

UNIVERSIDADE FEDERAL DE SÃO CARLOS

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

Programa de Pós-Graduação em Ecologia e Recursos Naturais

**Sincronia e Índice de Divergência de Diversidade de
Espécies Anemocóricas.**

KLÉCIA GILI MASSI

São Carlos – SP
2006

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Resumo

O Domínio do Cerrado é a segunda maior região fitogeográfica brasileira, originalmente cobrindo 23% do território brasileiro, sob influência de clima estacional. O cerrado apresenta variação florística e fisionômica, indo desde uma fisionomia campestre até uma florestal. Espécies anemocóricas são proporcionalmente mais importantes no cerrado do que em florestas tropicais, especialmente em fisionomias mais abertas. As características morfológicas dos diásporos anemocóricos parecem diminuir suas razões de descida, aumentando a chance de exposição aos ventos e de encontrar locais seguros para germinar. Espécies anemocóricas tendem a frutificar na melhor época para dispersar suas sementes. Também a altura de liberação e a vegetação circundante são fundamentais para a dispersão à longas distâncias. Selecionamos as espécies anemocóricas de três levantamentos fitossociológicos, um realizado em área nuclear, dois em área disjunta, e as classificamos em autogiro, autogiro-rotativas, flutuantes e planadoras, de acordo com a morfologia e comportamento do diásporo no ar parado. Tínhamos o período de frutificação para cada espécie anemocórica de uma área disjunta e tentamos observar a existência de estacionalidade na frutificação e a relação desta com algumas variáveis climáticas. O número de espécies frutificando foi maior na estação seca, coincidindo com o período de menores pluviosidade e umidade relativa do ar. Depois, estudamos os espectros de diásporos anemocóricos e os índices de divergência de diversidade (IDD) de espécies a tipos de diásporo anemocórico de três fisionomias do cerrado (*campo cerrado*, *cerrado sensu stricto* e *cerradão*) em uma área disjunta; e de três fisionomia de cerrado (*cerrado sensu stricto*) em províncias florísticas diferentes. Além de haver uma unidade florística na área disjunta, com a fisionomia ecotonal contendo elementos campestres e florestais, as áreas nuclear e disjuntas foram ecologicamente

semelhantes quanto à distribuição de espécies anemocóricas. No entanto, o tamanho das populações diferiu entre as três fisionomias e entre as três áreas, e levou a diferenças significativas quando as abundâncias das espécies foram consideradas. Em locais mais densos, a vegetação reduz a velocidade do vento no estrato inferior, restringindo a dispersão das espécies herbáceas, enquanto espécies anemocóricas de sementes mais pesadas, requerem o lançamento a partir de árvores ou lianas.

Palavras-chave: anemocoria, cerrado, dispersão pelo vento, divergência de diversidade intrínseca, fenologia, fisionomias, savana.

Abstract

The Cerrado Domain is the second largest Brazilian phytogeographic province, occupying originally 23% of Brazil's land surface, under seasonal climate. The cerrado presents a floristic and physiognomic variation, ranging from grassland to tall woodland. Anemochorous species are proportionally more important in the cerrado than in Brazilian rain forests, especially in open physiognomies. Morphological designs of wind-dispersed diaspores appear to slow their rates of descent, increasing their chances of exposure to winds and of reaching safe sites to germinate. Wind-dispersed species are constrained to fruit during the best time for seed dispersal. Also, the height of seed release and surrounding vegetation are fundamental to long-distance dispersal. We selected the wind-dispersed species from three phytosociological surveys (disjoint and core sites) and classified them into autogyro, rolling-autogyro, floater, or undulator, according to the diaspore morphology and aerodynamic behavior in still air. For each species, we had data on its fruiting period. We tried to assess whether there was a seasonality and, if there was, whether it was synchronized with some climatic conditions. The number of fruiting anemochorous cerrado species was highest at the dry season, coinciding with reduced precipitation. Next, we studied the anemochorous diaspore spectra and index of divergence from species to anemochorous diaspore diversity (IDD) in three cerrado physiognomies (*campo cerrado*, *cerrado sensu stricto*, and *cerradão*) in a disjoint site and three cerrado physiognomies (*cerrado sensu stricto*) in different floristic provinces. There was a floristic unit among the cerrado physiognomies, with the ecotonal ones containing both grassland and woodland elements. Both nuclear and disjoint sites were ecologically similar regarding the species distribution. However, there were differences when species abundances were considered. In denser sites, vegetation reduces wind velocity in

lower strata, constraining dispersal of herbaceous species and heavy-seeded, wind-dispersed species require launching from a tree or high climber.

Key-words: anemochory, cerrado, intrinsic diversity divergence, phenology, physiognomies, savanna, wind dispersal.

I. Introdução geral

Introdução Geral

A dispersão de sementes geralmente está relacionada a melhores condições para sua liberação e para o estabelecimento das plântulas e talvez por isso a maioria das espécies anemo ou autocóricas, com frutos secos e deiscentes, frutifique durante a estação seca (Morellato & Leitao-Filho 1996). A dispersão é um processo ecológico multifásico (Fuentes 2000) que não só determina a área potencial do recrutamento das novas gerações de plantas como também exerce influência em processos subseqüentes, tais como predação, competição e reprodução (Nathan & Muller-Landau 2000).

A dispersão é considerada como a partida de um diásporo (fruto ou semente) da planta matriz (Howe & Smallwood 1982), variando espaço-temporalmente (Solbrig 1980). No espaço, envolve o transporte dos diásporos por agentes físicos, como o vento ou a água, ou por agentes biológicos, os animais; no tempo, refere-se ao fato de que a semente pode assumir uma condição de dormência ou germinar, assim que for enterrada (Solbrig 1980). As características dos propágulos constituem síndromes de dispersão (Pijl 1969), que podem ser classificadas de acordo com o agente dispersor: saurocoria (dispersão por répteis), ornitocoria (aves), mamalocoria (mamíferos), mirmecocoria (formigas), anemocoria (vento), hidrocoria (água) e autocoria (mecanismos explosivos ou gravidade). A anemocoria conta com estruturas plumadas, aladas e pulverulentas (Harper 1977).

Na vegetação tropical, a anemocoria é, de forma geral, menos freqüente que os vetores bióticos (Pijl 1969). Nesta região, a dispersão pelo vento está associada aos ambientes mais secos (Frankie et al. 1974) e às áreas mais abertas (Howe & Smallwood 1982). Em florestas tropicais, no mínimo 50% e freqüentemente 75% ou mais das espécies arbóreas possuem frutos carnosos adaptados ao consumo e à dispersão por aves e por mamíferos, enquanto que,

nas savanas, essa proporção diminui, aumentando a anemocoria conseqüentemente (Howe & Smallwood 1982). Assim, em florestas tropicais, os principais vetores de sementes são os vertebrados frugívoros (Janzen 1967), sendo as espécies anemocóricas proporcionalmente mais importantes em habitats mais secos, como o cerrado (Oliveira & Moreira 1992) e as matas secas (McKey 1975).

O cerrado apresenta grande variação fisionômica, indo de uma fisionomia campestre (campo limpo) a uma florestal (cerradão), passando por fisionomias savânicas (campo sujo, campo cerrado e cerrado *sensu stricto*) (Coutinho 1978). No cerrado, há dois componentes, o arbustivo-arbóreo e o herbáceo-subarbustivo (Rizzini 1979), cujas importâncias variam de modo inverso. Enquanto que a importância do componente arbustivo-arbóreo aumenta do campo limpo ao cerradão, a do componente herbáceo-subarbustivo diminui (Coutinho 1978). A maioria dos estudos realizados em comunidades de cerrado não subdividiram a síndrome anemocórica (Mantovani & Martins 1988, Miranda 1995, Batalha et al. 1997, Batalha & Mantovani 2000, Bulhão & Figueiredo 2002, Vieira et al. 2002, Batalha & Martins 2004). O entendimento das relações específicas planta-agente dispersor (o vento na anemocoria) são fundamentais para se manter a dinâmica, a estrutura e a diversidade das comunidades tropicais (Figliolia & Kageyama, 1995).

Apresentamos a dissertação em capítulos, formatando-os de acordo com as normas das revistas científicas a que foram submetidos. O capítulo 1 foi formatado segundo as normas da revista 'Revista Brasileira de Botânica'. O capítulo 2 foi formatado segundo as normas da revista 'Biotropica'. Os capítulos foram redigidos na língua inglesa. O primeiro artigo já foi submetido à revista e estamos aguardando o parecer dos assessores. Como os capítulos são independentes, repetições tornaram-se inevitáveis.

No primeiro capítulo, procuramos observar a existência de estacionalidade na frutificação das espécies anemocóricas de uma área de cerrado localizada na Reserva Pé-de-Gigante

(Figura 1), Santa Rita do Passa Quatro, SP. Já no segundo capítulo procuramos comparar, a partir de um índice de divergência diferentes fisionomias de cerrado (campo cerrado, cerrado *sensu stricto* e cerradão) dentro da Reserva Pé-de-Gigante, e três áreas de cerrado *sensu stricto* situadas em províncias fitogeográficas distintas (Ratter et al. 2003), uma na região central (Figura 2) e duas na região sudeste do Brasil: Santa Rita do Passa Quatro, SP e Itirapina, SP (Figura 3).



Figura 1. Foto aérea da Gleba Cerrado Pé-de-Gigante, Santa Rita do Passa Quatro, SP (21°36-44'S, 47°34-41'W).

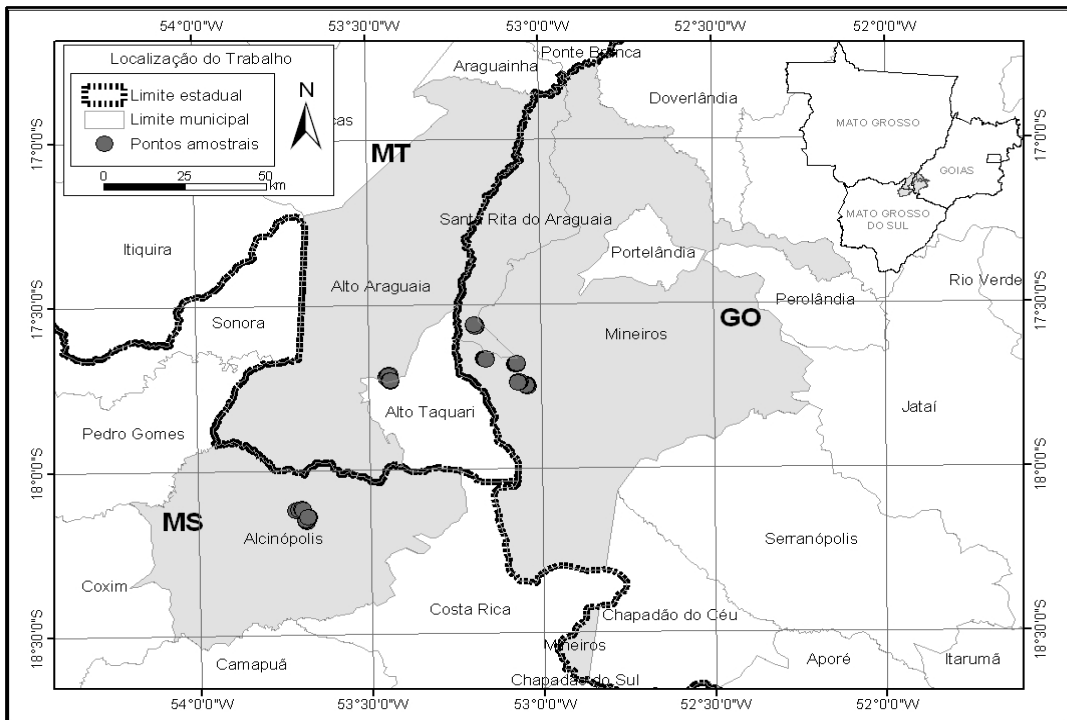


Figura 2. Localização das áreas amostradas, abrangendo os estados de GO, MT e MS.



