



Universidade Federal de São Carlos
Centro de Ciências Biológicas e da Saúde
Programa de Pós-graduação em Ecologia e Recursos Naturais

**Previsão de guildas de dispersão e de fenologia foliar com
base em atributos funcionais para espécies arbustivo-
arbóreas em uma área de cerrado *sensu stricto* em Itirapina
(SP)**

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Orientador: Prof. Dr. Marco Antônio Batalha

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Resumo

A classificação das plantas terrestres baseada em tipos funcionais, em vez de na identidade taxonômica, tem sido reconhecida como uma maneira promissora de lidar com questões ecológicas importantes em nível de comunidades, paisagens e biomas. Os objetivos de um esquema de estratégia ecológica vegetal (EEEV) são o entendimento das forças seletivas que moldam a ecologia das plantas e a descrição dos princípios gerais da relação entre as plantas e o ambiente sem necessidade de detalhamento taxonômico, a fim de que se construa uma linguagem comum para a comparação de espécies e tipos vegetacionais em escala mundial. Westoby (1998) propôs um EEEV para espécies arbustivo-arbóreas, constituído por três eixos: 1) área foliar específica (AFE); 2) altura da copa; e 3) massa da semente. Essas três características, folha-altura-semente (FAS), estão correlacionadas com várias outras e representam comprometimentos fundamentais que controlam as diferentes estratégias ecológicas das plantas. O objetivo deste trabalho foi testar, em uma área disjunta de cerrado *sensu stricto* em Itirapina – SP, se os traços funcionais propostos no esquema FAS são potenciais previsores das guildas de dispersão. Procuramos responder à seguinte pergunta: com base no esquema FAS, as espécies dispersas por mecanismos abióticos apresentam estratégias ecológicas diferentes das espécies dispersas por animais? Ainda, testamos, na mesma comunidade, se a área foliar específica e a altura da planta foram potenciais previsores da fenologia foliar (espécies decíduas e sempre-verdes). Nesse caso, tentamos responder à seguinte pergunta: a área foliar específica e a altura estão relacionadas com o hábito foliar da planta? De acordo com os nossos resultados, os atributos funcionais estudados não puderam prever nem as guildas de dispersão nem a fenologia foliar. A similaridade da área foliar específica nos dois casos pode ser devida a

dois fatores: altura similar das espécies (hábitats com disponibilidade de luz parecida) e esclerofilia. A deficiência nutricional do solo deve conduzir as espécies arbóreas de cerrado a ajustes adaptativos convergentes, tanto no que diz respeito à área foliar específica (baixos valores – esclerofilia) quanto no que diz respeito à altura. As guildas de dispersão foram similares quanto à massa da semente, tendo em vista que todas as espécies zoocóricas amostradas eram ornitocóricas, cuja massa da semente é tipicamente reduzida, e que as espécies abioticamente dispersas tiveram sementes com massas maiores do que o esperado. No cerrado, isto pode ocorrer em suporte à elevada razão raiz-parte aérea das sementes de algumas espécies do cerrado. Por outro lado, as espécies ornitocóricas são limitadas no tamanho e na massa por causa do pequeno tamanho da maioria das aves frugívoras. Além disso, no cerrado, algumas plantas ornitocóricas podem ter seus diásporos coletados por formigas, o que favoreceria a germinação de suas sementes.

Palavras-chave: cerrado *sensu stricto* – esquemas de estratégia ecológica vegetal – fenologia foliar – guildas de dispersão – traços funcionais.

Abstract

There is growing recognition that classifying terrestrial plant species on the basis of their function (into ‘functional types’) rather than their higher taxonomic identity is a promising way forward for tackling important ecological questions at the scale of communities, landscapes, and biomes. The aim of a plant ecology strategy scheme (PESS) is to express an understanding of important opportunities and selective forces that shape the ecologies of plants and to describe the general principles of plant-environment relations without taxonomic details, to provide a common language for comparing species and vegetation types worldwide. Westoby (1998) proposed a PESS for woody species consisted of three axes: 1) specific leaf area (SLA); 2) height of the canopy of the species; and 3) seed mass. These traits, leaf-height-seed (LHS), are correlated with a number of others and are fundamental trade-offs controlling plant strategies. The aim of this study was to test in a disjoint cerrado woodland site in southeastern Brazil whether traits of the LHS scheme are potential predictors of dispersal guilds. We tried to answer the following question: do the species dispersed by abiotic means present different ecological strategies to species dispersed by animals, considering the LHS scheme? Still, we tested in the same community whether specific leaf area and plant height are potential predictors of two phenological groups, that is, deciduous and evergreen species. We tried to answer the following question: are SLA and plant height related to leaf phenology? According to our results, neither dispersal guilds nor leaf phenological groups could be predicted by the functional traits studied. The similarity in SLA in both cases may be due to two factors: similar height of species (similar habitats in regard to light availability) and sclerophylly. Soil nutrient deficiency seems to lead cerrado woody species to convergent adaptative adjustments regarding both specific leaf area

and height. Dispersal guilds were similar concerning seed mass, given that all zoochorous species studied were ornithochorous, whose seed mass is typically low, and abiotically dispersed species had higher than expected seed masses. In the cerrado, the latter may occur as support to the investment in high root-to-shoot ratio of biomass allocation at the seedling stage. Seeds of bird-dispersed species are limited on the size and mass because of the small size of most frugivorous birds. Additionally, in the cerrado, some plants associated with bird dispersers may have their diaspores collected by ants, which favours their seed germination.

Keywords: cerrado woodland – dispersal guilds – functional traits – leaf phenology – plant ecology strategy schemes.

Introdução geral

Introdução geral

Há um crescente reconhecimento de que a classificação das plantas terrestres baseada nas suas funções (em tipos funcionais), em vez de na identidade taxonômica, é uma maneira promissora de lidar com questões ecológicas importantes em nível de comunidades, paisagens e biomas, relacionadas às respostas da vegetação às mudanças ambientais (por exemplo, mudanças no clima, na química atmosférica, uso da terra e outros distúrbios) e aos efeitos dela sobre estas (Cornelissen *et al.* 2003).

Os tipos funcionais de plantas são grupos de plantas – agrupamentos normalmente baseados nos atributos comuns das espécies em vez de nas relações filogenéticas – similares quanto: 1) às respostas aos fatores ambientais (disponibilidade de recursos, condições climáticas ou regime de distúrbio), por exemplo, xerofíticos *versus* mesofíticos, heliófilos *versus* umbrófilos, tolerantes ao fogo *versus* intolerantes ao fogo *etc.*; e 2) aos efeitos na comunidade (produtividade primária, ciclagem de nutrientes, transferência trófica), como, por exemplo, fixadores de nitrogênio, espécies promotoras de fogo *etc.* (Díaz & Cabido 2001).

As espécies funcionalmente similares, ou com uma mesma estratégia ecológica, são assim definidas, pois tendem a compartilhar um conjunto de traços funcionais, características de um organismo consideradas relevantes à sua resposta ao ambiente ou ao seu efeito sobre o funcionamento da comunidade (Cornelissen *et al.* 2003). O mérito da classificação baseada em traços funcionais é que os modelos quantitativos usados são baseados em traços e não em espécies, já que modelos baseados na taxonomia de espécies têm capacidade de generalização limitada devido ao elevado número de espécies no planeta (Keddy 1992).

De acordo com Westoby (1998), o agrupamento de espécies em categorias ou ao longo de

espectros, segundo seus atributos ecológicos (traços funcionais), pode ser feito por meio de Esquemas de Estratégia Ecológica Vegetal (EEEV), em que uma “estratégia” é a maneira pela qual uma espécie mantém sua população, o que se aplica a comparações interespecíficas, visto que a estratégia de uma espécie precisa ser pensada sobre uma série de gerações, e operando na presença de espécies competidoras, em diversos ambientes e sob variados regimes de distúrbios. Assim, se esses esquemas agrupam as espécies em categorias, então também podemos comparar guildas – grupos de espécies que exploram de maneira similar a mesma classe de recursos ambientais ou que ocupam o mesmo nicho ecológico (Root 1967) – quanto às estratégias ecológicas. Nesse sentido, podemos definir uma guilda de dispersão como um grupo de espécies caracterizado por um determinado agente dispersor de seus diásporos, por exemplo, espécies dispersas por mecanismos abióticos (incluindo espécies anemo e autocóricas) compondo uma guilda e espécies dispersas por agentes bióticos compondo outra (veja Van der Pijl 1972).

O espectro de dispersão varia de local para local (Willson *et al.* 1990), presumivelmente porque os méritos relativos dos diferentes modos de dispersão são afetados por atributos da planta em questão (tais como o tamanho da semente ou a altura da planta) e pelas circunstâncias ambientais sob as quais as plântulas se estabelecem, como, por exemplo, depois do fogo a partir do banco de sementes, sob sombra e em condições de solo seco (Hughes *et al.* 1994).

Os objetivos de um EEEV são o entendimento das forças seletivas que moldam a ecologia das plantas e a descrição dos princípios gerais da relação entre as plantas e o ambiente sem necessidade de detalhamento taxonômico, a fim de que se construa uma linguagem comum para a comparação de espécies e tipos vegetacionais em escala mundial (Westoby 1998). A busca por um EEEV que descreva de maneira eficiente as comunidades vegetais e que tenha

um bom poder de previsibilidade engloba toda a agenda de pesquisas em Ecologia Vegetal (Myerscough 1990).

