Brazilian Journal of Development

Reproductive biology of *Parkia platycephala* Benth (Leguminosae, Caesalpinioideae, clado mimosoide)

Biologia reprodutiva de *Parkia platycephala* Benth (Leguminosae, Caesalpinioideae, clado mimosoide)

DOI:10.34117/bjdv6n10-393

Recebimento dos originais: 08/09/2020
Aceitação para publicação: 19/10/2020

Samyra Ramos Chaves
Mestre em Ciências Biológicas (Botânica)/INPA
Doutoranda no Instituto Nacional de Pesquisas da Amazônia – INPA
Endereço: Av. André Araújo, 2936 – Aleixo – CEP 69060-001 – Manaus – AM - Brasil
E-mail: samyraramos.1@gmail.com

Ricardo Rodrigues dos Santos
Doutor em Psicobiologia (Comportamento Animal) Universidade Federal do Rio Grande do Norte
Professor na Universidade Federal do Maranhão – UFMA
Endereço: Universidade Federal do Maranhão, Centro de Ciências Agrárias e Ambientais, MA 230, KM 04, s/n, Boa Vista, Chapadinha – Maranhão, Brasil. CEP: 65500-000.
E-mail: Ricardo.ufma@gmail.com

André Luiz Gomes da Silva
Doutor em Ciências Biológicas (Botânica) /Museu Nacional – UFRJ
Professor no Instituto do Noroeste Fluminense de Educação Superior – Universidade Federal Fluminense
Endereço: Estra. João Jasbick, s/n- Dezessete, Santo Antônio de Pádua – RJ, CEP 28470-000
E-mail: algsilva@id.uff.br

ABSTRACT

The aim of this study was to investigate the reproductive biology of *Parkia platycephala*, a tree that occurs in the Cerrado biome (savanna-like tree vegetation), in Maranhão State, Northeast Brazil. The species is self-incompatible and under natural conditions fecundity is low. In Maranhão, *P. platycephala* blooms from June to August and set fruits from September to October. Flowers are inserted into ball-like capitulum with long peduncle and are of two types: the apex of the capitulum is functionally male and contains nectar-producing flowers, while basal flowers are hermaphrodite and do not produce nectar. Pollen grains are grouped in permanent indissoluble polyad. Anthesis is nocturnal and begins around 17:00h. The main resource offered by flowers to visitors is nectar produced by apical flowers. The unit of pollination is the capitulum visited by nectarivorous bats. Three species of bats were record visiting flowers: *Phyllostomus hastatus* (Phyllostominae) *Carolia perspicillata* (Carollinae) and *Glossophaga soricina* (Glossophaginae).

Keywords: Andromonoecy, Chiropterophily, Polyad.

RESUMO

O objetivo deste estudo foi o de investigar a biologia reprodutiva de *Parkia platycephala*, uma árvore que ocorre no bioma Cerrado (vegetação arbórea do tipo savana), no estado do Maranhão, região nordeste do Brasil. A espécie é auto-incompatível e sob condições naturais sua fecundidade é baixa. No Maranhão, *P. platycephala* floresce de junho a agosto e frutifica de setembro a outubro. Suas flores são inseridas em capítulos com pedúnculos longos e são de dois tipos: o ápice do capítulo é funcionalmente masculino e contém flores produtoras de néctar, enquanto as flores basais são hermafroditas e não produzem néctar. Os grãos de pólen são agrupados em políades indissolúveis permanente. A antese é noturna e se inicia por volta das 17:00h. O principal recurso oferecido pelas flores aos visitantes florais é o néctar produzido pelas flores apicais. A unidade de polinização é o capítulo visitado por morcegos nectarívoros. Três espécies de morcegos foram recordadas visitando flores: *Phyllostomus hastatus* (Phyllostominae) *Carolia perspicillata* (Carollinae) e *Glossophaga soricina* (Glossophaginae).

Palavras-chave: Andromonicia, Quiropterofilia, Políade.

1 INTRODUCTION

Fabaceae is the third largest Angiosperm family, with approximately 19.500 species, 770 genera (Schrire *et al*., 2005) and 36 tribes (Lewis *et al*., 2005) divided into six subfamilies: Duparquetioideae LPWG, Cercidoideae LPWG, Detarioideae Burmeist., Caesalpinioideae DC and Papilionoideae DC. (LPWG, 2017). The family has reat economic importance, and many species are used as food and fodder, in the recovery of degraded soils, urban tree planting, and in chemical and wood industries (Lewis *et al*., 2005).