Figura 3. Imagem de satélite da Estação Ecológica e Experimental de Itirapina ($22^{\circ}13'S$ e $47^{\circ}51'W$), São Paulo (Fonte: Embrapa).

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II. Capítulo 1

Sincronia na frutificação de espécies anemocóricas em uma área de cerrado (Santa Rita do Passa Quatro, São Paulo)¹

¹ Trabalho submetido ao periódico Revista Brasileira de Botânica com o título “Fruiting Synchrony of Anemochorous Species in a Disjoint Cerrado Site (Santa Rita do Passa Quatro, Southeastern Brazil)”.

Fruiting Synchrony of Anemochorous Species in a Disjoint Cerrado Site (Santa Rita do Passa Quatro, Southeastern Brazil)

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Running title: Fruiting synchrony of anemochorous species

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ABSTRACT – (Fruiting synchrony of anemochorous species in a disjoint cerrado site (Santa Rita do Passa Quatro, southeastern Brazil)). Plant species share reproductive characteristics that facilitate the process of dispersal by some vectors, which may be called ‘syndromes’, including dispersal by wind, or anemochory. In anemochory, there are dust, plumed, and winged dispersal units. From data collected in a disjoint cerrado reserve, we selected anemochorous species and classified them as autogyro, rolling-autogyro, floater or undulator species. For each species, we had data on its fruiting period. We tried to assess whether there was a fruiting peak and, if there was, whether it was synchronized with some climatic conditions. The number of fruiting anemochorous species was not uniformly distributed throughout the year and peaked in dry season, negatively related with air relative humidity and rainfall. The number of fruiting anemochorous cerrado species was highest at the dry season, coinciding with deciduousness of trees and shrubs, diminished air humidity during the day, reduced precipitation, and a higher permanent wind intensity. At the dry season, wind-dispersed fruits dehydrate and many species shed leaves, favoring diaspores dispersal. Floater and autogyro species were more frequent in the herbaceous component; and undulator species were more frequent in the woody component. Plumed and winged diaspores should prevail in open and closed physiognomies, respectively.

Key words – anemochory, cerrado, phenology, savanna, synchronization.

RESUMO – (Sincronia de frutificação de espécies anemocóricas em uma área disjunta de cerrado (Santa Rita do Passa Quatro, SP)). Espécies vegetais compartilham características reprodutivas que facilitam o processo de dispersão por alguns vetores, que podem ser chamadas de síndromes, incluindo a dispersão pelo vento, ou anemocoria. Na anemocoria, há unidades de dispersão aladas, plumadas e pulverulentas. A partir de dados coletados em uma

área disjunta de cerrado, selecionamos as espécies anemocóricas e as classificamos em autogiro, autogiro-rotativas, flutuantes e planadoras. Para cada espécie, tínhamos dados sobre seu período de frutificação. Procuramos testar se havia um pico na frutificação e, se houvesse, se ele era sincrônico com algumas condições climáticas. A frutificação das espécies anemocóricas não foi distribuída uniformemente ao longo do ano, tendo seu pico durante a estação seca e relacionando-se negativamente com a umidade relativa do ar e precipitação. O número de espécies anemocóricas com frutos foi maior na estação seca, coincidindo com a deciduidade de árvores e arbustos, menor umidade relativa do ar durante o dia, precipitação reduzida e ventos mais intensos. Na estação seca, frutos dispersos pelo vento desidratam e muitas espécies trocam suas folhas, favorecendo a dispersão dos diásporos. Espécies de diásporos autogiro e flutuantes foram mais freqüentes no componente herbáceo-subarbustivo. Espécies de diásporos planadores foram mais freqüentes no componente arbustivo-arbóreo. Diásporos plumados e alados devem prevalecer em fisionomias abertas e fechadas, respectivamente.

Palavras-chave: anemocoria, cerrado, fenologia, savana, sincronia.

Introduction

Plant species share reproductive characteristics that facilitate the process of dispersal by some vectors, which may be called ‘syndromes’ (Dalling 2002), including dispersal by wind, or anemochory (Pijl 1969). Morphological designs of wind-dispersed diaspores appear to slow their rates of descent, increasing their chances of exposure to winds and of reaching safe sites (Augsburger 1986). In anemochory, there are dust, plumed, and winged dispersal units (Harper 1977). Dust seeds, usually so small that movement in air is dominated by viscous forces, and plumed diaspores, which depend on structure such as the plumes on the seed or fruit coat, float downward in a vertical line (Harper 1977). Winged diaspores may have the seed mass concentrated in a central area (Pijl 1969) and glide and undulate (Augsburger 1986). When the seed mass is not concentrated in a central area, the seed may rotate around its end (autogyro), rotate on two axes simultaneously (rolling-autogyro), or spin tightly around a vertical line (helicopter) (Augsburger 1986).

The Cerrado Domain is the second largest Brazilian phytogeographic province, occupying originally 23% of Brazil’s land surface, especially in the Central Plateau, under seasonal climate, with wet summer and dry winter (Ratter *et al.* 1997). The cerrado flora has two components, a woody one and an herbaceous one, which are distinct and antagonistic (Coutinho 1990). The cerrado species present periodic variations in flower and fruit production that may represent adaptations to biotic and abiotic factors, like those of other savannas (Schaik *et al.* 1993). Anemochorous species are proportionally more important in the cerrado than in Brazilian rain forests, especially in open physiognomies (Oliveira & Moreira 1992).

Climatic conditions determine the time of fruit ripening, and wind-dispersed species are constrained to fruit during the best time for seed dispersal (Morellato & Leitão-Filho 1996;

Marques *et al.* 2004). This synchronization is a very effective means of increasing wind dispersal potential (Tackenberg *et al.* 2003). If the climate of the cerrado is seasonal and anemochorous cerrado species fruit mainly in the dry season (Mantovani & Martins 1988, Oliveira & Moreira 1992, Miranda 1995, Batalha *et al.* 1997, Batalha & Mantovani 2000, Batalha & Martins 2004), then they would have the whole rainy season to develop their roots before the next dry season (Morellato *et al.* 1989).

Regarding anemochorous species, even if, by definition, all diaspores are dispersed by wind, fruiting peak and synchronization with climatic variables of each subtype may be different. For instance, in a core cerrado area, on the one hand, different species with floater and helicopter diaspores presented similar patterns, with short fruiting periods at the dry season; on the other hand, species with undulator seeds presented longer fruiting periods, and the autogyro and rolling-autogyro species presented distinct fruiting periods for each species (Oliveira & Moreira 1992).

Batalha & Mantovani (2000) analyzed the fruiting patterns of anemochorous species in a disjoint cerrado site, in southeastern Brazil, but did not tested for differences among the types. So, given the existence of different types of wind-dispersed diaspores (autogyro, rolling-autogyro, floater, helicopter, and undulator) and the possibility of different fruiting patterns among them, we aimed to answer the following questions: when is the fruiting peak of anemochorous species in a disjoint cerrado site? Is this peaking period synchronized with some climatic conditions? Do the different types of wind-dispersed diaspores present similar fruiting patterns?

Material and Methods

This study was carried out in the Pé-de-Gigante (Giant's foot) Reserve, Santa Rita do

Passa Quatro, São Paulo State, southeastern Brazil, 21°36-39'S and 47°36-38'W, under Köppen's Cwag' climate, at 660 to 730 m high a.s.l., on Red-Yellow Latosol, with 1,269 ha, covered mainly by cerrado (Pivello *et al.* 1998, in which a more detailed characterization of the study area can be found). The climatic diagram (Fig. 1) shows that the dry period of the year lies from June to August, and the wet one from September to May (Batalha & Mantovani 2000). Mean annual rainfall and mean monthly temperature are, respectively, 1499 mm and 21.5°C.

Batalha & Mantovani (2000) collected the vegetation data used here, from September 1995 to February 1997, when they observed, among other things, whether each species was fruiting in a given month. We filtered their matrix and selected cerrado anemochorous species, classifying each one of them according to aerodynamic group into autogyro, rolling-autogyro, floater, helicopter, or undulator (Augsburger 1986). We consulted taxonomic descriptions of the species and observed the fruits in lodged vouchers at the University of São Paulo herbarium. We classified the species as belonging to either the woody component (phanerophytes, *sensu* Raunkiaer 1934) and or the herbaceous component (non-phanerophytes, *sensu* Raunkiaer 1934).

We applied circular statistics to our data and used Rayleigh test (Zar 1999) to check whether the anemochorous species fruited uniformly throughout the year. January corresponded to 0°; February, to 30°; March, to 60°; and so on. First, we applied Rayleigh test to all anemochorous species together and, then, to each aerodynamic group separately. To check whether the numbers of autogyro, rolling-autogyro, floater, helicopter, and undulator species were significantly different to an even distribution in each component, we applied the chi-square test (Zar 1999). To test the relationships of fruiting and climatic variables (mean air temperature, air relative humidity, and rainfall), we used simple linear regressions (Zar 1999).

Results

Of the 123 anemochorous species, we considered 36 as belonging to the woody component and 87 as belonging to the herbaceous component (Table 1). We did not find 37 out of the 123 species (30%) producing fruits. The number of fruiting anemochorous species was not uniformly distributed throughout the year ($z = 5.54$, $0.005 > P > 0.002$, Fig. 2). The mean angle for the fruiting anemochorous species was 230° , which corresponded to the end to August. The number of fruiting anemochorous species was negatively related with air relative humidity ($R^2 = 0.67$, $F = 19.96$, $P = 0.002$, Table 2) and with rainfall ($R^2 = 0.58$, $F = 13.75$, $P = 0.004$, Table 2), but not with temperature ($R^2 = 0.32$, $F = 4.79$, $P = 0.052$, Table 2).