Westoby (1998) propôs um EEEV para espécies arbustivo-arbóreas, constituído por três eixos: 1) área foliar específica, isto é, a área da folha fresca (madura) dividida por sua massa seca, expressa em $\text{m}^2 \text{kg}^{-1}$ (ou $\text{mm}^2 \text{mg}^{-1}$); 2) altura da copa da espécie na maturidade, expressa em metros; e 3) massa (seca) da semente, expressa em miligramas. Tais dimensões devem indicar a maneira pela qual as plantas assimilam carbono durante o crescimento vegetativo e asseguram a transmissão dos seus genes no futuro (Westoby *et al.* 2002). Essas três características, folha-altura-semente (FAS), estão correlacionadas com várias outras e representam compromettimentos fundamentais que controlam as diferentes estratégias ecológicas das plantas, porque não se espera que uma espécie: a) desenvolva uma grande área foliar e, ao mesmo tempo, construa folhas reforçadas que possuam ampla longevidade; b) suporte uma copa alta, sem custos com um caule alto; c) produza sementes grandes e ricas em material de reserva sem restringir o seu número no esforço reprodutivo (Westoby 1998). Ou seja, espera-se que haja um comprometimento por parte da planta com uma ou outra estratégia apenas, em cada um dos três componentes – folha, altura e semente.

A área foliar específica é crucial à longevidade da folha, ao tempo médio de residência dos nutrientes e à adaptação aos nutrientes do solo (Westoby 1998). Ela deve ser estimadora da taxa de retorno de investimento, ou seja, uma área foliar específica alta implica um menor tempo de retorno do investimento feito em cada grama de matéria seca na folha (Poorter 1994) e, conseqüentemente, uma resposta flexível com relação à disposição espacial dos recursos luminosos e do solo (Grime 1994). Já as espécies com reduzida área foliar específica apresentam folhas com maior longevidade (Reich *et al.* 1997), relacionada ao requerimento de

resistência estrutural extra (Wright & Cannon 2001) e à alocação de taninos, fenóis ou outros compostos de defesa (Coley 1988).

A altura da planta está associada não só ao vigor competitivo, à fecundidade e à duração do período de crescimento entre distúrbios como também à tolerância ou à evitação de estresses ambientais (climático ou nutricional), sendo que, por exemplo, algumas plantas altas podem evitar, com sucesso, que o fogo alcance as partes verdes e o meristema na copa (Cornelissen *et al.* 2003). Espécies com as copas em diferentes alturas devem operar em diferentes intensidades luminosas, temperaturas, turbulências e umidades relativas e, portanto, com diferentes custos para sustentar as folhas e transportar água a elas (Givnish 1995).

A massa da semente deve expressar a probabilidade da espécie dispersar com sucesso uma semente a um local propício e do indivíduo sobreviver às várias intempéries quando na fase de plântula (Westoby 1998). Sementes menores podem ser produzidas em maior número no período reprodutivo e enterradas mais profundamente no solo, particularmente se tiverem formato próximo do cilíndrico, o que confere elevada longevidade no banco de sementes (Westoby 1998; Cornelissen *et al.* 2003). Por outro lado, as sementes maiores mostraram experimentalmente que sobrevivem melhor sob várias condições desfavoráveis, por exemplo, seca, herbivoria e sombreamento (Westoby *et al.* 1996).

A área foliar específica, a altura e a massa da semente fazem parte de uma lista resumida de características vegetais sobre as quais devem se basear as classificações funcionais das plantas, porque apresentam um forte poder previsor em relação às respostas das comunidades frente às mudanças ambientais ou possuem elas mesmas um forte impacto sobre os processos da comunidade (ver Cornelissen *et al.* 2003). Diante disso, é importante aplicar esse esquema em tipos vegetacionais brasileiros. O protocolo simples do esquema FAS, com dimensões

prontamente mensuráveis (Westoby *et al.* 2002), abre caminho para comparações em escala mundial e meta-análises (Westoby 1998).

Ocupando originalmente cerca de 23% do território brasileiro, o cerrado é o segundo maior tipo vegetacional do país (Ratter *et al.* 1997) e apresenta diversidade alta de espécies, com mais de 900 espécies de árvores (Ratter *et al.* 2003). Como qualquer outra savana neotropical, o cerrado é caracterizado por um clima estacional, com estações chuvosa e seca marcantes (Franco 2002). Os padrões temporais de crescimento e reprodução das plantas – os padrões fenológicos –, em savanas tropicais, estão ligados à estacionalidade climática (Williams *et al.* 1997). As espécies arbóreas são parcialmente evitadoras da seca, isto é, os indivíduos de algumas espécies perdem todas as suas folhas e os indivíduos de outras espécies perdem apenas algumas das suas folhas (Eiten 1972).

O objetivo deste trabalho foi testar, em uma área disjunta de cerrado *sensu stricto*, de fisionomia densa, em Itirapina – SP (figuras 1 e 2), se os traços funcionais propostos no esquema FAS são potenciais previsores das guildas de dispersão (capítulo 1). Procuramos responder à seguinte pergunta: com base no esquema FAS, as espécies dispersas por mecanismos abióticos apresentam estratégias ecológicas diferentes das espécies dispersas por animais? Ainda, testamos, na mesma comunidade, se a área foliar específica e a altura da planta são potenciais previsores da fenologia foliar - espécies decíduas e sempre-verdes (capítulo 2). Nesse caso, tentamos responder à seguinte pergunta: a área foliar específica e a altura estão relacionadas com o hábito foliar da planta? Em outras palavras, podemos prever a fenologia foliar com base na área foliar específica e na altura?

Optamos por apresentar a dissertação em capítulos, formatados de acordo com as normas das revistas científicas a serem submetidos. Enviamos o primeiro capítulo ao periódico “Oecologia”.

O segundo, enviaremos ao “Australian Journal of Botany”. Como as revistas para as quais decidimos enviá-los exigiam a sua redação na língua inglesa, escrevemos os capítulos nesse idioma. Tendo em vista que estes são independentes, algumas repetições foram inevitáveis.

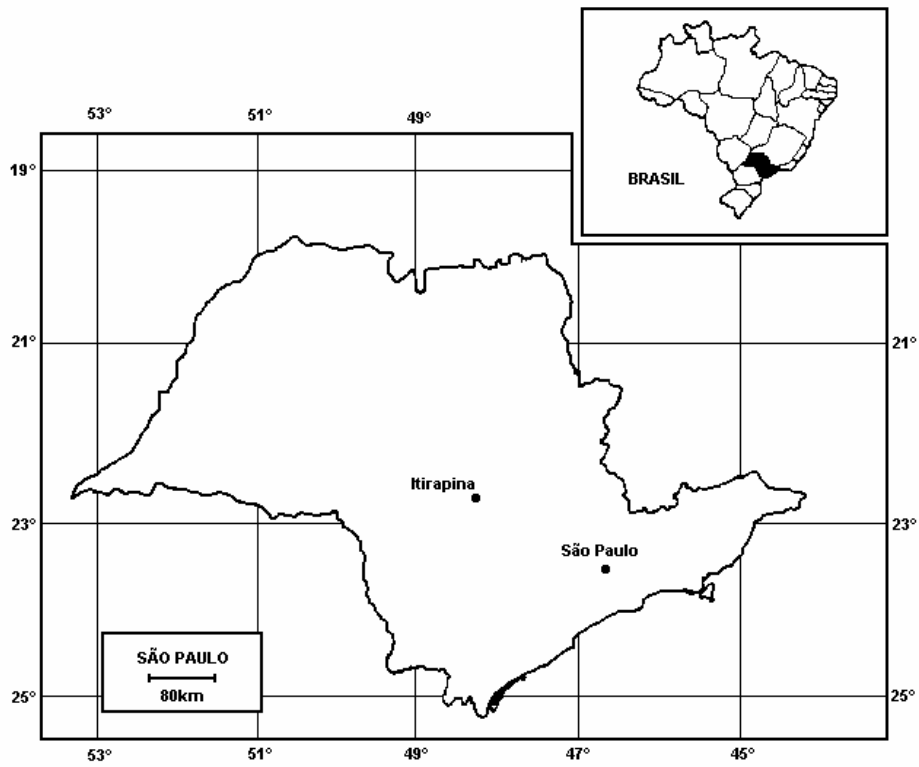


Fig. 1. Localização de Itirapina, SP, 22°12-13'S e 47°50-51'W (modificado de Salis *et al.* 1995).



Fig. 2. Fragmento de cerrado *sensu stricto* estudado (seta), em Itirapina, SP (22°12-13'S e 47°50-51'W; Google Earth - <http://earth.google.com>).

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Capítulo 1: O esquema de estratégia ecológica folha-
altura-semente: uma comparação entre duas guildas de
dispersão em uma área disjunta de cerrado *sensu stricto*¹

¹ Trabalho submetido à revista *Oecologia* com o título “The leaf-height-seed plant ecology strategy scheme: a comparison between two dispersal guilds in a disjoint cerrado woodland site”.

**The leaf-height-seed plant ecology strategy scheme: a comparison between
two dispersal guilds in a disjoint cerrado woodland site**

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Abstract Plant ecology strategy schemes describe the general principles of plant-environment relationships without taxonomic details, providing a common language for comparing species and vegetation types worldwide. The leaf-height-seed (LHS) scheme consists of three functional traits: specific leaf area, plant canopy height, and seed mass. We tested whether these traits are potential predictors of dispersal guilds in a disjoint cerrado woodland site in southeastern Brazil, trying to answer the following question: do the species dispersed by abiotic means present different ecological strategies from those dispersed by biotic means, regarding the LHS scheme? According to our results, none of the plant traits studied could predict dispersal guild. Similar SLA between abiotically and biotically dispersed species may be due not only to their occupation of similar stratum in the woodland site, which may indicate that there are no differences in their habitats regarding light availability, but also to sclerophylly, a common trait of cerrado species. The typical soil nutrient deficiency of cerrado may place constraints in plant canopy height regardless of the dispersal mode. Although not higher than the zoochorous species studied – all of them were bird-dispersed – the abiotically dispersed species studied had relatively high plant canopy heights, considering the average canopy height of the physiognomy of cerrado woodlands, which may confer high diaspore release height. Thus, they can produce relatively large seeds without compromising their dispersibility. In the cerrado, some abiotically dispersed trees might present higher than expected seed mass as support to the investment in high root-to-shoot ratio of biomass allocation at the seedling stage. Seeds of bird-dispersed species are limited on the size and mass because of the small size of most frugivorous birds. Additionally, in the cerrado, some plants associated with bird dispersers may have their diaspores collected by ants, which would favour their seed germination.