Mimosoideae, traditionally recognized as one of the three subfamilies, is currently recognized as a clade (mimosoide) nested in Caesalpinioideae (LPWG, 2017). Contains some 83 genera and 3.273 species (Lewis *et al*., 2005; LPWG, 2017), with a variety of growth forms including trees, shrubs, lianas and herbs (Ribeiro *et al*., 1999), and their representatives are characterized by trees, shrubs, lianas, rarely aquatic herbs; small regular flowers aggregated into heads or spikes; flowers actinomorphic, radially symmetrical; petals valvet in bud; sepals (and petals) generally united at the base. Extrafloral nectaries on the petioles or rachis are common (Lewis *et al*., 2005). Inflorescences are usually heads or spikes, although these are frequently aggregated into more complex compound structures (Lewis *et al*., 2005). Flowers are radially symmetrical, usually small, actinomorphic, with sepals and petals usually conate, corolla with valvar prefloration and seeds usually with a pleurogram in the form of 'U' or 'O' (Luckow *et al.* 2003).

Mimosoideae has a variety of floral types, with roughly equal proportion of species with generalist and specialist pollination systems. In the species *Parkia* and *Mimosa*, for example, inflorescences are dense and form a capitulum that functions as unit of pollination, which is visited by animals such as bees, hummingbirds or moths, while others are strictly adapted to pollination by bats (Baker *et al*. 1957; Gould, 1978; Hopkins, 1984, 1986; Vogel *et al*. 2005).

Parkia (Fabaceae - Mimosoideae) is a pantropical genus whith approximately 35 species of trees distributed in three taxonomic sections. These are divided based on the functional morphology of the globose capitulums. Section *Parkia* is pantropical with flowers of three functional types: each capitulum has an apical ball of fertile flowers, below that a constricted region of nectar-secreting ones, and at the base, a variable number of sterile flowers. These sometimes have elongated staminodia, forming a fringe that when well developed, hangs down and conceals the nectar-secreting flowers. In shape, the capitula range from clavate to biglobose. Section *Platyparkia* is entirely Neotropical with flowers of two types: the capitulum is oblate, with fertile flowers extending from the base to the middle, and the nectar-secreting flowers are at and around the apex, their surface forming an almost flat disc. And section *Sphaeroparkia* is again entirely Neotropical but the capitula are composed of only a single functional floral type (fertile), no morphologically distinct nectar-secreting or sterile flowers are present (Hopkins, 1986; Lewis *et al*, 2005). The natural distribution of *Parkia* in the neotropics extends from Honduras to the coastal forests of southeastern Brazil, with a centre of diversification in Amazonia (Hopkins, 1984, 1986).

Several papers have highlighted the importance of chiropterophily in the evolution of the genus *Parkia* (Baker *et al.* 1957; Vogel, 1968). In *Parkia* and *Platyparkia* sections are pollinated by distinct and distantly-related bats; bats of the Phyllostomidae for Neotropical species and Pteropodidae for Paleotropical species (Baker *et al.* 1957; Hopkins, 1984). According to Simmons (2005) only two of 18 families of bats contain species morphologically specialized for nectivory, and in Brazil 16 species are predominantly nectarivorous (Taddei, 1996). Flowers pollinated by bats share common characteristics, all of which promote and facilitate interactions with nectar-feeding bats Faegri & van der Pijl (1979). The three species in the *Sphaeroparkia* section are exclusively entomophilous, *P. velutina* is pollinated by nocturnal bees, *P. ulei* by diurnal bees and *P. multijuga* by small nocturnal insects (Hopkins, 1984, 1986; Hopkins, 2000; Chaves, 2015).

Parkia platycephala Benth. belongs to the section *Platyparkia* (Hopkins, 1984, 1986), and is popularly known in Brazil as “faveira”, “faveira-preta”, “visgueiro”, “fava-de-boi”, “sabiú” or “fava-de-bolota”. It is widely used both for wood and fodder, and the pods provide an excellent dietary supplement for ruminants (Cavada *et al*. 1997; Machado *et al*. 1999; Mann *et al*. 2001; Cavada *et al*. 2005; del Sol, 2005; Cavada *et al*. 2006; Alves *et al*. 2007; Figueiredo *et al*. 2008). The wood can be used in crates, boards for internal divisions in small buildings, ceilings, making toys, as well as for firewood to produce charcoal (Lorenzi, 1998).