Regarding the aerodynamic groups, 60 species were floater ones (48.8%); 26, rolling-autogyro (21.1%); 26, autogyro (21.1%); and 11, undulator (9.0%). None of them was helicopter-diaspore species. Considering the four aerodynamic groups found, these proportions were significantly different to an even distribution ($\chi^2 = 41.98$, $P < 0.001$). The distribution of aerodynamical groups was significantly different to an even distribution in the herbaceous component ($\chi^2 = 67.34$, $P < 0.001$), but not in the woody one ($\chi^2 = 3.33$, $P = 0.34$). On the one hand, the proportion of rolling-autogyro species was similar in both components; on the other hand, the proportions of autogyro and floater-diaspore species were higher in the herbaceous component and of undulator-diaspore species was higher in the woody component (Table 3).

The numbers of fruiting species with autogyro, rolling-autogyro, and undulator diaspores were uniformly distributed throughout the year (Fig. 3a, b and d, respectively). The only group with seasonal fruiting was those of the floater-diaspore species ($z = 6.13$, $0.005 > P > 0.002$, Fig. 3c), with mean angle at 258° , which corresponded to the end to September. The

number of fruiting floater-diaspore species was negatively related with temperature ($R^2 = 0.55$, $F = 12.04$, $P = 0.006$, Table 2), with rainfall ($R^2 = 0.80$, $F = 39.69$, $P < 0.001$, Table 2) and with air relative humidity ($R^2 = 0.53$, $F = 11.07$, $P = 0.008$, Table 2).

Discussion

Fruiting of anemochorous species in the community we studied was not uniformly distributed throughout the year, reflecting the seasonality of the cerrado climate (Monasterio & Sarmiento 1976). In cerrado sites, wind-dispersed species tend to fruit mainly in the dry season, when the dispersal of their diaspores is more efficient (Mantovani & Martins 1988, Miranda 1995, Batalha *et al.* 1997, Batalha & Martins 2004). In other tropical vegetation types, such as Brazilian dry forest (Griz & Machado 2001) and central American rain forest (Smythe 1970), wind-dispersed seeds fall chiefly throughout the dry season and the time of highest winds.

Despite this seasonality in fruiting of anemochorous species, a high proportion of them did not fruit in the sampling period. Individuals of many tropical trees may skip fruiting in some years, what may be compensated by efficient vegetative propagation (Gottsberger & Silberbauer-Gottsberger 1983). On the contrary, some species fruited for long periods, more than six months, as for example, *Banisteriopsis campestris*, *Machaerium acutifolium*, and *Qualea parviflora*. Ripening time for some of these species may be extended, reflecting the seasonal unpredictability or scarcity of resources needed for fruit development (Rathcke & Lacey 1985). The time of fruit ripening should reflect timing of conditions that influence dispersal success (Gottsberger & Silberbauer-Gottsberger 1983). Due to the exposure of diaspore to different conditions, dry fruits remaining on the trees could be beneficial for seed dispersal (Devineau 1999). For instance, longer release period for *Pinus* diaspores exposes

them to much greater variation in horizontal and vertical wind speeds (Greene & Johnson 1989).

The higher proportion of floater-diaspore species we found was different to other studies: in central Brazilian riparian forests, most species were autogyro (Pinheiro & Ribeiro 2001) and, in a core cerrado site, most species were autogyro and rolling-autogyro (Oliveira & Moreira 1992). In a more closed cerrado physiognomy, anemochorous species presented a higher proportion of winged (18%) than plumed (7%) dispersal units (Gottsberger & Silberbauer-Gottsberger 1983), whereas the opposite was found for us. We found a higher proportion of undulator dispersal units among woody species and of floater and autogyro dispersal units among herbaceous species, suggesting different ecological strategies between the two cerrado components. Indeed, woodiness is positively correlated with winged dispersal units, whereas, among herbs, plumed dispersal units are more common (Gottsberger & Silberbauer-Gottsberger 1983). We may, then, postulate that plumed and winged diaspores should prevail in open and closed physiognomies, respectively.

A seed is released at a height where there is sufficient wind speed to transport (Soons *et al.* 2004). Autogyro and rolling-autogyro species have structures that do not allow long-distance flights and, even if wind is strong, height of release is more important; floater diaspores, on the contrary, have high capacity of being transported, even in still air (Hensen & Muller 1997). Most helicopter-diaspore species are not tall, and the wind that blows in lower strata is weaker (Soons *et al.* 2004). Seeds that are released from lower heights are generally dispersed over shorter distances: first, they experience lower wind velocities; second, they fall over a shorter distance and hence have a shorter flight time; and third, they experience less organized wind turbulence and hence the probability of uplifting is lower (Soons *et al.* 2004). In short cerrado species, dispersal by wind may be dependent on casual events, such as occasional whirlwinds or burnings that clear the vegetation and allow dispersal over longer distances

(Coutinho 1978).

The only aerodynamic group with seasonal fruiting was the floater-diaspore species, maybe due to phylogenetic constraints. The other groups presented longer fruiting periods, well distributed throughout the year. Floater and undulator species should concentrate their fruiting periods at the dry season due to the hydrophobic behavior of hyaline wings and plumes (Hensen & Muller 1997).

There is a negative influence of humidity in anemochory, which requires auxiliary mechanisms to expose seeds at the right time (Pijl 1969) and find the most favorable period to ripening (Bawa & Hadley 1990). We found significant relationships between fruiting anemochorous species and air relative humidity and rainfall. Anemochory seems to be favoured by specific environmental conditions, such as greater wind circulation and less rainfall (Griz & Machado 2001). The number of fruiting anemochorous cerrado species is highest at early dry season, coinciding with deciduousness of trees and shrubs, diminished air humidity during the day, reduced precipitation, and a higher permanent wind intensity (Gottsberger & Silberbauer-Gottsberger 1983). At the dry season, wind-dispersed fruits dehydrate and many species shed leaves, favoring diaspores dispersal (Mantovani & Martins 1988). Additional studies on wind dispersal among cerrado species may include source density (Mc Euen & Curran 2004), height of seed release, terminal velocity, turbulence, wind speed (Harper 1977), convective updrafts, surrounding vegetation, uplifting of seeds (Soons *et al.* 2004), and the diaspore morphological structure (Hensen & Muller 1997).

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Table 1. Anemochorous species in the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, SP (21° 36-39`S, 47° 36-38`W). H = herbaceous, W = woody; A = autogyro, RA = rolling autogyro, F = floater, U = undulator.

Family/ species	component	aerodynamic group
Apocynaceae		
<i>Aspidosperma tomentosum</i> Mart.	W	U
<i>Forsteronia glabrescens</i> M. Arg.	H	F
<i>Himatanthus obovatus</i> (M. Arg.) Woods.	W	U
<i>Mandevilla vellutina</i> (Mart.) Woods.	H	U
<i>Odontadenia lutea</i> (Vell.) Markgr.	H	F
<i>Rhodocalyx rotundifolius</i> M. Arg.	H	U
<i>Temnadenia violacea</i> (Vell.) Miers	H	F
Aristolochiaceae		
<i>Aristolochia gilberti</i> Hook.	H	RA
Asclepidaceae		
<i>Astephanus carassensis</i> Malme	H	F
<i>Blepharodon nitidum</i> (Vell.) J. Macbr.	H	F
<i>Ditassa acerosa</i> Mart.	H	U
<i>D. nitida</i> E. Fourn	H	U
<i>Oxypetalum appendiculatum</i> Mart. & Zucc.	H	F
Asteraceae		
<i>Baccharis dracunculifolia</i> A. DC.	H	F
<i>B. humilis</i> Sch. Bip.	H	F
<i>B. rufescens</i> Spreng.	H	F
<i>Chaptalia integerrima</i> (Vell.) Burk	H	F
<i>Conyza canadensis</i> (Less.) Cronquist	H	F
<i>Dasyphyllum sprengelianum</i> (Gardner) Cabrera	H	F
<i>Elephantopus biflora</i> Less.	H	F
<i>E. mollis</i> Less.	H	F
<i>Emilia coccinea</i> (Simns) Sw.	H	F
<i>Eremanthus sphaerocephalus</i> Baker	W	F
<i>Eupatorium chlorolepsis</i> Baker	H	F
<i>E. maximiliani</i> Sch.	H	F
<i>E. squalidum</i> A. DC.	H	F
<i>Gochnatia barrosii</i> Cabrera	H	F
<i>G. pulchra</i> Cabrera	H	F
<i>Kanimia oblongifolia</i> Baker	H	F
<i>Mikania cordifolia</i> (Less.) Willd.	H	F
<i>Orthopappus angustifolius</i> (Sw.) Gleason	H	F
<i>Piptocarpha rotundifolia</i> (Less.) Baker	W	F
<i>Porophyllum angustissimum</i> Gardner	H	F
<i>P. ruderale</i> (Jacq.) Cass.	H	F
<i>Pterocaulon rugosum</i> (Vahl) Malme	H	F
<i>Trichogonia salviifolia</i> Gardner	H	F
<i>Vanillosmopsis erythropappa</i> (A. DC.) Sch. Bip.	W	F
<i>Vernonia apiculata</i> Mart.	H	F

(cont.)

<i>V. bardanoides</i> Less.	H	F
<i>V. cephalotes</i> A. DC.	H	F
<i>V. ferruginea</i> Less.	H	F
<i>V. herbacea</i> (Vell.) Rusby	H	F
<i>V. holosericea</i> Mart.	H	F
<i>V. lappoides</i> Baker	H	F
<i>V. obtusata</i> Less.	H	F
<i>V. onopordioides</i> Baker	H	F
<i>V. polyanthes</i> (Spr.) Less.	H	F
<i>V. rubriramea</i> Mart.	H	F
<i>V. scabra</i> Pers.	H	F
Bignoniaceae		
<i>Anemopaegma arvense</i> (Vell.) Stellfeld	H	U
<i>A. chamberlaynii</i> (Simms) Bur. & K. Schum.	H	U
<i>Arrabidaea brachypoda</i> (A. DC.) Bur.	H	RA
<i>A. craterophora</i> (A. DC.) Bur.	H	RA
<i>A. florida</i> A. DC.	H	RA
<i>Cremastus pulcher</i> (Cham.) Bur.	H	RA
<i>Cybistax antisiphilitica</i> (Mart.) Mart.	W	U
<i>Distictella mansoana</i> (A. DC.) Urban	H	RA
<i>Jacaranda caroba</i> (Vell.) A. DC.	W	RA
<i>J. decurrens</i> Cham.	H	RA
<i>J. rufa</i> Silva Manso	H	RA
<i>Memora peregrine</i> (Miers.) Sandwith.	H	RA
<i>Pyrostegia venusta</i> (Ker) Bur.	H	RA
<i>Tabebuia aurea</i> (Silva Manso) S. Moore	W	RA
<i>T. ochracea</i> (Cham.) Standl.	W	RA
<i>Zeyhera montana</i> Mart.	W	U
Celastraceae		
<i>Austroplenckia populnea</i> Reissek	W	RA
Clusiaceae		
<i>Kielmeyera coriacea</i> Mart.	W	RA
<i>K. rubriflora</i> Cambess.	W	RA
<i>K. variabilis</i> Mart.	W	RA
Cochlospermaceae		
<i>Cochlospermum regium</i> (Mart.) Pilg.	H	F
Fabaceae		
<i>Acosmium dasycarpum</i> (Vog.) Yakovlev	W	RA
<i>A. subelegans</i> (Mohl) Yakovlev	W	RA
<i>Bowdichia virgilioides</i> H. B. K.	W	RA
<i>Dyptichandra aurantiaca</i> (Mart.) Tul.	W	U
<i>Machaerium acutifolium</i> Vogel	W	A
<i>Mimosa gracilis</i> Benth.	H	RA
<i>M. xanthocentra</i> Mart.	H	RA
<i>Plathymentia reticulata</i> Benth.	W	U
<i>Platypodium elegans</i> Vogel	W	A
<i>Pterodon pubescens</i> Benth.	W	RA
<i>Sclerolobium paniculatum</i> Vogel	W	RA

