

UNIVERSIDADE FEDERAL DE SÃO CARLOS

Programa de Pós-Graduação em Ecologia e Recursos Naturais

Centro de Ciências Biológicas e da Saúde

FERNANDA QUINTAS MARTINS

**SISTEMAS DE POLINIZAÇÃO EM
FRAGMENTOS DE CERRADO NA REGIÃO DO
ALTO TAQUARI (GO, MS, MT)**

Orientador: Prof. Dr. Marco Antônio Batalha

São Carlos - SP

fevereiro de 2005

**Ficha catalográfica elaborada pelo DePT da
Biblioteca Comunitária da UFSCar**

M386sp

Martins, Fernanda Quintas.

Sistemas de polinização em fragmentos de Cerrado na região do Alto Taquari (GO, MS, MT) / Fernanda Quintas Martins. -- São Carlos : UFSCar, 2005.

90 p.

Dissertação (Mestrado) -- Universidade Federal de São Carlos, 2005.

1. Cerrados 2. Polinização 3. Distribuição espacial. I. Título.

CDD: 581.5264 (20ª)

Dedico este trabalho aos meus pais, Rita e Toninho, e ao Daniel, que, com amor, fizeram com que cada passo da minha vida fosse ainda mais especial.

Agradecimentos

Ao Prof. Dr. Marco Antônio Batalha, pela orientação cuidadosa, pelo valioso exemplo de conduta profissional e pelo apoio, compreensão e paciência, sem as quais não seria possível a realização deste trabalho;

Ao CNPq, pela bolsa a mim concedida (134362/03-9);

Ao Instituto Conservação Internacional do Brasil, em especial aos Drs. Mário Barroso Ramos-Neto e Paulo Gustavo do Prado Pereira, pelo apoio financeiro e logístico;

Às Fundações Emas e Oréades Núcleo de Geoprocessamento, sem as quais não conseguiríamos realizar nossas pesquisas nas áreas escolhidas;

Aos companheiros César Trento, Júlia Caram, André Vítor Fleuri Jardim e Rodrigo Rodrigues, pelas inesquecíveis horas passadas no campo. Aliás, sem vocês, minha tarefa de coleta e medição teria sido impossível;

Ao amigo Bufinha e à prefeitura de Alcinópolis, que muito ajudaram, dando-nos toda a atenção e apoio de que necessitamos;

Aos professores Manoel Martins, Maria Inês Salgueiro Lima e Dalva Maria da Silva Matos, pelas valiosas sugestões;

Ao PPG-ERN e ao Prof. Dr. José Eduardo dos Santos, por depositarem confiança no meu trabalho e fornecerem tudo de que precisei para a realização deste projeto;

Ao Prof. Dr. Fernando Roberto Martins, pelas orientações e sugestões em boa hora;

Aos colegas do laboratório de Ecologia Vegetal, Marcus, Igor, Priscilla e André, pelo companheirismo e apoio na convivência desfrutada;

A todos os colegas da pós-graduação, principalmente ao Alessandro, Manhães, Rodrigo e Fran, pelos momentos de descontração e ajuda mútua;

Aos amigos “de longe”, especialmente à Mariângela Alves, por ser uma grande amiga, de todas as horas, por toda a vida;

Aos amigos Lucas e Aniele, pelas palavras de incentivo e pelos momentos de descontração em nossos papos no fim de tarde;

A toda minha família, pelo apoio que sempre me dedicaram, principalmente à Renata, pelo carinho e amizade, além dos momentos de boas gargalhadas;

Aos meus irmãos, Marcelo e Murilo, pelo carinho, estímulo e confiança, além das boas ‘churrascadas’ nos raros fins de semana que nos víamos;

Às pessoas mais importantes da minha vida, meus pais, pelo ‘porto seguro’ que sempre representaram na minha vida, por todo o apoio, força, amor e confiança que sempre me dedicaram e que jamais conseguirei retribuir;

A Selminha, a quem muito devo por ter sempre estado presente na minha vida, dando-me todo o seu carinho, amor, atenção e paciência;

Ao Daniel, que, mais do que ter me apoiado, esteve comigo durante todas as etapas do meu trabalho, principalmente nas horas mais difíceis, sempre me ouvindo e ajudando, com muita paciência e carinho;

A todos que não foram citados, mas que estiveram presentes nestes dois anos de trabalho, auxiliando-me de uma forma ou de outra;

Por fim, agradeço a Deus, não apenas por mais esta realização em minha vida, mas também por ter colocado todas essas pessoas maravilhosas no meu caminho.

A TODOS, MUITO OBRIGADA!

“Eu poderia suportar, embora não sem dor,
que tivessem morrido todos os meus amores,
mas enlouqueceria se morressem todos os meus amigos!

A alguns deles não procuro, basta-me saber que eles existem.

Esta mera condição me encoraja a seguir em frente pela vida,

mas é delicioso que eu saiba e sinta que os adoro,

embora não declare e não os procure sempre...”

Vinicius de Moraes

Sumário

Resumo	8
Abstract	10
I - Introdução geral	12
Introdução geral	13
Referências bibliográficas	19
II – Capítulo 1	23
Pollination systems and floral traits in cerrado woody species of the Upper Taquari region (central Brazil)	25
Abstract.....	26
Resumo.....	26
Introduction.....	27
Material and Methods	29
Results	32
Discussion	33
References	36
III - Capítulo 2	49
Vertical and horizontal distribution of pollination systems in cerrado fragments of central Brazil.....	51
Abstract.....	52
Introduction.....	54
Material and Methods	56
Results	58
Discussion	59
References	62

IV - Apêndice	74
Tentativa para chave de identificação de sistemas de polinização em espécies arbustivo-arbóreas de cerrado	75
V - Conclusão Geral	77
V - Referências bibliográficas	80

Resumo

O Domínio do Cerrado ocupava originalmente cerca de 23% do território brasileiro (aproximadamente 2 milhões de km²), especialmente no Planalto Central, sendo a segunda maior província fitogeográfica do Brasil. A vegetação de cerrado não é uniforme na sua fisionomia, variando desde campo limpo a cerradão, mas a maior parte das fisionomias se enquadra na definição de ‘savana’. É estimado que ocorra de 3.000 a 7.000 espécies de plantas vasculares nesse tipo de vegetação, das quais de 1.000 a 2.000 espécies pertencem ao componente arbustivo-arbóreo.

Diferentes autores tentaram usar características reprodutivas para explicar os padrões gerais de diversidade e estrutura de comunidade encontrados em florestas tropicais, com a idéia de que a diversidade das plantas e a distribuição espacial são dependentes de processos reprodutivos. Estudos na biologia reprodutiva de espécies de planta de cerrado mostraram uma grande diversidade de sistemas de polinização, semelhantes àqueles encontrados em florestas neotropicais. Os dados que emergem para a biologia reprodutiva de plantas têm conseqüências importantes para conservação e entendimento da organização das comunidades de cerrado.

Amostramos cinco fragmentos de cerrado *sensu stricto* no Planalto Central brasileiro, em que amostramos os indivíduos arbustivo-arbóreos. Usando os dados florísticos de todas as nossas coletas, nós amostramos 2.280 indivíduos, representando 121 espécies e 38 famílias. As famílias mais ricas foram Fabaceae e Myrtaceae, sendo *Davilla elliptica* A. St-Hill e *Myrcia bella* Triana as espécies mais bem representadas. A maioria das espécies apresentou flores abertas, com antese diurna, cores claras e pólen como recompensa floral. Na vegetação de cerrado, as espécies com flores visitadas principalmente por abelhas e também pelos ‘insetos pequenos’ formaram os principais grupos ecologicamente relacionados com a polinização. Das 121 espécies, 65 foram polinizadas principalmente por abelhas; 30 por insetos pequenos; 15 por mariposas; cinco por morcegos; três por besouros; dois por beija-flores e um pelo vento.

A análise de ordenação dos caracteres florais e das espécies vegetais mostrou que houve um agrupamento entre espécies com alguns sistemas de polinização, para os quais inferências baseadas em caracteres florais são recomendadas, como as espécies polinizadas por morcegos, mariposas e aves. Já com relação às espécies polinizadas principalmente por abelhas e insetos pequenos, essas inferências baseadas em caracteres florais não são recomendadas devido à grande dispersão e sobreposição entre essas duas classes. A grande dispersão e sobreposição das classes de abelhas e insetos pequenos ocorreram provavelmente devido à ausência de especificidade nas relações planta-polinizador.

Para quatro dos cinco sistemas de polinização com pelo menos dez indivíduos, nós não encontramos nenhuma variação significativa em relação à distância da borda do fragmento, exceto para as plantas polinizadas por besouros, para as quais houve uma diminuição na frequência em direção ao interior do fragmento. De maneira semelhante, encontramos variação significativa em relação à altura somente para plantas polinizadas por morcegos, para as quais houve um aumento da frequência com a altura das árvores. Em geral, não encontramos variações horizontais e verticais nos sistemas de polinização, ao contrário do que foi encontrado em florestas, provavelmente, como consequência da fisionomia mais aberta dos fragmentos de cerrado.

Palavras-chave: Análise de Componentes Principais, Brasil central, caracteres florais, cerrado, distribuição espacial, estratificação, polinização.

Abstract

The Cerrado Domain occupied originally 23% of the Brazilian territory (ca. 2 million km²), especially in the Central Plateau, being the second largest phytogeographic province of Brazil. The cerrado vegetation is not uniform in physiognomy, ranging from grassland to tall woodland, but most of its physiognomies lie within the range defined as tropical savanna. It is estimated that 3,000 to 7,000 vascular plant species occur in this vegetation type, from which 1,000 to 2,000 belong to the woody component.

Different authors have attempted to use reproductive features to explain the general patterns of diversity and community structure found in tropical woodlands with the underlying idea that plant diversity and spatial distribution is dependent on reproductive processes. Studies on the reproductive biology of cerrado plant species have shown a great diversity of pollination systems, similar to those found in Neotropical forests. The data emerging for the reproductive biology of plants have important consequences for conservation and understanding of the organization of cerrado communities.

We sampled five cerrado fragments in the Brazilian Central Plateau, in which we sampled woody individuals. Using the floristic data of all our field trips, we sampled 2,280 individuals, representing 121 species and 38 families. The richest families were Fabaceae and Myrtaceae, and *Davilla elliptica* A. St-Hill and *Myrcia bella* Triana were the best represented species. Most species presented open flowers, with diurnal anthesis, pale colors and with pollen as floral reward. In the cerrado vegetation, species with flowers visited mainly by bees and 'small insects' were the main groups ecologically related to the pollination. Of the 121 species, 65 were pollinated mainly by bees; 30, by small insects; 15, by moths; five, by bats; three, by beetles; two, by hummingbirds; and one, by wind.

The ordination analysis of floral characteristics and plant species showed that there was a grouping of species with some pollination systems, for which inferences based on floral

characteristics are recommended, such as the species pollinated by bats, moths, and birds. On the other hand, for the species pollinated mainly by bees and small insects, these inferences are not recommended due their great dispersion throughout ordination axes and large overlapping. These dispersion and overlapping occurred probably due the absence of specificity between plants and pollinators.

For four of the five pollination systems with at least ten individuals, we found no significant variation in relation to distance from edge, except for plants pollinated by beetles, for which there was a decrease in the frequency to toward the fragment interior. Similarly, we only found significant variation in relation to the height for plants pollinated by bats, for which there was an increase of the frequency with the height of the trees. In general, we found no horizontal and vertical variations in the pollination systems, contrary to what was found in forests and, probably, as consequence of the more open physiognomy of the cerrado fragments.

Key words: central Brazil, cerrado, floral traits, pollination, Principal Components Analysis, spatial distribution, stratification.

I – INTRODUÇÃO GERAL

Introdução geral

O cerrado é conhecido por sua grande riqueza de espécies, compreendendo de 3.000 a 7.000 espécies de plantas vasculares (Castro *et al.* 1999). Estudos sobre os sistemas reprodutivo, sexual e de polinização na vegetação de cerrado têm sido realizados em diversos táxons, inclusive com abordagem comunitária, a maioria deles incluindo espécies do componente arbustivo-arbóreo (*e.g.*, Oliveira & Gibbs 2000). A biologia da polinização nos Neotrópicos, em nível de comunidade, tem sido estudada tanto em áreas florestais (Bawa *et al.* 1985, Kress & Beach 1994), quanto em áreas de cerrado (Silberbauer-Gottsberger & Gottsberger 1988, Barbosa 1997, Borges 2000, Oliveira & Gibbs 2000), ainda que, por enquanto, o número de trabalhos ainda seja relativamente baixo (Ramirez 2004).

Esses estudos têm uma importância fundamental para o entendimento de vários processos biológicos, principalmente daqueles relacionado às interações planta-animal (Ramirez & Brito 1987). A ecologia da polinização é de grande importância para a compreensão da estrutura das comunidades vegetais naturais (Silberbauer-Gottsberger & Gottsberger 1988, Machado 1990), fornecendo informações sobre a composição genética de populações vegetais (Proctor & Yeo 1972) e abordando aspectos da biologia floral, tais como período de antese e disponibilidade de néctar e pólen (Sazima *et al.* 1994). Além disso, esses estudos fornecem informações sobre a forma das flores, permitindo assim caracterizar mecanismos de polinização e adequação do visitante à flor (Sazima & Sazima 1990, Buzato *et al.* 1994). As relações entre planta-polinizador também são importantes na estruturação das comunidades, podendo influenciar a distribuição espacial das plantas, a riqueza, a abundância de espécies, a estrutura trófica e a fenodinâmica (Bawa *et al.* 1985, Morellato 1991), bem como a diversidade genética com a promoção do fluxo de genes (Nason *et al.* 1997). Essas informações podem ser utilizadas em estudos de regeneração de áreas degradadas, manejo de populações naturais e preservação do ambiente (Kevan & Baker 1983, Sazima & Sazima 1989, Kageyama 1992).

O espectro de visitantes para plantas em uma dada área é determinado por muitos fatores, sendo o mais óbvio a sobreposição entre o período de florescimento de cada espécie e os períodos de atividade dos animais naquela área (Bosch *et al.* 1997). Dada essa sobreposição, cada espécie de planta apresenta características morfológicas e fisiológicas específicas que podem atrair certos grupos de visitantes florais em detrimento de outros (Bosch *et al.* 1997). Tradicionalmente, a esse diferencial da atratividade tem sido dada uma maior importância, interpretando por que visitantes específicos são observados em determinadas flores, o que levou ao estabelecimento das síndromes de polinização (baseadas na cor e forma das flores, presença de recompensas e odores, e sistemas sexuais), supostamente adaptadas a tipos específicos de polinizadores (Faegri & Pijl 1979). A tradicional visão em estudos de polinização – baseados no conceito de síndrome (Faegri & Pijl 1979) – sustenta que sistemas de polinização tendem à especialização. Tal visão tem sido questionada há alguns anos, com base em evidências de uma ampla generalização dos sistemas de polinização (*e.g.*, McDade 1992, Waser *et al.* 1996, Herrera 1996, Ollerton 1996). Muitos fatores, tais como formas de vida da planta, estrato vegetacional, abundância, sistema sexual, fauna local, dentre outros, podem influenciar o grau de especialização e generalização dos sistemas de polinização. (Stebbins 1970, Ollerton 1996, Waser *et al.* 1996, Johnson & Steiner 2000).

Relações mais específicas são encontradas entre as espécies de determinadas famílias e categorias particulares de animais. Por exemplo, as espécies de Malpighiaceae e as abelhas coletoras de óleos são mutuamente adaptadas, estabelecendo forte inter-relação como consequência da produção de óleo e sua utilização por um grupo especializado de polinizadores (Anderson 1979, Buchman 1987, Vogel 1990). Flores com anteras poricidas necessitam de vibração dessas estruturas por abelhas para garantir a polinização, e as abelhas que visitam essas flores apresentam características morfológicas específicas que as permitem a exploração do pólen (Buchmann 1983). Interação de espécies de Annonaceae e besouros na polinização também ocorrem no cerrado (Gottsberger 1989, Gottsberger 1994). Flores com antese noturna

representam outra forma de interação específica, uma vez que limitam a polinização a determinados grupos de visitantes, como besouros, mariposas e morcegos (Borges 2000).

No entanto, muitas vezes, vários grupos diferentes de animais podem efetuar a polinização de uma só espécie (Silberbauer-Gottsberger & Gottsberger 1988). Os polinizadores costumam ser classificados como ‘exclusivos’, quando apenas este executa a polinização de uma determinada espécie vegetal; como ‘principais’, quando um grupo animal poliniza uma determinada espécie com mais eficácia que outros grupos, também envolvidos na polinização; e ‘adicionais’, quando este eventualmente poliniza determinada espécie, sendo o terceiro em importância. A participação de um grupo animal na polinização como exclusivo, principal ou adicional depende das condições morfológicas, fenológicas e ambientais existentes (Silberbauer-Gottsberger & Gottsberger 1988). Em resumo, o grau de habilidade dos visitantes e o sucesso reprodutivo de cada planta variam em função do número e do tipo de visitantes que a espécie atrai (Schemske & Horvitz 1984), com vários fatores influenciando o movimento do pólen, dentre os quais se destacam a densidade e a distribuição das plantas, as características estruturais do hábitat e as respostas comportamentais dos polinizadores (Barret & Eckert 1990). Quando a especialização ocorre, visitantes devem diferir não apenas em suas características gerais, mas também na forma de interferir na interação das características florais e da aptidão da planta (Schemske & Horvitz 1984).

Na vegetação de cerrado, as espécies com flores visitadas exclusivamente por abelhas e espécies visitadas por duas ou mais categorias de animais (‘insetos pequenos’) formam os principais grupos ecologicamente relacionados à polinização (Borges 2000, Oliveira & Gibbs 2000). O domínio das abelhas como polinizadores de plantas também é visto em outras formações tropicais (*e.g.*, Bawa *et al.* 1985, Ramirez 1989, Ramirez & Brito 1992, Kress & Beach 1994). Estudos da biologia reprodutiva de plantas de cerrado têm mostrado uma grande diversidade de sistemas de polinização, os quais são semelhantes àqueles encontrados em outras florestas neotropicais (Oliveira & Gibbs 2002).

Assim, na medida em que a importância da reprodução sexuada de plantas do cerrado fica evidente (Oliveira & Silva 1993, Saraiva *et al.* 1996, Oliveira & Gibbs 2000), pesquisas acerca dos mecanismos envolvidos em todas as suas etapas tornam-se cada vez mais necessárias. No presente trabalho, definimos os sistemas de polinização, considerando-se apenas as categorias principais de visitantes, sendo estabelecidos a partir de literaturas pertinentes, já que não houve observações diretas em campo. Amostramos cinco fragmentos de cerrado *sensu stricto* na região central do Brasil (Fig 1), abrangendo os estados de GO, MT (Fig 2) e MS (Fig 3). Procuramos analisar com que proporções os sistemas de polinização aparecem na vegetação de cerrado e se é possível inferir o principal sistema de polinização das espécies lenhosas baseados em caracteres florais (Capítulo 1) e como estes sistemas de polinização estavam distribuídos na comunidade, tanto em relação ao estrato vertical quanto ao horizontal (Capítulo 2).

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 'Brazilian Journal of Biology'. O capítulo 2 foi formatado segundo as normas da revista 'Biotropica'. Devido a essas normas, os capítulos foram redigidos na língua inglesa. Os dois artigos já foram submetidos às revistas e estamos aguardando os pareceres dos assessores. Como os capítulos são independentes, repetições tornaram-se inevitáveis. Nós incluímos ainda como apêndice uma primeira tentativa para uma chave dicotômica para se identificar os sistemas de polinização de espécies arbustivo-arbóreas de cerrado, com base nos resultados que encontramos. Quando testada e aprovada, uma chave como essa serviria para se determinar o principal grupo polinizador de espécies arbustivo-arbórea de cerrado sem que sejam necessárias observações diretas dos polinizadores.