The study of plant reproductive biology can provide data that answers questions regarding intraspecific gene-flow maintenance, reproductive success, sharing or competition by pollinators, as well as conservation of natural habitats affected by fragmentation processes (Machado *et al.*, 2002). In the case of species in the Mimosoideae such studies are especially important since a number of species are self-incompatible and andromonoecious (Arroyo, 1981).

Studies of the reproductive biology *P. platycephala* have not been undertaken until the current study and the pollination system remained unknown. This raised questions concerning pollinator behavior, data that could be directly applied to infer the evolution of pollination in the genus *Parkia*, as well as to questions about the reproduction system. Hopkins (1984) reported observations on a single individual of *P. platycephala* in cerrado in Piauí, but the flowering of this species was already ending and, in consequence, recorded data was sparse, especially regarding floral visitors and the reproductive system.

Considering that *P. platycephala* is a species that has a great ecological and economic importance, the present study aimed to complement the study of Hopkins (1984) by providing a complete set of data about the floral biology, pre-emergent reproductive success, and pollination biology of the species in an area of Cerrado in Northeastern Brazil.

2 MATERIALS AND METHODS

Study area- The study was conducted in a Brazilian North Cerrado located at Chapadinha (03°44'17"S; 43°20'29"W), Maranhão state, northeastern Brazil. The natural vegetation of the area is Cerrado *sensu lato*, consisting of scattered trees and shrubs, dominated by *Parkia platycephala, Caryocar brasiliense* Cambess and *Bowdichia virgilioides* Kunth (IBGE, 2012). The climate of the area is tropical with marked rainy and dry seasons, classified as Aw by. Precipitation is higher during January to June (1445mm) and lower from July to December (225mm) and average annual rainfall is 1670mm. The highest temperatures occur in the dry season Köppen (1948).

Species studied- *Parkia platycephala* is a semideciduous and heliophytic tree species that can reach 18m in height. It has indehiscent oblong pods with many seeds (Pio Correia, 1969). Is typical of the Cerrado *sensu stricto*, “campo sujo” (grassland with scattered trees and shrubs), and “cerradão” (woodland savanna habitat with a well-developed tree canopy). This species occurs naturally in the Brazilian Northeast, in Maranhão and Piauí States (Eiten, 1972), and in the “Campina” of Amazon (Lorenzi, 1998).

Flowering and fruiting phenology- Ten reproductive individuals were observed twice a month reproductive period from January 2008 to December 2010. We recorded the emergence of the inflorescences, the number of capitula per inflorescence and the number of pods per inflorescence in each sampling period.

Floral biology- Flower anthesis was analysed by recording the time and duration of flower opening, and the process of anther dehiscence per hour. Capitula (N=25) were collected in order to count apical and peripheral flower numbers. We measured the length and diameter of floral tube, ovary and length of the filaments and styles using digital calipers. Numbers of ovules per ovary (N=25) and polyads per anthers (N=25) were quantified in the laboratory of Botany of the Federal University of the Maranhão with a stereoscopic microscope. Measurements of ovules and polyads were conducted with an optical microscope with an image capture system.

Seed/ovule ratio was evaluated using the mean number of seeds per fruit (N = 25) and the mean number of ovules per ovary. Fruit/flower ratio was based on the number of fruits that developed after natural pollination. To assay for differences between means floral structures, we used the two-mean comparison test, with a level of significance of 5%. The “t” values observed were compared with tabulated theoretical “t” values (Pagano *et al*., 2004).

Nectar was collected from capitulum with 10 ml syringe. Sugar concentration of the total volume of flowers from each sample was analyzed with a portable refractometer with a scale from 0 to 32% Brix. Nectar collection was made during five days in different capitula (N = 8), starting at 06:00 pm and ending at 08:00 am at the next day. The amount of nectar from each flower was collected and measured with the aid of a 50 ml beaker attached to the inflorescence with a nylon string before of the anthesis and collected the next day at 08:00 am.