(cont.)		
<i>Vatairea macrocarpa</i> (Benth.)Ducke	W	A
Malpighiaceae		
<i>Banisteriopsis argyrophylla</i> (A. Juss.) B. Gates	H	A
<i>B. campestris</i> (A. Juss.) Little	H	A
<i>B. laevifolia</i> (A. Juss.) B. Gates	H	A
<i>B. pubipetala</i> (A. Juss.) Cuatrec	H	A
<i>B. stellaris</i> (Griseb) B. Gates	H	A
<i>B. variabilis</i> B. Gates	H	A
<i>Heteropteris byrsonimifolia</i> A. Juss.	W	A
<i>H. umbellata</i> A. Juss.	H	A
<i>Mascagnia cordifolia</i> (A. Juss.) Griseb	H	A
<i>Peixotoa tomentosa</i> A. Juss.	H	A
Malvaceae		
<i>Eriotheca gracilipes</i> (K.Schum.) A. Robyns	W	F
<i>Pseudobombax longiflorum</i> (Mart. & Zucc.)	W	F
Melastomataceae		
<i>Leandra lacunosa</i> Cogn.	W	F
<i>Tibouchina stenocarpa</i> (A. DC.) Cogn	W	F
Orchidaceae		
<i>Galeandra montana</i> Barb. Rodr.	H	F
<i>Ionopsis paniculata</i> Lindl.	H	F
Poaceae		
<i>Aristida jubata</i> (Arechav.) Herter	H	F
<i>Digitaria insularis</i> (L.) Fedde	H	F
<i>Gymnopogon foliosus</i> (Willd.) Nees	H	F
<i>Melinis minutiflora</i> P. Beauv.	H	F
<i>Rhynchelitrum repens</i> (Nees) C. E. Hubb.	H	F
<i>Schyzachirium condensatum</i> (Kunth.) Nees	H	F
Polygalaceae		
<i>Securidaca tomentosa</i> A. St-Hil.	H	A
Polypodiaceae		
<i>Adiantum fructuosum</i> Spreng.	H	F
<i>Polypodium latipes</i> Langsd. & Fisch.	H	F
Proteaceae		
<i>Roupala montana</i> Aubl.	W	U
Rhamnaceae		
<i>Crumenaria polygaloides</i> Reissek	H	A
Sapindaceae		
<i>Magonia pubescens</i> St.-Hil.	W	RA
<i>Paullinia elegans</i> Cambess.	H	RA
<i>Serjania erecta</i> Radlk.	H	A
<i>S. lethalis</i> A. St-Hil	H	A
<i>S. reticulata</i> Cambess.	H	A
<i>Toulicia tomentosa</i> Radlk.	H	A
Schizaeaceae		
<i>Anemia ferruginea</i> Kunth	H	F
Scrophulariaceae		
<i>Buchnera lavandulacea</i> Cham. & Schldl.	H	F
Vochysiaceae		

<i>Qualea dichotoma</i> Warm.	W	A
<i>Q. grandiflora</i> Mart.	W	A
<i>Q. multiflora</i> Mart.	W	A
<i>Q. parviflora</i> Mart.	W	A
<i>Vochysia cinamommea</i> Pohl	W	A
<i>V. tucanorum</i> Mart.	W	A

Table 2. Number of fruiting cerrado species and climatic factors in the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo State, southeastern Brazil (21°36-39'S, 47°36-38'W). ^{ns} P > 0.05, ** P < 0.01.

syndrome	climatic factor	b	R²
Anemochorous species	temperature	-2.17	0.32 ^{ns}
	air relative humidity	-0.98	0.67 **
	rainfall	-0.06	0.58 **
Floater diaspore species	temperature	-2.14	0.55 **
	air relative humidity	-0.67	0.53 **
	rainfall	-0.05	0.80 **

Table 3. Number of anemochorous species in the herbaceous and woody components of the cerrado in the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo State, Southeastern Brazil (21°36-39'S, 47°36-38'W). (A = autogyro-diaspore species, RA = rolling-autogyro-diaspore species, F = floater-diaspore species and U = undulator-diaspore species).

component	A	RA	F	U
herbaceous	16	13	54	4
woody	10	13	6	7

Figure 1. Climatic diagram following Walter (1986), constructed from data obtained at DAEE C4-107 meteorological station, located at Santa Rita do Passa Quatro (21°43'09"S, 47°28'38"W).

Figure 2. Percentage of anemochorous fruiting species throughout the year at the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo State, southeastern Brazil (21°36-39'S, 47°36-38'W).

Figure 3. Percentage of autogyro (a), rolling-autogyro (b), floater (c), and undulator (d) diaspore species fruiting throughout the year in the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo State, Southeastern Brazil (21°36-39'S, 47°36-38'W).

Estação Meteorológica DAEE (C4-107)
 SANTA RITA DO PASSA QUATRO - SP
 (21°43'09"S, 47°28'22"W, alt. 749m)
 [10]

[21.5] [1499]

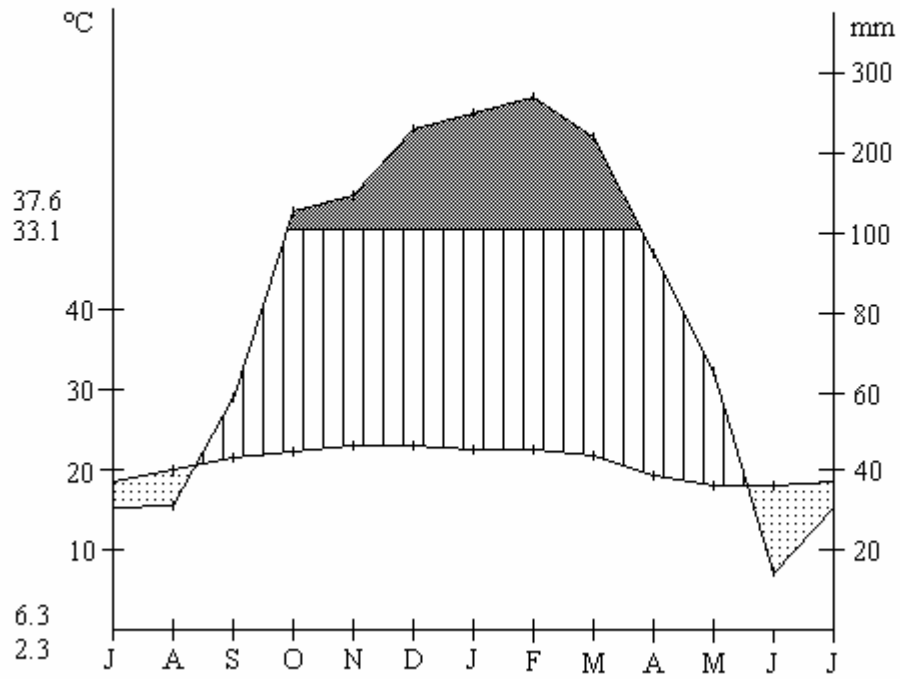


Figure 1.

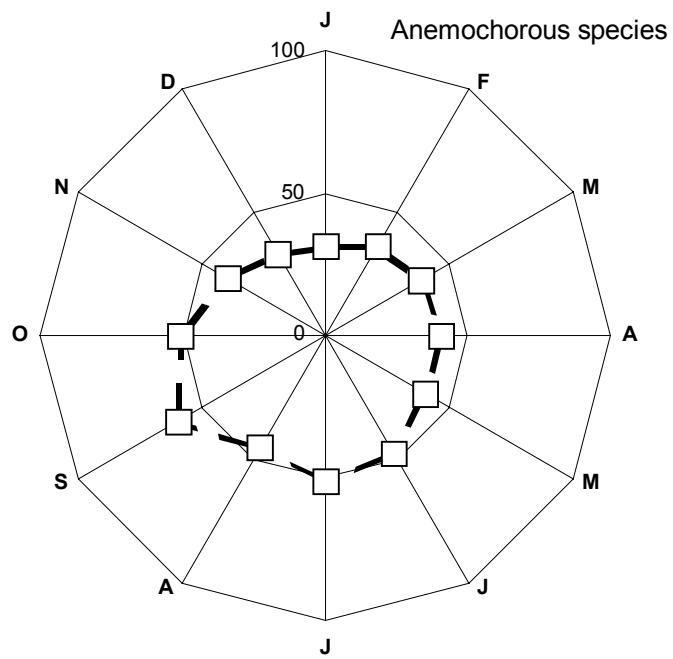


Figure 2.