Keywords Cerrado vegetation – Dispersal groups – Functional traits – Plant ecological strategy

Introduction

Classifying terrestrial plant species on the basis of their function – into ‘functional types’ – rather than their higher taxonomic identity is a promising way forward for answering important ecological questions at the scale of communities, landscapes, and biomes (Cornelissen et al. 2003). The arrangement of species in categories or along spectra according to their ecological attributes can be done through plant ecology strategy schemes (PESSs), whose aim is to express an understanding of important opportunities and selective forces that shape the ecologies of plants and to describe the general principles of plant-environment relationships without taxonomic details, to provide a common language for comparing species and vegetation types worldwide (Westoby 1998).

Westoby (1998) proposed a PESS for woody species consisted of three axes: 1) specific leaf area (SLA), crucial to leaf longevity, mean residence time of nutrients, and soil nutrient adaptation; 2) height of the plant’s canopy at maturity, associated with competitive vigour and tolerance or avoidance of environmental (climatic, nutritional) stress; and 3) seed mass, which influences dispersal and establishment ability. These traits, leaf-height-seed (LHS), are correlated with a number of others and are fundamental trade-offs controlling plant strategies, because it is ineluctable that a species cannot both deploy a large light-capturing area per photosynthesizing gram and also build strongly reinforced leaves that may have long lives; cannot support leaves high above the ground without incurring the expense of a tall stem; and cannot produce large, heavily-provisioned seeds without producing fewer of them per gram of reproductive effort (Westoby 1998). Thus, we expect that plants adopt just one of the two strategies at the different levels – leaf, height and seed.

Dispersal spectra vary from place to place (Willson et al. 1990), presumably because the relative merits of different dispersal modes are affected by attributes of the plant in question (e.g., seed size, height) and by the environmental circumstances under which seedlings establish or fail (e.g., after fire from soil seed bank, in deep shade, in dry soil conditions; see Hughes et al. 1994). A guild is defined as a group of species that exploit the same class of environmental resources in a similar way or that overlap significantly in their niche requirements (Root 1967). Thus, we may define a dispersal guild as a functional group characterized by a certain dispersal agent of diaspores, with species dispersed by abiotic mechanisms (including anemochorous and autochorous species) and species dispersed by biotic agents (zoochorous species; see Van der Pijl 1972).

The height of the seed fall is an important factor related to anemochory and autochory, because the slower the seed fall, the more efficient the dispersal of such species (Roth 1987; Nathan et al. 2002; Tackenberg 2003). In addition, in lower vegetation strata of cerrado woodlands with closed canopies, wind velocity, which is another important variable for wind dispersal, is reduced (Oliveira and Moreira 1992). Consequently, wind-dispersed species are associated with upper strata in Brazilian cerrado woodlands (Oliveira and Moreira 1992). So, in terms of the LHS plant ecology strategy scheme, we expect for cerrado woodlands higher values of plant height and lower values of seed mass in species dispersed by abiotic mechanisms when compared to those dispersed by biotic ones.

The smaller the leaves, and the greater the wind velocity, the more effectively is heat lost to the surrounding air by means of convection, thus avoiding injuries from strong irradiation and overheating (Larcher 1995). Among plant species of similar height in an Australian sclerophyll woodland community, smaller-leaved species tend to occur in more illuminated patches,

whereas large-leaved species occur in less illuminated patches (Bragg and Westoby 2002). In a chaparral patch, SLA of shrub species declines with increasing insolation (Ackerly et al. 2002). Under shade, increased SLA is a common response for tropical tree species (Souza and Válio 2003). Thus, for species dispersed by abiotic mechanisms, which are predominantly found in the upper strata of cerrado woodlands with closed canopies (Oliveira and Moreira 1992), we expect lower values of SLA than for animal-dispersed species.

The aim of this study was to test in a disjoint cerrado woodland site in southeastern Brazil whether traits of the LHS scheme are potential predictors of dispersal guilds. In other words, we tried to answer the following question: do the species dispersed by abiotic means present different ecological strategies to species dispersed by animals, considering the LHS scheme?

Materials and methods

We carried out our study in a cerrado site, at Itirapina, São Paulo State, southeastern Brazil (22°12-13'S and 47°50-51'W; Fig. 1). Following Coutinho (1990), the site is classified as *cerrado sensu stricto*, which is a woodland according to Sarmiento (1984), and presents a rather closed canopy. The climate is Köppens's (1931) Cwa, that is, macrothermic temperate with rainy summers and not severely dry winters. The soil in the region is classified as sandy soil – Quartzipsamment (Oliveira and Prado 1984; Embrapa 1999). The area belongs to the São Paulo State Forestry Institute and is surrounded by *Pinus* spp. and *Eucalyptus* spp. plantations and protected from fire for approximately 20 years.

In this fragment, there is a grid of 200 quadrats (each one with 5 m x 5 m), where other researchers have been carrying out studies on population dynamics and community structure.

We randomly picked 100 quadrats in this grid and carried out monthly field trips during a year, from May 2004 to April 2005. We sampled the woody component of the cerrado vegetation, defined as composed by all woody plants with stem diameter at soil level equal or larger than 3 cm (SMA 1997). We identified each individual in field or, when necessary, by collecting samples for subsequent comparison with lodged material at the Federal University of São Carlos herbarium (Hufscar) or identification keys based on vegetative characters (Batalha et al. 1998, Batalha and Mantovani 1999).

Of all woody species sampled, we selected those with at least ten individuals (Cornelissen et al. 2003) and that fruited during the sampling period. Because these species did not fruit in Itirapina, we collected the fruits of *Bauhinia rufa* Steud., *Dalbergia miscolobium* Benth., and *Schefflera vinosa* (Cham. & Schltldl.) Frodin & Fiaschi at the cerrado reserve of the Federal University of São Carlos, São Carlos, Brazil. We used the walking-and-gathering method with monthly observations along trails including two cerrado physiognomies found in the reserve – *campo cerrado* and *cerrado sensu stricto* (Coutinho 1990). We classified the sampled species according to two dispersal guilds: 1) species dispersed by abiotic mechanisms, which includes anemochorous species (with winged seeds, plumes, or other wind-dispersed features) and autochorous species (dispersed entirely by free fall or propelled explosively by a fruit that opens suddenly); and 2) species dispersed by biotic mechanisms, or zoochorous species, with diaspores attached to a fleshy pulp, aril, or other features typically associated with animal dispersal agents (Van der Pijl 1972).

We defined, measured and sampled plant height, specific leaf area (SLA), and seed mass following Cornelissen et al.'s (2003) protocol. We defined plant height as the distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level, expressed

in metres. We measured plant canopy height in 10 individuals per species, randomly sampled, using a telescopic stick. SLA is the one-sided area of a fresh leaf divided by its oven-dry mass, expressed in $\text{mm}^2 \text{mg}^{-1}$. From 10 individuals per species, randomly sampled, we collected 20 leaves (two leaves from each individual), took digital pictures of each leaf and measured its area with the ImageJ 1.33 software (Rasband 2004). The average SLA for each individual plant was one statistical observation. We defined seed mass as the oven-dry mass of an average seed of a species, expressed in milligrams. We collected 100 seeds from at least three individuals per species and used an analytical balance to weight the seeds. We took randomly 10 seeds per species to do the statistical analyses.

We applied logistic regression analysis (Hosmer and Lemeshow 1989; Ryan 1997) to test whether SLA, plant height, and seed mass could predict dispersal guild. First, we divided the total sample randomly into two subsamples, the analysis sample and the validation sample, following a proportionately stratified sampling procedure to make the analysis (Hair et al. 1998). The analysis sample and the validation sample comprised 60% and 40%, respectively, of the total sample. For each species considered, we sampled randomly six individuals for the analysis sample and four individuals for the validation sample to keep the same number of individuals of each species. Then, we modeled the relationship between the binary response variable (one = abiotic dispersal guild; zero = biotic dispersal guild) and each of the explanatory variables (univariate analyses). Before conducting the multivariate analysis (multiple logistic regression), we checked whether SLA, plant height, and seed mass were correlated, applying the Spearman correlation test (Sokal and Rohlf 1994). For the assessment of the significance of the models, we used the likelihood ratio test and the Wald statistic (Hosmer and Lemeshow 1989; Hair et al. 1998). For the measurement of the goodness of fit of the final model, we intended to

use: 1) the “Nalgerke R^2 ”, the only measure of goodness of fit calculated using the analysis data set; 2) the correct classification rate (CCR) with a cutoff value based on the proportion of 1’s; 3) the Pearson residuals; 4) the deviance residuals; and 5) the Hosmer and Lemeshow test (Hosmer and Lemeshow 1989; Neter et al. 1989; Ryan 1997). We conducted statistical analyses using Statistica 6.0 software (StatSoft Inc.) and Microsoft Office Excel 2003 (Microsoft Corporation).

Results

We found 11 species that fruited during the sampling period with at least 10 individuals, three of which dispersed by abiotic means and eight, by biotic means (Table 1). Thus, the total sample comprised 110 observations, 30 individuals dispersed by abiotic means and 80 individuals dispersed by biotic means. The analysis sample contained 66 observations (60% of the total sample), 18 for the abiotic guild and 48 for the biotic guild, and the validation sample contained 44 observations (40% of the total sample), 12 for the abiotic guild and 32 for the biotic guild.