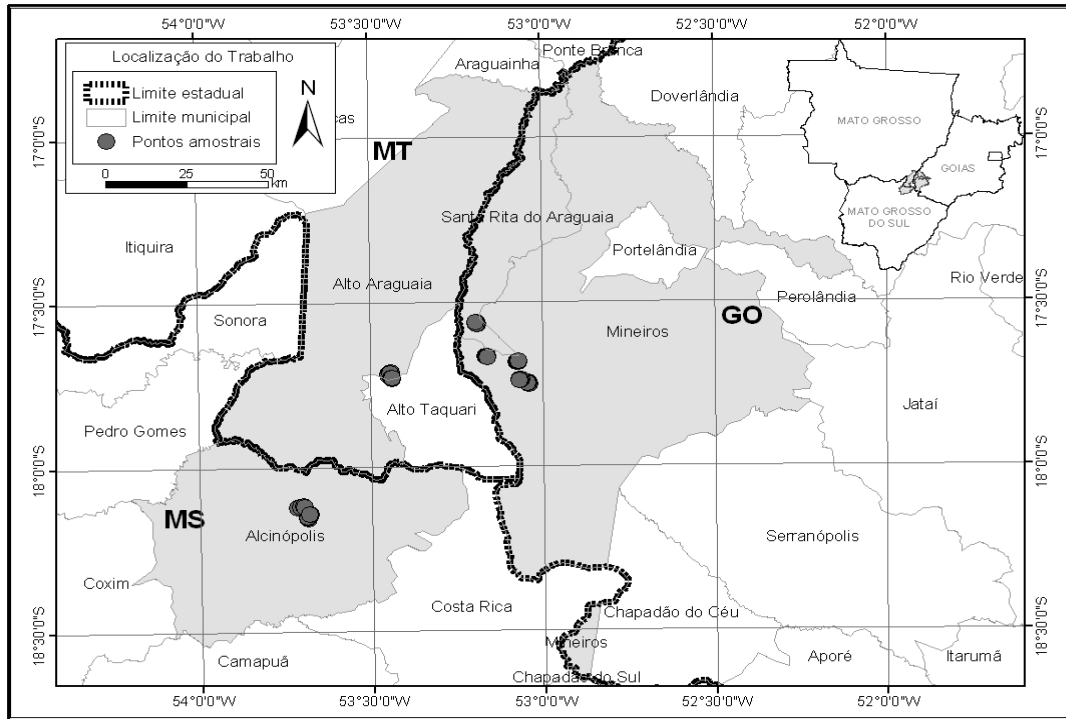


Figura 1 – Localização das áreas amostradas, abrangendo os estados de GO, MT e MS.

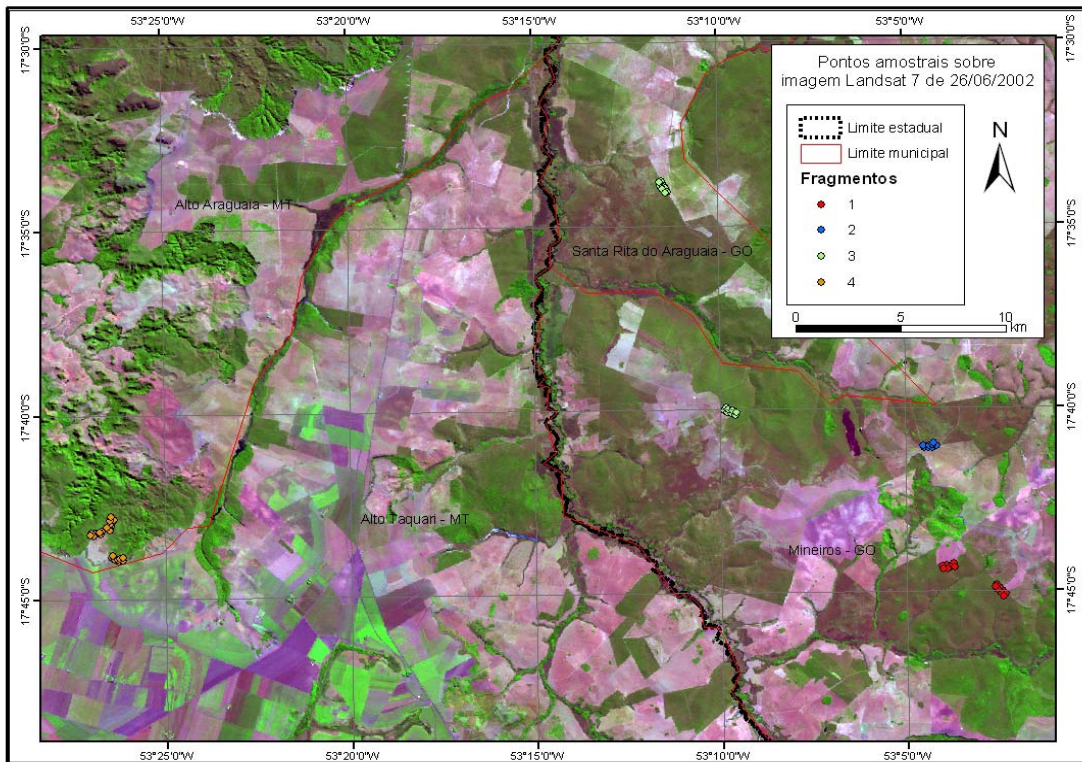


Figura 2 – Localização da área de estudo, mostrando os quatro fragmentos amostrados nos estados de Goiás e Mato Grosso.

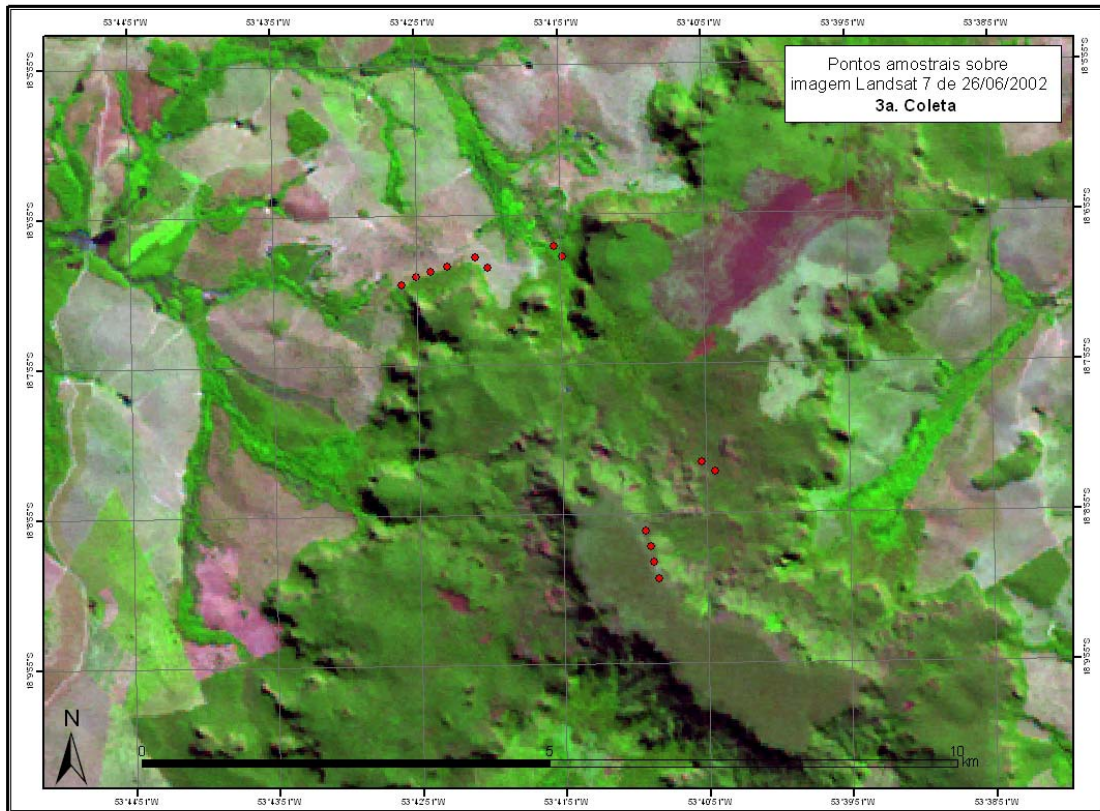


Figura 3 – Localização da área de estudo, mostrando o fragmento amostrado no estado de MS.

Referências bibliográficas

- Anderson W.R. 1979. Floral conservatism in Neotropical Malpighiaceae. *Biotropica* 11: 219-223.
- Barbosa A.A. 1997. *Biologia reprodutiva de uma comunidade de campo sujo, Uberlândia – MG*. Tese de Doutorado. Universidade Estadual de Campinas, Brasil.
- Barret S.C.H. & Eckert C.G. 1990. Current issues in Plant Reproductive Ecology. *Isr. J. Bot.* 39: 5-12.
- Bawa K.S., Bulloch S.H., Perry D.R., Coville R.E. & Grayum M.H. 1985. Reproduction biology of tropical lowland rain forest tree. II. Pollination system. *Am. J. Bot.* 72: 346-356.
- Borges H.B.N. 2000. *Biologia reprodutiva e conservação do estrato lenhoso numa comunidade do cerrado*. Tese de Doutorado. Universidade Estadual de Campinas, Brasil.
- Bosch J., Retana J. & Cerdá X. 1997. Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia* 109: 583-591.
- Buchmann S.L. 1983. Buzz pollination in angiosperms. In: Jones C.E. & Little R.J. (eds.), *Handbook of Experimental Pollination Biology*. Van Nostrand Reinhold, New York, pp. 73-113.
- Buchmann S.L. 1987. The ecology of oil flowers and their bees. *Annu. Rev. Ecol. Syst.* 18: 343-369.
- Buzato S., Franco A.L.M. & Sazima M. 1994. Adequação de *Camptosema scarlatinum* e *Collaea speciosa* à polinização por beija-flores. In: *Resumos do XLV Congresso Nacional de Botânica*: 64.
- Castro A.A.J.F., Martins, F.R., Tamashiro J.Y. & Shepherd G.J. 1999. How rich is the flora of the Brazilian cerrados? *Ann. Mo. Bot. Gard.* 86: 192-224.
- Faegri K. & Pijl L. van der. 1979. *The principles of pollination ecology*. Pergamon, New York.
- Gottsberger G. 1989. Beetle pollination and flowering rhythm of *Annona* sp. (Annonaceae) in Brazil. *Plant Syst. Evol.* 167: 165-187.
- Gottsberger G. 1994. As anonáceas do cerrado e a sua polinização. *Rev. Brasil. Biol.* 54: 391-402.

- Herrera C.M. 1996. Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. In: Lloyd D.G. & Barret S.C.H. (eds.), *Floral biology: studies on floral evolution in animal pollinated plants*. Chapman & Hall, New York, pp. 65-87.
- Johnson S.D. & Steiner K.E. 2000. Generalization versus specialization in plant pollinator systems. *Tree* 15: 140-143.
- Kageyama P.Y. 1992. Recomposição da vegetação com espécies arbóreas nativas em reservatórios de usinas hidrelétricas da CESP. *Série Técnica IPEF* 8(25): 1-43.
- Kevan P.G. & Baker H.G. 1983. Insects as flowers visitors and pollinators. *Annu. Rev. Entomol.* 28: 407-453.
- Kress W.J. & Beach J.H. 1994. Flowering plant reproductive systems. In: McDade L.A., Bawa K.S., Hespenheide H.A. & Hartshorn G.S. (eds.), *La Selva. Ecology and natural history of neotropical rain forest*. University Chicago, Chicago, pp. 161-182.
- McDade L.A. 1992. Pollinator relationships, biogeography, and phylogenetics. *BioScience* 42: 21-26.
- Machado I.C.S. 1990. *Biologia floral de espécies de caatinga no Município de Alagoinha (PE)*. Tese de Doutorado. Universidade Estadual de Campinas, Brasil.
- Morellato L.P.C. 1991. *Estudo da fenologia de árvores, arbustos e lianas de uma floresta semidecídua no Sudoeste do Brasil*. Tese de Doutorado. Universidade Estadual de Campinas, Brasil.
- Nason J.D., Aldrich P.R. & Hamrick J.L. 1997. Dispersal and the dynamics of genetic structure in fragmented tropical tree populations. In: Laurence W.F. & Bierregard Jr. R.O. (eds), *Tropical forest remnants. Ecology, management, and conservation of fragmented communities*. University of Chicago, Chicago.
- Ollerton J. 1996. Reconciling ecological process with phylogenetic patterns: the apparent paradox of plant-pollinator systems. *J.Ecol.* 84: 767-769.
- Oliveira P.E. & Silva J.C.S. 1993. Reproductive biology of two species of *Kielmeyera* (Guttiferae) in the cerrados of central Brazil. *J. Trop. Ecol.* 9: 67-79.

- Oliveira P.E. & Gibbs P.E. 2000. Reproductive biology of woody plants in a cerrado community of Central Brazil. *Flora* 195: 311-329.
- Oliveira P. E. & Gibbs P. E. 2002. Pollination and reproductive biology in cerrado plant communities. In: Oliveira P. E. & Marquis R. J. (eds.), *The cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, Columbia University, New York, pp. 329-347.
- Proctor M. & Yeo P. 1972. *The pollination of flowers*. Taplinger, New York.
- Ramirez N. 1989. Biología de polinización en una comunidad arbustiva tropical de la alta guayana Venezolana. *Biotropica* 21: 319-330.
- Ramirez N. 2004. Ecology of pollination in a tropical Venezuelan savanna. *Plant Ecol.* 173: 171-189.
- Ramirez N. & Brito Y. 1987. Patrones de floración y frutificación en una comunidad pantanosa tipo morichal (Calabozo-Guarico, Venezuela). *Acta Cient. Venez.* 38: 376-381.
- Ramirez N. & Brito Y. 1992. Pollination biology in a palm swamp community in the Venezuelan central plains. *Bot. J. Linn. Soc.* 110: 277-302.
- Saraiva L.C., Cesar O. & Monteiro R. 1996. Breeding systems of shrubs and trees of a Brazilian savanna. *Arq. Biol. Tecnol.* 39: 751-763.
- Sazima I. & Sazima M. 1989. Mamangavas e irapuás (Hymenoptera, Apoidea): visitas, interações e conseqüências para a polinização do maracujá (Passifloraceae). *Rev. Brasil. Ent.* 33: 109-118.
- Sazima I. & Sazima M. 1990. Hummingbird pollination in two species of *Vellozia* (Liliiflorae: Velloziaceae) in southeastern Brazil. *Bot. Acta* 103: 83-86.
- Sazima I., Sazima M. & Buzato S. 1994. Néctar by day and night: *Siphocampylus sulfuris* (Lobeliaceae) pollinated by hummingbird and bats. *Pl. Syst. Evol.* 191: 237-246.
- Schemske D.W. & Horvitz C. C. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science* 225: 519-521.
- Silberbauer-Gottsberger I. & Gottsberger G. 1988. A polinização de plantas do cerrado. *Rev. Brasil. Biol.* 48: 651-663.

- Stebbins G.L. 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. *Ann. Rev. Ecol. Syst.* 1: 307-326.
- Vogel S. 1990. History of the Malpighiaceae in the light of pollination ecology. *Mem. N. Y. Bot. Gard.* 55: 130-142.
- Waser N.M., Chittka L., Price M.V., Williams N.M. & Ollerton J. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043-1060.

II - CAPÍTULO 1

Sistemas de polinização e caracteres
florais em espécies lenhosas de cerrado
na região do Alto Taquari (Brasil
central)¹

¹Trabalho submetido à revista *Brazilian Journal of Biology* com o título "Pollination systems and floral traits in cerrado woody species of the Upper Taquari region (central Brazil)"

Pollination systems and floral traits in cerrado woody species of the Upper Taquari region (central Brazil)

MARTINS, F. Q. ¹ and BATALHA, M. A. ¹

¹ Department of Botany, Federal University of São Carlos, P.O. Box 676, 13565-905, São Carlos, SP, Brazil

Correspondence to: Marco Antônio Batalha, Department of Botany, Federal University of São Carlos, P.O. Box 676, 13565-905, São Carlos, SP, Brazil, email: marcobat@uol.com.br

(With 1 figure)

Palavras-chave: análise de componentes principais, cerrado, fenologia, polinização, savana

Key words: cerrado, phenology, pollination, principal components analysis, savanna

Running Title: Pollination systems and floral traits in cerrado species

ABSTRACT

Plant species present flowers with varied morphological and functional features, which may be associated to pollination systems, including species pollinated by wind, beetles, moths, bees, small insects, birds, or bats. We calculated the frequencies of the pollination systems among woody species in five cerrado fragments in central-western Brazil and tested whether the pollination systems were indeed related to floral traits. We sampled 2,280 individuals, belonging to 121 species, ninety-nine of which were described in relation to all floral traits. Most species had diurnal anthesis, pale colors, and open flowers. The most frequent groups were those composed by the species pollinated by bees, small insects, and moths. A Principal Component Analysis of the species and floral traits showed that there was a grouping among species with some pollination systems, such as those pollinated mainly by beetles, moths, birds, and bats, for which inferences based on the floral traits are recommended in cerrado sites. For the species pollinated mainly by bees or small insects, inferences based on the floral traits are not recommended, due to the large dispersion of the species scores and overlapping between these two groups, which occurred probably due to the specificity absence in plant-pollinator relationships.

RESUMO

Sistemas de polinização e caracteres florais em espécies lenhosas de cerrado na região do Alto Taquari (GO, MS e MT)

As espécies vegetais apresentam flores com características morfológicas e funcionais diversificadas, que podem ser associadas a sistemas de polinização, incluindo espécies polinizadas pelo vento, besouros, mariposas, abelhas, insetos pequenos, aves ou morcegos. Calculamos as frequências dos sistemas de polinização entre as espécies lenhosas em cinco fragmentos de cerrado no Brasil central e testamos se os sistemas de polinização estavam de fato relacionados às características florais. Amostramos 2.280 indivíduos, pertencentes a 121 espécies, das quais 99 foram descritas em relação a todas as características florais. A maioria dessas espécies possuía antese diurna, cores claras e flores abertas. Os grupos mais frequentes foram os das plantas polinizadas por abelhas, insetos pequenos e mariposas. Uma análise de ordenação das espécies e dos caracteres florais mostrou que houve agrupamentos entre as espécies com alguns sistemas de polinização, tais como as polinizadas principalmente por besouros, mariposas, aves e morcegos, para os quais inferências baseadas em características florais são recomendadas. No caso das espécies polinizadas por abelhas e insetos pequenos, inferências a partir dos caracteres florais não são recomendadas devido à grande dispersão dos escores das espécies e à sobreposição

entre esses dois grupos, que ocorreram, provavelmente, devido à ausência de especificidade nas relações planta-polinizador.

INTRODUCTION

Savannas are tropical and subtropical formations where the grass layer is almost continuous, interrupted only by shrubs and trees in varying proportions, and where the main growth patterns are closely associated with alternating wet and dry seasons (Bourlière & Hadley, 1983). The Cerrado Domain occupied formerly 2 million km² of the Brazilian territory (Ratter *et al.*, 1997), especially in the Central Plateau. As its name implies, in the Cerrado Domain, the cerrado vegetation prevails. The cerrado vegetation is not uniform in physiognomy (Coutinho, 1990), ranging from grassland to tall woodland, but with most of its physiognomies within the range defined as tropical savanna (Bourlière & Hadley, 1983). The cerrado vascular flora has an herbaceous and a woody component, which are antagonistic because both are heliophilous (Coutinho, 1990). Scholes & Archer (1997) postulated that the climatic seasonal pattern of tropical savannas, with alternating warm dry and hot wet seasons, provides a potential axis of niche separation by phenology for the herbaceous and woody components.