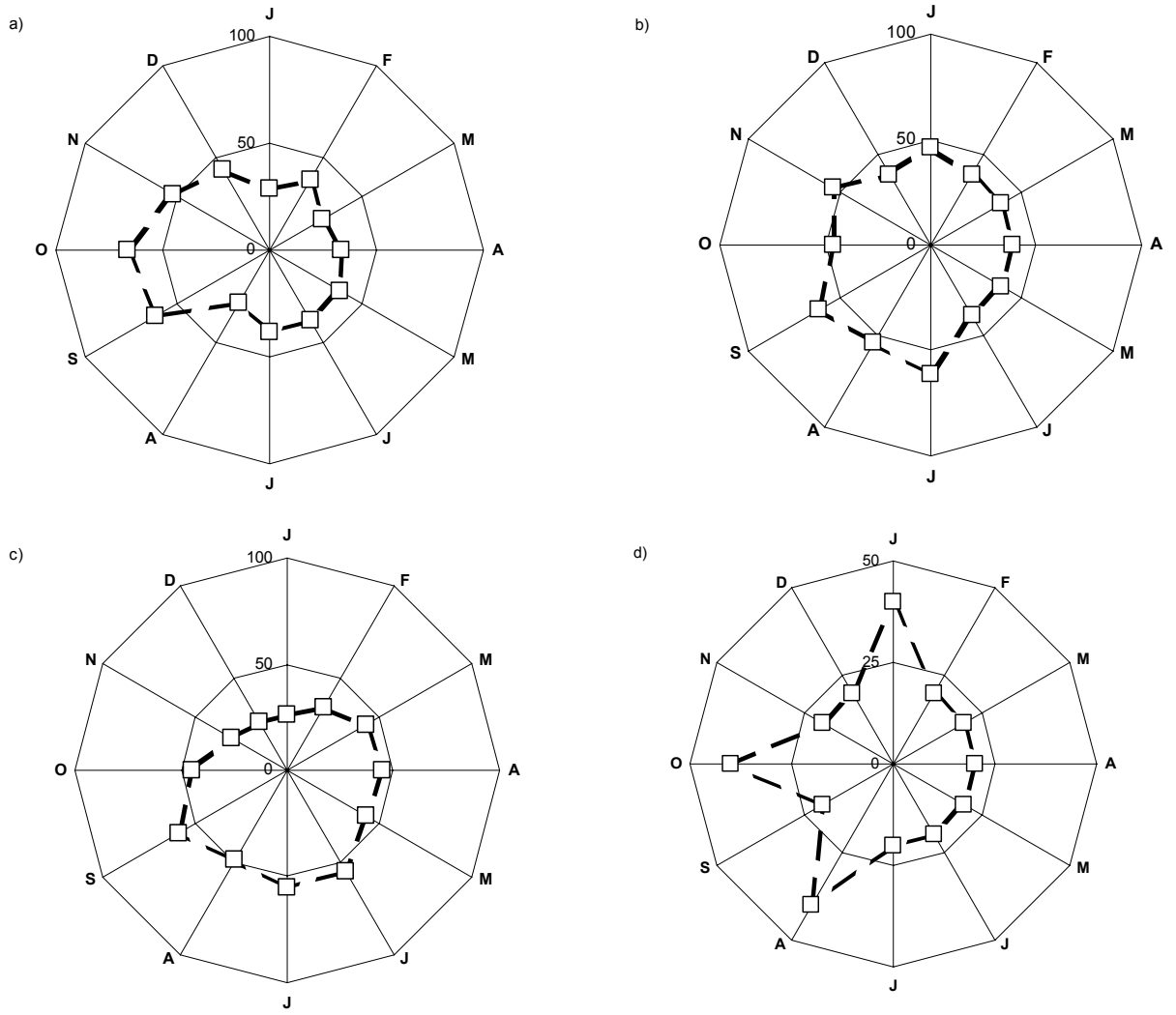


Figure 3.

III. Capítulo 2

Divergência de diversidade de espécies a diásporos anemocóricos em áreas de cerrado.¹

¹ Trabalho a ser submetido ao periódico *Biotropica* com o título “Divergence from Species to Anemochorous Diaspore Diversity in Cerrado Sites”.

1

2

3 LRH: Massi and Batalha

4 RRH: Divergence from Species to Diaspore Diversity

5

6 **Divergence from Species to Anemochorous Diaspore Diversity in Cerrado Sites.¹**

7

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9

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1 ABSTRACT – The cerrado presents a floristic and physiognomic variation, ranging from
2 grassland to tall woodland. Since the changes in the distribution of dispersal modes are
3 directly correlated with changes in vegetation structure, the index of divergence from species
4 to anemochorous diaspora diversity (IDD) is useful to compute the ecological similarity of
5 different communities. Our aim was to study the anemochorous diaspora spectra and IDD's in
6 cerrado physiognomies (*campo cerrado*, *cerrado sensu stricto*, and *cerradão*) in two Brazil
7 southern, disjoint sites and one cerrado physiognomy (*cerrado sensu stricto*) in a Brazil
8 central-western, core site. We conducted two anemochorous species surveys in a *cerrado*
9 *sensu stricto* physiognomy and compared with a phytosociological survey. The wind-
10 dispersed species were classified into autogyro, rolling-autogyro, floater, or undulator,
11 according to the diaspora morphology and aerodynamic behavior. We constructed the
12 anemochorous diaspora-types spectra and computed the IDD's of all physiognomies. We
13 applied a randomization test to test for differences among the IDD's, which we find in one
14 disjoint site. The high and equal divergence of the cerrado physiognomies indicated that they
15 are ecologically similar and structurally homogeneous, at least when concerning wind-
16 dispersed species. When individuals were considered, the proportions of winged-dispersed
17 diaspores were different. Both physical and biotic factors influence the success or failure of
18 seed dispersal. In denser sites, vegetation reduces wind velocity in lower strata, constraining
19 dispersal of herbaceous species and heavy-seeded, wind-dispersed species require launching
20 from a tree or high climber.

21

22 Key words: anemochory, cerrado, dispersal, intrinsic diversity divergence, savanna, wind
23 dispersal.

24

1 RESUMO – O cerrado apresenta variação florística e fisionômica, indo desde uma fisionomia
2 campestre até uma florestal. Uma vez que as mudanças na distribuição de modos de dispersão
3 estão diretamente relacionadas a mudanças na estrutura da vegetação, o índice de divergência
4 de diversidade (IDD) de espécies a diásporos anemocóricos é útil para calcular a similaridade
5 ecológica de diferentes comunidades. Nosso objetivo foi estudar os espectros de diásporos
6 anemocóricos e os IDDs de fisionomias de cerrado (*campo cerrado*, *cerrado sensu stricto* e
7 *cerradão*) em duas áreas disjuntas ao sul do Brasil, e de uma fisionomia de cerrado (*cerrado*
8 *sensu stricto*) em uma área nuclear no centro-oeste do Brasil. Conduzimos dois levantamentos
9 de espécies anemocóricas e o comparamos com um levantamento fitossociológico. As
10 espécies anemocóricas foram classificadas em autogiro, autogiro-rotativas, flutuantes e
11 planadoras, de acordo com a morfologia e comportamento do diásporo no ar parado.
12 Construimos os espectros de tipos de diásporos anemocóricos e calculamos os IDDs de todas
13 as fisionomias. Aplicamos um teste de randomização para testar as diferenças entre os IDDs,
14 que encontramos em uma área disjunta. As divergências altas e iguais das fisionomias de
15 cerrado indicaram que elas são ecologicamente similares e estruturalmente homogêneas, ao
16 menos em relação às espécies dispersas pelo vento. Quando indivíduos foram considerados,
17 as proporções de diásporos dispersos pelo vento foram diferentes. Fatores físicos e bióticos
18 influenciam o sucesso ou o fracasso da dispersão. Em locais mais densos, a vegetação reduz a
19 velocidade do vento no estrato inferior, restringindo a dispersão das espécies herbáceas,
20 enquanto espécies anemocóricas de sementes mais pesadas, requerem o lançamento a partir de
21 árvores ou lianas.

1 One of the most enlightening approaches to the study of the adaptations of plants to certain
2 ecological conditions is that focused on the careful consideration of the morphological
3 features (Sarmiento & Monasterio 1983). In the case of dispersal of plants, morphological
4 traits of diaspores may affect mean potential dispersal distance (Augspurger 1986). Wind
5 plays one of the most important role in seed dispersal, not only in scattering seeds far from the
6 parent plant (Greene & Johnson 1989), but by reducing intraespecific competition and to
7 reach new habitats (Howe & Smallwood 1982).

8 As long as seed dispersal lays the template from which communities develop, its pattern is
9 commonly believed to influence community structure (Levine & Murrel 2003). Seed dispersal
10 may contribute to species coexistence through tradeoffs between colonization ability and
11 other characters across species, as well as through the slowing of competitive exclusion when
12 seeds fail to arrive (Nathan & Muller-Landau 2000). The potential to influence above-ground
13 vegetation is one of the most relevant functions of soil seed banks (Fenner 1985). Above- and
14 below-ground community compartments are strongly related in terms of abundance and
15 species composition, at least in a semi-arid system (Olano *et al.* 2005).

16 There is a considerable variation in the ways by which wind acts as a disperser of seed
17 (Ridley 1930). An aerodynamic classification of seed and fruit groups is a logical
18 consequence of describing general motion to the distinct subsets and it may be based almost
19 entirely on a division of species only according to the similarity of equivalent distributions of
20 mass and geometry (Burrows 1975, Harper 1977). Based upon observations of diaspores
21 aerodynamic behavior in still air and their morphology, Augspurger (1986) placed each of the
22 34 species observed into one of six classes: autogyro (A), rolling-autogyro (RA), floater (F),
23 undulator (U), helicopter (H) or tumbler (T).

24 A seed is released at a height where there is sufficient wind speed to transport (Soons *et al.*
25 2004a). Autogyro and rolling-autogyro species have structures that do not allow long-distance

1 flights and, even if wind is strong, height of release is more important in these cases; floater
2 diaspores, on the contrary, have high capacity of being transported, even in still air (Hensen &
3 Muller 1997) and may be sufficient for explaining long-distance dispersal events and
4 relatively rapid migration through open, suitable landscapes (Soons *et al.* 2004b). So, winged-
5 diaspores species (A, RA, H, T and U) tends to present a seed rain pattern more clumped than
6 plumed-diaspore species (F).

7 The index of intrinsic diversity divergence (IDD), which ranges from zero to one,
8 quantifies the species convergence of a given community into ecologically relevant groups
9 irrespective of their systematic (Ricotta *et al.* 2002). Ricotta *et al.* (2002) used Raunkiaer's
10 (1934) life-forms to group the species, and the IDD was obtained by comparing the area under
11 the species diversity profile with the area under the corresponding life-form diversity profile.
12 When the IDD is applied, any classification of species into ecologically relevant groups may
13 be used (Ricotta *et al.* 2002). Since wind-dispersal is important to community dynamics
14 (Tackenberg *et al.* 2003, Soons *et al.* 2004a) and there are differences among wind-dispersed
15 diaspores (Augspurger 1986), we applied the IDD on the different wind-dispersed diaspores,
16 following Augspurger's (1986) classification, in some cerrado communities.

17 The cerrado vegetation occupied originally ca. 23 percent of Brazil's land surface, with a
18 core area in the Central Plateau and disjoint areas, such as those in the southeastern portion of
19 the country (Ratter *et al.* 1997). No species occurs at all cerrado sites, and the cerrado woody
20 flora includes many rare, characteristic species, together with accessory and ecotonal elements
21 (Ratter *et al.* 2003). These researchers proposed six cerrado floristic provinces, with distinct
22 floristic compositions: *i*) southern, *ii*) central, *iii*) central-western, *iv*) far-western, *v*) north-
23 eastern, and *vi*) Amazonian. The geographic distribution of cerrado species is limited (Gomes
24 *et al.* 2004) and there may be substitution of species belonging to the same genus or the same
25 family among the different cerrado floristic provinces (Bridgewater *et al.* 2004).