Analyzed individually, the SLA model was not significant, but the plant height model and the seed mass model were significantly related to dispersal guild (Table 2). Had not been correlated ($r_s = 0.36$; $p = 0.003$), considering the analysis data set, we would add both variables (plant height and seed mass) in the multivariate model. Instead, we proceeded the analysis by calculating the several measures of goodness of fit of the univariate models, the plant height model and the seed mass model. The Nalgerke R^2 values were 0.14 and 0.40 for the plant height model and the seed mass model, respectively. Using an optimal cutoff value of 0.278 (Neter et al. 1989), the CCR of the plant height model was 70.45%, with 50% of the abiotic dispersal

group and 78.12% of the biotic dispersal group being correctly classified. For the seed mass model, the CCR was 65.91%, with 41.67% of the abiotic dispersal group and 75% of the biotic dispersal group being correctly classified. The Pearson and the deviance tests were not significant neither to the plant height model [$\chi^2 = 51.13$ ($0.10 < p < 0.25$); $D = 48.89$ ($0.10 < p < 0.25$), respectively] nor to the seed mass model [$\chi^2 = 44.61$ ($0.25 < p < 0.50$); $D = 41.50$ ($0.25 < p < 0.50$), respectively]. We did not proceed with the Hosmer and Lemeshow test in both models, because none of the frequencies estimated by such models was higher than five and because there were several expected frequencies lower than one (see Hosmer & Lemeshow 1989). In summary, none of the studied variables could predict dispersal guild.

Discussion

We observed, during one year, more biotically than abiotically dispersed species fruiting in the woody component of the cerrado, what is expected, since the cerrado woody component is characterized by a higher proportion of zoochorous species, especially in closed physiognomies such as the one we studied (Batalha and Martins 2004). None of the studied variables – SLA, plant height, and seed mass – could predict dispersal guild in the area studied. Differences in SLA for plants in high- and low-light habitats may represent adaptive adjustments in leaf morphology for maximizing light interception in the shade and minimizing water loss in the sun (Larcher 1995). For cerrado trees, soil water availability *per se* does not limit their transpiration, but high atmospheric evaporative demand and hydraulic constraints possibly arising from their deep root habit do so (Meinzer et al. 1999). Similar adaptative adjustments in SLA of the cerrado woody species studied may be a consequence of their similar canopy heights –

abiotically and biotically dispersed species occupying similar stratum in the dense woodland site, which may indicate that there are no differences in their habitats regarding light availability.

The analysis of the light capture strategies of the groups of plants studied may be better viewed in terms of crown architecture instead of just SLA. For instance, during mid-morning to mid-afternoon, a cerrado species consisting of compound, pinnate leaves with nearly vertical leaflets receives greatly reduced radiant energy loads on its leaves when compared to others with nearly horizontal leaves (Meinzer et al. 1999). Since plant architecture affects light capture by crowns and its photosynthetic carbon gain, and may be influenced by the positioning of reproductive structures – for instance, a dispersal unit – (Percy et al. 2005), it is welcome to include it in future researches involving dispersal and light capture. However, although some architectural variables, both at leaf- (leaf angle and specific leaf area) and whole crown level (internode length), have an effect on foliage display efficiency (the fraction of foliage that is not self-shaded and is projected towards a given sky region), site to site variation in light availability is the main factor that determines the photosynthetic photon flux density absorbed per unit leaf area by individual plants (Valladares et al. 2002). This reinforces the suggestion that similar adjustments in SLA of both dispersal guilds studied are modulated, at least in part, by similar light availability.

Moreover, since plant height is a positive predictor of pathogen attack among cerrado plant species (Marquis et al. 2001), trees with similar canopy heights may intercept the same number of wind-borne spores, which would influence homogeneously SLA. Leaf toughness is another trait that should contribute to the non-difference of SLA in the studied species, since leaves of cerrado species are generally tough or sclerophyllous (Marquis et al. 2001). Sclerophylly in

cerrado plants has been related to soil nutrient deficiency, which limits their growth and could lead them to accumulate carbohydrates as mechanical structures, such as cellulose depositions, thick cuticle, and sclerenchyma (Arens 1958). According to such postulate, high light levels and lack of water stress would result in an abundance of assimilated CO₂, consumed in the production of structural elements in the leaves because of low availability of nutrients for growth.

Legumes have significantly higher leaf nitrogen (N) contents than non-legumes, which may be related to more efficient N assimilation processes in legumes (Bustamante et al. 2004). Since photosynthesis is strongly affected by N availability and maximum CO₂ assimilation on a mass basis and significantly correlated with leaf N and SLA (Franco et al. 2005), one could expect that the legumes sampled in this study – the abiotically dispersed guild was comprised exclusively by them – would present higher SLA rather than the lower values we expected initially. However, the legumes did not have higher SLA values, what may be explained by the possibility that, over time, fixing nitrogen can lead to a significant buildup of organic nitrogen that cycles through the litter and can become available to non-leguminous co-occurring species (Evans and Edwards 2001), which would influence at the same way the SLA of the latter.

The two cerrado dispersal guilds did not differ in their plant canopy heights either. The rather closed canopy of the studied site suggests an increased competition for light, which would favour increased investment in height growth (Givnish 1982). Indeed, along the cerrado physiognomic gradient, from pure grassland to woodland with a closed canopy, mean and maximum tree height increase (Castro and Kauffman 1998). In our study site, species from distinct dispersal guilds seem to behave similarly in regard to the running for light in terms of height. The typical soil nutrient deficiency of cerrado, however, may place constraints in plant

canopy height regardless of the dispersal mode. Low nutrient levels could result in low photosynthetic rates and, as a consequence, low growth rates (Franco 2002). For instance, in a core cerrado site, increasing soil nutrient availability resulted in higher plant canopy height (Haridasan 2000). Abiotically dispersed species rely on structural modifications that maintain a high diaspore release height to attain longer dispersal distances (Tackenberg et al. 2003). Although not higher than the zoochorous species studied, the abiotically dispersed species studied have relatively high plant canopy heights (Table 1), considering the average canopy height of 3 m of the cerrado woodland (Castro and Kauffman 1998), which may confer a high diaspore release height.

Species with abiotic dispersal usually have smaller seeds than species dispersed by animals (Moles et al. 2005). However, the species studied showed similar seed mass, irrespective of the dispersal group, a result influenced by the higher than expected seed mass values of the species dispersed by abiotic mechanisms and by the lower than expected seed mass values of the zoochorous group. Our findings agreed with Hughes et al. (1994), who concluded that most seeds in temperate floras are between 0.1 and 100 mg, and in this range all of the dispersal modes are feasible. One may suggest that the non-difference found between the dispersal guilds regarding the seed mass is consequence of phylogenetic constraint, given that the three species comprising the abiotically dispersed guild are of the same family (Fabaceae). Although seed mass is related to phylogeny, it could vary considerably within taxonomic groups, and there are no insuperable obstacles to the evolution of seed masses much higher or lower than group means; these outliers contradict intrinsic phylogenetic constraint (Lord et al. 1995). Moreover, divergences in seed mass have been much more strongly associated with divergences in other plant traits – mainly in growth form and dispersal syndrome – than with divergences in the

physical environment in which species occur; this means that the cross-species relationships have more predictive power than the phylogenetic relationships (Moles et al. 2005).

The seeds produced by a plant are under natural selection both to disperse and to establish successfully (Leishman and Westoby 1994). Species having large seed mass survive better under a variety of different seedling hazards (Westoby et al. 1996). If the height of the abiotically dispersed species – even similar to the animal-dispersed species – permits seeds to travel far in the study area and if there is a selective advantage for larger seeds, these plants can produce relatively larger seeds, compared to the expected low mass of the group (Moles et al. 2005), without compromising their dispersibility (Leishman and Westoby 1994). Among wind-assisted species, larger seeds tend to have larger wings or longer pappuses, because reduced dispersal associated with larger seed mass tends to be counteracted by investment in more expensive dispersal-assisting structures (Westoby 1998). However, heavy-seeded, wind-dispersed species require greater source densities to saturate sites with seed (McEuen and Curran 2004).

In the cerrado, some abiotically dispersed trees might present higher than expected seed mass to invest in high root-to-shoot ratio of biomass allocation at the seedling stage (Sasaki and Felipe 1999; Moreira and Klink 2000). In a core cerrado area with similar physiognomy of the studied site, the root-to-shoot ratio was 2.9, and the proportion of tree roots present at deeper levels was greater than in more open physiognomies (Castro and Kauffman 1998). Of eight abiotically dispersed species studied, Jackson et al. (1999) found that four (*Dalbergia miscolobium* included) were deep-rooted, one intermediate-rooted, and three shallow-rooted. The high root-to-shoot ratio seems to be an adaptation to allow cerrado seedlings to withstand the dry season during the first stages of life (Rizzini 1965), allow plants to resprout from

underground organs after fire (Franco 1998), and withstand the low soil nutrient content (Lilienfein et al. 2001).

All zoochorous species that fruited in the study period were bird-dispersed (Gottsberger and Silberbauer-Gottsberger 1983; Silva Júnior 2005), whose seeds are not typically large (Howe and Westley 1991; Kay 1992). The ornithochorous species accurately represents the zoochorous guild, since birds form the most important group of frugivores (Kay 1992). In a disjoint cerrado site, Gottsberger and Silberbauer-Gottsberger (1983) observed that, among trees, most species were dispersed by birds. Plant species with zoochorous dispersal may target birds more often than mammals and other animals, because of the greater species richness of the former (Willson et al. 1989). The small size of most frugivorous birds places an ecologically important limit on the size and mass of bird-dispersed seeds (Kay 1992). Not only are birds sensitive to the amount of ballast that they carry and tend to prefer trees with small fruits, but also trees with high ratios of edible aril to indigestible seed show the greatest removal success, especially during periods of fruit scarcity (Howe and Westley 1991). Additionally, in the cerrado, some plants associated with vertebrate dispersers, especially birds, may have their diaspores collected by ants (Gottsberger and Silberbauer-Gottsberger 1983; Leal and Oliveira 1998). Their seeds may benefit from being dropped by ants in safe spots beneath the leaf litter, where more appropriate microconditions, such as moisture, temperature, and nutrients, may favor seed germination (Harper 1977; Horvitz 1981). Pulp and aril removal from fruits of some bird-dispersed species of cerrado results in increased germination success for these species, probably because it reduces fungal attack on them (Leal and Oliveira 1998).

