento no recrutamento de plantas no Cerrado

Vanessa Mariano da Silva

Sorocaba - SP
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Dissertação apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação, para a obtenção do título de mestre em Diversidade Biológica e Conservação.

Orientador: Alexander V. Christianini

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VANESSA MARIANO DA SILVA

O PAPEL DA LIMITAÇÃO DE SEMENTES E DA LIMITAÇÃO NO ESTABELECIMENTO NO RECRUTAMENTO DE PLANTAS DO CERRADO

Dissertação apresentada ao Programa de Pós-Graduação para obtenção do título de mestre em Diversidade Biológica e Conservação.
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RESUMO

O recrutamento de plantas pode ser restringido pelas limitações de sementes e no estabelecimento, os quais afetam a composição e diversidade de uma comunidade. Em savanas neotropicais a importância relativa desses processos ainda não é clara em decorrência da falta de estudos. O objetivo desse estudo foi avaliar a importância das limitações de sementes e no estabelecimento para o recrutamento de uma comunidade de cerrado no sudeste do Brasil. Foram posicionados 49 coletores de sementes em uma parcela de 0,64 ha e a chuva de sementes foi monitorada mensalmente durante um ano. Além disso, foram realizados experimentos de adição de sementes. A produção de sementes apresentou um pico durante a estação chuvosa, sendo que as espécies zoocóricas produziram principalmente durante a estação chuvosa e as anomocóricas, durante a estação seca. Houve uma influência significativa da limitação de sementes no recrutamento, sendo que a maioria das espécies presentes na chuva de sementes apresentou valores dessa limitação maiores que 65%. Apenas 23% das espécies arbustivo-arbóreas presentes na parcela tiveram, pelo menos, uma semente coletada. As limitações de sementes e na fonte apresentaram uma relação negativa com o número de adultos, indicando que o aumento de fontes de sementes eleva o número de locais atingidos por sementes. Não houve relação entre limitações de sementes, na fonte e na dispersão com forma de vida, síndrome de dispersão e peso da semente. A adição de sementes não aumentou a regeneração de plântulas das quatro espécies testadas, as quais apresentaram valores elevados de limitação no estabelecimento. O presente estudo indica que o recrutamento de plantas de savanas neotropicais é restringido pelas limitações de sementes e no estabelecimento e ressalta a importância da produção e dispersão de sementes para a colonização de novos locais.

Palavras-chave: cerrado; limitação na dispersão; adição de sementes; dispersão de sementes; predação de sementes; tamanho das sementes; limitação na fonte; limitação no recrutamento.

ABSTRACT

Plant recruitment can be constrained by seed and establishment limitation and these processes can affect community species composition and diversity. In Neotropical savannas the relative importance of these processes for plant regeneration are unclear because of the scarcity of studies. The aim of this study was to evaluate the importance of seed and establishment limitation to plant recruitment on cerrado savanna in Itirapina, southeast Brazil (22°12'S, 47°52'W). We spread 49 seed traps in a 0.64-ha plot and monitored seed rain monthly for a year, and also conducted seed addition experiments. Seed production presented a peak in rainy season, with zoochoric and anemochoric species producing seeds mainly in rainy and dry season respectively. Our study indicates a strong influence of seed limitation on recruitment, with most seed rain species presenting seed limitation values higher than 65%. Only 23% of woody species in the plot had at least one seed trapped. Seed and source limitation was negative related to adult abundance, indicating that the increase of seed sources enhances the number of suitable sites reached by seeds. There was no relation between seed, source and dispersal limitation and plant life form, dispersal syndrome and seed mass. Seed addition was unable to increase seedling regeneration in the four species tested, which presented high values of establishment limitation. Our study shows that Neotropical savanna plants recruitment is restricted by seed and establishment limitation and highlights the role of seed production and dispersal to colonization of new sites.

Key words: cerrado; dispersal limitation; seed addition; seed dispersal; seed predation; seed size; source limitation; recruitment limitation.

SUMÁRIO

1. INTRODUÇÃO GERAL

O recrutamento é definido como a entrada de novos organismos em uma população ou comunidade (Ribbens *et al.* 1994). A limitação no recrutamento ocorre quando novos indivíduos não estão presentes em todos os locais favoráveis para seu crescimento e sobrevivência (Muller-Landau *et al.* 2002), influenciando composição, abundância, diversidade e riqueza de espécies de uma comunidade vegetal (Cornell & Lawton 1992, Tilman 1997). Os processos que restringem o recrutamento de plantas são a limitação no estabelecimento (*establishment limitation*) e a limitação de sementes (*seed limitation*) (Eriksson & Erlén 1992, Muller-Landau *et al.* 2002, Münzbergová & Herben 2005, Clark *et al.* 2007). A limitação no estabelecimento ocorre em decorrência da falta de locais adequados para o estabelecimento de sementes e plântulas (Muller-Landau *et al.* 2002). Já a limitação de sementes pode ser definida como a falha em atingir todos os locais adequados através das sementes, restringindo as taxas de crescimento da população e a abundância das espécies (Eriksson & Ehrlén 1992). A limitação de sementes pode ser dividida em limitação na fonte (*source limitation*), que é a limitação em decorrência do número reduzido de sementes produzidas e limitação na dispersão (*dispersal limitation*), que é a dispersão espacialmente limitada das sementes disponíveis (Turnbull *et al.* 2000, Muller-Landau *et al.* 2002). Estudos em florestas tropicais e temperadas sugerem que sementes e plântulas de várias espécies estão ausentes em locais aparentemente adequados para seu estabelecimento, indicando que a limitação de sementes é muito comum (Turnbull *et al.* 2000, Clark *et al.* 2007). O papel dessa limitação ainda não é claro em savanas neotropicais, como o cerrado, já que estudos sobre esse tema são extremamente raros em savanas (Salazar *et al.* 2012a). A limitação no estabelecimento e a limitação de sementes podem ser avaliadas através de experimentos de adição de sementes e da mensuração da chuva de sementes, os quais fornecem informações complementares sobre esses tipos de limitação (Muller-Landau *et al.* 2002).

Em estudo desenvolvido por Hubbell *et al.* (1999) em uma parcela de 50 ha de floresta tropical no Panamá durante 10 anos e que envolveu 314 espécies, a limitação no recrutamento foi o principal fator que determinou a riqueza local e composição de espécies. Do número total de espécies, 88% não forneceu nenhuma semente para qualquer um dos 200 coletores de sementes durante 10 anos de coleta. Além disso, 50% das espécies que depositaram sementes nos coletores tiveram sementes em seis (3%) ou menos coletores. Ou seja, a maior parte das espécies não é capaz de distribuir suas sementes em um número considerável de localidades. Este resultado é reforçado por um censo de plântulas realizados em 2000 parcelas de 1 m^2, onde 56% das espécies não possuíam nenhuma plântula, sendo que do total de espécies, mais de 70% estava presente em menos de 1% das parcelas amostradas. Desse modo, os autores concluíram que há uma forte limitação no recrutamento na área estudada. Em uma revisão de experimentos de adição de sementes em campo, Clark *et al.* (2007) concluíram que a maioria das espécies estudadas (n=159) possui limitação de sementes. Porém, em média os valores de limitação de sementes são baixos (cerca de 15%) e em cerca de 90% das espécies é menor que 50%. Além disso, espécies com sementes maiores e espécies com banco de sementes de curta duração apresentam maior limitação de sementes (Clark *et al.* 2007).