Plant reproductive processes are determinants of the composition and structure of communities (Bawa, 1990; Oliveira & Gibbs, 2000). Among such processes, the plant-pollinator interactions form a dynamic, yet somewhat cohesive, ecological subunit of a community (Moldenke & Lincoln, 1979). Pollination biology at community level in the Neotropics has been studied in forest areas (Bawa *et al.*, 1985; Kress & Beach, 1994) and also in the cerrado vegetation (Silberbauer-Gottsberger & Gottsberger, 1988; Barbosa, 1997; Oliveira & Gibbs, 2000). Pollination is an important ecological process to vegetation communities since it can directly affect the reproductive success of plants, being able to cause

loss of species if affected (Wunderlee, 1997). Pollination usually involves abiotic (water or wind) or biotic (animal) vectors, including from non-specialist insects to animals strictly dependent on flowers for their survival, such as bees, birds, and bats (Proctor *et al.*, 1996; Machado & Oliveira, 2000).

Plant species have flowers with many morphologic and functional features, which can be associated to pollination syndromes (Faegri & Pijl, 1979; Borges, 2000). These syndromes are composed of a set of attributes (*e.g.*, color, odor, shape, reward, and anthesis), which are common or specific to plant species adapted to a certain type of pollinator (Faegri & Pijl, 1979; Waser *et al.*, 1996). Pollination syndromes take into account these set of floral characters, which would allow determining the likeliest group of pollinators in certain species (Bawa *et al.*, 1985). However, the concept of pollination syndromes must be applied with caution (Herrera, 1996), since it presupposes pollinator-plant specialization, which, in general, is rare (Waser *et al.*, 1996). Pollination systems with a high level of specialization are exceptions; they often vary from less specialized to more generalized systems (Waser *et al.*, 1996). Thus, Oliveira & Gibbs (2000) grouped species according to pollination systems or functional guilds. In this sense, pollination service from different types of animals may be seen as a resource that unifies different pollination systems (Oliveira & Gibbs, 2000).

It is important to consider the attractive and floral resources displayed by species to their visitors, since these aspects ensure the presence and the fidelity of pollinators to the flowers (Borges, 2000). Pollinators are able to distinguish floral differences and have preferences for some colors, forms, sizes, and odors (Levin & Anderson, 1970). Cerrado species ensure the attraction and permanence of pollinators in their environment, offering resources in morphologically different flowers (Borges, 2000). This attraction is reinforced in some species by the emission of odors, and in other ones, by morphologic characteristics, so that these features act as guides of resources (Borges, 2000). Bees are considered better-adapted

animals to the pollination (Faegri & Pijl, 1979) and are the main pollinators of tropical areas (Bawa, 1990; Ramirez & Brito, 1992).

In the cerrado vegetation, bees also are the main pollinators (Silberbauer-Gottsberger & Gottsberger, 1988; Barbosa, 1997; Borges, 2000; Oliveira & Gibbs, 2000). Nevertheless, other pollinators are also important to the cerrado flora, since most species rely on a wide spectrum of pollinators, defined more by their size and foraging requirements than by specific interaction (Oliveira & Gibbs, 2002). Many species have small, apparently generalist flowers, pollinated by a range of insects of different groups, such as flies, bees, and wasps (Oliveira & Gibbs, 2002). As in other tropical communities, plant-pollinator relationships in cerrado seem to involve guilds of pollinators associated with a given plant or group of plants (Bawa, 1990; Oliveira & Gibbs, 2000). Studies on the reproductive biology of cerrado plants have shown a great diversity of pollination systems, which are similar to those found in Neotropical forests (Oliveira & Gibbs, 2002), but is it possible to infer the main pollination system of cerrado woody species based on floral traits? We studied the woody component of some cerrado fragments in central Brazil, attempting to answer the following questions: What are the main pollination systems among these species? What are their floral traits? Do species with a given pollination system form distinct groups when all their floral traits are taken into account? Which floral traits are related to a given pollination system?

MATERIAL AND METHODS

We carried out this study in 2003 in Alcinópolis (Mato Grosso do Sul State), Alto Araguaia and Alto Taquari (Mato Grosso State), and Mineiros and Santa Rita do Araguaia (Goiás State), central-western Brazil, in the southwestern extremity of the Brazilian Central Plateau. Regional climate is Aw (Köppen, 1948), humid tropical with wet summer and dry

winter. Annual rainfall varies from 1,200 to 2,000 mm, concentrated from October to March, and mean annual temperature lies around 24.6°C (Ramos-Neto & Pivello, 2000). This region was originally covered mainly by cerrado vegetation, from open (*campo limpo*, a grassland savanna) to closed (*cerradão*, a tall woodland) physiognomies, following Coutinho's (1990) classification.

Based on satellite images, we picked up randomly five fragments covered mainly by *cerrado sensu stricto* (a woodland). The first fragment (approximately, 22K0283659S and 8036276W UTM), with 8,278 ha and a perimeter of 124.6 km, was composed by cerrado (90.81%), seasonal and gallery forest (0.16%), and other vegetation types (9.03%). The second – and the smallest – fragment (approximately, 22K0279934S and 8043454W UTM), with 1,678 ha and a perimeter of 35.7 km, was composed by cerrado (85.62%) and other vegetation types (14.38%). The third – and the largest – fragment (approximately, 22K0267453S and 8056613W UTM), with 41,452 ha and a perimeter of 813.6 km, was composed by cerrado (92.11%), seasonal and gallery forest (0.29%), and other vegetation types (7.60%). The fourth fragment (approximately, 22K0240604S and 8039048W UTM), with 6.666 ha and a perimeter of 206.0 km, was composed by cerrado (58.67%), seasonal and gallery forest (32.34%), and other vegetation types (8.99%). The fifth fragment (approximately, 22K0215774S and 7990493W UTM), with 12,459 ha and a perimeter of 386.0 km, was composed by cerrado (40.75%), seasonal and gallery forests (26.54%), and other vegetation types (32.71%). All fragments were located inside private properties and surrounded by agriculture and pasture.

We randomly placed 38 transects, perpendicular to the edge, in the *cerrado sensu stricto* physiognomy of the five fragments: eight in the first and fourth, four in the second, twelve in the third; and six in the fifth. In each transect, we placed 15 sampling points, 10 m apart one from the other, starting at 10 m from the fragment edge. We used the point-quarter method

(Mueller-Dombois & Ellenberg, 1974) to sample the woody component. In each point, we sampled four woody plants with stem diameter at soil level equal to or larger than 3 cm (SMA, 1997). Thus, in the 38 transects, we placed 570 points and sampled 2,280 individuals. We collected the sampled individuals and identified them by comparison with lodged material at the São Paulo Botanical Institute (SP), by comparison with the Emas National Park reference collection (Batalha & Martins, 2002), or by using a key based on vegetative characters (Batalha & Mantovani, 1999).

We classified species into families following Judd *et al.* (1999) and determined their floral traits based on the literature (*e.g.*, Barbosa, 1997; Borges, 2000; Oliveira & Gibbs, 2000; Wanderley *et al.*, 2002; Wanderley *et al.*, 2003). We classified flowers according to their morphologic features (color and shape), functional features (time of anthesis, presence of odor, and presence of resource guides), and reward offered to pollinators (nectar and pollen). We considered the classes "opened", "closed" and "tubular" for flower shape and "white", "cream", "green", "lilac", "red", "orange" and "yellow" for flower color.

We classified those species for which we determined all floral traits into pollination systems based on the literature (*e.g.*, Silberbauer-Gottsberger & Gottsberger, 1988; Barbosa, 1997; Borges, 2000; Oliveira & Gibbs, 2000). Occasionally, when we could not find data for a given species, we classified its pollination system based on data for related species of the same genus. We recognized the following pollination systems: wind, beetles, moths, bees, small insects, hummingbirds, and bats, calculating the frequency of each system among the sampled individuals. The 'small insects' class included a varied assemblage of relatively small insects, such as small bees, beetles, flies, wasps, and butterflies (Bawa *et al.*, 1985).

We constructed a matrix of the floral traits in relation to the species, excluding those species for which we did not find information for all floral traits. For the two nominal variables – flower shape and flower color, we created dummy variables, which took value 1

when a given trait was present and value 0 when it was absent (Jongman *et al.*, 1995); for example, the dummy variable for tubular flowers took value 1 when the flower was tubular and value 0 when the flower was closed or open. To test for relationships between pollination systems and floral traits, we used a Principal Components Analyses (PCA) (Jongman *et al.*, 1995) with the Multivariate Statistical Package software (Kovach, 1999).

RESULTS

In the 2,280 sampled individuals, we found 121 species, and for 99 of which, we obtained information for all floral traits (Table 1). These 99 species comprised 2,085 individuals and 30 families. The most representative families were Myrtaceae (18 species), Fabaceae (17), and Apocynaceae, Malpighiaceae, and Melastomataceae, each one with five species. Most species had flowers with diurnal anthesis (79%) and pale colors (89%), that is, white, cream, yellow, or green. In relation to the shape, 68% of the species had open flowers; 24%, tubular flowers; and 8%, closed flowers. Pollen was a resource present in 65% of the species; and nectar, in 54%. Of the 99 species, 55.6% were mainly pollinated by bees; 20.2%, by small insects; 13.1%, by moths; 5.1%, by bats; 3.0%, by beetles; 2.0%, by hummingbirds; and 1.0%, by wind.

In the PCA, the eigenvalues of the first two axes were 0.73 and 0.37, explaining 46.8% of the variation in the data. In the ordination diagram (figure 1), the floral traits with longer vectors were shape, reward, anthesis, and, to a lesser extent, odor. Species pollinated by moths formed a distinct group, related to nocturnal anthesis and tubular flowers. These two characters, together with presence of odor, were also related to the species pollinated by beetles and bats. Species pollinated by birds presented positive scores in the first axis and negatives scores in the second one, being related to tubular flowers, diurnal anthesis, presence

of nectar, and showy colors. The only species we found pollinated by wind presented negative scores in both axes, with green, diurnal, and open flower. Species pollinated by bees and small insects were dispersed throughout both axes, one considerably overlapping with the other.

DISCUSSION

All plant species have particular morphological and physiological features that can attract some groups of floral visitors to the detriment of others (Bosch *et al.*, 1997). Many morphological and functional aspects of floral biology are important to the establishment of the plant-animal interaction (Faegri & Pijl, 1979; Waser, 1983). Shape and odor are floral traits that have been included in community studies, because they have important implications not only for the plant-pollinator relationship, but also for the reproductive success of the plant (Endress, 1994). Flower color was particularly good at separating bird- and hymenopteran-flowers for *Pentstemon* species (Wilson *et al.*, 2004). For us, however, color had a minor importance at separating pollination systems, since the two largest pollinator classes, bees and small insects, visit flowers of several colors. The exception was the white color, which had a relatively long vector, and was associated with moths, beetles, and bats in the second axis. We observed that the floral traits with longer vectors and, thus, best related to the pollination systems were flower shape, reward, anthesis, and odor.

Generally, the relationships between floral traits and pollination systems we found were similar to those described in other studies (*e.g.*, Faegri & Pijl, 1979; Silberbauer-Gottsberger & Gottsberger, 1988; Bawa, 1990; Barbosa, 1997; Oliveira & Gibbs, 2000). Flowers pollinated mainly by beetles were yellow, closed, nocturnal, and with odor; flowers pollinated mainly by birds were orange, tubular, diurnal, and with nectar; flowers pollinated mainly by

bats were white, nocturnal, and with odor; and flowers pollinated mainly by moths were pale, tubular, nocturnal, and with odor and nectar. Most of the flowers pollinated mainly by bees were open and yellow, white, cream, or lilac. Such colors, as well as the sweet and pleasant odor emitted by the flowers during the anthesis, are attributes related to the attraction of bees, since they are sensitive to olfactory and visual stimuli (Faegri & Pijl, 1979; Kevan & Baker, 1983).

Flowers pollinated mainly by small insects were small, usually open, and green or yellow. On the one hand, these traits imply floral rewards that are accessible to many insects; on the other hand, a certain insect from such group can visit flowers of several species, since there is a lot of species with these traits (Bawa & Opler, 1975; Bawa, 1980). Flowers pollinated by this group are generally small (less than 1 cm in length), pale green or pale yellow, and lack morphological specialization with the result that floral rewards are accessible to a wide variety of insects (Bawa *et al.*, 1985). We found a large overlapping between the two most frequent groups, bees and small insects, which probably occurred due to the absence of specificity, which is the most frequent condition in different vegetation types (Bawa, 1980), including the cerrado (Borges, 2000). In tropical forests, many species have morphologically simple flowers, allowing the access of different categories of visitors, such as bees, butterflies, moths, flies, and wasps (Bawa, 1990). Even species with more complex flowers are visited by several species that act as pollinators (Bawa, 1990).

In the cerrado, bird- and wind-pollinated flowers are rare (Silberbauer-Gottsberger & Gottsberger, 1988; Oliveira, 1991) and were the groups with lowest frequencies in the area we studied as well. Although hummingbirds are important pollinators of herbs in open cerrado areas (Silberbauer-Gottsberger & Gottsberger, 1988; Barbosa 1997), they seem to be only secondary or opportunistic visitors of cerrado woody species (Oliveira & Gibbs, 2000). The only species pollinated by wind that we sampled had inconspicuous flowers, without odor and

rewards, corroborating Faegri & Pijl (1979), who related these traits to abiotic pollination. Wind pollination, which has been associated with seasonally dry areas (Bullock 1994), is rare among cerrado woody species, and occurs commonly only among grasses and sedges (Silberbauer-Gottsberger & Gottsberger, 1988; Oliveira & Gibbs, 2002). We did not find butterfly-pollinated flowers, which are poorly represented among cerrado woody species (Oliveira & Gibbs, 2000, 2002).

Information from studies on pollination in cerrado sites (Silberbauer-Gottsberger & Gottsberger, 1988; Oliveira, 1991; Oliveira & Gibbs, 2000, 2002) pointed out the existence of several pollination systems, suggesting that plant species depend on the interaction with several groups of animals, and vice-versa. Our ordination analysis of floral traits and plant species showed that there was a grouping among species with some pollination systems (beetles, moths, birds, and bats), for which inferences based on the floral characters are recommended for cerrado sites. In these cases, one could infer the pollination system based on the floral traits. On the contrary, regarding the species pollinated mainly by bees or small insects, inferences based on the floral traits are not recommended, due to the large dispersion of the species scores and overlapping between these two classes, which occurred, probably, due to the specificity absence in the plant-pollinator relationships.

Acknowledgments – We are grateful to CNPq and Conservation International, especially Drs. Mário Barroso Ramos-Neto and Paulo Gustavo do Prado Pereira, for financial support; to Emas and Oréades Foundations, for satellite images; to André Vitor Fleuri Jardim and Júlia Caram, for help in field; and to an anonymous referee, for useful suggestions.

REFERENCES

- BARBOSA, A. A., 1997, *Biologia reprodutiva de uma comunidade de campo sujo, Uberlândia – MG*. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- BARROS, M. G., 1992, Fenologia da floração, estratégias reprodutivas e polinização de espécies simpátricas do gênero *Byrsonima* Rich (Malpighiaceae). *Rev. Brasil. Biol.*, 52: 343-353.
- BARROS, M. G., 1998, Sistemas reprodutivos e polinização em espécies simpátricas de *Erythroxylum* P.Br. (Erythroxylaceae) do Brasil. *Rev. Brasil. Bot.*, 21: 159-166.
- BARROS, M. G., 2001, Pollination ecology of *Tabebuia aurea* (Manso) Benth. & Hook. and *T. ochracea* (Cham.) Standl. (Bignoniaceae) in Central Brazil cerrado vegetation. *Rev. Brasil. Bot.*, 24: 255-261.
- BATALHA, M. A. & MANTOVANI, W., 1999, Chaves de identificação das espécies vegetais vasculares baseada em caracteres vegetativos para a ARIE Cerrado Pé-de-Gigante (Santa Rita do Passa Quatro, SP). *Rev. Inst. Flor.*, 11: 137-158.
- BATALHA, M. A. & MARTINS, F. R., 2002, The vascular flora of the cerrado in Emas National Park (Goiás, central Brazil). *Sida*, 20: 295-312.
- BAWA, K. S., 1980, Evolution of dioecy in flowering plants. *Ann. Rev. Ecol. Syst.*, 11: 15-39.
- BAWA, K. S., 1990, Plant-pollinator interactions in tropical rain forests. *Ann. Rev. Ecol. Syst.*, 21: 399-422.
- BAWA, K. S., BULLOCH, S. H., PERRY, D. R., COVILLE, R. E. & GRAYUM, M. H., 1985, Reproduction biology of tropical lowland rain forest tree. II. Pollination system. *Am. J. Bot.*, 72: 346-356.
- BAWA, K. S. & OPLER, P. A., 1975, Dioecism in tropical forest trees. *Evolution*, 29: 167-179.

- BORGES, H. B. N., 2000, *Biologia reprodutiva e conservação do estrato lenhoso numa comunidade do cerrado*. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- BOSCH, J., RETANA, J. & CERDÁ, X., 1997, Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia*, 109: 583-591.
- BOURLIÈRE, F. & HADLEY, M., 1983, Present-day savannas: an overview, pp. 1-17. In: D. W. Goodall (ed.), *Ecosystems of the world – tropical savannas*, Amsterdam, Elsevier.
- BULLOCK, S. H., 1994, Wind pollination of Neotropical dioecious trees. *Biotropica*, 26: 172-179.
- COUTINHO, L. M., 1990, Fire in the ecology of the Brazilian cerrado, pp. 82-105. In: J. G. Goldammer (ed.), *Fire in the tropical biota*, Springer, Berlin.
- CRESTANA, C. S. M. & KAGEYAMA, P. Y., 1989, Biologia reprodutiva de *Copaifera langsdorffii*. *Rev. Inst. Flor.*, 1: 201-214.
- ENDRESS, P. K., 1994, *Diversity and evolutionary biology of tropical flowers*. Cambridge University, Cambridge.
- FAEGRI, K. & PIJL, L. van der, 1979, *The principles of pollination ecology*. Pergamon, New York.
- FRANCO, A. L. M., 1995, *Ecologia da polinização e biologia reprodutiva de sete espécies de Phaseoleae*. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- FREITAS, C. V. & OLIVEIRA, P. E., 2002, Biologia reprodutiva de *Copaifera langsdorffii* Desf. (Leguminosae, Caesalpinioideae). *Rev. Brasil. Bot.*, 25: 311-321.
- GIBBS, P. E., OLIVEIRA, P. E. & BIANCHI, M. B., 1999, Postzygotic control of selfing in *Hymenaea stigonocarpa* (Leguminosae-Caesalpinioideae), a bat-pollinated tree of the Brazilian cerrados. *Int. J. Plant Sci.*, 160: 72-78.

- GOLDENBERG, R., 1994, *Estudos sobre a biologia reprodutiva de espécies de Melastomataceae de Cerrado em Itirapina, SP*. M.Sc. Dissertation. Universidade Estadual de Campinas, Brasil.
- GOTTSBERGER, G., 1999. Pollination and evolution in neotropical Annonaceae. *Pl. Sp. Biol.*, 14: 143-152.
- GOLDENBERG, R. & SHEPHERD, G. J., 1998, Studies on the reproductive biology of Melastomataceae in “cerrado” vegetation. *Plant Syst. Evol.*, 211: 13-29.
- GOTTSBERGER, G., 1994, As anonáceas do cerrado e a sua polinização. *Rev. Brasil. Biol.*, 54: 391-402.
- HERRERA, C. M., 1996, Floral traits and plant adaptation to insect pollinators: a devil’s advocate approach, pp. 65-87. In: D. G. Lloyd & S. C. H. Barrett (eds.), *Floral biology: studies on floral evolution in animal pollinated plants*, Chapman & Hall, New York.
- JONGMAN, R. H. G., TER BRAAK, C. J. F. & VAN TONGEREN, O. F. R., 1995, *Data analysis in community and landscape ecology*. Cambridge University, Cambridge.
- JUDD, W. S., CAMPBELL, C. S., KELLOG, E. A. & STEVENS, P. F., 1999, *Plant systematics: a phylogenetic approach*. Sinauer, Sunderland.
- KEVAN, P. G. & BAKER, H. G., 1983, Insects as flowers visitors and pollinators. *Annu. Rev. Entomol.*, 28: 407-453.
- KÖPPEN W., 1948, *Climatología*. Fondo de Cultura Económica, México.
- KOVACH, 1999, *Multivariate Statistical Package v.3.1*. Kovach Computing Services, Anglesey.
- KRESS, W. J. & BEACH, J. H., 1994, Flowering plant reproductive systems, pp. 161-182. In: L. A. McDade, K. S. Bawa, H. A. Hespenheide & G. S. Hartshorn (eds.), *La Selva. Ecology and natural history of neotropical rain forest*, University Chicago, Chicago.