As suggested by Westoby et al. (2002), the number of traits as predictors of ecological behavior does not need to stop at three. Although our predictions were clear and based on a

reasonable number of observations (Hair et al. 1998), our study considered a small number of species. Therefore, forthcoming studies on the relationship of plant traits and dispersal guilds with a larger number of species and a more detailed classification of dispersal groups, especially the biotically dispersed one, would reach more accurate predictions of the ecological strategies of groups with particular ecological affinities.

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Fig. 1 Location of Itirapina, São Paulo State, southeastern Brazil, 22°12-13'S and 47°50-51'W (modified from Salis et al. 1995).

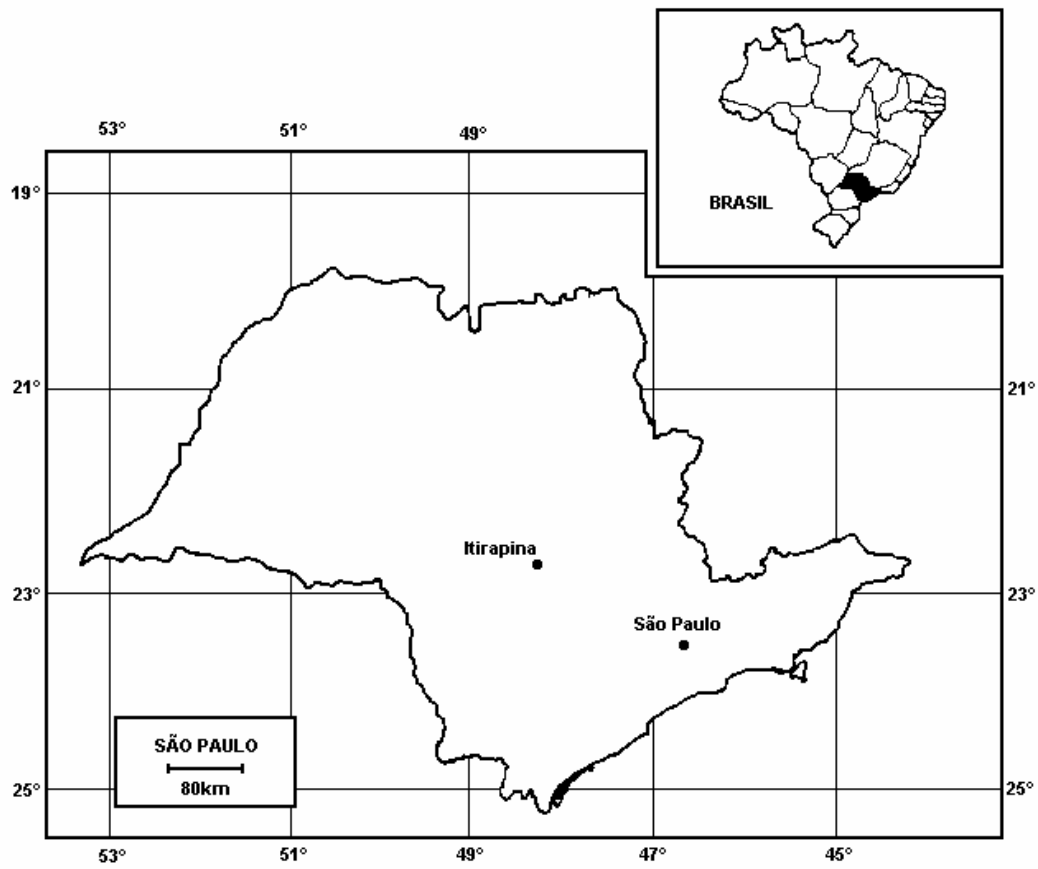


Table 1 Dispersal guild (DG; A = species dispersed by abiotic mechanisms, B = species dispersed by biotic mechanisms), specific leaf area (SLA), plant canopy height (H), and seed mass (SM) of species sampled in Itirapina, southeastern Brazil. The data presented refers to the analysis data set.

Species	Family ^a	DG	SLA (mm ² mg ⁻¹) ^b	H (m) ^b	SM (mg) ^b
<i>Anadenanthera falcata</i> (Benth.) Speg.	FAB	A	8.18 (1.17)	6.38 (2.45)	33.15 (2.92)
<i>Bauhinia rufa</i> Steud.	FAB	A	12.28 (1.90)	3.29 (0.47)	58.65 (27.68)
<i>Dalbergia miscolobium</i> Benth.	FAB	A	7.63 (0.70)	8.49 (2.80)	107.15 (11.27)
<i>Erythroxylum pelleterianum</i> St. Hil.	ERX	B	20.90 (1.65)	2.39 (0.65)	7.85 (0.87)
<i>Miconia albicans</i> Triana	MLS	B	7.88 (0.77)	2.43 (0.40)	0.27 (0.02)
<i>Miconia rubiginosa</i> (Bonpl.) A.DC.	MLS	B	6.94 (1.38)	4.11 (1.65)	2.65 (0.30)
<i>Myrcia lingua</i> Berg.	MRT	B	8.57 (1.39)	3.12 (0.93)	28.05 (5.47)
<i>Ocotea pulchella</i> Mart.	LAU	B	9.09 (0.97)	4.18 (0.66)	72.90 (8.25)
<i>Rapanea guianensis</i> (Aubl.) Kuntz.	MRS	B	9.65 (1.06)	4.21 (0.77)	18.05 (1.02)
<i>Schefflera vinosa</i> (Cham. & Schltdl.) Frodin & Fiaschi	ARL	B	7.12 (0.61)	3.20 (0.64)	12.60 (1.03)
<i>Xylopia aromatica</i> (Lam.) Mart.	ANN	B	11.29 (1.18)	4.97 (0.79)	41.05 (3.23)

^aFamily names are abbreviated according to Weber (1982)

^bMedians values (and median absolute deviation)

Table 2 Univariate logistic regression models. The univariate models are: specific leaf area model (“SLA”), plant height model (“H”), and seed mass model (“SM”); $\hat{\beta}$ = parameter estimate for the variable of the univariate model (the constants of the univariate models were omitted); \hat{SE} = estimated standard error of the parameter estimate; W = univariate Wald statistic; L = likelihood value for the univariate model; G = likelihood ratio test statistic. The first row shows the constant only model.

model	$\hat{\beta}$	\hat{SE}	W	p	L	G	p
constant	-0.981	0.276	12.594	< 0.001	-38.673		
SLA	-0.060	0.079	0.570	0.45	-38.360	0.625	0.42
H	0.318	0.129	6.088	0.01	-35.359	6.629	0.01
SM	0.041	0.011	14.741	< 0.001	-27.857	21.632	< 0.001

Capítulo 2: A área foliar específica e a altura não
predizem a fenologia foliar das espécies arbustivo-
arbóreas de uma área disjunta de cerrado *sensu*
*stricto*¹

¹ Trabalho a ser submetido à revista “Australian Journal of Botany” com o título “Specific leaf area and height do not predict leaf phenology of woody species in a disjoint cerrado woodland site”.

Specific leaf area and height do not predict leaf phenology of woody species in a disjoint cerrado woodland site

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Abbreviated title: Prediction of leaf phenology in cerrado woody species

Abstract. In tropical savannas such as the cerrado, the phenological patterns are linked to the climatic seasonality. Specific leaf area (SLA) and plant height are fundamental trade-offs controlling plant strategies. We postulated that evergreen species would present lower specific leaf area and shallower roots than deciduous species. Thus, we tried to answer the following question: can we predict leaf phenology of woody species based on SLA and height in a disjoint savanna woodland (*cerrado sensu stricto*) site? We found that both plant traits could not predict leaf phenology for the species studied. The majority of the species of both phenological groups could be considered sclerophyllous (low SLA), a common feature in cerrado associated with the low soil nutrient content. The similarity in SLA between deciduous and evergreen cerrado species may be due to the likely small difference between them regarding leaf life span. The effects of the soil nutrient deficiency not only on specific leaf area but also on plant height of cerrado woody plants seem to lead to convergent adaptative adjustments. Our findings reinforce the suggestion that cerrado tree species may possess a limited number of physiological and morphological solutions for coping with seasonal drought.

Introduction

Like any other neotropical savanna, the Brazilian cerrado is characterized by a strongly seasonal climate, with distinctive wet and dry seasons (Franco 2002). In tropical savannas, the temporal patterns in growth and reproduction – phenological patterns – of the plant species are linked to the climatic seasonality (Williams *et al.* 1997). In the cerrado, during the prolonged dry season, the low relative humidity and moderately high daytime temperatures impose a consistently high evaporative demand (Jackson *et al.* 1999). During this period, water in the upper soil layers is severely depleted as

evidenced by the extremely low water potentials in the first few centimeters of soil and by the dieback of grasses (Franco 1998). The woody plants, on the other hand, are only partially drought-evading, that is, individuals of some species lose all their leaves and individuals of others lose only some of them (Eiten 1972).

Whereas deciduous species drop their entire canopy in the dry season and hence do not transpire significantly, evergreen species maintain a canopy and transpire (Eamus 1999). This might be made possible by a root system that accesses deeper layers of soil than deciduous species (Sarmiento and Monasterio 1983; Sobrado 1986). Indeed, in an Australian wet-dry tropical savanna, the dominant evergreen species had high daily maximum leaf conductance during the dry season, which suggests they had access to groundwater (Myers *et al.* 1997). However, in a study with 10 cerrado woody species most of the deciduous species extracted water from deep soil layers in the dry season, whereas the evergreen species showed a broader range of water extraction patterns, from shallow-rooted to deep-rooted, indicating a complex pattern of water exploitation of the soil profile (Jackson *et al.* 1999).

The degree of soil water partitioning and variation in the timing of leaf production and loss among cerrado woody species suggests that resource partitioning may play an important role in maintenance of the high diversity of woody species in the cerrado (Franco 2002). This resource partitioning may be reflected not only in belowground traits (*e.g.*, soil water uptake) but also in leaf- (*e.g.*, specific leaf area) and whole-plant traits (*e.g.*, plant height).