A dispersão tem sementes tem sido apontada como um dos principais processos que governam a ecologia de populações de plantas, uma vez que a maioria das plantas depende de sementes para sua reprodução e o local para onde a semente é dispersa exerce uma enorme influência nas probabilidades de sobrevivência e germinação das sementes e na transição do estágio de plântula para juvenil e adulto (Schupp & Fuentes 1995). Além disso, é uma interação que contribui reconhecidamente para a manutenção da estrutura e diversidade de comunidades vegetais (Christian 2001), diminuindo as densidades de sementes e plântulas da mesma espécie e distanciando as sementes dos arredores da planta-mãe onde se concentram patógenos e insetos predadores especializados (Janzen 1970, Connell 1971). A limitação na dispersão faz com que os propágulos fiquem agregados e, portanto, reduz a frequência da competição interespecífica e aumenta a frequência da intraespecífica (Pacala & Levin 1997). Além disso, de acordo com Webb & Peart (2001) uma maior diversidade de espécies é promovida quando há limitação na dispersão, uma vez que ela diminui a chance de dominância de espécies competitivamente superiores, permitindo que outras espécies se estabeleçam.

A predação de sementes também desempenha um papel chave na estruturação da comunidade de plantas e estudos conduzidos em vários ecossistemas têm demonstrado que a predação pós-dispersão causa significativas perdas de sementes (Andersen 1989, Ehrlén 1996, Curran & Webb 2000, Ferreira *et al.* 2011). A predação pós-dispersão pode variar de acordo com o habitat, micro-habitat, espécie, densidade, características das sementes e estação do ano (Hulme 1994, Ferreira *et al.* 2011). Sabe-se que essa interação pode limitar o recrutamento de plântulas no cerrado e que formigas granívoras desempenham papel importante nesta restrição (Ferreira *et al.* 2011). Porém, poucos estudos ligam diretamente a predação de sementes com o estabelecimento de plântulas e, portanto, a ligação entre predação de sementes e a dinâmica das populações de plantas ainda não é clara (Ferreira *et al.* 2011).

O cerrado e a limitação de sementes e no estabelecimento

O Cerrado ocupava mais de 2 milhões de km², sendo o segundo maior domínio do Brasil e representando cerca de 20% da área do país (Ratter *et al.* 1997, Klink & Machado 2005). É a savana tropical mais rica do mundo, possuindo alta diversidade de habitats e de espécies (Klink & Machado 2005), e é destacada como um dos *hotspots* globais de biodiversidade (Myers *et al.* 2000). Está presente em locais com climas sazonais, com cerca de seis meses de baixa pluviosidade (Veloso *et al.* 1991). A estação chuvosa ocorre de outubro a março e a seca de abril a setembro e as temperaturas variam de 22° a 27°C (Klink & Machado 2005). A precipitação média anual é de ca. 1500 mm (Klink & Machado 2005).

Estudos sobre dinâmica de sementes e estabelecimento de plântulas em nível de comunidade são raros em savanas (Salazar 2010). De acordo com estudo de Salazar *et al.* (2012a), que avaliou 23 espécies, as médias de limitação de sementes, limitação na fonte e limitação na dispersão foram de mais de 80%, 60% e 70% em cerrado *sensu stricto*, respectivamente. Além disso, para 17 espécies estudadas, em média mais de 60% das sementes foram removidas em um período de 30 a 45 dias, indicando que eventos pós-dispersão podem ter um papel importante na redução da disponibilidade das sementes (Salazar *et al.* 2012a). A média da limitação no recrutamento de plântulas foi de mais de 90% (Salazar *et al.* 2012b). Os estudos citados acima foram os únicos encontrados sobre o tema no Cerrado brasileiro e foram desenvolvidos na porção central do país (Brasília). Não foram encontrados estudos sobre limitação de sementes e no estabelecimento na porção sul da distribuição do cerrado. Desse modo, o presente estudo fornece informações inéditas sobre a limitação no recrutamento nessa porção do cerrado, as quais são importantes para o entendimento desses processos nesse bioma.

2. OBJETIVO GERAL

Avaliar a importância da limitação de sementes e da limitação no estabelecimento para o recrutamento das espécies vegetais de uma comunidade de cerrado.

3. MATERIAL E MÉTODOS

Área de estudo

Este estudo foi desenvolvido na Estação Experimental de Itirapina (Figura 1). O fragmento estudado tem 127,6 ha de cerrado *stricto sensu* (São Paulo 2006). A vegetação é dominada por árvores e arbustos, atingindo até 8 metros de altura. A precipitação anual média na área de estudo é de 1459 mm, sendo que a média no período chuvoso (outubro a março) é de 1228 mm e no período seco (abril a setembro) é de 331 mm, e a temperatura média anual é de 21,9ºC (São Paulo 2006).

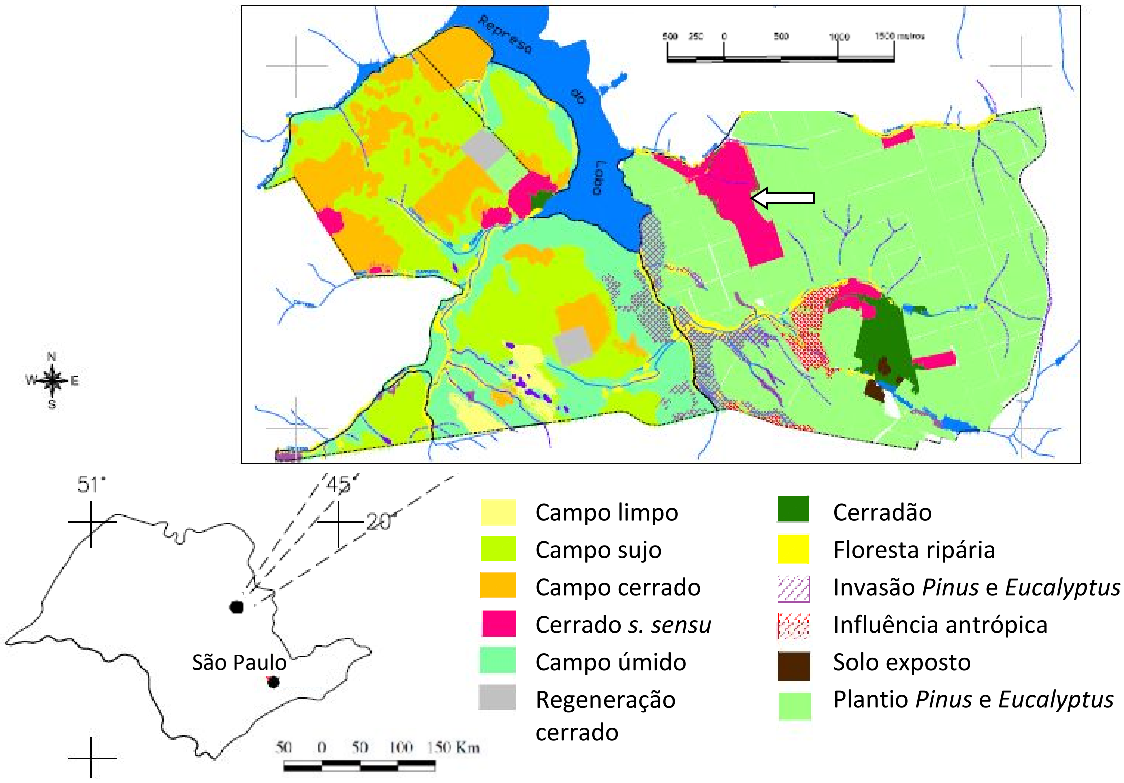

Figura 1. Localização da Estação Ecológica de Itirapina no estado de São Paulo, Brasil, e as fisionomias presentes na Unidade (adaptado de São Paulo, 2006). A seta branca indica o fragmento florestal no qual foi realizado o presente estudo.