Viability of polyads from apical and peripheral flowers was tested via studies of pollen tube growth. Polyads were immersed in 20% sucrose solution following collection and 24 hours later, assayed with an optical microscope for pollen tubes presence (Kearns *et al*. 1993). A pollen grain was considered to have germinated when the length of the germinated pollen tube was equal to or longer than the diameter of the grain.

Floral visitors- Floral visitors were observed, collected, and identified during flowering period of five pre-selected reproductive adult plants. Observations were carried out from 06:00 pm to 06:00 am, across ten sequential days, totaling 120 hours of observation. Floral visitors were classified as “effective” when the behavior of visitors may promote the contact of anthers with stigma and the frequency of visits is high, more than 10 visits per day; “occasional” when the behavior of visitors promotes the contact of anthers with stigma and frequency of visits is low, less than 10 visits per day or floral resources robbers when visitors do not touch the stigma nor the anthers. We record the visitors with the aid of binocular and camera. Camera was positioned to the inflorescences with chapters in the process of anthesis to determine the frequency of floral visitors.

The collection of insects was performed using a killing jar. All flower visitors were individually collected and identified. Bats were collected from 18:00 to midnight every alternate night for three days, using mist nets (12m x 2.5m) strung in front of the canopies of two individual *P. platycephala*.

Reproductive system- Hand pollination was carried out on whole capitula, instead of individual flowers. Four experimental tests were carried out: 1- Hand self-pollination (autogamy); 2-Cross-pollination (xenogamy). These tests were conducted with previously bagged capitula one day before the anthesis; 3- Control- unbagged capitula; 4-Automatic self-pollination-calculated from the proportion of fruits formed from bagged capitula. Tests were conducted in both apical and peripheral flowers and analyzed separately.

Preemergent reproductive success- To estimate fecundity rate, we followed Cruden (1972) and used a value that is the product of two ratios (seed/ovule and fruit/flower).

3 RESULTS AND DISCUSSION

Flowering phenology- The *P. platycephala* study population flowered annually and in synchrony, which concurs with Hopkins (1984). This pattern is typical of species in the section *Platyparkia* (Hopkins, 1984; Piechowski *et al*., 2010). Each individual tree flowered for about four weeks. According to the classification proposed by Gentry (1974), flowering of *P. platycephala* can be classified as a cornucopia pattern, as many capitula are receptive and flowering per night is extended, which is common to species of section *Platyparkia* (Hopkins, 1984).

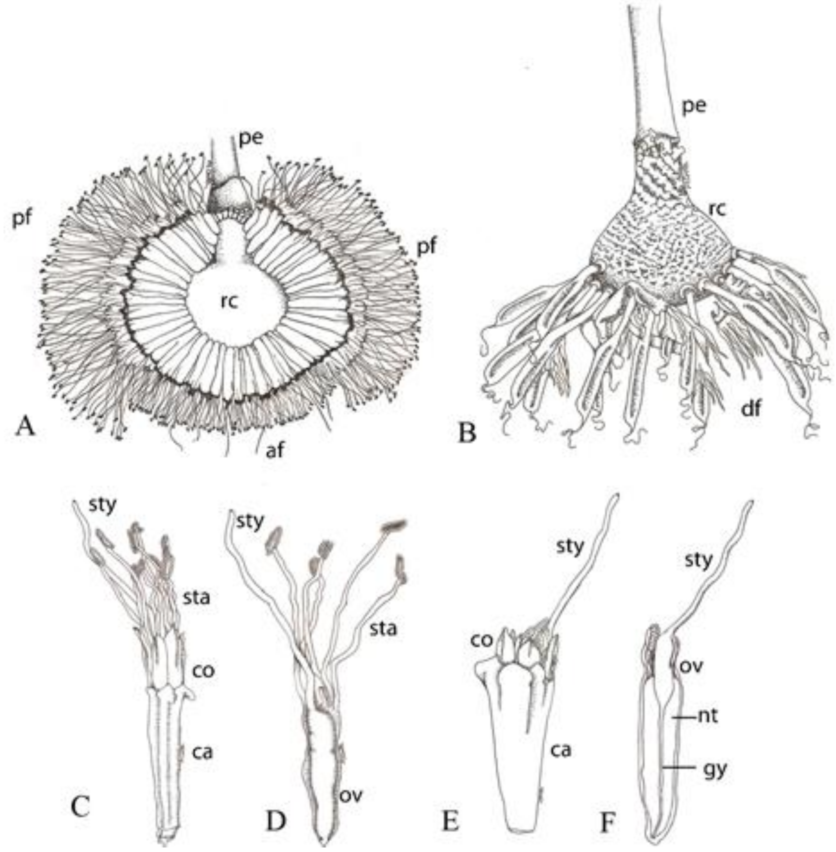
Fruiting occured from August to November, with the fruits attached to the plant for some four months. This long maturation period may be a strategy to avoid the adverse conditions of the soil seed bank (Gutterman, 1972; Cowling *et al*. 1987 Lamont, 1991; Baskin *et al*., 1998.