Specific leaf area (SLA) and plant height are correlated with a number of other traits and are fundamental trade-offs controlling plant strategies, because it is ineluctable that a species cannot both deploy a large light-capturing area per photosynthesizing gram

and also build strongly reinforced leaves that may have long lives; and cannot support leaves high above the ground without incurring the expense of a tall stem (Westoby 1998).

SLA of a species is in many cases a good positive correlate of its potential relative growth rate or mass-based maximum CO₂ assimilation (Westoby 1998; Franco *et al.* 2005). Lower values tend to correspond with relatively high investments in leaf “defences” (particularly structural ones) and long leaf lifespan, increasing the leaf construction costs (Eamus 1999; Cornelissen *et al.* 2003). High SLA species can have strategies associated with rapid production of new leaves during early life; faster leaf turnover of plant parts (*e.g.*, faster leaf turnover rate, which implies short lived leaves) permits also a more flexible response to the spatial patchiness of light and soil resources (Grime 1994).

To survive harsh dry-season conditions, leaves of evergreen species should be sclerophyllous, with low SLA (Eamus 1999). On contrary, deciduous species should have high photosynthetic rates (maximizing the light-catching area per unit of photosynthesizing mass – high SLA), to compensate their shorter payback period (Eamus 1999). Indeed, in four different habitats in northern Australia, deciduous species had higher SLA, lower leaf life span, and larger foliar N and P contents, associated with higher photosynthetic rates (see Franco *et al.* 2005), than did evergreen species (Prior *et al.* 2003). Analyzing data compiled from a wide range of vegetation types encompassing more than 2,000 species, Wright *et al.* (2005a) concluded that evergreen woody species had longer mean leaf life span and lower mean SLA than deciduous woody species, yet some evergreens showed leaf lifespans almost as short as for deciduous species with the shortest leaf life spans, and similarly high SLA. In the

cerrado, a study with 11 cerrado woody species found that deciduous species produced leaves with higher SLA and maximum CO₂ assimilation on a mass basis than evergreen ones (Franco *et al.* 2005). However, another study with 39 woody species of a *cerrado sensu stricto* site in southeastern Brazil did not find differences in SLA among evergreen, deciduous, semideciduous, and brevideciduous species (Paula 2002).

Plant height is associated with competitive vigour, whole plant fecundity, time intervals that plant species are generally given to grow between disturbances, and with tolerance or avoidance of environmental (climatic, nutrient) stress, as some tall plants may successfully avoid fire reaching the green parts and meristems in the canopy (Cornelissen *et al.* 2003). For instance, the survival of shrub species in a temperate woodland of semi-arid Australia increased with height (Hodgkinson 1998).

Along the cerrado physiognomic gradient, from pure grassland to woodland with a closed canopy of tall shrubs and scattered trees, mean and maximum tree height increase, and greater proportion of tree roots is present at deeper levels in the woodland (Castro and Kauffman 1998). Thus, closed cerrado physiognomies seem to present not only taller trees but also deeper-rooted trees. In this sense, although some small woody plants have deep roots (Eiten 1972), it is likely that in such physiognomies the trees presenting deeper roots are taller. For instance, in a northern Australian savanna, the volume of soil encountered by the roots of small trees was less than that of large trees (Prior and Eamus 1999). Jackson *et al.* (1999) measured the heights of both deciduous and evergreen species (five species for each group) in a cerrado woodland site, but did not analyze them. Apparently, the deciduous species were taller than the evergreen ones. Therefore, we may postulate, since the majority of the roots of the deciduous species are deeper (Jackson *et al.* 1999), that, in cerrado woodlands, deciduous species

are taller than evergreen ones.

We may also postulate that, in cerrado woodlands, deciduous species have higher SLA. Many of researcher assumptions about evergreen and deciduous habit (*e.g.*, associating deciduousness with high SLA) apply only to the extent that evergreenness is associated with long leaf lifespan (Reich *et al.* 1992). Many tropical rain forest species are evergreen, yet have leaf lifetimes lower than one year (Reich *et al.* 1991) and leaf traits (high SLA) that are similar to those of deciduous plants (from other biomes) with similar leaf lifetimes (Reich *et al.* 1992). Thus, differences in leaf traits researchers associate with evergreen *vs.* deciduous contrasts may be a result primarily of differences in leaf lifespan, and not with anything intrinsic in the evergreen *vs.* nonevergreen habit *per se* (Reich *et al.* 1992). Although Sarmiento and Monasterio (1983) concluded that leaves of savanna trees lived for about one year, Franco *et al.* (2005) found variation among cerrado evergreen species in regard to leaf longevity, ranging from 12 to 24 months. In the present study, we did not associate evergreenness in cerrado with long leaf lifespan. Instead, we related evergreenness and deciduousness with *longer* (not necessarily long) and *shorter* leaf lifespan, respectively, though not dealing with leaf lifespan itself but with SLA, a trait strongly correlated with the other (Reich *et al.* 1992).

The aim of this study was to test, in a disjoint savanna woodland (*cerrado sensu stricto*) site, with a rather closed canopy, in southeastern Brazil, whether two plant traits, specific leaf area and plant height, are potential predictors of two phenological groups, that is, deciduous and evergreen species. We tried to answer the following question: are SLA and plant height related to leaf phenology? In other words, can we predict leaf phenology of woody species in a cerrado woodland site based on SLA and

height?

Materials and methods

We conducted our study in a cerrado site, at Itirapina, São Paulo State, southeastern Brazil (22°12-13'S and 47°50-51'W, Fig. 1). The site is classified as *cerrado sensu stricto* (Coutinho 1990), which is a woodland according to Sarmiento (1984), and presents a rather closed canopy. The climate is Köppens's (1931) Cwa, that is, macrothermic temperate with rainy summers and not severely dry winters. The soil in the region is classified as sandy soil – Quartzipsamment (Oliveira and Prado 1984; Embrapa 1999). The area belongs to the São Paulo State Forestry Institute and is surrounded by *Pinus* spp. and *Eucalyptus* spp. plantations and protected from fire for approximately 20 years.

In this fragment, there is a grid of 200 quadrats (each one with 5 m x 5 m), where other researchers have been carrying out studies on population dynamics and community structure. We randomly picked 100 quadrats in this grid and conducted monthly field trips throughout a year, from May 2004 to April 2005. We sampled the woody component of the cerrado vegetation, defined as composed by all woody plants with stem diameter at soil level equal to or larger than 3 cm (SMA 1997). We identified each individual in field or, when necessary, by collecting samples for subsequent comparison with lodged material at the Federal University of São Carlos herbarium (Hufscar) or identification keys based on vegetative characters (Batalha *et al.* 1998; Batalha and Mantovani 1999).

We selected the species with at least 10 individuals (Cornelissen *et al.* 2003) and classified them according to their leaf phenology, based on the literature, as: 1) evergreen species (plants that maintain a canopy, including brevideciduous and semideciduous species; see Williams *et al.* 1997); and 2) deciduous species (plants that lose all leaves and remain leafless for some period, including briefly deciduous species; see Franco *et al.* 2005; Table 1). We classified the species not found in the literature [*Erythroxylum pelleterianum* A. St.-Hil., *Eugenia puniceifolia* (Kunth) A. DC., *Miconia rubiginosa* (Bonpl.) A. DC., *Myrcia lingua* (O. Berg) Mattos & D. Legrand] according to our data. In monthly field trips, we recorded whether a given individual had or had not lost all its leaves. After that, we calculated the proportion of individuals that lost all leaves throughout the study period for each species not found in the literature. Based on this proportion, we classified them as deciduous or evergreen species. The four species analyzed had low proportion of leafless individuals – *E. puniceifolia* had the highest proportion,

one leafless individual among eight studied (12.5%) –, so we classified all of them as evergreen species.

We followed the Cornelissen *et al.*'s (2003) protocol to sample plant height, and specific leaf area. We defined plant height as the distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level, expressed in metres, and measured it in 10 individuals per species, randomly sampled, using a telescopic stick. Specific leaf area is the one-sided area of a fresh leaf divided by its oven-dry mass, expressed in $\text{mm}^2 \text{mg}^{-1}$, so we took 20 leaves (two leaves from each individual) from 10 individuals per species, randomly sampled. We took digital pictures of each leaf and measured its area with the ImageJ V.1.33 software (Rasband 2004)). The average SLA for each individual plant was one statistical observation.

We applied logistic regression analysis (Hosmer and Lemeshow 1989; Ryan 1997) to test whether SLA and plant height could predict leaf phenology. First, we divided the total sample randomly into two subsamples, the analysis sample and the validation sample, following a proportionately stratified sampling procedure to make the analysis (Hair *et al.* 1998). The analysis sample and the validation sample comprised 60% and 40%, respectively, of the total sample, so, for each species considered, we sampled randomly six individuals for the analysis sample and four individuals for the validation sample to keep the same number of individuals for each species. Then, we modeled the relationship between the binary response variable (one = deciduous individual; zero = evergreen individual) and each of the explanatory variables (univariate analyses). Before conducting the multivariate analysis (multiple logistic regression), we checked whether the specific leaf area and the plant height were correlated, applying the Spearman correlation test (Sokal and Rohlf 1994). For the assessment of the significance of the models, we used the likelihood ratio test and the Wald statistic (Hosmer and Lemeshow 1989; Hair *et al.* 1998). For the measurement of the goodness of fit of the final model, we intended to use: 1) the “Nalgerke R^2 ”, the only measure of goodness of fit calculated using the analysis data set; 2) the correct classification rate (CCR) with a cutoff value based on the proportion of 1's; 3) the Pearson residuals; 4) the deviance residuals; and 5) the Hosmer and Lemeshow test (Hosmer and Lemeshow 1989; Neter *et al.* 1989; Ryan 1997). We carried out statistical analyses using Statistica 6.0 software (StatSoft Inc.) and Microsoft Office Excel 2003 (Microsoft Corporation).