Coleta de dados

Para avaliar a composição e abundância das espécies da comunidade vegetal foram instaladas 64 parcelas contíguas de 10 x 10 m, formando um quadrado de 80 x 80 m, totalizando 6400 m^2 (Figura 2), sendo que a localização e a distância da borda foram definidos ao acaso. Foram amostrados todos os indivíduos vegetais lenhosos arbustivo-arbóreos presentes nas parcelas que tinham Diâmetro à Altura do Solo (DAS) maior ou igual a 3 cm e/ou altura maior que 60 cm e identificados com o auxílio de chaves de identificação. Para avaliar as limitações de sementes, na fonte e na dispersão foi avaliada a chuva de sementes da comunidade vegetal mensalmente durante um ano (janeiro a dezembro de 2014), utilizando-se 49 coletores de 30 x 50 cm, distantes 10 m entre si de maneira sistemática (Figura 2). Para avaliar a limitação de plântulas e a limitação no estabelecimento foram realizados experimentos de adição de sementes e para avaliar a influência da predação de sementes na regeneração foi feito um experimento de exclusão de predação. Foi realizada uma avaliação mensal da germinação das sementes durante 6 meses (Bruna 1999, Ferreira *et al.* 2011). As espécies utilizadas foram *Dalbergia miscolobium*, *Pyrostegia venusta*, *Banisteriopsis stellaris* e *Siparuna guianensis* (Tabela 1). Detalhes dos métodos e da análise dos dados estão presentes no Artigo que acompanha essa dissertação.

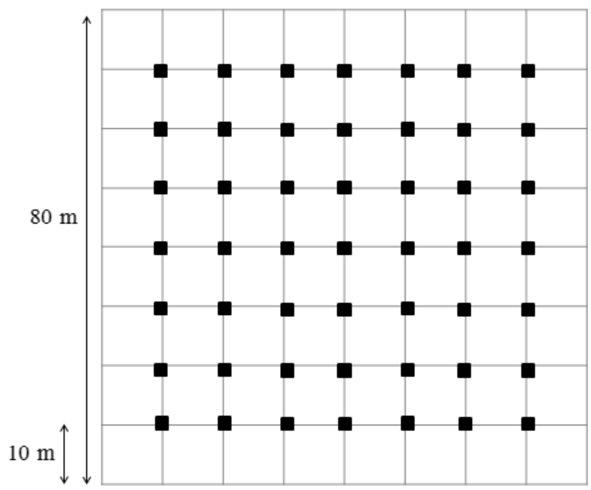

Figura 2. Distribuição das parcelas nas quais foram amostrados os indivíduos arbustivo-arbóreos e dos coletores de sementes instalados no fragmento de cerrado *stricto sensu* na Estação Ecológica de Itirapina. Os coletores estão representados pelos quadrados pretos e os limites das parcelas (10 x 10 m) como linhas.

Tabela 1. Espécies utilizadas nos experimentos de adição e de predação de sementes e suas respectivas famílias, formas de vida e síndromes de dispersão.

Espécie	Família	Forma de vida	Dispersão
Banisteriopsis stellaris	Malpighiaceae	Liana	Anemocórica
Dalbergia miscolobium	Fabaceae	Árvore	Anemocórica
Pyrostegia venusta	Bignoniaceae	Liana	Anemocórica
Siparuna guianensis	Siparunaceae	Arvoreta	Zoocórica

A partir dos dados da chuva de sementes foram calculados os valores de limitação de sementes, limitação na fonte e limitação na dispersão a partir de fórmulas apresentadas por Muller-Laudau *et al.* (2002). A limitação de sementes (SL) está relacionada com o número de coletores que não foram atingidos por sementes de uma determinada espécie e é definida pela fórmula:

$$SL = 1 - \frac{a}{n}$$

sendo *a* o número de coletores em que as sementes foram encontradas e *n*, o número total de coletores. A limitação na fonte (SC) se relaciona com a baixa produção de frutos e pode ser calculada como

$$SC = \exp(-\frac{s}{n})$$

sendo *s* a soma do número de sementes encontradas em todos os coletores. Para determinar a restrição na dispersão das sementes foi calculada a limitação na dispersão (DL) a partir da seguinte fórmula:

$$DL = 1 - \frac{a/n}{1-SC}$$

A partir dos dados dos experimentos de adição de sementes foram calculados os valores de limitação de plântulas e de limitação no estabelecimento, de acordo com Muller-Laudau *et al.* (2002). A limitação de plântulas (SDL) é avaliada utilizando-se o número de locais em que plantas se estabeleceram (*r*) e o número total de locais em que foram adicionadas sementes (*n*) a partir da seguinte equação

$$SDL = 1 - \frac{r}{\mathrm{n}}$$

Esse índice releva a proporção de locais nos quais nenhuma nova plântula emerge em um determinado período de tempo. A limitação no estabelecimento (EL) é a proporção de locais que não receberam sementes e que nenhuma planta emergiu e é mensurada como

$$EL = 1 - \frac{r}{a}$$

Todos os índices citados variam de 0 a 1, sendo que 1 indica limitação máxima e 0 indica ausência de limitação. Maiores detalhes e implicações podem ser encontrados no artigo, a seguir.

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CAPÍTULO I

Artigo

Formatado para o periódico “Biotropica”

Seed and establishment limitation in a Neotropical savanna

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ABSTRACT

Plant recruitment can be constrained by seed and establishment limitation and these processes can affect species composition and diversity in a community. In Neotropical savannas the relative importance of these processes from plant regeneration are unclear because of the scarcity of studies. The aim of this study was to evaluate the importance of seed and establishment limitation to plant recruitment on cerrado savanna in southeast Brazil. We spread 49 seed traps in a 0.64-ha plot and monitored seed rain monthly for a year, and also conducted seed addition experiments. Seed production presented a peak in rainy season, with zoochoric species producing seed mainly in rainy season and anemochoric, in dry season. Our study indicates a strong influence of seed limitation on recruitment, with most seed rain species presenting seed limitation values higher than 65%. Only 23% of woody species in the plot had at least one seed trapped. Seed and source limitation was negative related to adult numbers, indicating that the increase of seed sources enhances the number of suitable sites reached by seeds. There was no relation between seed, source and dispersal limitation and plant life form, dispersal syndrome and seed mass. Seed addition was unable to increase seedling regeneration in the four species tested. Our study shows that Neotropical savanna plants recruitment is restricted by seed and establishment limitation and highlights the role of seed production and dispersal to colonization of new sites.

Key words: Cerrado; dispersal limitation; seed addition; seed dispersal; seed predation; seed size; source limitation; recruitment limitation.

RECRUITMENT LIMITATION IS THE FAILURE OF THE PLANTS IN RECRUIT NEW INDIVIDUALS IN ALL SUITABLE SITES FOR THEIR GROWTH AND SURVIVAL (Hubbell *et al.* 1999, Muller-Landau *et al.* 2002). This limitation may have strong effects on species richness, abundance, composition and diversity from a plant community (Cornell & Lawton 1992,Tilman 1997) and may occur on different spatial and temporal scales (Ribbens *et al.* 1994). For example, recruitment limitation is the major factor determining local species richness and composition in a species rich tropical forest in Panama (Hubbell *et al.* 1999). A mean of 88% of the species sampled (N=314) failure to deliver at least one seed to any seed trap (N=200) in ten years of study (Hubbell *et al.* 1999). In a seedling census in 2000 m^2 at the same site, 56% of the species had no seedlings found (Hubbell *et al.* 1999). Furthermore, seed density presents a strong negative relation with seedling recruitment, increasing the importance of seed dispersal on recruitment (Harms *et al.* 2000). Seed species pools structure plant communities, with local species richness being strongly limited by seed arrival and by species composition in the seed pool (Myers & Harms 2009). Although the importance of seed dispersal is undisputable, the dispersal capabilities of most plants remain unknown and barely quantified.