1 Besides the floristic variation, the cerrado presents a wide physiognomic variation, ranging
2 from grassland (*campo limpo*), through savannas (*campo sujo*, *campo cerrado*, and *cerrado*
3 *sensu stricto*), to tall woodland (*cerradão*). The cerrado flora has two components, a woody
4 one and an herbaceous one, which are distinct and antagonistic (Coutinho 1990). Winged
5 dispersal units prevail in the woody component, whereas plumed dispersal units are more
6 common in the herbaceous component (Gottsberger & Silberbauer-Gottsberger 1983). From
7 open to closed cerrado physiognomies, thus, the importance of winged diaspores (A, RA, and
8 U) should increase, whereas the importance of plumed diaspores (F) should decrease.

9 As long as there may be substitution of species belonging to the same genus or family
10 among different cerrado floristic provinces, we may expect that, for the same physiognomy,
11 even in different provinces, the proportions of winged-dispersed woody species and
12 individuals, and the IDD_s are equal. Hence, we tried to answer the following question: are the
13 proportions of winged-dispersed diaspores and IDD_s equal between cerrado sites? Moreover,
14 since changes in the distribution of dispersal modes are directly correlated with changes in
15 vegetation structure (Gottsberger & Silberbauer-Gottsberger 1983), we may expect, for a
16 given site, different proportions of winged-dispersed diaspores and different IDD_s from open
17 to closed cerrado physiognomies. Hence, we also tried to answer the following questions:
18 does the proportion of winged dispersal units increase towards closed cerrado physiognomy?;
19 does the proportion of plumed dispersal units decrease towards closed cerrado physiognomy?;
20 and are the IDD_s different among cerrado physiognomies?

21 22 **METHODS**

23
24 **COMPARISON AMONG PHYSIOGNOMIES** –We used data collected by Batalha & Mantovani
25 (2000). The site is the Pé-de-Gigante (Giant's foot) Reserve, Santa Rita do Passa Quatro, São

1 Paulo State, southeastern Brazil, 21°36-39'S and 47°36-38'W, under Köppen's Cwag'
 2 climate, at 660 to 730 m high a.s.l., on Oxisol, with 1,269 ha, covered mainly by cerrado
 3 (Pivello *et al.* 1998). From September 1995 to February 1997, they carried out a
 4 phytosociological survey and sampled both the herbaceous and the woody components of
 5 three cerrado physiognomies, *campo cerrado*, *cerrado sensu stricto*, and *cerradão*. In each
 6 physiognomy, they placed ten quadrats, in which they sampled both the woody and the
 7 herbaceous individuals, sampling 1,335 individuals in the *campo cerrado*, 1,086 individuals
 8 in the *cerrado sensu stricto*, and 1,072 individuals in the *cerradão*.

9 We filtered the matrices, excluding all non-anemochorous species. Then, we classified
 10 each anemochorous species, according to the movement of its diaspore while being dispersed,
 11 into autogyro, rolling-autogyro, floater, or undulator (Augsburger 1986). To assess this, we
 12 consulted taxonomic descriptions of the species and observed the fruits in lodged vouchers at
 13 the University of São Paulo herbarium (SPF). We had, thus, data on abundance and type of
 14 wind dispersal for all anemochorous species in three physiognomies. We tested for
 15 differences in the proportions of wind-dispersal types by applying pair-wise comparisons with
 16 the chi-square test (Zar 1999), considering either the number of species or the number of
 17 individuals.

18 To determine the IDD of each physiognomy, first we computed the intrinsic diversity
 19 profiles for species (α_{SP}) and the intrinsic diversity profiles for anemochorous diaspore-types
 20 (α_{DT}), which are related, respectively, to the area under the species diversity profile and the
 21 area under wind-dispersal type diversity profile. We constructed the diversity profiles
 22 following the procedures of Patil & Tailie (1982) and determined the area under a given
 23 profile as:

24 $\alpha = I \times (N/2)$, in which

$$I = [(2 \sum_{i=1}^H i \times p_i) - 1]/N$$

1 and i ($1 \leq i \leq N$) was the rank of the relative abundances p_i arranged in descending order
 2 (Ricotta *et al.* 2002). We calculated the index of intrinsic divergence (IDD) of each cerrado
 3 as:

$$4 \quad \text{IDD} = 1 - [(\alpha_{\text{DT}} - 0.5) / (\alpha_{\text{SP}} - 0.5)]$$

5 We applied a randomization test (Manly 1997), with 5,000 permutations, to test whether
 6 the IDD of the *campo cerrado*, *cerrado sensu stricto*, and *cerradão* were significantly
 7 different ($\alpha = 0.05$).

8

9 COMPARISON AMONG SITES –We used data from three sites, a core cerrado site in the central-
 10 western province and two disjoint cerrado sites in the southern province. The core site is
 11 located in Alcinópolis (Mato Grosso do Sul State), Alto Araguaia and Alto Taquari (Mato
 12 Grosso State), and Mineiros and Santa Rita do Araguaia (Goiás State), central-western Brazil,
 13 in the southwestern extremity of the Brazilian Central Plateau. Regional climate is Aw
 14 (Köppen 1948), humid tropical with wet summer and dry winter. This region was originally
 15 covered mainly by cerrado vegetation, from open (*campo limpo*, a grassland savanna) to
 16 closed (*cerradão*, a tall woodland) physiognomies, following Coutinho's (1990)
 17 classification. The first disjoint site is located in Itirapina Municipality, São Paulo State,
 18 southeastern Brazil, approximately at 22°13'S and 47°51'W, 760m high above sea level. The
 19 site is classified as *cerrado sensu stricto* following Coutinho's (1990) classification. The
 20 climate is Köppen's Cwa, that is, macrothermic temperate with rainy summer and not
 21 severely dry winter. The second disjoint site is located in the Pé-de-Gigante Reserve (see
 22 description above).

23 In the core site, we randomly placed 32 lines, keeping at least 100 m between two of them.
 24 In each line, we placed 15 points, 10 m apart one from the other, and sampled 60 woody
 25 individuals with the point-quarter method (Müller-Dombois & Ellenberg 1974). So, in all

1 lines, we sampled 1,920 woody individuals. In the first disjoint site, there is a grid of 100
 2 quadrats (each one with 25m²), where we randomly surveyed 50 quadrats at the middle of the
 3 rainy season (March 2004), sampling 1595 woody individuals. In the second disjoint site,
 4 Batalha & Mantovani (2000) sampled 687 woody individuals in the *cerrado sensu stricto*. We
 5 defined the woody component as composed by the woody individuals with stem diameter at
 6 soil level higher than 3 cm (SMA 1997).

7 Again we filtered the matrices, classified each anemochorous species, and tested for
 8 differences in the proportions of wind-dispersal types by applying pair-wise comparisons with
 9 the chi-square test (Zar 1999), considering either the number of species or the number of
 10 individuals. We calculated the index of intrinsic divergence (IDD) of each cerrado site
 11 (according to the description) and we applied a randomization test (Manly 1997), with 5,000
 12 permutations, to whether the IDD of the *cerrado sensu stricto* in the disjoint and core sites
 13 were significantly different ($\alpha = 0.05$).

14

15 **RESULTS**

16

17 COMPARISON AMONG PHYSIOGNOMIES – We sampled 36 anemochorous species in the *campo*
 18 *cerrado*; 36, in the *cerrado sensu stricto*, and 35, in the *cerradão* (Table 1). Within this site,
 19 16 species were common to the three physiognomies. The proportions of wind-dispersal types
 20 were not different when we took into account the number of species, but, when considered the
 21 number of individuals, they were (Table 2). The IDD of the *campo cerrado*, *cerrado sensu*
 22 *stricto*, and *cerradão* were, respectively, 0.868 ($\alpha_{SP} = 8.072$ and $\alpha_{DT} = 1.496$), 0.883 ($\alpha_{SP} =$
 23 8.918 and $\alpha_{DT} = 1.483$), and 0.844 ($\alpha_{SP} = 7.361$ and $\alpha_{DT} = 1.569$) (Fig. 1). The IDD were not
 24 significantly different (*campo cerrado* vs. *cerrado sensu stricto*, $p = 0.757$; *campo cerrado* vs.
 25 *cerradão*, $p = 0.636$; *cerrado sensu stricto* vs. *cerradão*, $p = 0.443$).

1

2 COMPARISON AMONG SITES – We sampled 28 anemochorous woody species in the core site;
3 14, in the first disjoint site (Itirapina), and 21, in the second disjoint site (Pé-de-Gigante) ; and
4 7 species were common to the three *cerrado sensu stricto* sites (Table 3). The proportions of
5 wind-dispersal types were not different when we took into account the number of species, but,
6 when considered the number of individuals, they were (Table 4). The IDD of the *cerrado*
7 *sensu stricto* in the core site, Itirapina disjoint site and Pé-de-Gigante disjoint site were,
8 respectively 0.839 ($\alpha_{SP} = 5.151$ and $\alpha_{DT} = 1.249$), 0.589 ($\alpha_{SP} = 2.95$ and $\alpha_{DT} = 1.506$), and
9 0.827 ($\alpha_{SP} = 5.137$ and $\alpha_{DT} = 1.301$) (Fig. 2). The IDD comparisons with the first disjoint site
10 were significantly different (core vs. first disjoint site, $p = 0.0364$; core vs. second disjoint
11 site, $p = 0.864$; first vs. second disjoint site, $p = 0.0468$).

12

13 **DISCUSSION**

14

15 COMPARISON AMONG PHYSIOGNOMIES – Since the importance of trees and shrubs increases
16 from open to closed physiognomies (Coutinho 1978), we expected the proportions of
17 autogyro, rolling-autogyro, and undulator species also to increase in this direction and the
18 proportion of floater species to decrease. Nevertheless, the distributions of wind-dispersed
19 diaspore types were the same among the three cerrado physiognomies, at least when just the
20 species were considered. The hypothesis that the woody component increases towards closed
21 physiognomies, while the herbaceous component diversity decreases, was not confirmed by
22 Batalha *et al.* (2001). Because the difference between the IDD was not significant, we may
23 postulate that there is a cerrado floristic unit with the ecotonal physiognomy containing
24 grassland and woodland elements.

1 Eiten (1977) stated that cerrado floristic composition changes gradually across the
2 physiognomic gradient. Therefore, the canopy cover, type of plant cover, and species
3 composition would distinguish the diverse structure of the cerrado vegetation (Jepson
4 2005), from small and scattered to large and clumped trees (Goodland & Pollard 1973). On
5 the contrary, Coutinho (1978) considered the savanna formations as wide ecotones between
6 the *cerradão* and the *campo limpo*, since a great number of species present are common to
7 both these extreme formations. Under the prevailing equilibrium viewpoint, communities are
8 assumed to be composed of species that differ in their resource use within that community
9 (Pickett 1980), which make possible their occurrence together (Whittaker 1965).