Results

We found 26 species with at least 10 individuals, 12 of which classified as deciduous and 14 as evergreen (Table 1). Thus, the total sample comprised 260 observations, 120 coded as “deciduous” (code “one”) and 140 as “evergreen” (code “zero”). The analysis sample contained 156 observations (60% of the total sample), 72 for the deciduous group and 84 for the evergreen group, and the validation sample contained 104 observations (40% of the total sample), 48 for the deciduous group and 56 for the evergreen group.

Any variable whose univariate test has a p-value < 0.25 should be considered as a candidate for the multivariate logistic regression model (Mickey and Greenland 1989). The use of a more traditional level (such as 0.05) often fails to identify variables known to be important (Mickey and Greenland 1989). Besides, any univariate approach ignores the possibility that a collection of variables, each of which is weakly associated with the outcome, can become an important predictor of outcome when taken together (Hosmer and Lemeshow 1989).

Although the p-value of the univariate tests of the explanatory variables exceeded the level of 0.25 (Table 2), we decided to keep them as candidates for the multivariate model to search for a possible property when taken together and to explore the possibility of interaction between them. However, considering the analysis data set, specific leaf area and plant height were negatively correlated ($r_s = -0.33$; $p < 0.001$) and, consequently, we could not test the bivariate model. Thus, we considered the model containing just the plant height as the explanatory variable, since its association with the response variable was stronger, shown by the higher values of both Wald statistic and likelihood ratio test statistic. Because such model was not significant (Table 2), we did

not measure its goodness of fit. Therefore, specific leaf area and plant height could not predict leaf phenology for the species studied.

Discussion

Nearly half (46%) of the species sampled were deciduous, although most species of savanna trees appear as evergreen or as brevideciduous (Sarmiento and Monasterio 1983). The Brazilian cerrado, with a woody flora richer than any other tropical savanna area, has a larger number of deciduous species, but, nevertheless, they are far less numerous than the brevideciduous and evergreen species (Rizzini 1965; Sarmiento and Monasterio 1983). In a *cerrado sensu stricto* site, 33% of the species studied were deciduous (Paula 2002), whereas in a north Australian tropical savanna this proportion decreased to 27% (Williams *et al.* 1997).

Neither specific leaf area nor plant height could predict leaf phenology in the species studied. One may suggest that these results have phylogenetic influence, but in this study, if it exists, it is reduced for several reasons: the species studied belong to several families in each phenological group; although leaf phenology varies mainly among families, it also varies within them; and phenological patterns differ even within monophyletic groups in cerrado, namely Fabaceae (Bulhão and Figueiredo 2002).

Median values of specific leaf area ranged from 6.51 to 17.92 mm² mg⁻¹ and from 6.94 to 20.90 mm² mg⁻¹ for deciduous and evergreen species, respectively. Leaf mass per area (LMA), simply the inverse of SLA, is a useful index to assess sclerophylly (Witkowski and Lamont 1991). According to Rizzini (1979), leaves whose mass-area ratio is higher than 0.6 g dm⁻² (lower than 16.67 mm⁻² mg) can be considered sclerophyllous. In this sense, the majority of the species studied of both phenological

groups, except *Cybistax antisiphylitica* Mart. (deciduous species) and *Erythroxylum pelleterianum* A. St.-Hil. (evergreen species), could be considered sclerophyllous.

Sclerophylly in cerrado plants is common (Marquis *et al.* 2001) and has been related to soil nutrient deficiency, which limits the growth of plants and could lead them to accumulate carbohydrates as mechanical structures, such as cellulose depositions, thick cuticle, and sclerenchyma (Arens 1958). Low SLA, which is related to sclerophyllous leaves, is a common trait in nutrient-poor environments, probably because it allows a longer leaf life span and increased nutrient-use efficiency (Reich *et al.* 1992). SLA is also under selection according to light and water availability (Gutschick 1999; Niinemets 2001), so the high irradiances and seasonal drought typical of cerrado environments are likely to have contributed to the evolution of low SLA of species (Hoffmann *et al.* 2005). In this sense, soil nutrient deficiency, high irradiances, and seasonal drought seem to converge both phenological guilds of the cerrado woodland studied to similar values of SLA. Among evergreens, SLA is positively correlated with both mean annual temperature (MAT) and rainfall, whereas among deciduous species SLA decreases with MAT and shows no relationship to rainfall (Wright *et al.* 2005b).

Since SLA is strongly correlated with leaf life span (Reich *et al.* 1992), the similarity in SLA between deciduous and evergreen cerrado species may be due to the likely small difference between them regarding leaf life span. Although Franco *et al.* (2005) observed in cerrado that leaf lifespan of five deciduous species was about 10-11 months, whereas leaf lifespan of the six evergreen species varied from 12 to 24 months, Paula (2002) did not observe differences in some leaf traits (SLA included) among 39 cerrado species (divided in evergreen, deciduous, semideciduous, and brevideciduous species) and suggested that all species had similar leaf lifespan in spite of differences in

deciduousness degrees. Truly deciduous species – that is, those remaining leafless for several months – are less frequent and they often represent pioneering forest species colonizing certain savannas (Sarmiento and Monasterio 1983).

Similar values of plant height for both deciduous and evergreen species suggest two interpretations. First, the association between root depth and height would not exist for cerrado species in a manner that neither deep-rooted deciduous species would be necessarily taller nor shallow-rooted evergreen species would be necessarily shorter. Second, the association between root depth and height would exist, but it would be independent of leaf phenology. The latter implies that there would not be a link between leaf phenology and root depth, given that there is no link between the former and plant height, contrary to Jackson *et al.* (1999). Other studies in cerrado dealing with these traits – rooting depth, plant height, and leaf phenology – in larger number of species are needed to give good predictions.

Bulhão and Figueiredo (2002) suggested that the association between evergreen species and shallow roots (and, consequently, between deciduous species and deep roots) is simply due to the variation in leaf habit. Deciduous and semideciduous species that renew leaves at the end of the dry season may be facultative evergreen (Bulhão and Figueiredo 2002). Evergreen species may present deciduousness due to higher water loss caused by very dry periods or by dryer microsites (Borchert 1994). The deciduousness degree both within and between species may vary temporally and spatially, so correlations involving leaf habit should be taken cautiously (Morais *et al.* 1995; Bulhão and Figueiredo 2002). Sampling longer periods of leaf production and fall in cerrado is needed to investigate patterns of leaf habit.

The rather closed canopy of the woodland cerrado studied suggests an increased

competition for light, which would favour increased investment in height growth (Givnish 1982). In our study site, both phenological guilds seem to respond equally to the running for light in terms of height. The typical soil nutrient deficiency of cerrado, however, may place constraints in plant canopy height regardless of the leaf habit. Increasing soil nutrient availability results in higher plant canopy height (Haridasan 2000), and the height of reproductive individuals of savanna species averages half that of congeneric forest species (Hoffmann *et al.* 2003).

According to Franco *et al.* (2005), deciduous and evergreen trees share common relationships between leaf traits, which suggests that selective pressures impose strong constraints on functional trait variability in cerrado environments. Six co-occurring cerrado species shared similar functional relationships between wood density and leaf- and whole-plant level traits, which meant that rather than differing intrinsically in physiological responsiveness to the cerrado environment, such species appeared to have operating ranges along common physiological response curves (Bucci *et al.* 2004). Additionally, damage caused by either insects or pathogens was similar among cerrado species despite their interspecific differences in leaf phenology (Marquis *et al.* 2001).

Following Bucci *et al.* (2004), resource allocation patterns often result in enhancement of a particular function at the expense of another, particularly in resource-limited environments, such as those with low water and nutrient availability. The same authors showed for some cerrado trees that allocation of resources to the production of wood of high density constrains other patterns of resource allocation in a manner that individuals with dense wood had leaves with low SLA and relatively shallow root systems. Since woody density is associated with several leaf properties and variation in woody density is a strong predictor of variation in a suite of characteristics related to

water transport properties and regulation of leaf water deficits (Bucci *et al.* 2004), incorporating such trait in the studies of phenological groups in cerrado would be welcome.

High atmospheric evaporative demand and hydraulic constraints result in strong stomatal limitation of transpiration and a prolonged midday depression of photosynthetic rates in both evergreen and deciduous species during both wet and dry seasons (Meinzer *et al.* 1999; Franco and Lüttge 2002; Bucci *et al.* 2005). According to Prado *et al.* (2004), however, there was no severe water stress during the dry season for 22 species of a cerrado woodland site. The same authors found no relationship between leaf phenology and morning leaf water status or gas exchange throughout the year and concluded that: 1) distinct leaf shedding intensity could represent only how much leaf area each species needs to lose to keep transpiration in pace with water extraction and water lift capacity in the dry season and 2) the remaining leaves after shedding tend to respond in the same way under drought despite species deciduousness, prevailing a general behavior for leaf gas exchange and leaf water status maintenance. Periods of vegetative growth and dormancy in the cerrado may be more synchronized with variation of the photoperiod, thermoperiod, and irradiance than seasonal variations of water availability (Bulhão & Figueiredo 2002).

Stressed or not, both deciduous and evergreen species in cerrado woodland seem to behave similarly in regard to leaf gas exchange and water status throughout the year. These similarities are reflected in several traits and our results suggest that SLA and plant height are two of them, though deciduous and evergreen species may adopt distinct strategies concerning other traits. For example, deciduous cerrado species are related to organ preformation in buds, early budding, and reduced shoot growth pattern

(in time and space), whereas evergreen species are linked to continuous budding and branching throughout the year (Damascos *et al.* 2005; Damascos in press).

In summary, SLA and plant height could not predict leaf phenology for the species studied. The majority of the species of both phenological groups could be considered sclerophyllous (low SLA), a common feature in cerrado associated with the low soil nutrient content. The similarity in SLA between deciduous and evergreen cerrado species may be due to the likely small difference between them regarding leaf life span, and the effects of the soil nutrient deficiency not only on specific leaf area but also on plant height of cerrado woody plants seem to lead to convergent adaptative adjustments – sclerophylly and occupation of similar vertical stratum. The absence of relationship between leaf phenology and the two plant traits studied reinforces the suggestion of Bucci *et al.* (2004), according to whom cerrado tree species may possess a limited number of physiological and morphological solutions for coping with seasonal drought.