Recruitment limitation can occur due to establishment limitation and seed limitation (Eriksson & Erlén 1992, Muller-Landau *et al.* 2002, Münzbergová & Herben 2005, Clark *et al.* 2007). Establishment limitation is defined as the lack of recruitment in result of the absence of suitable sites to seed and seedling establishment (Muller-Landau *et al.* 2002). Seed limitation occurs when seeds do not reach all suitable sites, limiting population growth levels and species abundance (Eriksson & Ehrlén 1992). Seed limitation can be divided into two processes: (1) source limitation, which is limitation duo to the small number of seed produced; and (2) dispersal limitation, which is the spatially limited dispersal of available seeds (Muller-Landau *et al.* 2002, Turnbull *et al.* 2000). Therefore, seed dispersal is an interaction that contributes to the maintenance of the structure and diversity of plant communities (Christian 2001). Increase of dispersal limitation produce aggregate patterns of seedling of single species, reducing the frequency of interspecific competition and increasing intraspecific (Pacala & Levin 1997). Therefore a greater diversity of species is allowed when there is dispersal limitation, which reduces the chance of dominance by superior competitors allowing the establishment of other species (Webb & Peart 2001).

Studies in temperate and tropical forests have demonstrated that seeds and seedlings of many species are apparently absent in suitable sites for their establishment, indicating that seed limitation is very common (Turnbull *et al.* 2000, Clark *et al.* 2007). In a review of seed augmentation experiments Clark *et al.* (2007) concluded that most studied species presented seed limitation. Despite the great importance for plant populations and communities, few studies quantified seed limitation (Clark *et al.* 2007, Muller-Landau *et al.* 2002), with studies focusing on woodlands and sand dunes (Turnbull *et al.* 2000). Factors such as the number of adults, traits of dispersers and pollinators and environmental conditions can affect seed production and dispersal (Nathan & Muller-Landau 2000). Establishment limitation appears to be another important process that limits recruitment, exhibiting high levels in different habitats (Hubbell *et al.* 1999, Clark *et al.* 2007, Salazar *et al.* 2012b, Vargas & Stevenson 2013). It is known that seed predation can also limit the establishment of seedlings in cerrado and ants often play an important role in this restriction (Ferreira *et al.* 2011).

Certain plant traits such as seed mass, growth form and dispersal syndrome are often correlated with dispersal mechanisms that on their hand influence distances of dispersal and interactions with animals (Thomson *et al.* 2010). Large-seeded plants produce less seeds per square meter of canopy and per adult plant per year, compared with small-seeded species (Moles & Westoby 2006), exhibiting a negative correlation between seed mass and seed number (Leishman 2001). Therefore, seed size may be an important determinant to recruitment, with large-seeded species presenting higher seed limitation levels (Clark *et al.* 2007) and smaller establishment limitation due to the great survival to shade, drought and physical damage (Westoby *et al.* 1996, Moles & Westoby 2002). Growth form also influences species ecological traits (Dorrepaal 2007) and seems to be another factor that influences recruitment limitation in some communities (*e.g.* Mendoza *et al.* 2009). Dispersal syndromes may affect species dispersal patterns (Thomson *et al.* 2010, Buoro *et al.* 2014) and few studies explore the ecological consequences of these syndromes, mainly to the dynamics of populations (Buoro *et al.* 2014). We still need more studies addressing how all those traits influence dispersal limitation (*e.g.* Leishman 2001, Mendoza *et al.* 2009, Buoro *et al.* 2014), especially in vegetation types such as savannas.

Cerrado is the savanna with the highest species richness of the world (Klink & Machado 2005), and is highlighted as a global hotspot of biodiversity (Myers *et al.* 2000). It once covered more than 2 million square km and it is the second largest ecosystem of Brazil, representing nearly 20% of the country (Ratter *et al.* 1997, Klink & Machado 2005). Although Neotropical savannas such as the cerrado bear a rich flora with a high level of endemism (Myers *et al.* 2000), there is a great scarcity of studies describing patterns of seed rain and factors that affect dispersal and plant regeneration. Only one study (Salazar *et al.* 2012a) evaluate dispersal limitation at community level (23 species) limiting our ability to understand the role of dispersal and establishment limitation to plant regeneration in this savanna. Many Brazilian savanna species presented vegetative reproduction and fire events affect negatively sexual reproduction and increase the importance of vegetative reproduction to recruitment (Hoffmann 1998, Hoffmann 1999, Salazar & Goldstein 2014). However, in long-unburned areas the relative importance of these processes is unclear (Salazar & Goldstein 2014). Without an evaluation of the role of seed limitation in plant regeneration in savannas the relative role of vegetative versus seed propagation may be misleading.

The aim of this study was to evaluate the importance of seed and establishment limitation to plant recruitment on a Neotropical savanna. For this we (a) described seed limitation at community level, (b) evaluate the influence of number of adults, life form, dispersal syndrome and seed mass on seed limitation, (c) described establishment limitation for four species and (d) the influence of predation and seed addition on recruitment.

METHODS

STUDY SITE

This study was carried out at the Estação Experimental de Itirapina, a 127 ha fragment (22º12'S, 47°52'W) in southeast Brazil (São Paulo 2006). The fragment is covered by cerrado *stricto sensu*, a Brazilian savanna defined by vegetation dominated by trees and shrubs, with a herbaceous layer and canopy cover greater than 30% (Oliveira-Filho & Ratter 2002). The average annual precipitation in the study site is 1459 mm, and during the rainy season (October to March) the average is 1228 mm of precipitation and during the dry season (April to September) is 331 mm (São Paulo 2006). The average annual temperature is 21.9°C (São Paulo 2006). Trees may reach up to 8 m tall and Myrtaceae, Rubiaceae and Melastomataceae stand out in number of species (Gianotti & Leitão Filho 1992).

SEED RAIN AND SEED LIMITATION

To evaluate seed limitation we quantified seed rain using seed traps from January to December 2014. In the study site we haphazardly delimitated a 80 x 80 m plot. All wooded plants within the plot with diameter at the base larger than 3 cm and/or 60 cm tall were mapped, sampled and identified. According to field observations and other studies (*e.g.* Hoffmann 1998), all sampled individuals were considered adults. The plot was also subdivided by each 10 x 10 m generating a grid of 64 quadrats of 100 m² each. In the intersection of the limits of four adjacent quadrats we set a seed trap, 10 m distant from each other in a systematic design (total of 49 seed traps in the plot, see Suplementary material).Traps consisted of 30 x 50 cm plastic boxes that were kept 45 cm above ground by four stakes and covered with a 0.1 mm mesh. Traps were covered with a wire mesh to avoid access by vertebrates and stakes were coated by a sticky resin (Tanglefoot) to prevent ants from reaching seeds and fruits. The content of each trap was collected monthly between January and December 2014. Seeds and fruits were identified to the lowest taxonomic level based on specialized literature. All seeds were inspected and those with no predation marks or decomposition signs were considered viable.