- LEVIN, D. A. & ANDERSON, W. W., 1970, Competition for pollinators between simultaneously flowering species. *Am. Nat.*, 104: 455-467.
- MACHADO, A. O. & OLIVEIRA, P. E., 2000, Biologia floral e reprodutiva de *Casearia grandiflora* Camb. (Flacourtiaceae). *Rev. Brasil. Bot.*, 23: 283-290.
- MOLDENKE, A. R. & LINCOLN, P. G., 1979, Pollination ecology in montane Colorado. *Phytologia*, 42: 349-379.
- MUELLER-DOMBOIS, D. & ELLENBERG, H., 1974, *Aims and methods of vegetation ecology*. John Willey & Sons, New York.
- OLIVEIRA, P. E., 1991, *The pollination and reproductive biology of a cerrado woody community in Brazil*. Ph.D. Thesis, University of St. Andrews, St. Andrews.
- OLIVEIRA, P. E. & GIBBS, P. E., 1994, Pollination biology and breeding systems of six *Vochysia* species (Vochysiaceae) in Central Brazil. *J. Trop. Ecol.*, 10: 509-522.
- OLIVEIRA, P. E. & GIBBS, P. E., 2000, Reproductive biology of woody plants in a cerrado community of Central Brazil. *Flora*, 195: 311-329.
- OLIVEIRA, P. E. & GIBBS, P. E., 2002, Pollination and reproductive biology in cerrado plant communities, pp. 329-347. In: P. E. Oliveira & R. J. Marquis (eds.), *The cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, Columbia University, New York.
- OLIVEIRA, P. E., GIBBS, P. E. & BARBOSA, A. A., 2004, Moth pollination of woody species in the Cerrados of Central Brazil: a case of so much owed to so few? *Plant Syst. Evol.*, 245: 41-54.
- OLIVEIRA, P. E., GIBBS, P. E., BARBOSA, A. A. & TALAVERA, S., 1992, Contrasting breeding systems in two *Eriotheca* (Bombacaceae) species of the Brazilian cerrados. *Plant Syst. Evol.*, 179: 207-219.

- OLIVEIRA, P. E. & PAULA F. R., 2001, Fenologia e biologia reprodutiva de plantas de Matas de galeria, pp. 303-331. In: J. F. Ribeiro, C. E. L. Fonseca da & J. C. Souza-Silva (eds.), *Cerrado: caracterização e recuperação de Matas de Galeria*, Embrapa, Planaltina.
- OLIVEIRA, P. E. & SAZIMA, M., 1990, Pollination biology of two species of *Kielmeyera* (Guttiferae) from Brazilian cerrado vegetation. *Plant Syst. Evol.*, 172: 35-49.
- PROCTOR, M., YEO, P. & LACK, A., 1996, *The natural history of pollination*. Harper Collins, New York.
- PROENÇA, C. E. B. & GIBBS, P. E., 1994, Reproductive biology of eight sympatric Myrtaceae from Central Brazil. *New Phytol.*, 126: 343-354.
- RAMIREZ, N. & BRITO, Y., 1992, Pollination biology in a palm swamp community in the Venezolana central plains. *Bot. J. Linn. Soc.*, 110: 277-302.
- RAMOS-NETO, M. B. & PIVELLO, V. R., 2000, Lightning fires in a Brazilian savanna National Park: rethinking management strategies. *Environ. Manage.*, 26: 675-684.
- RATTER, J. A., RIBEIRO, J. F. & BRIDGEWATER, S., 1997, The Brazilian cerrado vegetation and threats to its biodiversity. *Ann. Bot.*, 80: 223-230.
- SARAIVA, L. C., CESAR, O. & MONTEIRO, R., 1988, Biologia da polinização e sistemas de reprodução de *Styrax camporum* Pohl e *S. ferrugineus* Nees et Mart. (Styracaceae). *Rev. Brasil. Bot.*, 11: 71-80.
- SAZIMA, M. & SAZIMA, I., 1975, Quiropterofilia em *Lafoensia pacari* St. Hil. (Lythraceae), na Serra do Cipó, Minas Gerais. *Ciênc. Cult.*, 27: 405-416.
- SCHOLES, R. J. & ARCHER, S. R., 1997, Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.*, 28: 517-544.
- SIGRIST, M. R., 2001, *Biologia reprodutiva de doze espécies simpátricas de Malpighiaceae em mata semidecídua do sudoeste Brasileiro*. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.

- SILBERBAUER-GOTTSBERGER, I. & GOTTSBERGER, G., 1988, A polinização de plantas do cerrado. *Rev. Brasil. Biol.*, 48: 651-663.
- SILBERBAUER-GOTTSBERGER, I., GOTTSBERGER, G. & WEBBER, A. C., 2003, Morphological and functional flower characteristics of New and Old World Annonaceae with respect to their mode of pollination. *Taxon*, 52: 701-718.
- SMA. Secretaria de Estado do Meio Ambiente, 1997, *Cerrado: bases para conservação e uso sustentável das áreas de cerrado do estado de São Paulo*. Secretaria de Estado do Meio Ambiente, São Paulo.
- TOREZAN-SILINGARDI, H. M. & DEL-CLARO, K., 1998, Behavior of visitors and reproductive biology of *Campomanesia pubescens* (Myrtaceae) in cerrado vegetation. *Ciênc. Cult.*, 50: 281-284.
- VIANA, B. F., KLEINERT, A. M. P. & IMPERATRIZ-FONSECA, V. L., 1997, Abundance and flower visits of bees in a Cerrado of Bahia, Tropical Brazil. *Stud. Neotrop. Fauna Environ.*, 32: 212-219.
- WANDERLEY, M. G. L., SHEPHERD, G. J., GIULIETTI, A. M. & MELHEM, T. S., 2002, *Flora Fanerogâmica do Estado de São Paulo*. Fapesp e Hucitec, São Paulo. v2.
- WANDERLEY, M. G. L., SHEPHERD, G. J. & GIULIETTI, A. M., 2003, *Flora Fanerogâmica do Estado de São Paulo*. Fapesp e Hucitec, São Carlos. v3.
- WASER, N. M., 1983, The adaptive nature of floral traits: ideas and evidence, pp. 241-285. *In: L. Real (ed.), Pollination biology*, Academic, New York.
- WASER, N. M., CHITTKA, L., PRICE, M. V., WILLIAMS, N. M. & OLLERTON J., 1996, Generalization in pollination systems, and why it matters. *Ecology*, 77: 1043-1060.
- WEBER, W. A., 1982, Mnemonic three-letter acronyms for the families of vascular plants: a device for more effective herbarium curation. *Taxon*, 31: 74-88.

WILSON, P., CASTELLANOS, M. C., HOGUE, J. N., THOMSON, J. D. &

ARMBRUSTER, W. S., 2004, A multivariate search for pollination syndromes among penstemons. *Oikos*, 104: 345-361.

WUNDERLEE, J. M., 1997, The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecol. Manag.*, 99: 223-235.

Fig. 1 – Principal component analysis of floral traits and woody species of the cerrado fragments in Upper Taquari region (central-western Brazil). Species were classified according their pollination system: ▲= bees, ▲ = small insects, △= moths, ■ = bats, ■ = hummingbirds, □ = beetles, and ○ = wind.

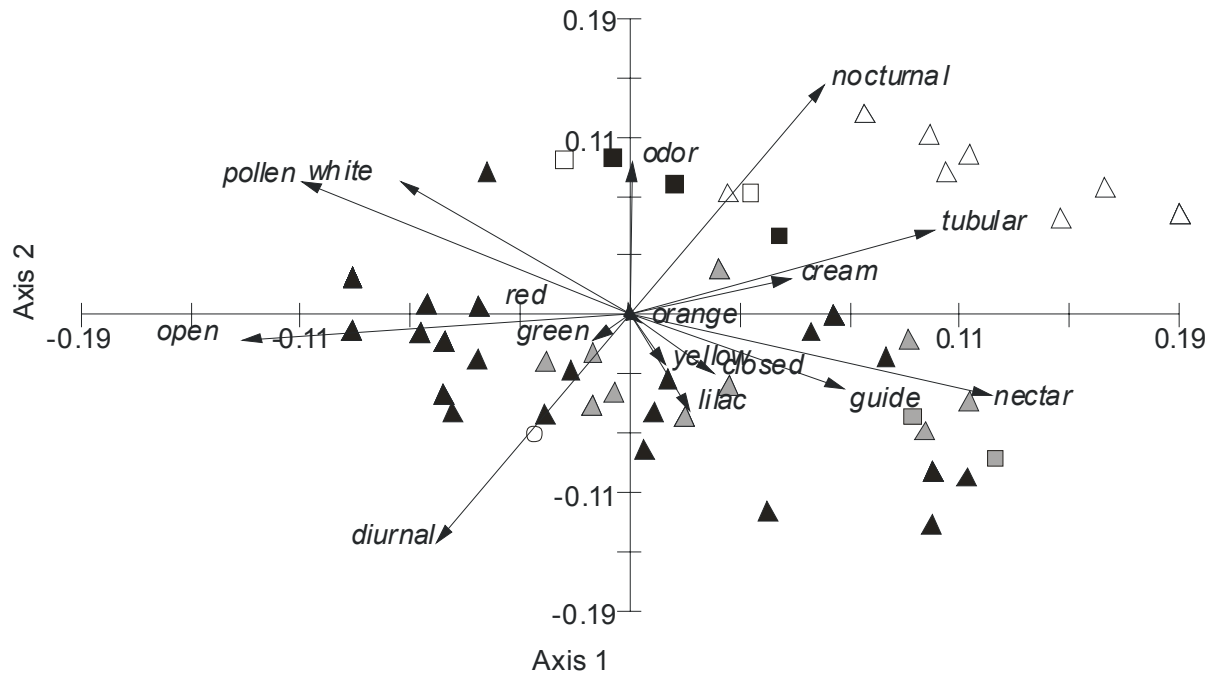
TABLE 1 – Floral traits and pollination systems of woody species in cerrado fragments located in Upper Taquari region (central-western Brazil). Family names were abbreviated according to Weber (1982). Pol – pollination systems; CO – color; A – anthesis; RG – resource guide; O – odor; N – nectar; P – pollen; S – shape; ba – bats; be – bees; bt – beetles; hb – hummingbird; mo – moths; si – small insects; wi – wind; cr – cream; gr – green; li – lilac; or – orange; re – red; wh – white; ye – yellow; d – diurnal; n – nocturnal; 0 – absent; 1 – present; cl – closed; op – open; tu – tubular. Sources: 1 – Barbosa (1997), 2 – Barros (1992), 3 – Barros (1998), 4 – Barros (2001), 5 – Bawa *et al.* (1985), 6- Borges (2000), 7- Crestana & Kageyama (1989), 8- Franco (1995), 9- Freitas & Oliveira (2002), 10- Gibbs *et al.* (1999), 11- Goldenberg (1994), 12- Goldenberg & Shepherd (1998), 13- Gottsberger (1994), 14- Gottsberger (1999), 15- Oliveira & Gibbs (1994), 16- Oliveira & Gibbs (2000), 17- Oliveira & Paula (2001), 18- Oliveira & Sazima (1990), 19- Oliveira *et al.* (1992), 20- Oliveira *et al.* (2004), 21- Proença & Gibbs (1994), 22- Saraiva *et al.* (1988), 23- Sazima & Sazima (1975), 24- Sigrist (2001), 25- Silberbauer-Gottsberger & Gottsberger (1988), 26- Silberbauer-Gottsberger *et al.* (2003), 27- Torezan-Silingardi & Del-Claro (1998), 28- Viana *et al.* (1997); * classification of the pollination systems based on the genus.

Family	Species	Pol	CO	A	RG	O	N	P	S	Source
ANA	<i>Anacardium humile</i> A. St-Hil.	si	wh	d	0	1	1	0	op	1*
ANN	<i>Annona coriacea</i> Mart.	bt	ye	n	0	1	0	1	cl	13
ANN	<i>Annona crassiflora</i> Mart.	bt	ye	n	0	1	0	1	cl	13, 16
ANN	<i>Bocageopsis mattogrossensis</i> (R.E. Fries) R.E. Fries	si	wh	d	0	0	0	1	op	14*, 26*
ANN	<i>Duguetia furfuracea</i> (A. St-Hil.) Benth. & Hook.f.	bt	re	n	0	1	0	1	op	6, 13
API	<i>Didymopanax macrocarpum</i> (Cham. & Schltdl.) Seem.	si	gr	d	0	1	0	1	op	16
API	<i>Didymopanax vinosum</i> (Cham. & Schltdl.) Marchal	si	gr	d	0	1	0	1	op	16*
APO	<i>Aspidosperma macrocarpon</i> Mart.	mo	cr	n	1	1	1	0	tu	16, 20
APO	<i>Aspidosperma nobile</i> Müll. Arg.	mo	cr	n	1	1	1	0	tu	16*, 20*
APO	<i>Aspidosperma polyneuron</i> Müll. Arg.	mo	cr	n	1	1	1	0	tu	16*, 20*
APO	<i>Aspidosperma tomentosum</i> Mart.	mo	cr	n	1	1	1	0	tu	16, 20
APO	<i>Hancornia speciosa</i> Gomez	mo	wh	n	0	1	1	0	tu	16*, 20
APO	<i>Himatanthus obovatus</i> (Müll. Arg.) Woods.	mo	wh	n	1	1	1	1	tu	6, 20
AST	<i>Eremanthus erythropappus</i> Sch. Bip.	si	wh	d	0	1	1	1	tu	16*
AST	<i>Eremanthus glomerulatus</i> Less.	si	wh	d	0	1	1	1	tu	16

Family	Species	Pol	CO	A	RG	O	N	P	S	Source
AST	<i>Piptocarpha rotundifolia</i> (Less.) Baker	si	wh	d	0	1	1	0	tu	16, 17
BIG	<i>Tabebuia aurea</i> (Silva Manso) S. Moore	be	ye	d	0	1	1	1	tu	4, 6
BIG	<i>Tabebuia ochracea</i> (Cham.) Standl.	be	ye	d	1	1	1	1	tu	4, 16
BIG	<i>Zeyheria montana</i> Mart.	hb	ye	d	1	0	1	0	tu	1
CAC	<i>Caryocar brasiliense</i> Cambess.	ba	wh	n	0	1	1	1	op	6, 20
CEL	<i>Peritassa campestris</i> (Cambess.) A.C. Sm.	be	gr	d	0	1	0	1	op	1*
CLU	<i>Kielmeyera coriacea</i> Mart.	be	wh	d	0	1	0	1	op	17, 18
CLU	<i>Kielmeyera rubriflora</i> Cambess.	be	wh	d	0	1	0	1	op	18
CMB	<i>Buchenavia tomentosa</i> Eichl.	si	cr	d	0	0	1	0	tu	
CNN	<i>Connarus suberosus</i> Planch.	si	ye	d	0	1	1	0	op	6, 16
CNN	<i>Rourea induta</i> Planch.	be	wh	d	0	1	1	1	op	1
DLL	<i>Davilla elliptica</i> A. St-Hil.	be	ye	d	0	1	0	1	op	1, 6
ERX	<i>Erythroxylum campestre</i> A. St-Hil.	si	cr	d	0	1	1	0	op	1, 3
ERX	<i>Erythroxylum suberosum</i> A. St-Hil.	si	wh	d	0	0	1	0	op	3, 6
ERX	<i>Erythroxylum tortuosum</i> Mart.	si	wh	d	0	0	1	0	op	3, 16
EUP	<i>Manihot caerulescens</i> Pohl	be	gr	d	0	0	1	1	op	6*
FAB	<i>Acosmium subelegans</i> (Mohl.) Yakovlev	be	wh	d	1	1	1	0	op	6
FAB	<i>Anadenanthera falcata</i> (Benth.) Speg	si	cr	d	0	0	1	1	op	17*
FAB	<i>Andira anthelmia</i> (Vell.) J.F. Macbr.	be	li	d	1	1	1	0	cl	6*
FAB	<i>Andira cuiabensis</i> Benth.	be	li	d	1	1	1	0	cl	6
FAB	<i>Andira laurifolia</i> Benth.	be	li	d	1	1	1	0	cl	6*
FAB	<i>Andira vermifuga</i> (Mart.) Benth.	be	li	d	1	1	1	0	cl	6*
FAB	<i>Bauhinia rufa</i> Steud.	ba	wh	n	0	1	1	1	op	10, 17
FAB	<i>Bowdichia virgilioides</i> Kunth	be	li	d	1	0	1	0	cl	6, 17
FAB	<i>Copaifera langsdorffii</i> Desf.	be	wh	d	0	1	1	1	op	7, 9
FAB	<i>Dimorphandra mollis</i> Benth.	si	cr	d	0	1	1	0	op	6, 16
FAB	<i>Dioclea bicolor</i> Benth.	be	li	d	1	1	1	1	op	8*
FAB	<i>Hymenaea stigonocarpa</i> Mart.	ba	wh	n	1	1	1	1	op	6, 10
FAB	<i>Machaerium acutifolium</i> Vogel	be	cr	d	1	0	1	0	cl	6*

Family	Species	Pol	CO	A	RG	O	N	P	S	Source
FAB	<i>Sclerolobium aureum</i> (Tul.) Benth.	si	ye	d	0	1	1	0	op	6
FAB	<i>Sclerolobium paniculatum</i> Vogel	si	ye	d	0	1	1	0	op	16, 17
FAB	<i>Senna silvestris</i> (Vell.) H.S. Irwin & Barneby	be	ye	d	0	1	1	1	op	17, 28
FAB	<i>Stryphnodendron obovatum</i> Benth.	si	wh	d	1	1	1	0	tu	6, 16
FLC	<i>Casearia sylvestris</i> Sw.	si	gr	d	0	1	1	1	op	1, 6
LOG	<i>Strychnos pseudoquina</i> A. St-Hil.	mo	cr	n	0	1	1	0	tu	16, 20
LYT	<i>Lafoensia pacari</i> A. St-Hil.	ba	ye	n	1	1	1	1	op	6, 23
MLP	<i>Banisteriopsis stellaris</i> (Griseb.) B.Gates	be	wh	d	0	0	0	1	op	1, 24*
MLP	<i>Byrsonima basiloba</i> A. Juss.	be	ye	d	0	0	0	1	op	1, 24*
MLP	<i>Byrsonima coccolobifolia</i> A. Juss.	be	li	d	0	0	0	1	op	2, 6
MLP	<i>Byrsonima crassa</i> Nied.	be	ye	d	0	0	0	1	op	2, 17
MLP	<i>Byrsonima intermedia</i> A. Juss.	be	ye	d	0	0	0	1	op	1, 24*
MLS	<i>Miconia albicans</i> Triana	be	wh	d	0	0	0	1	op	12, 17
MLS	<i>Miconia fallax</i> A. DC.	be	wh	d	0	1	0	1	op	12, 16*
MLS	<i>Miconia ferruginata</i> A. DC	be	wh	d	0	1	0	1	op	12*
MLS	<i>Miconia ligustroides</i> (A. DC.) Naud.	be	wh	d	0	1	0	1	op	12
MLS	<i>Mouriri elliptica</i> Mart.	be	wh	d	0	0	0	1	op	11*
MLV	<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns	be	wh	d	0	0	1	1	op	17, 19
MLV	<i>Pseudobombax longiflorum</i> (Mart. & Zucc.) A. Robyns	ba	wh	n	0	1	1	1	op	6, 20
	Robyns									
MOR	<i>Brosimum gaudichaudii</i> Trec.	wi	gr	d	0	0	0	0	op	1, 6
MRT	<i>Campomanesia adamantium</i> (Cambess.) O. Berg	be	wh	d	1	1	0	1	op	1, 27*
MRT	<i>Campomanesia pubescens</i> (A. DC.) O. Berg	be	wh	d	1	1	0	1	op	1, 27
MRT	<i>Eugenia aurata</i> O. Berg	be	wh	d	0	1	0	1	op	1, 6*
MRT	<i>Eugenia bimarginata</i> A. DC.	be	wh	d	0	1	0	1	op	1, 6*
MRT	<i>Eugenia piauihiensis</i> O. Berg	be	wh	d	0	1	0	1	op	1, 6*
MRT	<i>Eugenia puniceifolia</i> (Kunth) A. DC.	be	wh	d	0	1	0	1	op	1
MRT	<i>Myrcia bella</i> Cambess.	be	wh	d	0	1	0	1	op	6*, 21*
MRT	<i>Myrcia camapuanensis</i> N.F.E. Silveira	be	wh	d	0	1	0	1	op	6*, 21*

