

POLLINATION SYSTEMS AND FLORAL TRAITS IN CERRADO WOODY SPECIES OF THE UPPER TAQUARI REGION (CENTRAL BRAZIL)

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Received November 8, 2004 – Accepted February 16, 2005 – Distributed May 31, 2006

(With 1 figure)

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 probably occurred due to the specificity absence in plant-pollinator relationships.

Keywords: cerrado, phenology, pollination, principal components analysis, savanna.

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.

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

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 formerly occupied 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 heliophylous (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 for 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 pollination (Faegri & Pijl, 1979) and are the main pollinators of tropical areas (Bawa, 1990; Ramirez & Brito, 1992).

In the cerrado vegetation, bees are also the main pollinators (Silberbauer-Gottsberger & Gottsberger, 1988; Barbosa, 1997; Borges, 2000; Oliveira & Gibbs, 2000). Nevertheless, other pollinators are also important for 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. The regional climate is Aw (Köppen, 1948), humid tropical with a wet summer and dry winter. Annual rainfall varies from 1,200 to 2,000 mm, concentrated from October to March, and the mean annual temperature is 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 randomly picked up 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. At each point, we sampled four woody plants with a 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 “open”, “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 had 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 had 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; 5.0%, 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 (Fig. 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 the 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 negative 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 for the establishment of 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 in separating pollination systems, since the two largest pollinator classes, bees and small insects, visit flowers of several colors. The exception was white, 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 &

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- Sigríst (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. & Schltld.) Seem.	si	gr	d	0	1	0	1	op	16
API	<i>Didymopanax vinosum</i> (Cham. & Schltld.) 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
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>Conarus 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*

TABLE 1
Continued...

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
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 piauhiensis</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*
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 ribesoides</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

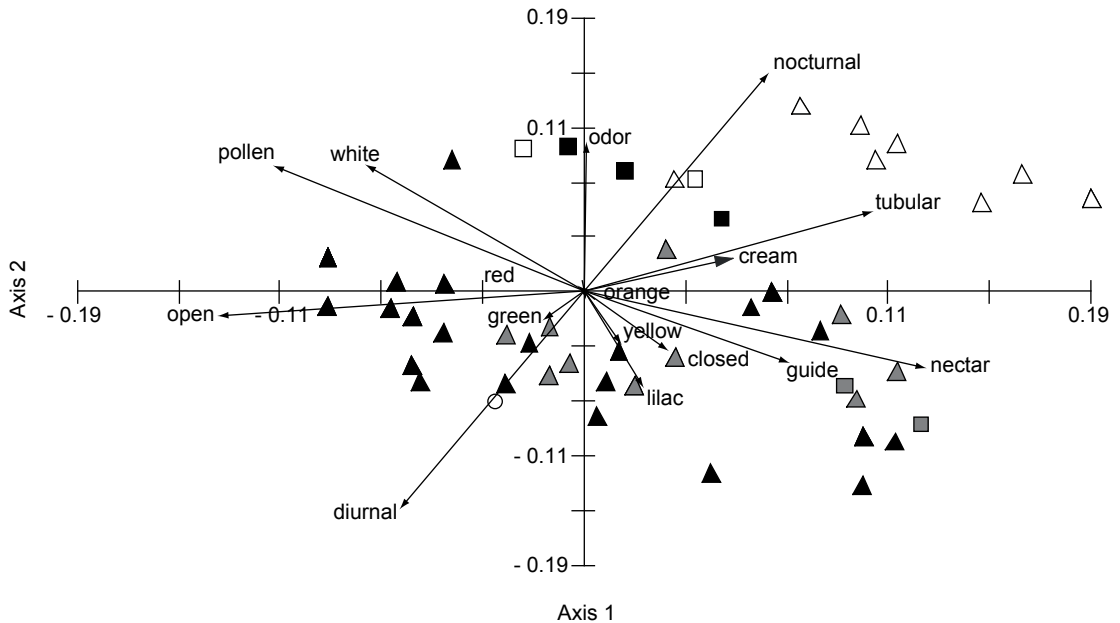


Fig. 1 — Principal component analysis of floral traits and woody species of the cerrado fragments in Upper Taquari region (central-western Brazil). Species were classified according to their pollination system: ▲ = bees; ▲ = small insects; △ = moths; ■ = bats; ■ = hummingbirds; □ = beetles; and ○ = wind.

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 a 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 the Emas and Oréades Foundations, for satellite images; to André Vitor Fleuri Jardim and Júlia Caram, for help in the field; and to an anonymous referee, for useful suggestions.

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