From the seed rain data we calculated seed, source and dispersal limitation values following the formulas found in Muller-Laudau *et al.* (2002). To evaluate the influence of life form, dispersal syndrome and seed mass on seed limitation values we classified the species with at least one seed trapped based on literature (*e.g.* Kullmann 2012, Silva Júnior 2012).

SEED ADDITION AND SEED PREDATION EXPERIMENTS

To assess seedling and establishment limitation we conducted seed addition experiments with four species: *Banisteriopsis stellaris*, *Dalbergia miscolobium*, *Pyrostegia venusta* and *Siparuna guianensis*. To evaluate the influence of seed predation on regeneration an experiment was done with exclusions from predators. Exclusion treatments consisted in a plastic frame of 35 x 26cm covered with a metal mesh of 1.5 cm, and the frame was secured to the ground with metal rods. For each plant species we combined four treatments with 10 cm distance from each other in a factorial design (Hoffmann 1996): (i) seed addition without exclusion of predators; (ii) seed addition and predation exclusion; (iii) no seed addition and with exclusion of predators; (iv) no seed addition and without predation exclusion. Each set of treatments (block) was replicated 15 times for each species. The location of the blocks inside the plot was defined randomly, observing a minimum distance of 20 m from each other. We added 10 seed of *D. miscolobium*, 5 of *P. venusta*, 7 of *B. stellaris* and 2 of *S. guianensis* in each seed addition treatment. The number of seeds added varied with the availability of seeds for each specie (Hoffmann 2000). Seeds were collected from ripe fruits of at least 3 adult individuals per specie and seed were added during the natural period of fruiting. A monthly evaluation of seed germination was carried out for 6 months (Bruna 1999, Ferreira *et al.*2011). We used the number of sites with seedlings, total number of sites and number of sites reached by seeds to calculate seedling and establishment limitation, according to Muller-Laudau *et al.* (2002). The number of sites reached by seeds was defined by the nearest seed traps. As the area of a seed trap is smaller than the area of the set of treatments, the values of establishment limitation were underestimated.

DATA ANALYSIS

To evaluate if the number of seeds trapped (a proxy for seed production) is related to the number of traps we used linear regression. To evaluate if seed, source and dispersal limitation were related with seed mass and number of individuals within the 80 x 80 m plot linear regressions were used. One-way ANOVAs were used to examine the relation between life form and dispersal syndrome with seed, source and dispersal limitation. We did not include in our analyses *Miconia* seeds that could not be identified at species level, but this seeds would respond to 0.2% and 0.01% to total number of seeds of *M. albicans* and *M. rubiginosa*, respectively. To assess the abundance-based similarity between seed traps we used the program Estimates to calculate Chao-Jaccard similarity index using data of species that reached each seed trap.

RESULTS

SEED RAIN AND SEED LIMITATION

In the study plot we sampled 3,915 individuals of shrubs and trees, belonging to 74 species (Supporting Information). The three most abundant species (*Xylopia aromatica*, *Miconia albicans* and *M. rubiginosa*) represented almost 75% of the total. There were 45 zoochorics, 20 anemochoric and 3 autochoric species among the adult plants in the plot. Zoochory also predominates in number of individuals, followed by anemochory and autochory (Supporting Information). Zoochory exceeded anemochory and autochory in number of seeds, but zoochory and anemochory had the same number of seed species (Table 2).

During one year we sampled 367,682 viable seeds in traps belonging to 24 species, including the exotic *Pinus* sp. (Table 1). There was a peak of seed rain from February to

April (Fig. 1), which was strongly influenced by the large amount of zoochoric seeds. The number of viable seeds trapped, the number of traps in which they were found and seed, source and dispersal limitation values are presented on Table 1. There was great variation of limitation values among species and only two species, the tree *M. rubiginosa* and the liana *Serjania* sp., have zero seed limitation values. Almost 70% of the seed species had seed limitation values higher than 65%. Notable exceptions were two melastomes, *M. albicans* and *M. rubiginosa* from which more than 99% of total viable seeds came from. There was a relationship between the number of seeds sampled in traps and the number of traps hit by seeds of a given species ($p<0.01$; $r^2=0.64$; Fig. 2), indicating that the increase in the seed number increases the number of sites reached by seeds.

Only 34% of the total number of shrub and tree species sampled in the study plot had at least one seed trapped. Species that had no seeds sampled (66%) presented maximum seed limitation values. The mean Chao-Jaccard similarity index among seed traps was 0.88 ± 0.24 (mean ± SD), indicating a high similarity of the seed rain between sites. Seed limitation was not related to life form, dispersal syndrome and seed mass, as source and dispersal limitation (Fig. 3; Table 3). However, seed and source limitation have significant negative relationships with the number of adult individuals sampled (Fig. 3; Table 3).

SEED ADDITION AND SEED PREDATION

We found 17 seedlings of *D. miscolobium* and one of *P. venusta* in the seed addition experiments, but no seedlings of *B. stellaris* and *S. guianensis*. We found 0.47 ± 0.64 (mean ± SD) seedlings of *D. miscolobium* in the treatment with seed addition and no predation exclusion, 0.2 ± 0.41 seedlings in seed addition and exclusion treatment, 0.13 ± 0.35 in the treatment with no addition and no exclusion and 0.33 ± 0.72 seedlings in the treatment with only predation exclusion. Seed addition (F=0.49; p=0.49) and seed predation treatments (F=0.05; p=0.82) had no influence in *D. miscolobium* seedling numbers, as the interaction between treatments (F=2.66; p=0.11). *D. miscolobium* had the lowest values of seedling and establishment limitation and *B. stellaris*, *P. venusta* and *S. guianensis* had high limitation values (Table 4).

DISCUSSION

Our study indicates a potential influence of seed limitation on recruitment, with most seed rain species presenting seed limitation values higher than 65%. Similar seed limitation values were found for tropical forest (Hubbel *et al.* 1999, Dalling *et al.* 2002) and Neotropical savanna (Salazar *et al*. 2012a). A higher number of seeds produced (measured by the amount of seeds sampled in traps) increased the number of sites reached by seeds, indicating that seed number is an important determinant for successful colonization of suitable sites.

Seed rain presented a peak in rainy season, with zoochoric species producing seeds mainly in rainy season and anemochorics in dry season, corroborating other studies in Cerrado (Batalha & Mantovani 2000, Munhoz & Felfili 2007, Salazar *et al.* 2012a). Zoochory had higher number of adult and seed species, compared to anemochory and autochory. Similar results were found in other Neotropical savanna communities (Batalha & Mantovani 2000, Vieira *et al.* 2002, Salazar *et al.* 2012a), confirming that animals are important dispersal agents and probably have an important role for savanna plant recruitment.

Seed dispersal has a great importance in spatial processes of plant regeneration, determining the potential sites for recruitment and influencing subsequent chances of seed losses, germination and seedling competition (Nathan & Muller-Landau 2000). Local plant species richness may be limited by the seed arrival from sorts of local and regional species pools (Myers & Harms 2009, Myers & Harms 2011). Thus, high levels of seed limitation affect diversity and composition of communities and it is a key process to recruitment. Therefore, diversity seems to be influenced by the availability of species that are able to exploit the environmental heterogeneity and a seed species-pool with a range of functional traits seems to allow species coexistence (Questad & Foster 2008). The high similarity of the seed rain between traps highlights the large dispersal capacity of some species, like *D. miscolobium*, *M. albicans*, *M. rubiginosa*, *Serjania* sp. and *X. aromatica*, and the importance of a rich species-pool to establishment in a wide range of sites.