Family	Species	Pol	CO	A	RG	O	N	P	S	Source
MRT	<i>Myrcia crassifolia</i> (O. Berg) Kiaersk.	be	wh	d	0	1	0	1	op	6*, 21*
MRT	<i>Myrcia fallax</i> (Rich.) A. DC.	be	wh	d	0	1	0	1	op	6*, 21*
MRT	<i>Myrcia guianensis</i> A. DC.	be	wh	d	0	1	0	1	op	6*, 21*
MRT	<i>Myrcia laruotteana</i> Cambess.	be	wh	d	0	1	0	1	op	6*, 21*
MRT	<i>Myrcia linguaeformis</i> Kiaersk.	be	wh	d	0	1	0	1	op	6*, 21*
MRT	<i>Myrcia rhodosepala</i> Kiaersk.	be	wh	d	0	1	0	1	op	21
MRT	<i>Myrcia</i> sp. nov.	be	wh	d	0	1	0	1	op	6*, 21*
MRT	<i>Myrcia torta</i> A. DC.	be	wh	d	0	1	0	1	op	6*, 21*
MRT	<i>Myrcia uberavensis</i> O. Berg	be	wh	d	0	1	0	1	op	1
MRT	<i>Psidium laruotteanum</i> Cambess.	be	wh	d	0	1	0	1	op	6*, 21*
NYC	<i>Guapira noxia</i> (Netto) Lundell	si	wh	d	0	1	1	0	tu	16, 17
NYC	<i>Neea theifera</i> Oerst.	si	ye	d	0	0	1	0	tu	6, 16
OCH	<i>Ouratea acuminata</i> (A. DC.) Engl.	be	ye	d	0	1	0	1	op	1, 6*
OCH	<i>Ouratea castaneaefolia</i> (A. DC.) Engl.	be	ye	d	0	1	0	1	op	6, 17
OCH	<i>Ouratea semiserrata</i> (Mart. & Nees) Engl.	be	ye	d	0	1	0	1	op	6
OCH	<i>Ouratea spectabilis</i> (Mart.) Engl.	be	ye	d	0	1	0	1	op	1, 6*
PRT	<i>Roupala montana</i> Aubl.	mo	wh	n	0	1	1	0	op	6, 20
RUB	<i>Chomelia ribesioides</i> Benth.ex A. Gray	mo	wh	d	0	1	1	0	tu	6*
RUB	<i>Palicourea rigida</i> Kunth	hb	or	d	0	0	1	0	tu	1, 16
RUB	<i>Tocoyena formosa</i> (Cham. & Schltdl.) K. Schum.	mo	ye	n	0	1	1	0	tu	6, 16
SPT	<i>Pouteria ramiflora</i> (Mart.) Radlk.	mo	cr	n	0	1	0	1	tu	25
SPT	<i>Pouteria torta</i> (Mart.) Radlk.	mo	cr	n	0	1	0	1	tu	25
STY	<i>Styrax ferrugineum</i> Nees & Mart.	be	wh	d	0	1	1	0	tu	16, 22
VOC	<i>Qualea grandiflora</i> Mart.	mo	ye	n	0	1	1	1	tu	6, 20
VOC	<i>Qualea multiflora</i> Mart.	be	wh	d	1	1	1	0	op	16, 17
VOC	<i>Qualea parviflora</i> Mart.	be	li	d	1	0	1	0	op	6, 16
VOC	<i>Vochysia thyrsoidea</i> Pohl	be	ye	d	1	0	1	1	op	15, 16



III - CAPÍTULO 2

Distribuição vertical e horizontal dos sistemas de polinização em fragmentos de cerrado do Brasil central.

² Trabalho submetido à revista *Biotropica* com o título "Vertical and horizontal distribution of pollination systems in cerrado fragments of central Brazil"

Vertical and horizontal distribution of pollination systems in cerrado fragments of central Brazil

Fernanda Quintas Martins^{1*} and Marco Antônio Batalha¹

¹ *Department of Botany, Federal University of São Carlos, PO Box 676, 13565-905, São Carlos, SP, Brazil; * Author for correspondence (e-mail: fernanda_quintas@uol.com.br)*

Key words: Central-western Brazil, Phenology, Savanna, Spatial distribution, Stratification

Abstract

The relationships between plants and pollinators are important to the structure and biological organization of communities. The main selective pressures on pollination strategies stem mainly from the environment in which the plants occur, such as subcanopy, canopy, edge, or interior of a given fragment. Different environmental conditions between the edge and the interior of the fragments or between the lower and the upper strata – differences in humidity, illumination, and airflow – increase the differences between ecological niches and may imply differences in the proportions of pollination systems. Plant-pollinator relationships in the cerrado, a Brazilian savanna, seem to involve guilds of pollinators associated with a given plant or group of plants. In some fragments covered by cerrado vegetation, we determined the frequency of pollination systems in the woody component and analyzed their spatial distribution both horizontally – in relation to distance from edge – and vertically – in relation to height. We placed randomly 38 transects and 570 points, sampling 2,280 individuals and 121 species. As expected in Neotropical regions, bee-pollination was the most frequent pollination system. To test whether the frequencies of the pollination systems varied with distance from edge and with height, we used regression analyses. For four of the five pollination systems (moths, bees, small insects, and bats), we found no significant variation in relation to distance from edge. We found a decrease in the frequency of plants pollinated by beetles toward the fragment interior. Similarly, for four of the five pollination systems (beetles, moths, bees, and small insects), we found no significant variation in relation to height. We found an increase in the frequency of plants pollinated by bats toward higher heights. In general, we found no horizontal and vertical variation in the pollination systems,

contrary to what was found in forests and, probably, as consequence of the more open physiognomy of the cerrado vegetation.

Introduction

Different authors (e.g., Bawa 1974; Kaur et al. 1978; Bawa 1990) have attempted to use reproductive features to explain the general patterns of diversity and community structure found in tropical woodlands with the underlying idea that plant diversity and spatial distribution is dependent on reproductive processes (Heithaus 1974). Studies on the reproductive biology of cerrado plant species have shown a great diversity of pollination systems, similar to those found in Neotropical forests (Oliveira and Gibbs 2002). The data emerging for the reproductive biology of plants have important consequences for conservation and understanding of the organization of cerrado communities (Oliveira and Gibbs 2002). Geographical and environmental distribution patterns of the different pollination systems have been identified, and the dominance of some groups may, to a certain extent, characterize those communities (Regal 1982; Bawa 1990).

The Cerrado Domain occupied originally 23% of the Brazilian territory (ca. 2 million km²), especially in the Central Plateau, being the second largest phytogeographic province of Brazil (Ratter et al. 1997). As its name implies, in the Cerrado Domain, the cerrado vegetation prevails. The cerrado vegetation is not uniform in physiognomy (Coutinho 1990), ranging from grassland to tall woodland, but most of its physiognomies lie within the range defined as tropical savanna (Sarmiento 1983). Castro et al. (1999) estimated that 3,000 to 7,000 vascular plant species occur in this vegetation type, from which 1,000 to 2,000 belong to the woody component.

As in other tropical communities (Bawa 1990), plant-pollinator relationships in the cerrado seem to involve guilds of pollinators associated with a given plant or group of plants (Oliveira and Gibbs 2000). There are few one-to-one plant-pollinator relationships, although many taxa are still poorly studied (Oliveira and Gibbs 2002). Bee pollination is dominant both in cerrado

and Neotropical forests (Oliveira and Gibbs 2000; Dulmen 2001; Ramírez 2004). Many large-bee genera observed in cerrado were also reported for wet and dry forests in Costa Rica (Bawa et al. 1985; Kress and Beach 1994), as were the small Meliponinae and Halictidae bees. In the cerrado, bees are the main pollinators, but others pollinators have a role for both woody and herbaceous cerrado species (Oliveira and Gibbs 2002). Rare and almost absent groups are butterflies and hummingbirds, which are frequent opportunist visitors or only secondary visitors of many woody species (Oliveira and Gibbs 2000).

The relationships between plants and pollinators are very important to the structure and biological organization of communities, affecting spatial distribution, abundance, richness, trophic structure, and phenodynamic (Heithaus 1974; Frankie 1975; Bawa et al. 1985; Morellato 1991), as well as genetic diversity by providing flow of genes (Nason et al. 1997). The structure of the vegetation can also be related to its reproduction, since it interferes in the horizontal and vertical organization of the plants (Ramírez 1993). Pollination system patterns can vary according to climate, altitude, geographic region, and vegetation type (Silberbauer-Gottsberger and Gottsberger 1988). The main selective pressures on pollination strategies stem mainly from the environment in which the plants occur, such as subcanopy, canopy, edge, or interior of a given fragment (Opler et al. 1980a; Waller 1988; Morellato 1991). Thus, different environmental conditions between the edge and the interior of the fragments or between the lower and the upper strata – differences in humidity, illumination, and airflow – increase the differences between ecological niches (Roth 1987) and may imply differences in the proportions of pollination systems (Smith 1973).

Pollination systems are not randomly distributed in the community (Bawa et al. 1985). There are, for example, differences between the species that reach the canopy and the inferior strata (Bawa et al. 1985). As long as the vertical structure of the vegetation results in stratification of food resources and microclimate, the animal community may be also stratified

(Smith 1973). Thus, each vegetation strata may have its own characteristic pollinators (Smith 1973), which, in turn, may be related to vertical differences in flower shapes and pollinator sizes (Bawa and Opler 1975; Opler et al. 1980a; Bawa et al. 1985). Vertical stratification of pollination systems may occur also in the cerrado (Oliveira and Gibbs 2002). Moths and bats are pollinators mostly of trees, whereas wind and hummingbird pollination appear mostly in the herbaceous layer (Oliveira and Gibbs 2002). Even though Araújo (2001) found no significant difference in the distribution of the pollination systems between the border and the interior of woodland fragments in the Brazilian Pantanal, species pollinated by wind, bats, and hummingbirds were not found inside seasonal forest fragments (Opler et al. 1980b; Morellato 1991).

Community level studies on different pollination systems may ultimately prove to be vital in understanding community structure and organization (Bawa et al. 1985). We determined the frequency of pollination systems in the woody component and analyzed the spatial distribution of these systems horizontally – in relation to distance from edge – and vertically – in relation to height – in some cerrado fragments. We tried to answer the following questions: What are the frequencies of the pollination systems among cerrado woody species? Do those frequencies vary from the edge to the interior of the fragments? Do those frequencies vary in relation to height?

Material and Methods

We carried out this study in Alto Taquari (Mato Grosso State), Alcinópolis (Mato Grosso do Sul State), and Mineiros (Goiás State), central-western Brazil, in the southwestern portion of the Brazilian Central Plateau. Regional climate is classified as Aw (Köppen 1931), that is, humid tropical with wet summer and dry winter. Annual rainfall varies from 1,200 to 2,000

mm, concentrated from October to March, and mean annual temperature lies around 24.6°C (Ramos-Neto & Pivello 2000). This region was originally covered mainly by cerrado vegetation, from open (*campo limpo*, a grassland savanna) to closed (*cerradão*, a tall woodland) physiognomies, following Coutinho's (1990) classification.

Based on satellite images, we picked randomly five fragments covered mainly by *cerrado sensu stricto* (a woodland). The first fragment (approximately, 22K0283659S and 8036276W UTM), with 8,278 ha; the second one (approximately, 22K0279934S and 8043454W UTM), with 1,678 ha; the third one (approximately, 22K0267453S and 8056613W UTM), with 41,452 ha; the fourth one (approximately, 22K0240604S and 8039048W UTM), with 6.666 ha; and the fifth (approximately, 22K0215774S and 7990493W UTM), with 12,459 ha. All fragments were located inside private properties and surrounded by agriculture and pasture.

We randomly placed 38 transects in the five fragments: eight in the first and fourth ones, four in the second one, twelve in the third one; and six in the fifth one. In each transect, we placed 15 sampling points, 10 m apart one from another, starting at 10 m from the fragment edge. We used the point-quarter method (Mueller-Dombois & Ellenberg 1974) to sample the woody component. In each point, we sampled four woody plants with stem diameter at soil level equal or larger than 3 cm. Thus, in the 38 transects, we placed 570 points and sampled 2,280 individuals. We collected the sampled individuals and identified them by comparison with lodged material at the São Paulo Botanical Institute or at the Federal University of São Carlos herbaria, by comparison with the Emas National Park reference collection (Batalha and Martins 2002), or by using identification keys based on vegetative characters (Batalha and Mantovani 1999).

We classified the species into families following Judd et al. (1999) and into pollination systems based on the literature (e.g., Silberbauer-Gottsberger and Gottsberger 1988; Barbosa 1997; Borges 2000; Oliveira and Gibbs 2000). Occasionally, when we could not find data for

a given species, we classified its pollination system based on data for related species of the same genus or based on their floral traits. We recognized the following pollination systems: wind, beetles, moths, bees, small insects, hummingbirds, and bats. The ‘small insects’ class included a varied assemblage of relatively small insects, such as small bees, beetles, flies, wasps, and butterflies (Bawa et al. 1985). We calculated the frequency of each pollination system among the sampled individuals.

To test whether the frequencies of the pollination systems with at least ten individuals varied with distance from edge and with height, we used regression analyses (Zar 1999). In relation to distance from edge, we grouped the sampled individuals according to their distance from edge; that is, for a given distance, we sampled 152 individuals (four individuals per point and 38 points for each distance) and calculated the frequencies of each pollination system among these 152 individuals. In relation to height, we arranged the individuals in decreasing order of height and divided them in eight classes with similar number of individuals (Table 1). We calculated median height and the frequencies of each pollination system in each class. In the regression analyses, “distance from edge” or “height class” were the independent variables and “frequency of a given pollination system” was the dependent one.

Results

We sampled 2,280 individuals, representing 121 species and 38 families (Table 2). The richest families were Fabaceae (24 species) and Myrtaceae (18 species), and *Davilla elliptica* A. St-Hil (337 individuals) and *Myrcia bella* Triana (246 individuals) were the best represented species. Of the 121 species, one was pollinated mainly by wind (0.83%); three, by beetles (2.48%); 15, by moths (12.40%); 65, by bees (53.72%); 30, by small insects (24.79%);

two, by hummingbirds (1.65%); and five, by bats (4.13%). Of the 2,280 individuals, two were pollinated mainly by wind (0.09%); ten, by beetles (0.44%); 204, by moths (8.95%); 1,712, by bees (75.09%); 310, by small insects (13.59%); three, by hummingbirds (0.13%); and 39, by bats (1.71%).

For four of the five pollination systems with at least ten individuals, we found no significant variation in relation to distance from edge (moths: $p = 0.604$; bees: $p = 0.733$; small insects: 0.790; bats: $p = 0.227$; Figure 1). We found a decrease in the frequency of plants pollinated by beetles toward the fragment interior ($p = 0.034$; Figure 1). Similarly, for four of the five pollination systems with at least ten individuals, we found no significant variation in relation to height (moths: $p = 0.155$; beetles: $p = 0.247$; bees: $p = 0.075$; small insects: 0.067; Figure 2). We found an increase in the frequency of plants pollinated by bats toward higher heights ($p = 0.005$; Figure 2).

Discussion

Most woody species in the cerrado fragments we sampled were pollinated mainly by bees, followed by small insects and moths. Bees were the main pollinators in other cerrado sites as well, such as in Botucatu, southeastern Brazil (Silberbauer-Gottsberger and Gottsberger 1988), and Brasilia, central Brazil (Oliveira and Gibbs 2000), and in other vegetation types, such as rain forest (e.g., Bawa et al. 1985). Pollination by bees is the most frequent pollination system not only in the cerrado, but also in the Neotropical flora as a whole (Gentry 1982).

During most of the first third of angiosperm evolution, a time during which many of the modern orders and families of plants arose, South America was a part of the West Gondwanaland, cradle of the angiosperms (Raven and Axelrod 1974). However, during virtually all of the Tertiary and much of the Cretaceous, South America was an island

continent, at least from the perspective of tropical plants, and most of the evolution of its rich and varied flora took place in isolation following separation from Africa and Laurasia (Gentry 1982). Plants with rather conspicuous, often large, tubular flowers pollinated by specialized large and medium-sized bees mostly belong to Amazonian-centered families, which are also the most frequent families in the cerrado flora, as, for example, Apocynaceae, Bignoniaceae, Lecythidaceae, and many Fabaceae (Gentry 1982).

Corroborating Oliveira and Gibbs (2000), who stated that butterflies and hummingbirds are rare groups as main pollinators of cerrado woody species, we found no species pollinated mainly by butterflies and only two pollinated mainly by hummingbirds. Silberbauer-Gottsberger and Gottsberger (1988) postulated that some environmental conditions, especially high temperatures and low air humidity, would explain the low incidence of hummingbird pollination in cerrado sites. Pollinating birds seem to be more abundant in habitats with a less seasonal climate, dominated by favorable conditions, which is associated with more constant and abundant food resources throughout the year (Ramírez 2004). Even though not frequent among cerrado woody species, butterfly and wind pollination may be important, respectively, among Asteraceae (Silberbauer-Gottsberger and Gottsberger 1988) and grasses and sedges (Barbosa 1997; Oliveira and Gibbs 2000), families that are frequent among herbaceous woody species (Batalha and Martins 2002).

Morellato (1991) found higher frequencies of bat-, bird-, and wind-pollinated species in the edge of rain forest fragments and of bee-pollinated species in the interior. Whereas the frequency of pollination systems varied from the edge to the interior in rain forest fragments (Morellato 1991, Opler *et al.* 1980b), we did not find such trend for the pollination systems in cerrado fragments, except for the plants pollinated mainly by beetles, whose frequency decreased towards the fragment interior. That non-variation of most pollination system in cerrado fragments in relation to the distance from edge could be a consequence of the open

physiognomy of the sampled vegetation. Since the *cerrado sensu stricto* physiognomy fits the definition of a tropical savanna (Bourlière and Hadley 1983), the differences in environmental conditions between edge and core regions of those fragments may be not as large as those in forest fragments.

Species pollinated mainly by hummingbirds, small insects, beetles, butterflies, and moths should be particularly common in the subcanopy, whereas species pollinated mainly by medium-sized to large bees should be predominant in the canopy (Bawa et al. 1985; Ramirez 1993). In forests, pollination systems present maximum diversity in the subcanopy, and although almost all systems occur in the canopy, approximately two thirds of the species in this stratum are pollinated by medium-sized to large bees and small diverse insects (Appanah 1981; Bawa et al. 1985; Ramírez 1989; Ramalho 2004; Ramírez 2004). Hummingbird and moths pollination systems are almost completely absent in the canopy trees (Appanah 1981; Bawa et al. 1985; Ramirez 1989).