Floral biology- Flowers of *Parkia platycephala* were inserted into a ball-like capitulum with a long peduncle, some 31.5 cm in length (N = 25, ± 4.1). Flowers at the capitulum apex were functionally male and produced nectar, while those on the basal portion were hermaphrodite and did not produce nectar. Each capitulum had a mean of 151 apical flowers (N = 15, ± 33) and 830 peripheral flowers (N = 15, ± 73). Each branch has 9.64 capitula (N = 25, ± 4.54) (Figure 1A).

Both apical and peripheral flowers had a gamosepalous calyx with five predominantly cream lobes with touches of brown and red. The corolla was gamopetalous with five lobes in red color (Figures 1C, E). Morphometric measurements of the two flowers types are given in Tab.1. The gynoecium is red, unilocular and pluriovular, and there were no recorded differences in the number of eggs formed in the two flower types ($t_{obs}= 1,39 < t_{teor}=2.04$) (Table 1). According Hopkins (1984), a gynoecium is present in section *Platyparkia,* although pods are not usually formed and absent in section *Parkia*. The style is filiform and the apical flowers are larger than the peripheral flowers (Table 1). The stigma is terminal and small, with internal stigmatic papillae. The diameter of stigmatic cavity is 22µm, which corresponds to the mean diameter of a polyad~~s~~. One stigma can only receive one polyad.

The ovary of apical flowers is shorter than that of the peripheral flowers (Figure 1F) while ovules from the peripheral flowers are significantly larger than those of apical flowers ($t_{obs}= 4,2 > t_{teor}=2.14$). It is therefore likely that possession of a shorter ovary and a smaller ovule by apical flowers is the cause of their sterility, especially since such flowers do not produce fruit in hand-crossing experiments. This has also been reported for flowers of *P. pendula* (Piechowski *et al*., 2010). However, studies of ovules development and floral anatomy are needed to confirm the causes of female sterility in apical flowers of *P. platycephala*.

Figure 1: Floral morphology of Parkia platycephala. A - Capitulum; B - Receptacle of the capitulun with developing fruits; C - Peripheral flower (functionally hermaphrodite); D - Gynoecium of peripheral flower; E - Apical flower (functionally male); F - Gynoecium of apical flower. Legends: pf - peripheral flower; pe - peduncule; rc - receptacle of the capitulum; af - apical flower; df - developing fruits; sty - style; sta - stamen; co - corolla; ca - calix, ov - ovary; nt - nectariferous tissue; gy – gynophore.



The androecium is monadelphous and composed of ten stamens. The filaments are red, the same color as the corolla lobes. Anthers show rimosa dehiscence (with longitudinal opening) and are brown in color. Filaments of apical flowers are shorter than those of peripheral flowers.

Apical flowers have a floral receptacle filled by nectariferous tissue and the ovary is suspended by a gynophore so that it reaches the height of the lobes of the sepals (Figure 1F).

The capitulum releases a strong and unpleasant odor during anthesis, which is more intense at the beginning of the night, coinciding with the period of greatest nectar production and release. Piechowski *et al*. (2010) reported eleven substances in the floral scent of *P. pendula*, and that monoterpenoids were prominent, with (E)-b-ocimene being the dominant compound. The scent of bat-pollinated flowers has often been described as fetid or pungent (Heithaus, 1982; Endress, 1994; Knudsen, *et al*., 1996). The strong floral scent, along with the excessive production of nectar, nocturnal anthesis and red flowers are strong evidence of specialization for this species in chiropterophily (Hopkins, 1984; Piechowski *et al*., 2010).