Seed and source limitation had a negative relation with adult numbers, which means that more seed sources increases the number of sites reached by seeds, as can be illustrated by *M. albicans*, *M. rubiginosa* and *X. aromatica*. There was no relation between seed, source and dispersal limitation with plant life form, dispersal syndrome and seed mass. Clark *et al.* (2007) found similar results for life form and dispersal syndrome in their meta-analysis with 159 species around the world. In our site of cerrado anemochorous plants produced a lower number of seeds compared to zoochorous at community level, but this did not affected limitations values. However, seeds dispersed by animals may probable reach farther distances (Thomson *et al.* 2011). However, contrary to the expectations, our findings indicate that seed mass does not influence seed limitation at community level. Nevertheless, there is evidence that seed mass influence establishment limitation in savanna sites subjected to frequent burning (Lahoreau *et al.* 2006). Most of seeds trapped were from

M albicans or *M. rubiginosa* that reached almost all traps, indicating that those species saturated available sites with seeds.

A low number of seedlings emerged from our seed addition experiments, and two of four species had no single seedling found. Seed addition experiments can demonstrate if suitable sites are unoccupied at the time of experiment and the lack of effect on recruitment may indicate that these sites are not available (Turnbull *et al.* 2000). Our study indicates that establishment limitation may decrease recruitment for these species, in addition with seed limitation. This low rate of seedling regenaration was also founded in tropical forest (Vargas & Stevenson 2013, Hubbel *et al.* 1999), tropical savana (Hoffmann *et al.* 2004, Salazar *et al.* 2012b, Lima *et al.* 2014) and subtropical forest (Luo *et al.* 2013), and may be related to specific requirements for seed germination and survival such as light, temperature and moisture. For *D. miscolobium*, Salazar *et al.* (2012b) founded seedling limitation values higher than 90% for this species, compared to 53% in our study site. Seed and establishment limitation had similar effects on recruitment for *D. miscolobium* and *S. guianensis*, indicating that seed and seedling-related processes have similar importance in constraining opportunities of plant recruitment for these species. For *P. venusta* and *B. stellaris* establishment limitation had a stronger influence, reaching maximum values. Thus the relative importance of these processes varies between species.

Exclusion of seed predators does not affect the number of *D. miscolobium* seedlings. Other studies found high levels of seed removal and predation in savanna communities, mainly by ants, and there was great variation among seed species (Christianini *et al.* 2007, 2009, 2010, Ferreira *et al.* 2011, Salazar *et al.* 2012b). Any of these studies included *D. miscolobium*. Moreover, our exclusion treatment did not exclude invertebrates and this may have influenced our results.

Our study suggests the importance of seed and establishment limitation to plant recruitment in Neotropical savannas, with a high variation of the relative importance of each process among species. Seed dispersal also seems to be an important factor that influences the colonization of new sites and long-term maintenance of the populations, indicating the value of reproductive processes to recruitment. We emphasize the importance of similar studies to better understand plant regeneration process.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Species sampled in the 0.64 ha plot of cerrado *sensu stricto* and the number of individuals, dispersal syndrome and life form (N=72). Species are arranged by decreasing order of abundance in the plot.

Fig S1. Spatial distribution of seed traps inside the 0.64 ha plot which woody species were sampled. Seed traps are represented by black squares.

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TABLES

Table 1. Number of seed traps reached by seeds (a), total number of seeds (s) and seed, source and dispersal limitation index for each species found in 49 seed traps from January to December 2014.

Species	a	s	Seed limitation	Source limitation	Dispersal limitation
Asteraceae sp1	17	77	0.65	0.21	0.56
Asteraceae sp2	16	300	0.67	0	0.67
Asteraceae sp3	2	2	0.96	0.96	-0.021
Asteraceae sp4	1	1	0.98	0.98	-0.010
Banisteriopsis sp.	28	209	0.43	0.01	0.42
Bowdichia virgilioides	4	5	0.92	0.90	0.16
Byrsonima sp.	7	50	0.86	0.36	0.78
Dalbergia miscolobium	34	122	0.31	0.08	0.24
Erythroxylum pelleterianum	1	1	0.98	0.98	0
Forsteronia glabrescens	12	19	0.76	0.68	0.24
Kielmeyera coriacea	1	1	0.98	0.98	-0.010
Miconia albicans	39	25728	0.20	0	0.20
Miconia rubiginosa	49	339067	0	0	0
Miconia fallax	1	49	0.98	0.37	0.97
Myrcia guianensis	12	77	0.76	0.21	0.69
Pera glabrata	5	5	0.90	0.90	-0.052

Pinus sp.	39	208	0.20	0.01	0.19
Pouteria torta	1	3	0.98	0.94	0.66
Pyrostegia venusta	30	114	0.39	0.10	0.32
Serjania sp.	49	682	0	0	0
Siparuna guianensis	4	249	0.92	0.01	0.92
Stryphnodendron obovatum	1	7	0.98	0.87	0.85
Styrax ferrugineus	8	20	0.84	0.66	0.51
Xylopia aromatica	38	123	0.22	0.08	0.16
Mean (±SD)			0.66±0.34	0.43±0.41	0.35±0.34

Table 2. Seed rain number of seeds and number of species, according with dispersal syndrome.

	Number of seeds	%	Number of species	%
Zoochoric	365,877	99.58	11	47.83
Anemochoric	1532	0.42	11	47.83
Autochoric	7	<0.01	1	4.35

Table 3. Influence of life form, dispersal syndrome, seed mass and number of adults on seed, source and dispersal limitation values (n=24). Bold rows indicate significant relationships between factors. See also Fig. 3.

	Life form		Dispersal syndrome		Seed mass			Number of adults		
	$F_{(2,16)}$	P	$F_{(1,20)}$	p	r	p	Slope	r	p	Slope
Seed limitation	1.41	0.27	0.03	0.87	0.04	0.91	0.08	**-0.71**	**<0.01**	**-0.37**
Source limitation	0.88	0.43	0.28	0.6	0.1	0.74	0.14	**-0.65**	**<0.01**	**-0.4**
Dispersal limitation	0.45	0.64	1.48	0.24	0.04	0.89	0.09	-0.21	0.43	-0.02

Table 4. Seedling and establishment limitation values, total number of seedlings found (r) and total number of sites reached by seeds (a) for four species used in seed addition and predation experiments in a Brazilian savanna fragment.

Species	Family	Life form	Dispersal syndrome	r	a	Seedling limitation	Establishment limitation
Banisteriopsis stellaris	Malpighiaceae	Liana	Anemochoric	0	7	1	1
Dalbergia miscolobium	Fabaceae	Tree	Anemochoric	7	10	0.53	0.3
Pyrostegia venusta	Bignoniaceae	Liana	Anemochoric	1	10	0.93	0.9
Siparuna guianensis	Siparunaceae	Treelet	Zoochoric	0	2	1	1
Mean ± SD						0.87±0.22	0.8±0.34

FIGURE LEGENDS

Fig. 1. Total number of viable seeds trapped monthly in 49 seed traps from January to December 2014, according with dispersal syndrome: (a) total number of seeds for each month, (b) number of zoochoric seeds, and (c) number of anemochoric seeds trapped.

Fig. 2. Relation between number of seeds trapped and number of traps reached by seeds (R^2= 0.64; y=10,69x+2,44).

Fig. 3. Seed, source and dispersal limitation according to life form (mean ± SD), dispersal syndromes (mean ± SD), seed mass and number of adults, based on annual seed rain sampled in 49 seed traps in a Cerrado in southeast Brazil.