Notwithstanding, we found no significant variation of the pollination system frequencies in relation to height, except for those plants pollinated by bats, whose frequency increased toward higher heights. The relative proportion of various pollination systems seems to be related to vegetation structure and floristic composition (Ramírez 1989), and, in tropical communities, most pollinators act in a wide vertical space and only a few of them can be considered as exclusive of a determined strata (Ramírez 1993). In a savanna, such as the *cerrado sensu stricto* we sampled, trees are much lower than in a forest, and, thus, exclusiveness of pollinators to a determined strata should be much less frequent than in forests.

In our study, bees were the main pollinators; as expected in a Neotropical flora (Gentry 1982). In general, we found no horizontal and vertical variation in the pollination systems, contrary to what was found in forests and, probably, as consequence of the more open

physiognomy of the cerrado fragments. There are still few studies that evaluated the distribution of pollination systems in relation to distance from the edge in fragments and tree height (Ramirez 1993). Detailed studies on the ecological and geographical variations of the pollination systems in cerrado fragments are still lacking, especially those concerning the herbaceous component and throughout the cerrado physiognomic gradient.

Acknowledgments

We are grateful to Conservation International, especially Drs. Mário Barroso Ramos-Neto and Paulo Gustavo do Prado Pereira, and CNPq, for financial support; to Emas and Oréades Foundations, for satellite images; and to André Vitor Fleuri Jardim and Júlia Caram, for help in field.

References

- Appanah S. 1981. Pollination in Malaysian primary forest. *The Malaysian Forester* 44: 37-42.
- Araújo A.C. 2001. Flora, fenologia de floração e polinização em capões do Pantanal Sul Mato Grossense. Ph.D. Thesis. State University of Campinas, Campinas, Brasil.
- Barbosa A.A. 1997. Biologia reprodutiva de uma comunidade de campo sujo, Uberlândia – MG. Ph.D. Thesis. State University of Campinas, Campinas, Brasil.
- Barros M.G. 1992. Fenologia da floração, estratégias reprodutivas e polinização de espécies simpátricas do gênero *Byrsonima* Rich (Malpighiaceae). *Revista Brasileira de Biologia* 52: 343-353.
- Barros M.G. 1998. Sistemas reprodutivos e polinização em espécies simpátricas de *Erythroxylum* P.Br. (Erythroxylaceae) do Brasil. *Revista Brasileira de Botânica* 21: 159-166.
- Barros M.G. 2001. Pollination ecology of *Tabebuia aurea* (Manso) Benth. & Hook. and *T. ochracea* (Cham.) Standl. (Bignoniaceae) in Central Brazil cerrado vegetation. *Revista Brasileira de Botânica* 24: 255-261.

- Batalha M.A. and Mantovani W. 1999. Chaves de identificação das espécies vegetais vasculares baseadas em caracteres vegetativos para a ARIE Cerrado Pé-de-Gigante (Santa Rita do Passa Quatro, SP). *Revista Instituto Florestal* 11: 137-158.
- Batalha M.A. and Martins F.R. 2002. The vascular flora of the cerrado in Emas National Park (Goiás, central Brazil). *Sida* 20: 295-312.
- Bawa K.S. 1974. Breeding system of tree species of lowland tropical community. *Evolution* 28: 85-92.
- Bawa K.S. 1990. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21: 399-422.
- Bawa K.S., Bulloch S.H., Perry D.R., Coville R.E. and Grayum M.H. 1985. Reproduction biology of tropical lowland rain forest tree. II. Pollination system. *American Journal of Botany* 72: 346-356.
- Bawa K.S. and Opler P.A. 1975. Dioecism in tropical forest trees. *Evolution* 29: 167-179.
- Borges H.B.N. 2000. Biologia reprodutiva e conservação do estrato lenhoso numa comunidade do cerrado. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- Bourlière F. and Hadley M. 1983. Present-day savannas: an overview. In: Goodall D.W. (ed), *Ecosystems of the world – tropical savannas*. Elsevier, Amsterdam, pp. 1-17.
- Castro A.A.J.F., Martins F.R., Tamashiro J.Y. and Shepherd G.J. 1999. How rich is the flora of Brazilian cerrados? *Annals of the Missouri Botanical Gardens* 86: 192-224.
- Coutinho L.M. 1990. Fire in the ecology of the Brazilian cerrado. In: Goldammer J.G. (ed), *Fire in the tropical biota*. Springer, Berlin, pp. 82-105.
- Dulmen van A. 2001. Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. *Plant Ecology* 153: 73-85.
- Franco A.L.M. 1995. Ecologia da polinização e biologia reprodutiva de sete espécies de Phaseoleae. Ph.D. Thesis. State University of Campinas, Campinas, Brasil.
- Frankie G.W. 1975. Tropical forest phenology and pollinator plant coevolution. In: Gilbert L.E. and Haven P.H. (eds.), *Coevolution of animals and plants*. University of Texas Press, Austin.
- Freitas C.V. and Oliveira P.E. 2002. Biologia reprodutiva de *Copaifera langsdorffii* Desf. (Leguminosae, Caesalpinioideae). *Revista Brasileira de Botânica* 25: 311-321.
- Gentry A.H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean Orogeny? *Annals of the Missouri Botanical Garden* 69: 557-593.

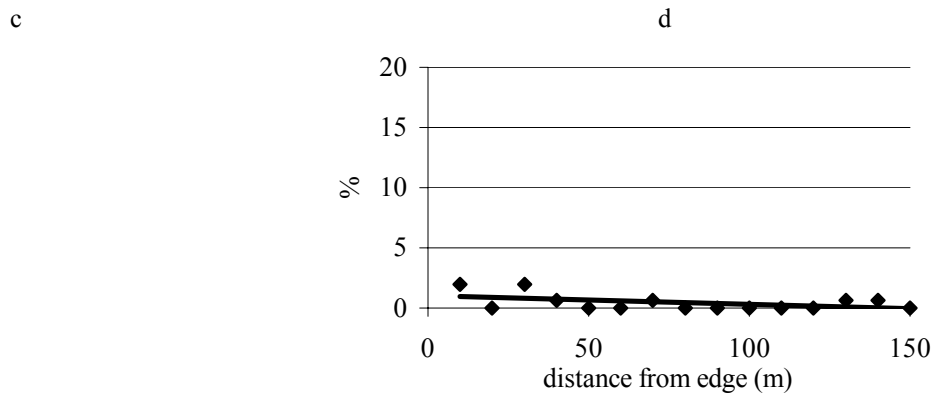
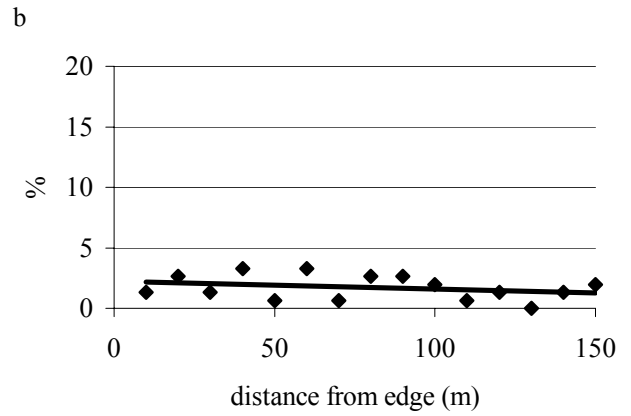
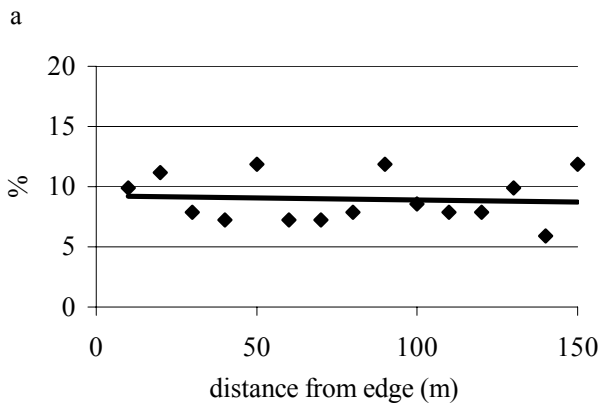
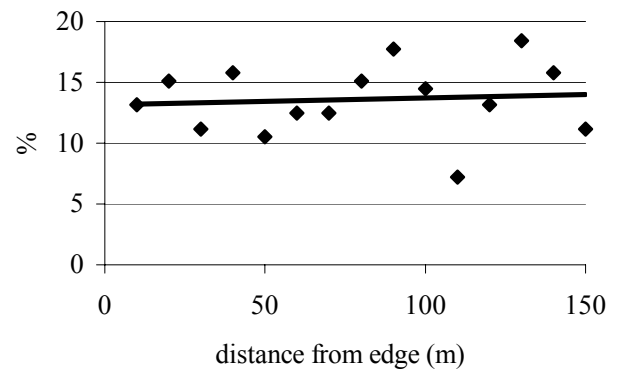
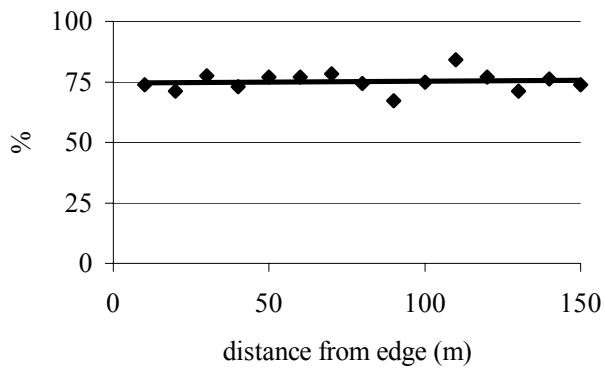
- Gibbs P.E., Oliveira P.E. and Bianchi M.B. 1999. Postzygotic control of selfing in *Hymenaea stigonocarpa* (Leguminosae-Caesalpinioideae), a bat-pollinated tree of the Brazilian cerrados. *International Journal of Plant Sciences* 160: 72-78.
- Goldenberg R. and Shepherd G.J. 1998. Studies on the reproductive biology of Melastomataceae in "cerrado" vegetation. *Plant Systematics and Evolution* 211: 13-29.
- Gottsberger G. 1986. Some Pollination Strategies in Neotropical Savannas and Forests. *Plant Systematics and Evolution* 152: 29-45.
- Gottsberger G. 1994. As anonáceas do cerrado e a sua polinização. *Revista Brasileira de Biologia* 54: 391-402.
- Gottsberger G. 1999. Pollination and evolution in neotropical Annonaceae. *Plant Species Biology* 14: 143-152.
- Heithaus E.R. 1974. The role of plant-pollinator interactions in determining community structure. *Annals of the Missouri Botanical Garden* 61: 675-691.
- Judd W.S., Campbell C.S., Kellog E.A. and Stevens P.F. 1999. *Plant systematics: a phylogenetic approach*. Sinauer, Sunderland.
- Kaur A., Ha C.D., Jong K., Sands V.E., Chan H.T., Solpadmo E. and Ashton P.S. 1978. Apomixis may be widespread among trees of the climax rain forest. *Nature* 271: 440-442.
- Köppen W. 1931. *Grundriss der Klimakunde*. Gruyter, Berlin.
- Kress W.J. and Beach J.H. 1994. Flowering plant reproductive systems. In: McDade L.A., Bawa K.S., Hespenheide H.A. and Hartshorn G.S. (eds), *La Selva. Ecology and natural history of neotropical rain forest*. University Chicago, Chicago, pp. 161-182.
- Morellato, L.P.C. 1991. *Estudo da fenologia de árvores, arbustos e lianas de uma floresta semidecídua no Sudoeste do Brasil*. Ph.D. Thesis. State University of Campinas, Campinas, Brasil.
- Mueller-Dombois D. and Ellenberg H. 1974. *Aims and methods of vegetation ecology*. John Willey & Sons, New York.
- Nason J.D., Aldrich P.R. and Hamrick J.L. 1997. Dispersal and the dynamics of genetic structure in fragmented tropical tree populations. In: Laurence W.F. and Bierregard Jr. R.O. (eds), *Tropical forest remnants. Ecology, management, and conservation of fragmented communities*. University of Chicago, Chicago.
- Oliveira P.E. and Gibbs P.E. 1994. Pollination biology and breeding systems of six *Vochysia* species (Vochysiaceae) in Central Brazil. *Journal of Tropical Ecology* 10: 509-522.
- Oliveira P.E. and Gibbs P.E. 2000. Reproductive biology of woody plants in a cerrado community of Central Brazil. *Flora* 195: 311-329.

- Oliveira P.E. and Gibbs P.E. 2002. Pollination and reproductive biology in cerrado plant communities. In: Oliveira P.E. and Marquis R.J. (eds), *The cerrados of Brazil: ecology and natural history of a Neotropical savanna*. Columbia University, New York, pp. 329-347.
- Oliveira P.E. and Paula F.R. 2001. Fenologia e biologia reprodutiva de plantas de matas de galeria. In: Ribeiro J.F., Fonseca da C.E.L. and Souza-Silva J.C. (eds), *Cerrado: caracterização e recuperação de matas de galeria*. Embrapa, Planaltina, pp. 303-331.
- Oliveira P.E. and Sazima M. 1990. Pollination biology of two species of *Kielmeyera* (Guttiferae) from Brazilian cerrado vegetation. *Plant Systematics and Evolution* 172: 35-49.
- Oliveira P.E., Gibbs P.E., Barbosa A.A. and Talavera S. 1992. Contrasting breeding systems in two *Eriotheca* (Bombacaceae) species of the Brazilian cerrados. *Plant Systematics and Evolution* 179: 207-219.
- Oliveira P.E., Gibbs P.E. and Barbosa A.A. 2004. Moth pollination of woody species in the cerrados of central Brazil: a case of so much owed to so few? *Plant Systematics and Evolution* 245: 41-54.
- Opler P.A., Baker H.G. and Frankie G.W. 1980a. Plant reproductive characteristics during secondary succession in Neotropical lowland forest ecosystems. *Biotropica* 12 (Supplement): 40-46.
- Opler P.A., Frankie G.W. and Baker H.G. 1980b. Comparative phenology studies of treelet and shrub species in tropical wet and dry forest in the lowland of Costa Rica. *Journal of Ecology* 68: 189-209.
- Proença C.E.B. and Gibbs P.E. 1994. Reproductive biology of eight sympatric Myrtaceae from Central Brazil. *New Phytologist* 126: 343-354.
- Ramalho M. 2004. Stingless bees and mass flowering trees in the canopy of Atlantic Forest: a tight relationship. *Acta Botanica Brasilica* 18: 37-47.
- Ramirez N. 1989. Biología de polinización en una comunidad arbustiva tropical de la alta guayana Venezolana. *Biotropica* 21: 319-330.
- Ramírez N. 1993. Reproductive biology in a tropical shrubland of Venezuelan Guayana. *Journal of Vegetation Science* 4: 5-12.
- Ramirez N. 2004. Ecology of pollination in a tropical Venezuelan savanna. *Plant Ecology* 173: 171-189.
- Ramos-Neto M.B. and Pivello V.R. 2000. Lightning fires in a Brazilian savanna National Park: rethinking management strategies. *Environmental Management* 26: 675-684.
- Ratter J.A., Ribeiro J.F. and Bridgewater S. 1997. The Brazilian cerrado vegetation and threats to its biodiversity. *Annals of Botany* 80: 223-230.

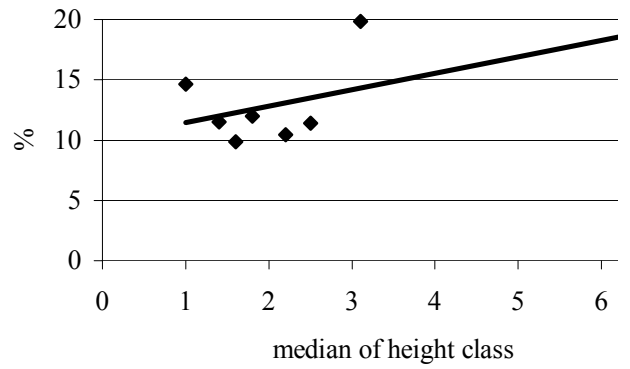
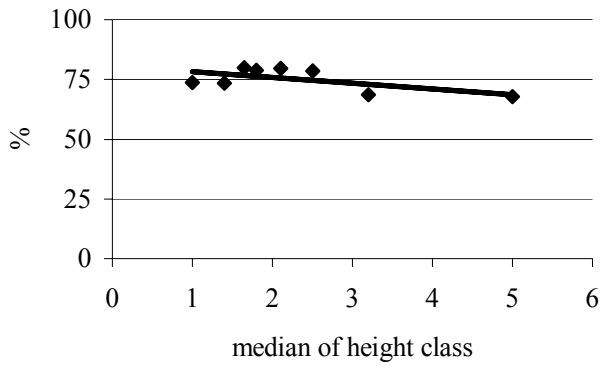
- Raven P.H. and Axelrod D.I. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539-673.
- Regal P.J. 1982. Pollination by Wind and animals: Ecology of geographic patterns. *Annual Review of Ecology and Systematics* 13: 497-524.
- Roth I. 1987. Stratification of a tropical forest as seen in dispersal types. Dr W. Junk, Dordrecht.
- Saraiva L.C., Cesar O. and Monteiro R. 1988. Biologia da polinização e sistemas de reprodução de *Styrax camporum* Pohl e *S. ferrugineus* Nees et Mart. (Styracaceae). *Revista Brasileira de Botânica* 11: 71-80.
- Sarmiento G. 1983. The savannas of tropical America. In: Goodall D.W. (ed), *Ecosystems of the world: tropical savannas*. Elsevier, Amsterdam, pp. 245-288.
- Sazima M. and Sazima I. 1975. Quiropterofilia em *Lafoensia pacari* St. Hil. (Lythraceae), na Serra do Cipó, Minas Gerais. *Ciência e Cultura* 27: 405-416.
- Sigrist M.R. 2001. Biologia reprodutiva de doze espécies simpátricas de Malpighiaceae em mata semidecídua do sudoeste Brasileiro. Ph.D. Thesis. State University of Campinas, Campinas, Brasil.
- Silberbauer-Gottsberger I. and Gottsberger G. 1988. A polinização de plantas do cerrado. *Revista Brasileira de Biologia* 48: 651-663.
- Silberbauer-Gottsberger I., Gottsberger G. and Webber A.C. 2003. Morphological and functional flower characteristics of New and Old world annonaceae with respect to their mode of pollination. *Taxon* 52: 701-718.
- Smith A.P. 1973. Stratification of temperate and tropical forest. *American Naturalist* 107: 671-683.
- Torezan-Silingardi H.M. and Del-Claro K. 1998. Behavior of visitors and reproductive biology of *Campomanesia pubescens* (Myrtaceae) in cerrado vegetation. *Ciência e Cultura* 50: 281-284.
- Viana B.F., Kleinert A.M.P. and Imperatriz-Fonseca V.L. 1997. Abundance and flower visits of bees in a Cerrado of Bahia, Tropical Brazil. *Studies on Neotropical Fauna and Environment* 32: 212-219.
- Waller D.M. 1988. Plant morphology and reproduction. In: Doust J.L. and Doust L.L. (ed), *Plant Reproductive Ecology- Patterns and Strategies*. Oxford University, New York.
- Weber W.A. 1982. Mnemonic three-letter acronyms for the families of vascular plants: a device for more effective herbarium curation. *Taxon* 31: 74-88.
- Zar J.H. 1999. *Biostatistical analysis*. Prentice Hall, Upper Saddle River.

Figure 1. Regression analysis of the distance from edge in fragments of cerrado *sensu stricto* of central Brazil: a - bees, b - small insect, c - moth, d - bats, and e - beetles.

Figure 2. Regression analysis of the height of woody species in *sensu stricto* cerrado fragments of central Brazil: a - bees, b - small insect, c - moth, d - bats, and e - beetles.