Table 1: Morphometry of two floral types of Parkia platycephala in Chapadinha Cerrado, Maranhão, Brazil.

	N	Apical flowers	Peripheral flowers
Length of floral tube	30	7.86 ± 0.55	8.29 ± 0.58
Diameter of floral tube	25	1.98 ± 0.23	1.59 ± 0.14
Length of ovary	25	2.97 ± 0.32	5.37 ± 0.66
Diameter of ovary	25	0.82 ± 9	0.8 ± 0.1
Length of filament	30	4.00 ± 1.20	9.11 ± 1.60
Length of style	30	5.63 ± 1.70	10.5 ± 1.06
Number of polyads	25	36.96 ± 3.81	36 ± 3
Diameter of polyads	15	18.20 ± 1.98	1.59 ± 0.14
Number of ovules	25	34.40 ± 3.12	33.16 ± 3.10
Diameter of ovules	15	217.7 ± 19.4	244.6 ± 14.2

Nectar was the main floral resource available at *P. platycephala* flowers. However, since polyads are produced in large quantities, they are also a potential food source (Hopkins, 1984). Nectar is produced by the nectariferous tissue inserted into the apical floral receptacle of the flowers and their production is more intense at the beginning of anthesis. Each capitulum produces 6.63ml of nectar per night (N= 14, ± 1.49). Sugar nectar concentration of the nectar is 15% in Brix scale (N = 58, ± 0.02) during anthesis.

Polyads from the apical flowers are white and measure 18.20 µm in diameter (N=25, ±1.98), while polyads from the basal flowers are yellow and measure 19.09 µm in diameter (N=25, ±2.61). However, these values are not statistically different (t_{obs}= 1.36 < t_{teor}=2.04).

In basal flowers the mean number of polyads per anther was 36.00 (N= 25, ± 3.00), for apical flowers 36.96 (N=25, ±3.81). Statistical tests found no significant difference in the production of polyads between the two floral types (t_{obs}=0.96 < t_{teor}=2.04).

Polyads from both apical and basal flowers are fertile. However, polyads from the apical flowers were a hit of 12% of germination of the pollen tube, while the polyads from the peripheral flowers have 68% of germination. These results indicate that the apical flowers are functionally male and, therefore, *P. platycephala* can be considered an andromonoic species. According Hopkins (1986), andromonoecy has been detected in most species of *Parkia*, and in many cases, the capitulum contain a mixture of functional male and hermaphrodite flowers.

Floral Visitors and pollination biology

The main nocturnal floral visitors of *P. platycephala* are three Phyllostomid bats: *Phyllostomus hastatus* (Phyllostominae), *Carolia perspicillata* (Carollinae) and *Glossophaga soricina* (Glossophaginae). These bats species visit flowers searching for nectar.

Bat visits begin at dusk, around 18:00 pm and are intense until 22:00 pm. After this, visits become scarce. In the period of greatest bat activity, each capitulum receives an average of some 60 visits every minutes. Each visit in a capitulum lasts from one to five seconds at most. This pattern is according by Hopkins (1986). According to Piechowski *et al.*, (2010), timing of visits by bats tracks the temporal pattern of nectar production.

During a visit, the bat holds on by its hind legs to the base of a capitulum positioning itself upside down and hugs the capitulum while collecting nectar with its tongue. In this position, the tail membrane (uropatagium or interfemoral membrane) is positioned in the midline of the capitulum comes into contact with the reproductive organs of basal flowers, receiving the polyads passively and transferring some of polyads collected on previous visits to other capitula. This helps explain why fruits arise only in the mid-region of a capitulum following pollination (Figure 1B). Similar behavior has been described for *P. pendula* (Hopkins, 1986; Piechowski *et al.*, 2010).

Bats pollinating *P. platycephala* are traplining foragers, a strategy which results in high levels of pollen transfer and thus enhances genetic diversity in plant populations, reduces inbreeding depression, and contributions of floral traits to plant fitness, which should in turn affect the rates and directions of floral evolution (Ohashi, *et al*., 2009). By their morphological and behavioral characteristics, bats are effective pollinators of *P. platycephala*.