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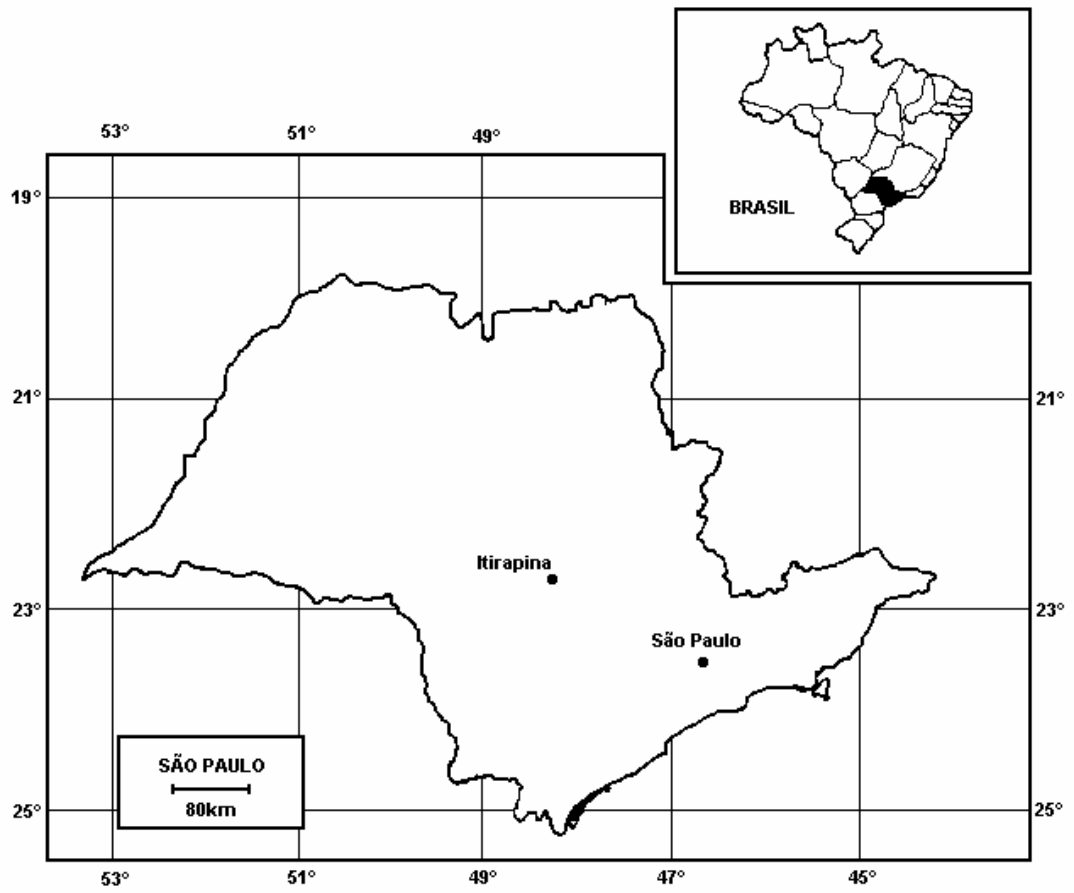


Fig. 1. Location of Itirapina, São Paulo State, southeastern Brazil, 22°12-13'S and 47°50-51'W (modified from Salis *et al.* 1995).

Table 1. Leaf phenology (LP) – evergreen (e) or deciduous (d) – with its respective reference, and specific leaf area (SLA) and plant canopy height (H) of the species sampled in Itirapina, southeastern Brazil

The data presented are median values with their respective median absolute deviation

Species	Family ^A	LP ^B	reference for LP ^C	SLA (mm ² /mg)	H (m)
<i>Acosmium subelegans</i> (Mohl.) Yakovlev	FAB	e	Lorenzi 2000	11.55 (0.67)	2.54 (0.60)
<i>Eriotheca gracilipes</i> (K.Schum.) A.Robyns	MLV	e	Paula 2002	9.07 (0.64)	2.86 (0.62)
<i>Erythroxylum pelleterianum</i> A.St.-Hil.	ERX	e (0/4)	PO	20.90 (1.65)	2.39 (0.65)
<i>Eugenia puniceifolia</i> (Kunth) DC.	MRT	e (1/8)	PO	9.73 (2.44)	5.07 (0.56)
<i>Miconia albicans</i> Triana	MLS	e	Paula 2002	7.88 (0.77)	2.43 (0.40)
<i>Miconia rubiginosa</i> (Bonpl.) DC.	MLS	e (2/28)	PO	6.94 (1.38)	4.11 (1.65)
<i>Myrcia lingua</i> (O.Berg) Mattos and D.Legrand	MRT	e (8/130)	PO	8.57 (1.39)	3.12 (0.93)
<i>Ocotea pulchella</i> Mart.	LAU	e	Lorenzi 2000	9.09 (0.97)	4.18 (0.66)
<i>Ouratea spectabilis</i> Engl.	OCH	e	Leitão 1998	8.16 (1.11)	4.47 (1.27)
<i>Pouteria torta</i> Radlk.	SPT	e	Silva Júnior 2005	9.66 (0.97)	4.15 (1.28)
<i>Rapanea guianensis</i> Aubl.	MRS	e	Morais <i>et al.</i> 1995	9.65 (1.06)	4.21 (0.77)
<i>Schefflera vinosa</i> (Cham. and Schltdl.) Frodin and Fiaschi	ARL	e	Prado <i>et al.</i> 2004	7.12 (0.61)	3.20 (0.64)
<i>Vochysia tucanorum</i> Mart.	VOC	e	Lorenzi 2000	12.43 (0.72)	3.27 (1.37)
<i>Xylopia aromatica</i> Mart.	ANN	e	Paula 2002	11.29 (1.18)	4.97 (0.79)
<i>Anadenanthera falcata</i> (Benth.) Speg.	FAB	d	Paula 2002	8.18 (1.17)	6.38 (2.45)
<i>Aspidosperma tomentosum</i> Mart.	APO	d	Paula 2002	10.46 (1.07)	1.84 (0.62)
<i>Bauhinia rufa</i> (Bongard) Stendel	FAB	d	Prado <i>et al.</i> 2004	12.28 (1.90)	3.29 (0.47)
<i>Blepharocalyx salicifolius</i> (Camb.) Burr.	MRT	d	Morais <i>et al.</i> 1995	10.77 (1.72)	5.42 (1.65)
<i>Bowdichia virgilioides</i> Kunth	FAB	d	Paula 2002	7.50 (0.92)	6.11 (1.28)
<i>Byrsonima coccolobifolia</i> A.Juss.	MLP	d	Marquis <i>et al.</i> 2001	11.80 (2.66)	3.56 (1.22)
<i>Cydistax antisiphylitica</i> Mart.	BIG	d	Silva Júnior 2005	17.92 (1.25)	1.84 (0.73)
<i>Dalbergia miscolobium</i> Benth.	FAB	d	Franco <i>et al.</i> 2005	7.63 (0.70)	8.49 (2.80)
<i>Diospyros hispida</i> A.DC.	EBN	d	Paula 2002	8.09 (1.43)	1.62 (0.50)
<i>Guapira noxia</i> (Netto) Lundell	NYC	d	Silva Júnior 2005	12.08 (0.59)	1.89 (0.58)
<i>Pouteria ramiflora</i> Radlk.	SPT	d	Silva Júnior 2005	9.10 (1.44)	4.81 (1.50)
<i>Qualea grandiflora</i> Mart.	VOC	d	Franco <i>et al.</i> 2005	6.51 (1.50)	4.50 (1.45)

^AFamily names are abbreviated according to Weber (1982)

^BProportion of leafless individuals, in parentheses, for each species not found in the literature

^CPO = personal observation

Table 2. Univariate logistic regression models

The univariate models are: specific leaf area model (“SLA”) and plant height model (“H”); $\hat{\beta}$ = parameter estimate of the variable for the univariate model (the constants of the univariate models were omitted); \hat{SE} = estimated standard error of the parameter estimate; W = univariate Wald statistic; L = likelihood value for the univariate model; G = likelihood ratio test statistic. The first row shows the constant only model.

model	$\hat{\beta}$	\hat{SE}	W	p	L	G	p
constant	-0.154	0.161	0.921	0.337	-107.669		
SLA	-0.001	0.046	0.001	0.979	-107.669	0.001	0.979
H	0.056	0.078	0.516	0.473	-107.410	0.518	0.472

Conclusão geral

Conclusão geral

Este trabalho permitiu-nos chegar às seguintes conclusões:

- Os três atributos funcionais propostos no esquema por Westoby (1998) – área foliar específica, altura da planta e massa da semente – não puderam prever as guildas de dispersão – espécies abioticamente dispersas de um lado e espécies dispersas por agentes bióticos de outro – no cerrado *sensu stricto*; em outras palavras, as duas guildas de dispersão nesse local são compostas por espécies que não diferem quanto aos três atributos funcionais estudados;
- A área foliar específica e a altura da planta também não puderam prever os dois grupos fenológicos, espécies decíduas e sempre-verdes, na área estudada; ou seja, os dois grupos fenológicos são compostos por espécies que não diferem com relação a esses atributos;
- No cerrado *sensu stricto*, a similaridade entre as duas guildas de dispersão e entre os dois grupos fenológicos, no que diz respeito à área foliar específica, deve ser influenciada pela similaridade na altura das plantas (hábitats com disponibilidade de luz parecida) e pela esclerofilia, característica relacionada à deficiência nutricional do solo do cerrado;
- As espécies arbustivo-arbóreas do cerrado *sensu stricto* possuem ajustes adaptativos convergentes, tanto no que diz respeito à área foliar específica (baixos valores –

esclerofilia) quanto no que diz respeito à altura (ocupação do mesmo estrato vegetacional).