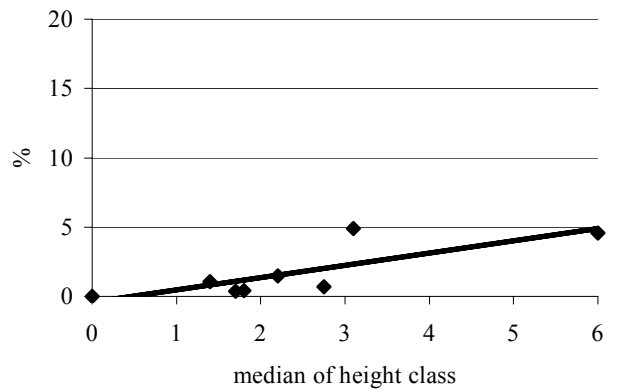
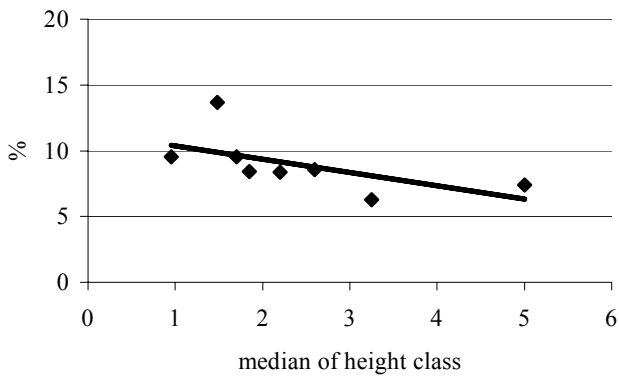


e



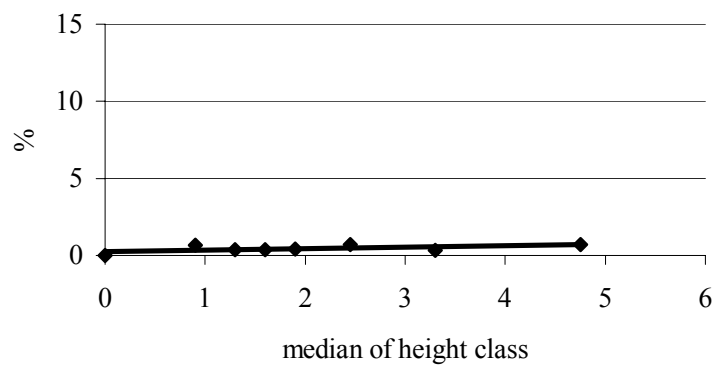
a

b



c

d



e

Table 1. Height classes with number of individuals in five cerrado fragments of central Brazil.

height (m)	individuals
lower limit – upper limit	
0.00 – 1.20	294
1.20 – 1.55	278
1.55 – 1.78	273
1.78 – 1.90	250
1.90 – 2.30	335
2.30 – 2.85	280
2.85 – 3.80	287
3.80 – 12.50	283

Table 2. Pollination systems of the woody species sampled in five cerrado fragments, central Brazil. Family names were abbreviated according to Weber (1982). Pol – pollination systems; ba – bats; be – bees; bt – beetles; hb – hummingbird; mo – moths; si – small insects; wi – wind. Sources: 1 - Araújo (2001), 2 - Barbosa (1997), 3 - Barros (1992), 4 - Barros (1998), 5 - Barros (2001), 6 - Bawa et al. (1985), 7 - Borges (2000), 8 - Franco (1995), 9 - Freitas and Oliveira (2002), 10 - Gibbs et al. (1999), 11 - Goldenberg and Shepherd (1998), 12 - Gottsberger (1986), 13 - Gottsberger (1994), 14 - Gottsberger (1999), 15 - Oliveira and Gibbs (1994), 16 - Oliveira and Gibbs (2000), 17 - Oliveira and Paula (2001), 18 - Oliveira and Sazima (1990), 19 - Oliveira et al. (1992), 20 - Oliveira et al. (2004), 21 - Proença and Gibbs (1994), 22 - Ramirez 2004, 23 - Saraiva et al. (1988), 24 - Sazima and Sazima (1975), 25 - Sigrist (2001), 26 - Silberbauer-Gottsberger et al. (2003), 27 - Silberbauer-Gottsberger and Gottsberger (1988), 28 - Torezan-Silingardi and Del-Claro (1998), 29 - Viana et al. (1997); * classification of the pollination systems based on the genus; + based in floral traits.

Family	Species	Pol	Source
Anacardiaceae	<i>Anacardium humile</i> A. St-Hil.	si	2 ⁺
Anacardiaceae	<i>Tapirira guianensis</i> Aubl.	si	17
Annonaceae	<i>Annona coriacea</i> Mart.	bt	12, 13
Annonaceae	<i>Annona crassiflora</i> Mart.	bt	13, 16
Annonaceae	<i>Bocageopsis mattogrossensis</i> (R.E. Fries) R.E. Fries	si	15*, 28*
Annonaceae	<i>Duguetia furfuracea</i> (A. St-Hil.) Benth. & Hook.f.	bt	2, 13
Apiaceae	<i>Didymopanax macrocarpum</i> (Cham. & Schltdl.) Seem.	si	16, 17*
Apiaceae	<i>Didymopanax vinosum</i> (Cham. & Schltdl.) Marchal	si	16*, 17*
Apocynaceae	<i>Aspidosperma macrocarpon</i> Mart.	mo	16, 20
Apocynaceae	<i>Aspidosperma nobile</i> Müll. Arg.	mo	16*, 17*
Apocynaceae	<i>Aspidosperma polyneuron</i> Müll. Arg.	mo	16*, 20*
Apocynaceae	<i>Aspidosperma tomentosum</i> Mart.	mo	16, 20
Apocynaceae	<i>Hancornia speciosa</i> Gomez	mo	16*, 20
Apocynaceae	<i>Himatanthus obovatus</i> (Müll. Arg.) Woods.	mo	7, 20
Asteraceae	<i>Eremanthus erythropappus</i> Sch. Bip.	si	2*, 16*
Asteraceae	<i>Eremanthus glomerulatus</i> Less.	si	16
Asteraceae	<i>Piptocarpha rotundifolia</i> (Less.) Baker	si	16, 17
Bignoniaceae	<i>Tabebuia aurea</i> (Silva Manso) S. Moore	be	5, 7
Bignoniaceae	<i>Tabebuia ochracea</i> (Cham.) Standl.	be	5, 16
Bignoniaceae	<i>Zeyheria montana</i> Mart.	hb	2
Caryocaraceae	<i>Caryocar brasiliense</i> Cambess.	ba	7, 20
Celastraceae	<i>Austroplenkia populnea</i> (Reissek) Lund	si	17
Celastraceae	<i>Peritassa campestris</i> (Cambess.) A.C. Sm.	be	2 ⁺
Chrysobalanaceae	<i>Couepia grandiflora</i> (Mart. & Zucc.) Benth. Ex Hook.f.	mo	17, 27
Chrysobalanaceae	<i>Licania humilis</i> Cham. & Schltdl.	be	1*, 22*
Clusiaceae	<i>Kielmeyera coriacea</i> Mart.	be	17, 18
Clusiaceae	<i>Kielmeyera rubriflora</i> Cambess.	be	18
Combretaceae	<i>Buchenavia tomentosa</i> Eichl.	si	+
Connaraceae	<i>Connarus suberosus</i> Planch.	si	7, 16
Connaraceae	<i>Rourea induta</i> Planch.	be	2
Dilleniaceae	<i>Davilla elliptica</i> A. St-Hil.	be	2, 7
Ebenaceae	<i>Diospyros hispida</i> A. DC.	mo	20, 27
Erythroxylaceae	<i>Erythroxylum campestre</i> A. St-Hil.	si	2, 4
Erythroxylaceae	<i>Erythroxylum suberosum</i> A. St-Hil.	si	4, 7
Erythroxylaceae	<i>Erythroxylum tortuosum</i> Mart.	si	4, 16
Euphorbiaceae	<i>Manihot caerulescens</i> Pohl	be	1*
Euphorbiaceae	<i>Maprounea guianensis</i> Aubl.	si	17

Family	Species	Pol	Source
Euphorbiaceae	<i>Pera glabrata</i> (Schott.) Baill.	si	17
Fabaceae	<i>Acosmium subelegans</i> (Mohl.) Yakovlev	be	7
Fabaceae	<i>Anadenanthera falcata</i> (Benth.) Speg	si	17*
Fabaceae	<i>Andira anthelmia</i> (Vell.) J.F. Macbr.	be	7*
Fabaceae	<i>Andira cuiabensis</i> Benth.	be	7
Fabaceae	<i>Andira laurifolia</i> Benth.	be	7*
Fabaceae	<i>Andira vermifuga</i> (Mart.) Benth.	be	7*
Fabaceae	<i>Bauhinia rufa</i> Steud.	ba	10, 17
Fabaceae	<i>Bowdichia virgilioides</i> Kunth	be	7, 17
Fabaceae	<i>Copaifera langsdorffii</i> Desf.	be	9, 17
Fabaceae	<i>Dalbergia cuiabensis</i> Benth.	be	16*, 17*
Fabaceae	<i>Dalbergia miscolobium</i> Benth.	be	16, 17
Fabaceae	<i>Dimorphandra mollis</i> Benth.	si	7, 16
Fabaceae	<i>Dioclea bicolor</i> Benth.	be	8*
Fabaceae	<i>Diptychandra aurantiaca</i> Tul.	be	+
Fabaceae	<i>Harpalyce brasiliana</i> Benth.	be	+
Fabaceae	<i>Hymenaea stigonocarpa</i> Mart.	ba	7, 10
Fabaceae	<i>Machaerium acutifolium</i> Vogel	be	7*, 22*
Fabaceae	<i>Plathymenia reticulata</i> Benth.	si	+
Fabaceae	<i>Pterodon pubescens</i> Benth.	be	16*
Fabaceae	<i>Sclerolobium aureum</i> (Tul.) Benth.	si	7
Fabaceae	<i>Sclerolobium paniculatum</i> Vogel	si	16, 17
Fabaceae	<i>Senna silvestris</i> (Vell.) H.S. Irwin & Barneby	be	17, 29
Fabaceae	<i>Stryphnodendron obovatum</i> Benth.	si	7, 16*
Fabaceae	<i>Vatairea macrocarpa</i> (Benth.) Ducke	be	+
Flacourtiaceae	<i>Casearia sylvestris</i> Sw.	si	2, 7
Icacinaceae	<i>Emmotum nitens</i> (Benth.) Miers	si	16, 17
Lauraceae	<i>Ocotea corymbosa</i> (Meissn.) Mez.	si	17
Lecythidaceae	<i>Eschweilera nana</i> (O.Berg) Miers	be	6*
Loganiaceae	<i>Strychnos pseudoquina</i> A. St-Hil.	mo	16, 20
Lythraceae	<i>Lafoensia pacari</i> A. St-Hil.	ba	7, 24
Malpighiaceae	<i>Banisteriopsis stellaris</i> (Griseb.) B.Gates	be	2*, 12
Malpighiaceae	<i>Byrsonima basiloba</i> A. Juss.	be	2, 3*
Malpighiaceae	<i>Byrsonima coccolobifolia</i> A. Juss.	be	3, 7
Malpighiaceae	<i>Byrsonima crassa</i> Nied.	be	3, 17
Malpighiaceae	<i>Byrsonima intermedia</i> A. Juss.	be	2, 12
Malpighiaceae	<i>Peixotoa reticulata</i> Griseb.	be	2, 25*
Malvaceae	<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns	be	17, 19
Malvaceae	<i>Pseudobombax longiflorum</i> (Mart. & Zucc.) A. Robyns	ba	7, 20
Melastomataceae	<i>Miconia albicans</i> Triana	be	11, 17
Melastomataceae	<i>Miconia fallax</i> A. DC.	be	11, 16
Melastomataceae	<i>Miconia ferruginata</i> A. DC	be	11*
Melastomataceae	<i>Miconia ligustroides</i> (A. DC.) Naud.	be	11
Melastomataceae	<i>Mouriri elliptica</i> Mart.	be	11*
Moraceae	<i>Brosimum gaudichaudii</i> Trec.	wi	2, 7
Myristicaceae	<i>Virola sebifera</i> Aubl.	si	17
Myrtaceae	<i>Campomanesia adamantium</i> (Cambess.) O. Berg	be	2*, 28*
Myrtaceae	<i>Campomanesia pubescens</i> (A. DC.) O. Berg	be	2, 28
Myrtaceae	<i>Eugenia aurata</i> O. Berg	be	2, 7
Myrtaceae	<i>Eugenia bimarginata</i> A. DC.	be	2*, 7*
Myrtaceae	<i>Eugenia piuhensis</i> O. Berg	be	2*, 7*
Myrtaceae	<i>Eugenia puniceifolia</i> (Kunth) A. DC.	be	2
Myrtaceae	<i>Myrcia bella</i> Cambess.	be	7*, 21*
Myrtaceae	<i>Myrcia camapuanensis</i> N.F.E. Silveira	be	7*, 21*
Myrtaceae	<i>Myrcia crassifolia</i> (O. Berg) Kiaersk.	be	7*, 21
Myrtaceae	<i>Myrcia fallax</i> (Rich.) A. DC.	be	7*, 21*
Myrtaceae	<i>Myrcia guianensis</i> A. DC.	be	7*, 21*
Myrtaceae	<i>Myrcia laruotteana</i> Cambess.	be	7*, 21*
Myrtaceae	<i>Myrcia linguiformis</i> Kiaersk.	be	7*, 21*

Family	Species	Pol	Source
Myrtaceae	<i>Myrcia rhodosepala</i> Kiaersk.	be	21
Myrtaceae	<i>Myrcia</i> sp. Nov.	be	7*, 21*
Myrtaceae	<i>Myrcia torta</i> A. DC.	be	7*, 21*
Myrtaceae	<i>Myrcia uberavensis</i> O. Berg	be	2
Myrtaceae	<i>Psidium laruotteanum</i> Cambess.	be	7*, 21*
Nyctaginaceae	<i>Guapira noxia</i> (Netto) Lundell	si	16, 17
Nyctaginaceae	<i>Neea theifera</i> Oerst.	si	7, 16
Ochnaceae	<i>Ouratea acuminata</i> (A. DC.) Engl.	be	2*, 7*
Ochnaceae	<i>Ouratea castaneaefolia</i> (A. DC.) Engl.	be	7, 17
Ochnaceae	<i>Ouratea semiserrata</i> (Mart. & Nees) Engl.	be	7, 16*
Ochnaceae	<i>Ouratea spectabilis</i> (Mart.) Engl.	be	2*, 7*
Proteaceae	<i>Roupala montana</i> Aubl.	mo	7, 20
Rubiaceae	<i>Chomelia ribesioides</i> Benth.ex A. Gray	mo	7*
Rubiaceae	<i>Genipa americana</i> L.	be	6
Rubiaceae	<i>Palicourea rigida</i> Kunth	hb	2, 16
Rubiaceae	<i>Tocoyena formosa</i> (Cham. & Schltdl.) K. Schum.	mo	7, 16
Sapindaceae	<i>Toulicia tomentosa</i> Radlk.	si	+
Sapotaceae	<i>Pouteria ramiflora</i> (Mart.) Radlk.	mo	27
Sapotaceae	<i>Pouteria torta</i> (Mart.) Radlk.	mo	27
Simaroubaceae	<i>Simarouba amara</i> Aubl.	si	6, 17
Styracaceae	<i>Styrax ferrugineum</i> Nees & Mart.	be	16, 23
Vochysiaceae	<i>Qualea grandiflora</i> Mart.	mo	7, 20
Vochysiaceae	<i>Qualea multiflora</i> Mart.	be	7, 16
Vochysiaceae	<i>Qualea parviflora</i> Mart.	be	7, 16
Vochysiaceae	<i>Vochysia thyrsoidea</i> Pohl	be	15, 16

IV – APÊNDICE

Tentativa para chave de identificação de sistemas de polinização em espécies arbustivo- arbóreas de cerrado

- 1. Corola tubulosa
 - 2. Antese noturna mariposas
 - 2'. Antese diurna
 - 3. Flores grandes (>3 cm), odor ausente..... aves
 - 3'. Flores pequenas (≤ 1 cm) ou médias ($1 \leq 3$ cm), odor presente
 - 4. Guias de recurso presentes..... abelhas
 - 4'. Guias de recurso ausentes
 - 5. Cor amarela, laranja ou vermelha..... abelhas
 - 5'. Cor branca, creme, esverdeada ou roxa
 - 6. Flor média ($1 \leq 3$ cm)..... abelhas
 - 6'. Flor pequena (≤ 1 cm)
 - 7. Longevidade de 0,5 ou 1 dia, pólen como recurso abelhas
 - 7'. Longevidade de 1 dia, néctar ou pólen como recurso insetos pequenos
 - 1'. Corola aberta ou fechada
 - 8. Guias de recurso presentes
 - 9. Antese noturna, flores grandes (>3 cm) morcegos
 - 9'. Antese diurna, flores pequenas (≤ 1 cm) ou médias ($1 \leq 3$ cm) abelhas
 - 8'. Guias de recurso ausentes
 - 10. Cor amarela, laranja ou vermelha
 - 11. Corola aberta abelhas
 - 11'. Corola fechada
 - 12. Antese diurna, flor pequena (≤ 1 cm) ou média ($1 \leq 3$ cm)..... abelhas

- 12'. Antese noturna, flor média ($1 \leq 3$ cm) ou grande (>3 cm)..... besouros
- 10'. Cor branca, creme, esverdeada ou roxa
13. Flor grande (>30 mm), antese noturnamorcegos
- 13'. Flor pequena (≤ 1 cm) ou média ($1 \leq 3$ cm), antese diurna
14. Flor média ($1 \leq 3$ cm) abelhas
- 14'. Flor pequena (≤ 1 cm)
15. Odor ausente, recursos ausentes vento
- 15'. Odor presente, recursos presentes
16. Longevidade de 0,5 ou 1 dia, pólen como recurso..... abelhas
- 16'. Longevidade de 1 dia, néctar ou pólen como recurso insetos pequenos

V – CONCLUSÃO GERAL

Com este trabalho, chegamos às seguintes conclusões:

- Nos cinco fragmentos de cerrado estudados, encontramos 121 espécies pertencentes a 38 famílias, totalizando 2.280 indivíduos amostrados;
- As famílias mais representativas foram Fabaceae, com 24 espécies, e Myrtaceae, com 18 espécies;
- As espécies mais abundantes foram *Davilla elliptica*, com 337 indivíduos e *Myrcia bella*, com 246 indivíduos;
- Os caracteres florais que demonstraram uma maior importância para a polinização foram a forma da flor, o tipo de recompensa, o período de antese e, em menor escala, o odor;
- A maioria das espécies apresentou flores com antese diurna, cores claras (amarela, verde, branca e creme) e flores abertas;
- Na vegetação de cerrado, as espécies com flores visitadas principalmente por abelhas (54%) e por insetos pequenos (25%) formaram os principais grupos ecologicamente relacionados à polinização, corroborando o predomínio das abelhas como polinizadores (*e.g.* Oliveira & Gibbs 2000, Silberbauer-Gottsberger & Gottsberger 1988);
- Os sistemas de polinização menos frequentes foram os beija-flores e o vento, não havendo ainda nenhuma espécie polinizada principalmente por borboletas. As porcentagens desses sistemas devem aumentar, caso se considere o componente herbáceo-subarbustivo;
- Com relação à análise de ordenação, encontramos formação de grupos distintos para as espécies vegetais polinizadas por mariposas, besouros e morcegos, estando relacionados com antese noturna, flores tubulares, e nos dois últimos casos, com o odor;
- As aves e o vento também formaram grupos distintos, estando o primeiro relacionado com flores tubulares, antese diurna, presença de néctar e cores chamativas; e o segundo relacionado com flores abertas, antese diurna e cores verdes;

- As classes das abelhas e dos insetos pequenos apresentaram uma grande dispersão e sobreposição, devido, provavelmente, a uma ausência de especificidade entre a relação planta-polinizador;
- Encontramos uma variação horizontal significativa para apenas um dos cinco sistemas de polinização: houve uma diminuição das espécies polinizadas por besouros em direção ao interior;
- Encontramos uma variação vertical significativa para apenas um sistema de polinização: houve um aumento do número de espécies polinizadas por morcegos em plantas mais altas;
- Nossos resultados não corroboraram a idéia de que a distribuição espacial dos polinizadores não é aleatória (Bawa et al. 1985). Essa não variação da maioria dos sistemas de polinização nos fragmentos de cerrado *sensu stricto* pode ser uma consequência da fisionomia aberta da vegetação amostrada e das árvores serem muito mais baixas do que as de florestas;

Há ainda poucos estudos que avaliaram a distribuição espacial dos sistemas de polinização na vegetação de cerrado. Estudos detalhados são necessários para o entendimento das variações ecológicas e geográficas dos sistemas de polinização, especialmente ao que concerne o componente herbáceo-subarborescente e o gradiente fisionômico do cerrado.