FIGURES

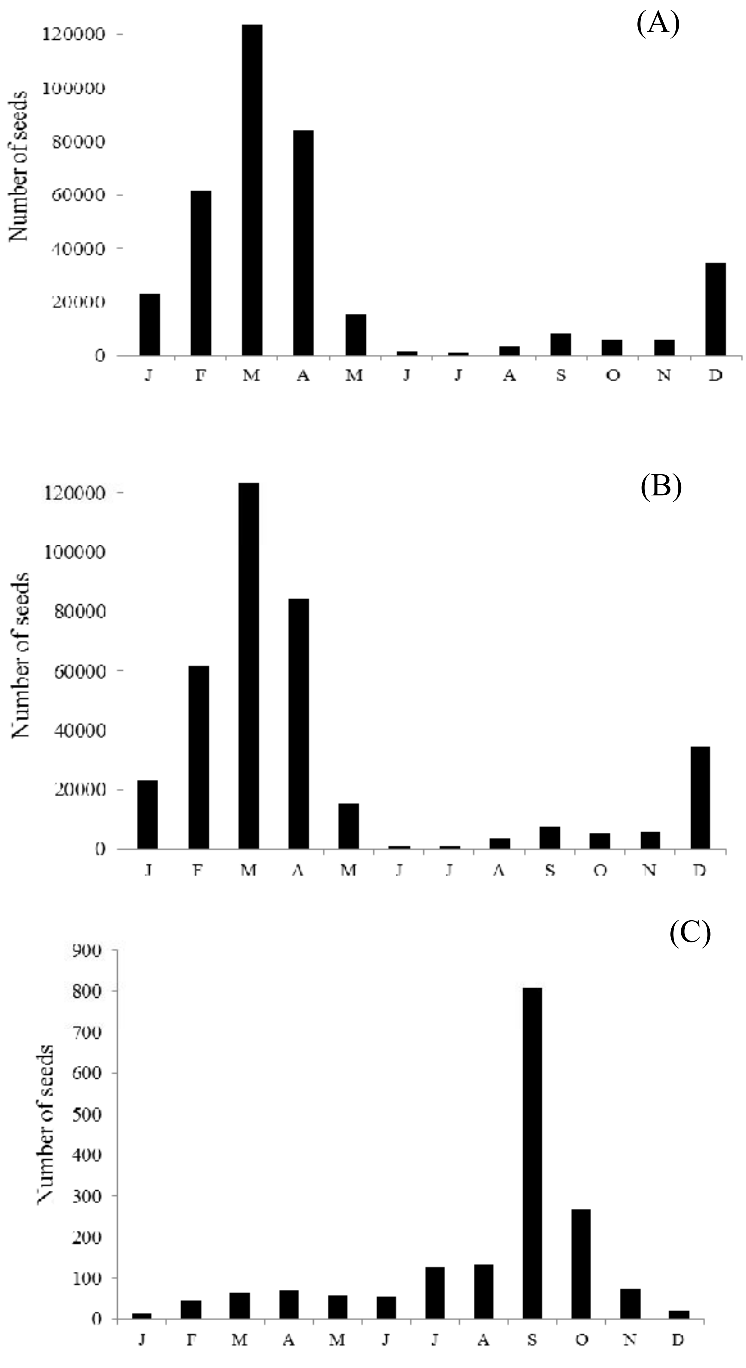
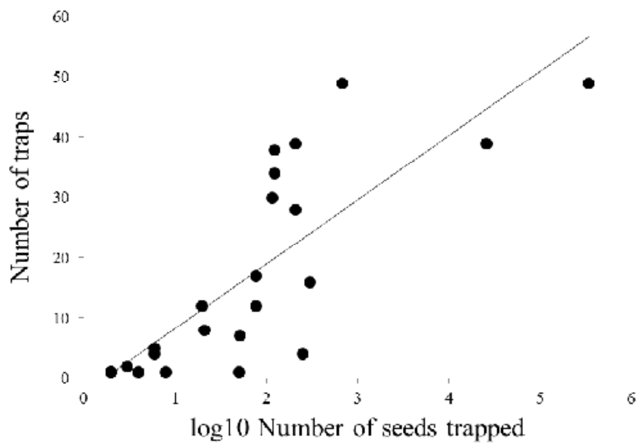


Fig. 1. Total number of viable seeds trapped monthly in 49 seed traps from January to December 2014, according with dispersal syndrome: (a) total number of seeds for each month, (b) number of zoochoric seeds, and (c) number of anemochoric seeds trapped.



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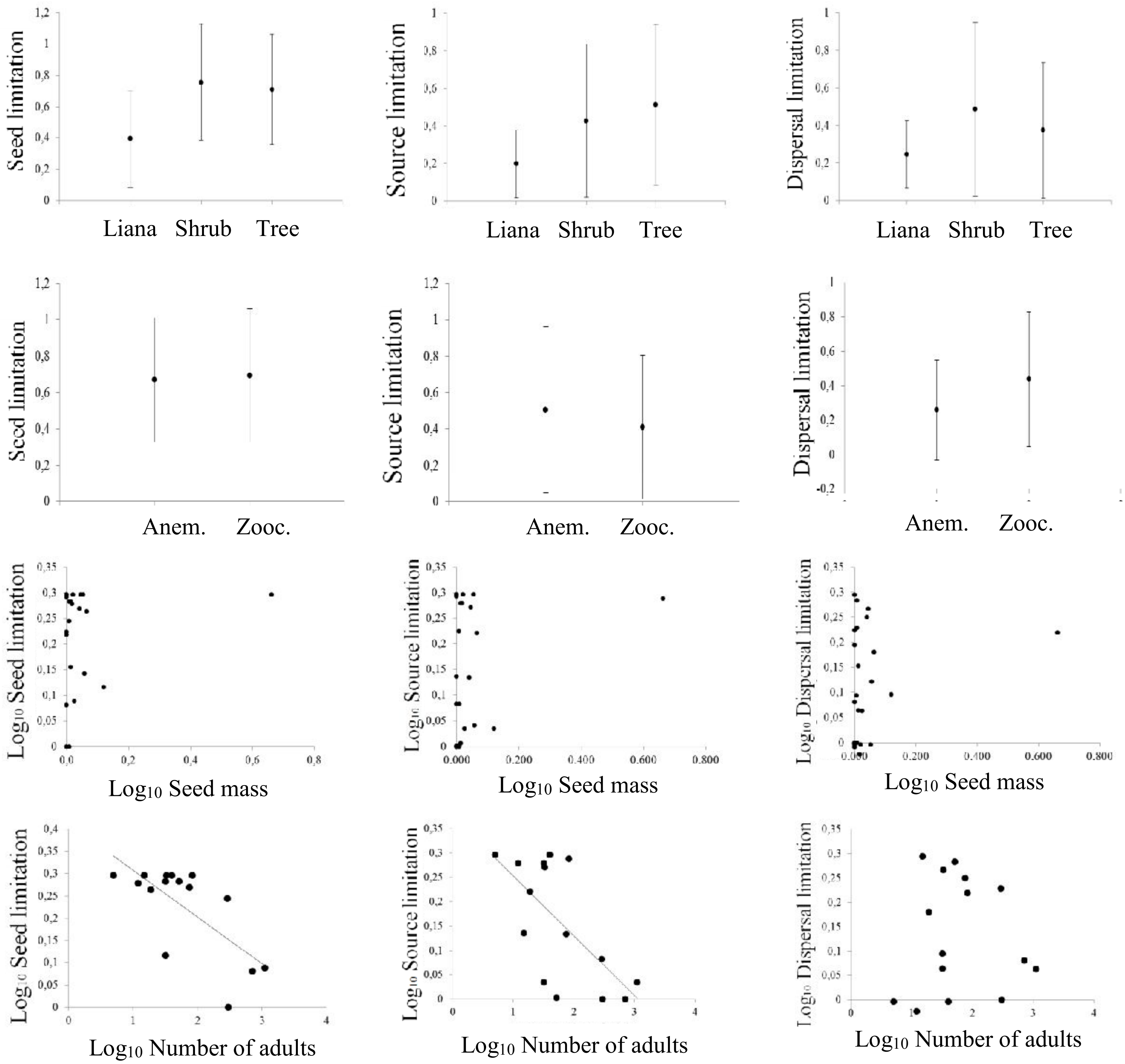