10 Possession of plumed seeds or fruits is rare in forests and frequent in open vegetations (Pijl
11 1969). Indeed, in a gallery forest within the Cerrado domain (Pinheiro & Ribeiro 2001) and in
12 a semi-deciduous forest in Barro Colorado Island (Augsburger 1986), the most abundant
13 diaspore class was the autogyro one. Tropical species show significant differences in seed
14 weight among trees, shrubs, and herbs (Rockwood 1985). In addition, species with large
15 flowers, fruits, and seeds tend to have large leaves, and one of the reasons could be to support
16 the fruit photosynthetically (Primack 1987). On the contrary, the herbaceous species recycle
17 the mineral elements internally by relocating them to the below-ground organs when the aerial
18 apparatus starts to dry out and before it is burned (Sarmiento 1984). To Ozinga *et al.* (2004)
19 the constraints of nutrient availability and seed weight may, in herbaceous species, lead to a
20 selection pressure against morphological adaptations, such as wings and plumes.

21 The proportions of winged-dispersed diaspores when individuals were considered were
22 different between the *campo cerrado*, *cerrado sensu stricto*, and *cerradão*. The occurrence of
23 a given physiognomy is maybe not defined by qualitative floristic changes, but by the
24 dominance of certain species that characterize the physiognomy (Oliveira & Moreira 1992).

1 The ecological processes and dynamics of the cerrado vegetation are the product of spatial
2 and temporal variability of several resources (Joly *et al.* 1999). If a location is characterized
3 by conditions within acceptable limits for a given species and contains all necessary
4 resources, the species can occur and persist (Begon *et al.* 1996).

5 The trees are supposed to be limited in growth by severe shortage of nutrients in the soil of
6 the grasslands (Goodland & Pollard 1973). Nascimento & Saddi (1992) concluded that the
7 high level of aluminum in a soil is a factor that could explain the greater number of *Qualea*
8 *parviflora* individuals. Moreover the differences in soil water availability between savannas
9 and dense hill forest were the principal environmental cause of variation in distribution of tree
10 species (Borchert 1994). Although most woody species are strongly fire-adapted, fires at too
11 frequent intervals damage them and favor the ground layer, thus producing more open
12 physiognomies (Gomes *et al.* 2004).

13 For a species to be dispersed, optimization would occur when dispersal agents presented
14 optimal conditions to act (Mantovani & Martins 1988). In denser sites, vegetation reduces
15 wind velocity in lower strata, constraining dispersal of herbaceous species (Oliveira &
16 Moreira 1992). The wind velocities necessary to transport most seeds away from the crown
17 constrain the number of seed dispersed (Clark *et al.* 2005). Seeds that are released from a
18 lower height above the vegetation are generally dispersed over shorter distances (Soons *et al.*
19 2004b). Heavy-seeded, wind-dispersed species require greater source densities to saturate
20 sites with seed (McEuen & Curran 2004), being launched from a tree or high climber (Pijl
21 1969).

22 High density of seeds deposited under the canopy may influence the fate of seeds and
23 subsequent patterns of plant recruitment (Clark *et al.* 2005). However, ants, rodents birds,
24 dungbeetles, and abiotic factors such as wind and water can move seeds after primary
25 dispersal (Vander Wall *et al.* 2005). Seeds deposited far from parent plants are likely to have

1 different survival and germination rates than those deposited nearby, and might have a
2 disproportionate influence on the resulting vegetation (Wang & Smith 2002). Nevertheless,
3 species without particular adaptations for long-range seed dispersal are regarded as very
4 sensitive to isolation (Hensen & Müller 1997).

5 COMPARISON AMONG SITES – The proportions of winged-dispersed species were equal among
6 a core cerrado site and two disjoint cerrado sites, with the same physiognomy. In the past, the
7 extent of tropical forest increased in warmer, wetter periods and contracted as savanna
8 dominated the vegetation in the cooler and drier periods; today, the present distributions of
9 both plant and animal species provide evidence of the positions once occupied by these
10 “tropical islands in a sea of savanna” (Begon *et al.* 1996).

11 Due to its extension, environmental heterogeneity, and proximity to other tropical
12 vegetation types, the cerrado has a high diversification at the level of species; and most of
13 these species exhibit morphological and physiological adaptations to the climatic and edaphic
14 conditions that prevail in the region (Joly *et al.* 1999). Each of these regions has species that
15 are endemic to them, but in many cases these species are part of a closely related species
16 complex (Prado & Gibbs 1993). Also there are too many species having wide distribution,
17 nearly occurring in whole cerrado domain (Leitão-Filho 1992).

18 A high IDD value of a given community indicates that such community is structurally very
19 homogeneous, because most species diversity is distributed in few classes (Ricotta *et al.*
20 2002). In the case of the core and one disjoint sites (Pé-de-Gigante Reserve), they are
21 structurally homogeneous due to the prevalence of one anemochorous diaspore-type and with
22 the others poorly represented. The Itirapina disjoint site showed its species diversity well
23 distributed in diaspore classes. As long as IDD is a measure to quantify the ecological
24 similarity of different communities (Ricotta *et al.* 2002), we may conclude that the core and
25 Pé-de-Gigante disjoint sites are ecologically similar, and both are ecologically different from

1 Itirapina. The *cerrado sensu stricto* from Itirapina is opened, with soil exposure and this can
2 be explained by several perturbation factors (Pagano *et al.* 1989). We postulated that this
3 would favoured any diaspore type.

4 On the contrary, when individuals were considered, the proportions of winged-dispersed
5 diaspores were different. Even when there is a large number of common species between
6 sites, the size of the species population is very variable from place to place (Felfili *et al.*
7 2004). The dominance of species and the number of their individuals varies strongly in
8 different cerrado sites; this is certainly influenced by different altitudes (Gottsberger &
9 Silberbauer-Gottsberger 1983), geomorphology, soil physic and chemical features, fire
10 frequency (Coutinho 1978), climatic factors, herbivory, and human disturbances (Miranda *et*
11 *al.* 2002). Both physical and biotic factors influence the success or failure of seed dispersal
12 (Howe & Westley 1986).

13 In an Australian savanna, sexual regeneration of the species is disadvantaged by current
14 burning practices because both seed supply and the number of microsites are reduced
15 (Setterfield 2002). The losses of reproductive structures due to fire must be important, mainly
16 in smaller trees (Garcia-Nuñez *et al.* 2001). However, dispersal by wind may be dependent on
17 casual events, such as occasional whirlwinds or burnings that clear the vegetation and allow
18 dispersal over longer distances (Coutinho 1978). Hoffmann (1998) concluded that current fire
19 regimes must cause a shift is savanna species composition, favoring species capable of
20 vegetative reproduction.

21 The substrate available for deposition might also affect seed-dispersion patterns – that is,
22 seeds might be preferentially deposited or retained on some microsites. For example, wind-
23 dispersed seeds might be more likely to end up on rough surfaces (Nathan & Muller-Landau
24 2000). Johnson & Fryer (1992) studying the wind dispersal of samaras, concluded that on

1 rougher surfaces, seeds remained stationary for a sufficient length of time to imbibe water to
2 start the germination sequence.

3 We think that are important the comparisons between individuals and species. To
4 Whittaker (1965), comparing number of species is the most convenient way to compare
5 diversities in different communities as it seems inappropriate to compare on the same scale
6 individuals as disparate in size as trees and herbs.

7

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9

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11

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1 TABLE 1. *Percentage of autogyro, rolling-autogyro, undulator, and floater diaspora*
 2 *individuals and species in the campo cerrado, cerrado sensu stricto and cerradão of the Pé-de-*
 3 *Gigante Reserve.*

physiognomy	total	autogyro (%)	rolling-autogyro (%)	undulator (%)	floater (%)
<i>campo cerrado</i>					
Species	36	36.1	22.2	8.3	33.4
Individuals	262	31.7	15.6	12.2	40.5
<i>cerrado sensu stricto</i>					
Species	36	41.7	27.8	16.6	13.9
Individuals	304	42.8	22.7	25.3	9.2
<i>cerradão</i>					
Species	35	37.2	31.4	11.4	20.0
Individuals	361	33.0	33.0	28.2	5.8

4

1 TABLE 2. Comparisons of wind-dispersed diaspore spectra among physiognomies of the Pé-
 2 de-Gigante Reserve.

Comparison	species	Individuals
<i>campo cerrado</i> vs. <i>cerrado sensu stricto</i>	$\chi^2 = 4.247$ ^{NS}	$\chi^2 = 78.796$ ^{***}
<i>campo cerrado</i> vs. <i>cerradão</i>	$\chi^2 = 1.919$ ^{NS}	$\chi^2 = 125.330$ ^{***}
<i>cerrado sensu stricto</i> vs. <i>cerradão</i>	$\chi^2 = 0.910$ ^{NS}	$\chi^2 = 13.489$ ^{**}

3 NS = $P > 0.05$; ** $P < 0.01$; *** $P < 0.001$

1 TABLE 3. *Percentage of autogyro, rolling-autogyro, undulator, and floater diaspora*
 2 *individuals and species in the cerrado sensu stricto of the core (central-western Brazil) and*
 3 *disjoint sites (southeastern Brazil).*

sites	total	autogyro (%)	rolling-autogyro (%)	undulator (%)	floater (%)
core site					
Species	28	21.4	42.9	25	10.7
Individuals	427	52.0	29.0	11.0	8.0
Itirapina disjoint site					
Species	14	35.7	42.9	14.3	7.1
Individuals	329	36.5	32.2	25.5	5.8
Pé-de-Gigante disjoint site					
Species	21	38.1	23.8	23.8	14.3
Individuals	171	39.8	15.8	41.5	2.9

4

- 1 TABLE 4. *Comparisons of wind-dispersed diaspore spectra among sites of cerrado sensu*
 2 *stricto physiognomy.*

Comparison	species	Individuals
core site vs. Itirapina disjoint site	$\chi^2 = 1.352$ ^{NS}	$\chi^2 = 34.400$ ***
core site vs. Pé-de-Gigante disjoint site	$\chi^2 = 2.553$ ^{NS}	$\chi^2 = 74.619$ ***
Itirapina disjoint site vs. Pé-de-Gigante disjoint site	$\chi^2 = 1.738$ ^{NS}	$\chi^2 = 22.926$ ***