VI – REFERÊNCIAS BIBLIOGRÁFICAS

- Anderson W.R. 1979. Floral conservatism in Neotropical Malpighiaceae. *Biotropica* 11: 219-223.
- Appanah S. 1981. Pollination in Malaysian primary forest. *The Malaysian Forester* 44: 37-42.
- Araújo A.C. 2001. Flora, fenologia de floração e polinização em capões do Pantanal Sul Mato Grossense. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- Barbosa A.A. 1997. Biologia reprodutiva de uma comunidade de campo sujo, Uberlândia – MG. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- Barret S.C.H. & Eckert C.G. 1990. Current issues in Plant Reproductive Ecology. *Israel Journal of Botany* 39: 5-12.
- Barros M.G. 1992. Fenologia da floração, estratégias reprodutivas e polinização de espécies simpátricas do gênero *Byrsonima* Rich (Malpighiaceae). *Revista Brasileira de Biologia* 52: 343-353.
- Barros M.G. 1998. Sistemas reprodutivos e polinização em espécies simpátricas de *Erythroxylum* P.Br. (Erythroxylaceae) do Brasil. *Revista Brasileira de Botânica* 21: 159-166.
- Barros M.G. 2001. Pollination ecology of *Tabebuia aurea* (Manso) Benth. & Hook. and *T. ochracea* (Cham.) Standl. (Bignoniaceae) in Central Brazil cerrado vegetation. *Revista Brasileira de Botânica* 24: 255-261.
- Batalha M.A. & Mantovani W. 1999. Chaves de identificação das espécies vegetais vasculares baseadas em caracteres vegetativos para a ARIE Cerrado Pé-de-Gigante (Santa Rita do Passa Quatro, SP). *Revista Instituto Florestal* 11: 137-158.
- Batalha M.A. & Martins F.R. 2002. The vascular flora of the cerrado in Emas National Park (Goiás, central Brazil). *Sida* 20: 295-312.
- Bawa K.S. 1974. Breeding system of tree species of lowland tropical community. *Evolution* 28: 85-92.
- Bawa K.S. 1980. Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* 11: 15-39.

- Bawa K.S. 1990. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21: 399-422.
- Bawa K.S., Bulloch S.H., Perry D.R., Coville R.E. & Grayum M.H. 1985. Reproduction biology of tropical lowland rain forest tree. II. Pollination system. *American Journal of Botany* 72: 346-356.
- Bawa K.S. & Opler P.A. 1975. Dioecism in tropical forest trees. *Evolution* 29: 167-179.
- Borges H.B.N. 2000. Biologia reprodutiva e conservação do estrato lenhoso numa comunidade do cerrado. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- Bosch J., Retana J. & Cerdá X. 1997. Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia* 109: 583-591.
- Bourlière F. & Hadley M. 1983. Present-day savannas: an overview. In: Goodall D.W. (ed), *Ecosystems of the world – tropical savannas*. Elsevier, Amsterdam, pp. 1-17.
- Buchmann S.L. 1983. Buzz pollination in angiosperms. In: Jones C.E. & Little R.J. (eds.), *Handbook of Experimental Pollination Biology*. Van Nostrand Reinhold, New York, pp. 73-113.
- Buchmann S.L. 1987. The ecology of oil flowers and their bees. *Annual Review of Ecology and Systematics* 18: 343-369.
- Bullock S.H. 1994. Wind pollination of Neotropical dioecious trees. *Biotropica* 26: 172-179.
- Buzato S., Franco A.L.M. & Sazima M. 1994. Adequação de *Camptosema scarlatinum* e *Collaea speciosa* à polinização por beija-flores. In: Resumos do XLV Congresso Nacional de Botânica: 64.
- Castro A.A.J.F., Martins F.R., Tamashiro J.Y. & Shepherd G.J. 1999. How rich is the flora of Brazilian cerrados? *Annals of the Missouri Botanical Garden* 86: 192-224.
- Coutinho L.M. 1990. Fire in the ecology of the Brazilian cerrado. In: Goldammer J.G. (ed), *Fire in the tropical biota*. Springer, Berlin, pp. 82-105.

- Crestana C.S.M. & Kageyama P.Y. 1989. Biologia reprodutiva de *Copaifera langsdorffii*. Revista Instituto Florestal 1: 201-214.
- Dulmen van A. 2001. Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. Plant Ecology 153: 73-85.
- Endress P.K. 1994. Diversity and evolutionary biology of tropical flowers. Cambridge University, Cambridge.
- Faegri K. & Pijl L. van der. 1979. The principles of pollination ecology. Pergamon, New York.
- Franco A.L.M. 1995. Ecologia da polinização e biologia reprodutiva de sete espécies de Phaseoleae. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- Frankie G.W. 1975. Tropical forest phenology and pollinator plant coevolution. In: Gilbert L.E. & Haven P.H. (eds.), Coevolution of animals and plants. University of Texas Press, Austin.
- Freitas C.V. & Oliveira P.E. 2002. Biologia reprodutiva de *Copaifera langsdorffii* Desf. (Leguminosae, Caesalpinioideae). Revista Brasileira de Botânica 25: 311-321.
- Gentry A.H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean Orogeny? Annals of the Missouri Botanical Garden 69: 557-593.
- Gibbs P.E., Oliveira P.E. & Bianchi M.B. 1999. Postzygotic control of selfing in *Hymenaea stigonocarpa* (Leguminosae-Caesalpinioideae), a bat-pollinated tree of the Brazilian cerrados. International Journal of Plant Sciences 160: 72-78.
- Goldenberg R. 1994. Estudos sobre a biologia reprodutiva de espécies de Melastomataceae de Cerrado em Itirapina, SP. M.Sc. Dissertation. Universidade Estadual de Campinas, Brasil.
- Goldenberg R. & Shepherd G.J. 1998 Studies on the reproductive biology of Melastomataceae in “cerrado” vegetation. Plant Systematics and Evolution 211: 13-29.
- Gottsberger G. 1986. Some Pollination Strategies in Neotropical Savannas and Forests. Plant Systematics and Evolution 152: 29-45.

- Gottsberger G. 1989. Beetle pollination and flowering rhythm of *Annona* sp. (Annonaceae) in Brazil. *Plant Systematics and Evolution* 167: 165-187.
- Gottsberger G. 1994. As anonáceas do cerrado e a sua polinização. *Revista Brasileira de Biologia* 54: 391-402.
- Gottsberger G. 1999. Pollination and evolution in neotropical Annonaceae. *Plant Species Biology* 14: 143-152.
- Heithaus E.R. 1974. The role of plant-pollinator interactions in determining community structure. *Annals of the Missouri Botanical Garden* 61: 675-691.
- Herrera C.M. 1996. Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. In: Lloyd D.G. & Barret S.C.H. (eds.), *Floral biology: studies on floral evolution in animal pollinated plants*. Chapman & Hall, New York, pp. 65-87.
- Johnson S.D. & Steiner K.E. 2000. Generalization versus specialization in plant pollinator systems. *Tree* 15: 140-143.
- Jongman R.H.G. Ter Braak C.J.F. & Van Tongeren O.F.R. 1995. *Data analysis in community and landscape ecology*. Cambridge University, Cambridge.
- Judd W.S., Campbell C.S., Kellogg E.A. & Stevens P.F. 1999. *Plant systematics: a phylogenetic approach*. Sinauer, Sunderland.
- Kageyama P.Y. 1992. Recomposição da vegetação com espécies arbóreas nativas em reservatórios de usinas hidrelétricas da CESP. *Série Técnica IPEF* 8(25): 1-43.
- Kaur A., Ha C.D., Jong K., Sands V.E., Chan H.T., Solpadmo E. & Ashton P.S. 1978. Apomixis may be widespread among trees of the climax rain forest. *Nature* 271: 440-442.
- Kevan P.G. & Baker H.G. 1983. Insects as flowers visitors and pollinators. *Annual Review of Entomology* 28: 407-453.
- Köppen W. 1931. *Grundriss der Klimakunde*. Gruyter, Berlin.
- Kovach 1999. *Multivariate Statistical Package v.3.1*. Kovach Computing Services, Anglesey.

- Kress W.J. & Beach J.H. 1994. Flowering plant reproductive systems. In: McDade L.A., Bawa K.S., Hespenheide H.A. & Hartshorn G.S. (eds), *La Selva. Ecology and natural history of neotropical rain forest*. University Chicago, Chicago, pp. 161-182.
- Levin D.A. and Anderson W.W. 1970. Competition for pollinators between simultaneously flowering species. *American Naturalist* 104: 455-467.
- Machado I.C.S. 1990. *Biologia floral de espécies de caatinga no Município de Alagoinha (PE)*. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- Machado A.O. & Oliveira P.E. 2000. *Biologia floral e reprodutiva de Casearia grandiflora* Camb. (Flacourtiaceae). *Revista Brasileira de Botânica* 23: 283-290.
- McDade L.A. 1992. Pollinator relationships, biogeography, and phylogenetics. *BioScience* 42: 21-26.
- Moldenke A.R. & Lincoln P.G. 1979. Pollination ecology in montane Colorado. *Phytologia* 42: 349-379.
- Morellato L.P.C. 1991. *Estudo da fenologia de árvores, arbustos e lianas de uma floresta semidecídua no Sudoeste do Brasil*. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- Mueller-Dombois D. & Ellenberg H. 1974. *Aims and methods of vegetation ecology*. John Wiley & Sons, New York.
- Nason J.D., Aldrich P.R. & Hamrick J.L. 1997. Dispersal and the dynamics of genetic structure in fragmented tropical tree populations. In: Laurence W.F. & Bierregard Jr. R.O. (eds), *Tropical forest remnants. Ecology, management, and conservation of fragmented communities*. University of Chicago, Chicago.
- Ollerton J. 1996. Reconciling ecological process with phylogenetic patterns: the apparent paradox of plant-pollinator systems. *Journal of Ecology* 84: 767-769.
- Oliveira P.E. 1991. *The pollination and reproductive biology of a cerrado woody community in Brazil*. Ph.D. Thesis. University of St. Andrews, St. Andrews.

- Oliveira P.E. & Gibbs P.E. 1994. Pollination biology and breeding systems of six *Vochysia* species (Vochysiaceae) in Central Brazil. *Journal of Tropical Ecology* 10: 509-522.
- Oliveira P.E. & Gibbs P.E. 2000. Reproductive biology of woody plants in a cerrado community of Central Brazil. *Flora* 195: 311-329.
- Oliveira P.E. & Gibbs P.E. 2002. Pollination and reproductive biology in cerrado plant communities. In: Oliveira P.E. & Marquis R.J. (eds), *The cerrados of Brazil: ecology and natural history of a Neotropical savanna*. Columbia University, New York, pp. 329-347.
- Oliveira P.E. & Paula F.R. 2001. Fenologia e biologia reprodutiva de plantas de matas de galeria. In: Ribeiro J.F., Fonseca da C.E.L. & Souza-Silva J.C. (eds), *Cerrado: caracterização e recuperação de matas de galeria*. Embrapa, Planaltina, pp. 303-331.
- Oliveira P.E. & Sazima M. 1990. Pollination biology of two species of *Kielmeyera* (Guttiferae) from Brazilian cerrado vegetation. *Plant Systematics and Evolution* 172: 35-49.
- Oliveira P.E. & Silva J.C.S. 1993. Reproductive biology of two species of *Kielmeyera* (Guttiferae) in the cerrados of central Brazil. *Journal of Tropical Ecology* 9: 67-79.
- Oliveira P.E., Gibbs P.E., Barbosa A.A. & Talavera S. 1992. Contrasting breeding systems in two *Eriotheca* (Bombacaceae) species of the Brazilian cerrados. *Plant Systematics and Evolution* 179: 207-219.
- Oliveira P.E., Gibbs P.E. & Barbosa A.A. 2004. Moth pollination of woody species in the cerrados of central Brazil: a case of so much owed to so few? *Plant Systematics and Evolution* 245: 41-54.
- Opler P.A., Baker H.G. & Frankie G.W. 1980a. Plant reproductive characteristics during secondary succession in Neotropical lowland forest ecosystems. *Biotropica* 12 (Supplement): 40-46.
- Opler P.A., Frankie G.W. & Baker H.G. 1980b. Comparative phenology studies of treelet and shrub species in tropical wet and dry forest in the lowland of Costa Rica. *Journal of Ecology* 68: 189-209.

- Proctor M. & Yeo P. 1972. The pollination of flowers. Taplinger, New York.
- Proctor M., Yeo P. & Lack A. 1996. The natural history of pollination. Harper Collins, New York.
- Proença C.E.B. & Gibbs P.E. 1994. Reproductive biology of eight sympatric Myrtaceae from Central Brazil. *New Phytologist* 126: 343-354.
- Ramalho M. 2004. Stingless bees and mass flowering trees in the canopy of Atlantic Forest: a tight relationship. *Acta Botanica Brasilica* 18: 37-47.
- Ramirez N. 1989. Biología de polinización en una comunidad arbustiva tropical de la alta guayana Venezolana. *Biotropica* 21: 319-330.
- Ramírez N. 1993. Reproductive biology in a tropical shrubland of Venezuelan Guayana. *Journal of Vegetation Science* 4: 5-12.
- Ramirez N. 2004. Ecology of pollination in a tropical Venezuelan savanna. *Plant Ecology* 173: 171-189.
- Ramirez N. and Brito Y. 1987. Patrones de floración y fructificación en una comunidad pantanosa tipo morichal (Calabozo-Guarico, Venezuela). *Acta Científica Venezolana* 38: 376-381.
- Ramirez N. & Brito Y. 1992. Pollination biology in a palm swamp community in the Venezuelan central plains. *Botanical Journal of the Linnean Society* 110: 277-302.
- Ramos-Neto M.B. & Pivello V.R. 2000. Lightning fires in a Brazilian savanna National Park: rethinking management strategies. *Environmental Management* 26: 675-684.
- Ratter J.A., Ribeiro J.F. & Bridgewater S. 1997. The Brazilian cerrado vegetation and threats to its biodiversity. *Annals of Botany* 80: 223-230.
- Raven P.H. & Axelrod D.I. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539-673.
- Regal P.J. 1982. Pollination by Wind and animals: Ecology of geographic patterns. *Annual Review of Ecology and Systematics* 13: 497-524.
- Roth I. 1987. Stratification of a tropical forest as seen in dispersal types. Dr W. Junk, Dordrecht.

- Saraiva L.C., Cesar O. & Monteiro R. 1988. Biologia da polinização e sistemas de reprodução de *Styrax camporum* Pohl e *S. ferrugineus* Nees et Mart. (Styracaceae). Revista Brasileira de Botânica 11: 71-80.
- Saraiva L.C., Cesar O. & Monteiro R. 1996. Breeding systems of shrubs and trees of a Brazilian savanna. Arquivos de Biologia e Tecnologia 39: 751-763.
- Sarmiento G. 1983. The savannas of tropical America. In: Goodall D.W. (ed), Ecosystems of the world: tropical savannas. Elsevier, Amsterdam, pp. 245-288.
- Sazima M. & Sazima I. 1975. Quiropterofilia em *Lafoensia pacari* St. Hil. (Lythraceae), na Serra do Cipó, Minas Gerais. Ciência e Cultura 27: 405-416.
- Sazima I. & Sazima M. 1989. Mamangavas e irapuás (Hymenoptera, Apoidea): visitas, interações e conseqüências para a polinização do maracujá (Passifloraceae). Revista Brasileira de Entomologia. 33: 109-118.
- Sazima I. & Sazima M. 1990. Hummingbird pollination in two species of *Vellozia* (Liliiflorae: Velloziaceae) in southeastern Brazil. Botanica Acta 103: 83-86.
- Sazima I., Sazima M. & Buzato S. 1994. Néctar by day and night: *Siphocampylus sulfurus* (Lobeliaceae) pollinated by hummingbird and bats. Plant Systematics and Evolution 191: 237-246.
- Schemske D.W. & Horvitz C.C. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. Science 225: 519-521.
- Scholes R.J. & Archer S.R. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28: 517-544.
- Sigrist M.R. 2001. Biologia reprodutiva de doze espécies simpátricas de Malpighiaceae em mata semidecídua do sudoeste Brasileiro. Ph.D. Thesis. Universidade Estadual de Campinas, Brasil.
- Silberbauer-Gottsberger I. & Gottsberger G. 1988. A polinização de plantas do cerrado. Revista Brasileira de Biologia 48: 651-663.

- Silberbauer-Gottsberger I., Gottsberger G. & Webber A.C. 2003. Morphological and functional flower characteristics of New and Old world Annonaceae with respect to their mode of pollination. *Taxon* 52: 701-718.
- SMA. Secretaria de Estado do Meio Ambiente 1997. Cerrado: bases para conservação e uso sustentável das áreas de cerrado do estado de São Paulo. Secretaria de Estado do Meio Ambiente, São Paulo.
- Smith A.P. 1973. Stratification of temperate and tropical forest. *American Naturalist* 107: 671-683.
- Stebbins G.L. 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. *Annual Review of Ecology and Systematics* 1: 307-326.
- Torezan-Silingardi H.M. & Del-Claro K. 1998. Behavior of visitors and reproductive biology of *Campomanesia pubescens* (Myrtaceae) in cerrado vegetation. *Ciência e Cultura* 50: 281-284.
- Viana B.F., Kleinert A.M.P. & Imperatriz-Fonseca V.L. 1997. Abundance and flower visits of bees in a Cerrado of Bahia, Tropical Brazil. *Studies on Neotropical Fauna and Environment* 32: 212-219.
- Vogel S. 1990. History of the Malpighiaceae in the light of pollination ecology. *Memoirs of the New York Botanical Garden* 55: 130-142.
- Waller D.M. 1988. Plant morphology and reproduction. In: Doust J.L. & Doust L.L. (ed), *Plant Reproductive Ecology- Patterns and Strategies*. Oxford University, New York.
- Wanderley M.G.L., Shepherd G.J., Giulietti A.M. & Melhem T.S. 2002. *Flora Fanerogâmica do Estado de São Paulo*. Fapesp e Hucitec, São Paulo. v2.
- Wanderley M.G.L., Shepherd G.J. & Giulietti A.M. 2003. *Flora Fanerogâmica do Estado de São Paulo*. Fapesp e Hucitec, São Carlos. v3.
- Waser N.M. 1983. The adaptive nature of floral traits: ideas and evidence. In: Real L. (ed.), *Pollination biology*, Academic, New York, pp. 241-285.

- Waser N.M., Chittka L., Price M.V., Williams N.M. & Ollerton J. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043-1060.
- Weber W.A. 1982. Mnemonic three-letter acronyms for the families of vascular plants: a device for more effective herbarium curation. *Taxon* 31: 74-88.
- Wilson P., Castellanos M.C., Hogue J.N., Thomson J.D. & Armbruster W.S. 2004. A multivariate search for pollination syndromes among penstemons. *Oikos* 104: 345-361.
- Wunderlee J.M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99: 223-235.
- Zar J.H. 1999. *Biostatistical analysis*. Prentice Hall, Upper Saddle River.

“É necessário abrir o coração à bondade,
o cérebro à compreensão, a existência ao trabalho,
o passo ao bem, o verbo à fraternidade”.

Emmanuel (Chico Xavier)