Fig. 3. Seed, source and dispersal limitation according to life form (mean ± SD), dispersal syndromes (mean ± SD), seed mass and number of adults, based on annual seed rain sampled in 49 seed traps in a Cerrado in southeast Brazil.

SUPPORTING INFORMATION

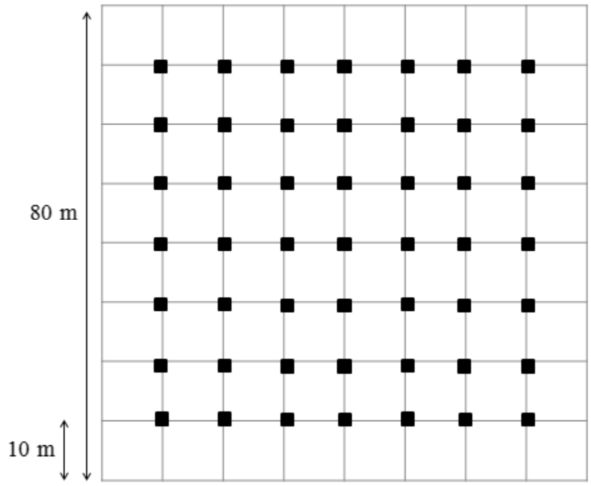

Fig S1. Spatial distribution of seed traps inside the 0.64 ha plot which woody species were sampled. Seed traps are represented by black squares.

Table S1. Species sampled in the 6,400 m² plot of cerrado *sensu stricto* and the number of individuals, dispersal syndrome and life form (N=72). Species are arranged by decreasing order of abundance in the plot.

Species	Number of individuals	Dispersal syndrome	Life form
Xylopia aromatica	1101	Zoochoric	Tree
Miconia albicans	705	Zoochoric	Tree
Miconia rubiginosa	298	Zoochoric	Tree
Myrcia guianensis	289	Zoochoric	Tree
Ocotea pulchella	177	Zoochoric	Tree
Aspidosperma tomentosum	135	Anemochoric	Tree
Eugenia punicifolia	94	Zoochoric	Shrub
Schefflera vinosa	92	Zoochoric	Tree
Campomanesia pubescens	87	Zoochoric	Shrub
Pouteria torta	81	Zoochoric	Tree
Pouteria ramiflora	50	Zoochoric	Tree
Siparuna guianensis	50	Zoochoric	Tree
Vochysia tucanorum	48	Anemochoric	Tree
Byrsonima coccolobifolia	43	Zoochoric	Shrub
Erythroxylum pelleterianum	42	Zoochoric	Shrub
Eriotheca gracilipes	39	Anemochoric	Tree
Anadenanthera peregrina falcata	38	Autochoric	Tree
Bowdichia virgilioides	36	Anemochoric	Tree

Pinus sp.	35	Anemochoric	Tree
Dalbergia miscolobium	32	Anemochoric	Tree
Stryphnodendron obovatum	32	Autochoric	Tree
Byrsonima verbascifolia	31	Zoochoric	Tree
Annona coriacea	30	Zoochoric	Tree
Diospyros hispida	27	Zoochoric	Tree
Tocoyena formosa	27	Zoochoric	Tree
Acosmium subelegans	26	Anemochoric	Tree
Styrax ferrugineus	22	Zoochoric	Tree
Ouratea spectabilis	18	Zoochoric	Tree
Myrcia bella	17	Zoochoric	Shrub
Blepharocalix salicifolius	14	Zoochoric	Tree
Miconia fallax	14	Zoochoric	Shrub
Qualea grandiflora	11	Anemochoric	Tree
Pera glabrata	11	Zoochoric	Tree
Bauhinia rufa	10	Autochoric	Tree
Alibertia edulis	9	Zoochoric	Shrub
Asteraceae sp1	8	Anemochoric	Shrub
Asteraceae sp3	6	Anemochoric	Shrub
Piptocarpha rotundifolia	5	Anemochoric	Tree
Qualea multiflora	5	Anemochoric	Tree
Morphospecies 4	5	-	Shrub
Kielmeyera coriacea	4	Anemochoric	Tree

Machaerium acutifolium	4	Anemochoric	Tree
Erythroxylum suberosum	4	Zoochoric	Tree
Guapira noxia	4	Zoochoric	Tree
Myrsine umbellata	4	Zoochoric	Shrub
Protium heptaphyllum	4	Zoochoric	Tree
Morphoespecies 1	4	-	Tree
Morphoespecies 6	4	-	
Duguetia furfuracea	3	Zoochoric	Tree
Morphoespecies 2	3	-	Tree
Handroanthus ochraceus	2	Anemochoric	Tree
Jacaranda caroba	2	Anemochoric	Tree
Tibouchina stenocarpa	2	Anemochoric	Tree
Aegiphila verticillata	2	Zoochoric	Tree
Brosimium gaudichaudii	2	Zoochoric	Tree
Copaifera langsdorfii	2	Zoochoric	Tree
Cordiera elliptica	2	Zoochoric	Shrub
Coussarea hydrangeifolia	2	Zoochoric	Shrub
Hancornia speciosa	2	Zoochoric	Tree
Melastomataceae sp1	2	Zoochoric	Shrub
Strychnos bicolor	2	Zoochoric	Shrub
Asteraceae sp2	1	Anemochoric	Shrub
Asteraceae sp4	1	Anemochoric	Shrub
Vochysia cinnamomea	1	Anemochoric	Tree

Amaioua guianensis	1	Zoochoric	Tree
Ocotea corymbosa	1	Zoochoric	Tree
Palicourea marcgravii	1	Zoochoric	Shrub
Palicourea rigida	1	Zoochoric	Tree
Strychnos pseudoquina	1	Zoochoric	Tree
Syagrus romanzoffiana	1	Zoochoric	Palm
Trichilia pallida	1	Zoochoric	Tree
Virola sebifera	1	Zoochoric	Tree
Morphospecies 5	1	-	Tree

6 CONSIDERAÇÕES FINAIS

O presente estudo indica a importância da limitação de sementes e da limitação no estabelecimento para o recrutamento de plantas do cerrado, assim como da produção e dispersão de sementes. A avaliação da chuva de sementes, juntamente com os experimentos de adição, mostraram-se métodos eficientes na avaliação dessas limitações. Apesar da relação desses processos com a composição e diversidade espécies, ainda há uma grande demanda de estudos, especialmente em savanas. O cerrado é a savana tropical mais rica do mundo e, portanto, trabalhos que avaliem as restrições no recrutamento de plantas desse bioma são relevantes para a conservação da biodiversidade e podem guiar ações e políticas de manejo das espécies estudadas.