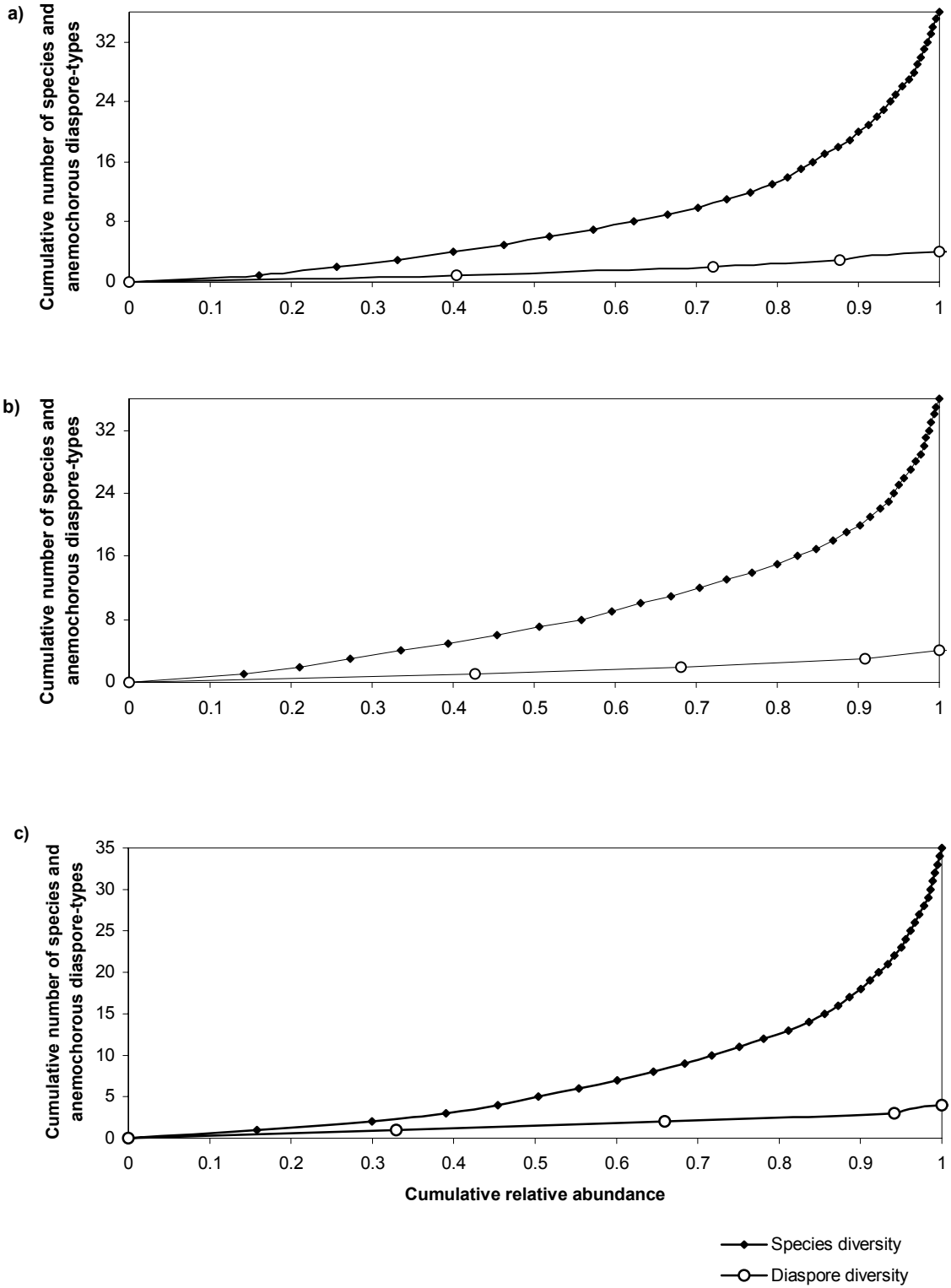
3 NS = $P > 0.05$; *** $P < 0.001$

1 FIGURE 2. Intrinsic diversity profile for species and anemochorous diaspore-types relative
2 abundances of the *campo cerrado* (a), *cerrado sensu stricto* (b) and *cerradão* (c) of the Pé-de-
3 Gigante Reserve.

4

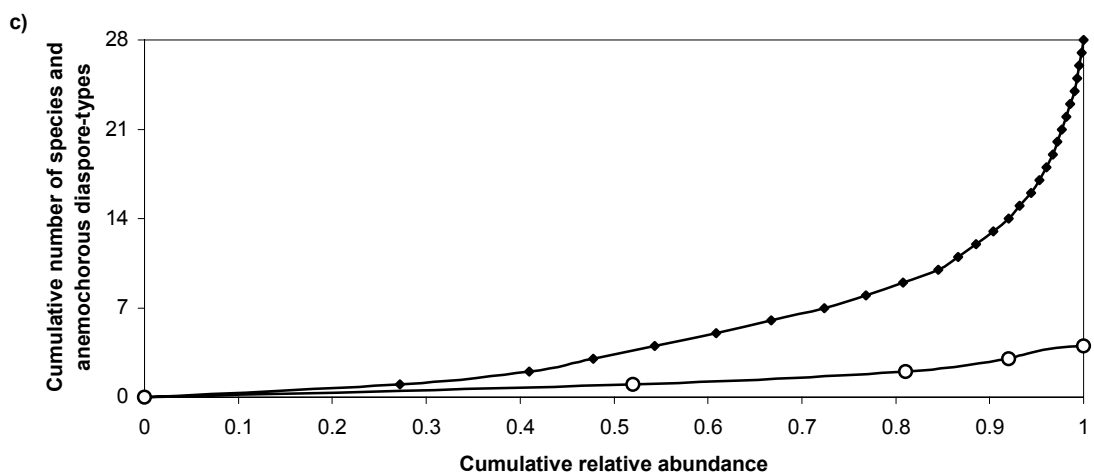
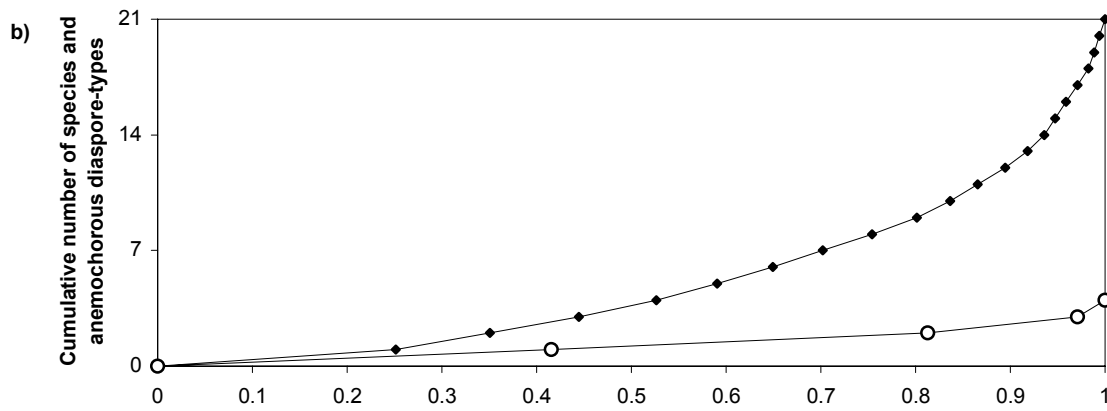
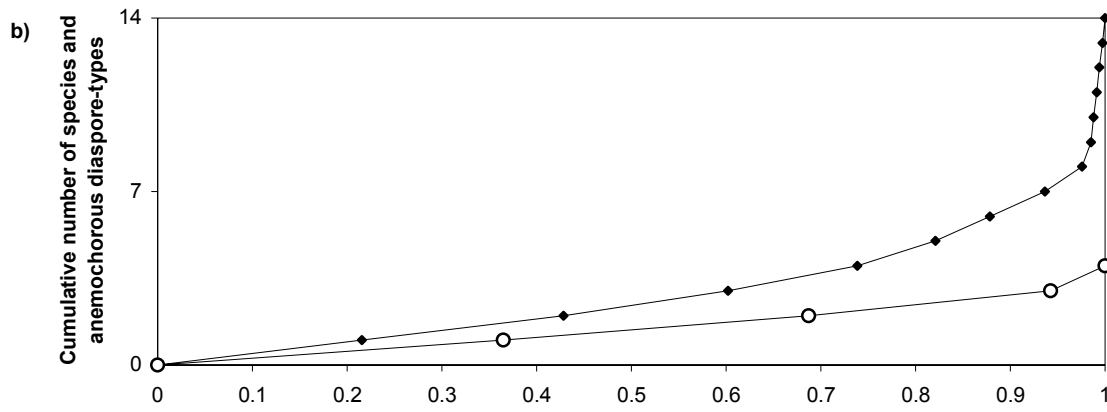
5 FIGURE 1. Intrinsic diversity profile for species and anemochorous diaspore-types relative
6 abundances of the *cerrado sensu stricto* of Itirapina (a) and Pé-de-Gigante (b) disjoint sites
7 (southeastern Brazil) and the core site (c) (central-western Brazil).

1



2

1



—●— Species diversity
—○— Diaspore diversity

IV. Conclusão Geral

Conclusão Geral

Com este trabalho chegamos às seguintes conclusões:

- a frutificação das espécies anemocóricas na Reserva Pé-de-Gigante (SP), foi estacional; logo a estação seca favorece a dispersão dos diásporos anemocóricos, que são secos, corroborando Mantovani & Martins (1988), Miranda (1995), Batalha et al. (1997) e Batalha & Martins (2004);
- o número de espécies anemocóricas frutificando relacionou-se negativamente com a precipitação e com a umidade relativa. Na estação seca, frutos dispersos pelo vento desidratam e muitas espécies trocam suas folhas, favorecendo a dispersão dos diásporos;
- os grupos de espécies com diásporos autogiro, autogiro-rotativos e planadores tiveram períodos de frutificação bem distribuídos ao longo do ano. O grupo de espécies com unidade de dispersão flutuante frutificou estacionalmente com pico na estação seca, relacionando-se negativamente à temperatura, umidade relativa do ar e precipitação. Isso pode ser devido às restrições filogenéticas, porém espécies com sementes flutuantes devem concentrar seus períodos de frutificação durante a estação seca, devido ao comportamento hidrofóbico das plumas (Hensen & Muller 1997);
- os componentes herbáceo-subarbustivo e arbustivo-arbóreo apresentaram maior proporção de espécies com diásporos flutuantes e planadores, respectivamente. Portanto, diásporos plumados e alados devem prevalecer em fisionomias abertas e fechadas, respectivamente;

- as fisionomias de cerrado *sensu stricto*, nas áreas nuclear e disjuntas, apresentaram a mesma distribuição de espécies dentro dos grupos de tipos de diásporo anemocórico; logo a distribuição de espécies entre os diferentes tipos de diásporos anemocóricos entre as espécies deve se manter independente da província geográfica em que a comunidade se encontre;
- o número de indivíduos dentro dos grupos de tipos de diásporo anemocórico variou de uma área para outra; logo, pode haver restrições à dispersão ou uso diferenciado dos recursos disponíveis;
- as fisionomias campo cerrado, cerrado *sensu stricto* e cerradão de uma área disjunta apresentaram a mesma distribuição de espécies dentro dos grupos de tipos de diásporo anemocórico; logo, a distribuição de tipos de diásporos anemocóricos entre as espécies deve se manter independentemente da fisionomia de cerrado;
- quando a abundância das espécies foi considerada, as proporções de tipos de diásporos anemocóricos variaram entre as fisionomias de uma mesma área; logo, processos ecológicos que atuem em escalas menores e que influenciem o tamanho das populações afetam a distribuição de tipos de diásporos anemocóricos na comunidade.