At the beginning of anthesis capitula were also visited three bee species: *Trigona branneri, T. guianensis, Apis mellifera,* and other unidentified species of Hymenoptera. Visits by insects ceased in the early evening. The foraging behavior and morphology of these insects indicate that they act only as robbers of floral resources. The resources collected by these insects were nectar and polyads.

During the night, two unidentified species of Lepidoptera were observed visiting *P. platycephala* capitula. Visits were quick, lasting from two to five seconds, and these animals remained for several minutes visiting the capitulum of the same tree. Also, by their morphological and behavioral characteristics they are considered nectar robbers. Orthoptera were also observed on the capitulum and Diptera were very common on post-anthesis capitula. According to Hopkins (1984), many species of insects visit the capitulum of *Parkia* exclusively pollinated by bats.

Breeding system

Parkia platycephala is self-incompatible, as it produced no fruit in experiments of manual and passive pollination of both apical and basal flowers, respectively (see Table 2). This is line with pollination biology work carried out with other *Parkia* species, such as Piechowski (2010), in *P. pendula.*

In the test of xenogamy in basal flowers, only two capitula produced fruit, one produced seven and the other, five. From total fruit used in this experiment the capitulum produced 0.86 fruits (N=14 ± 2. 21).

Whereas the total number of flowers in 14 capitula was 11.620, fruit set was very low, with a fruit/flower ratio of 0.001. In the control experiment, the number of fruits per capitulum was 5.56 (N= 25, ± 1.96), and the fruit/flower ratio was 0.007. Apical flowers produced no fruit in xenogamy experiments and control tests.

Table 2: Breeding system of Parkia platycephala in Chapadinha Cerrado, Maranhão, Brazil.

	Apical flowers		**Peripheral flowers**	
Tests	**N**	**Fr/cap**	**N**	**Fr/cap**
Control	10	0	25	5.56 ± 1.96
Xenogamy	10	0	14	0.86 ± 2.21
Self-pollination	10	0	10	0
Automatic self- pollination	10	0	10	0

Low fruit production by basal flowers, both in experiments of xenogamy and control tests, are far below those established by Wiens *et al*. (1987) for self-incompatible tree species. However, many other Fabaceae species also show low fruit/flower ratios, which may be related to sexual selection and the availability of nutrients for fruit production (Bawa *et al*., 1989). In *P. platycephala* the inflorescence base does not change its size after initial fruit formation thus making it both physiologically and topologically impossible for many fruits to develop (Figure 1B). The highest number of fruits we observed per capitulum under natural and experimental conditions was 21.

Basal flowers have a seed/ovule ratio of 0.76, a value considered high for both woody species in general (Wiens *et al*. 1987) and for fabaceous species (Bawa *et al*., 1989). The fertility rate (product of seed/ovule and fruit/flower ratios) under natural conditions was 0.005 (Table 3), which is considered low for self-incompatible species (Wiens *et al*., 1987).

Table 3: Reproductive success pre-emergence on natural conditions of Parkia platycephala in Chapadinha Cerrado, Maranhão State, Brazil.

	Apical flowers	**Peripheral flowers**
Flowers/capitulum	151 ± 33 (N= 15)	830 ± 73 (N= 15)
Ovules/flowers	34.4 ± 3.12 (N=25)	33.16 ± 3.1 (N= 25)
Fruits/capitulum	0	5.56 ± 1.96 (N=25)
Fruit/flower	-	0.007
Healthy seed/fruit	-	25.36 ± 6.02
Aborted seeds/fruit	-	2.84 ± 3.06
Seed/ovule	-	0.76
Fecundity rate	-	0.005

The fertility rate of *P. platycephala* is influenced mainly by the low fruit/flower ratio. However, the high production of seeds may also be involved in low fruit production, since for each capitulum produced a mean of 141 morphologically healthy seeds available for dispersal. This value can be considered satisfactory for the population dynamics of this species that have their seeds dispersed by autocory.

4 CONCLUSION

The species is self-incompatible and under natural conditions the fecundity is low. In Maranhão, *P. platycephala* blooms from June to August and set fruit from September to October. Flowers are inserted into ball-like capitulum with long peduncle and are of two types: the apex of the capitulum is functionally male and contains nectar-producing flowers, while basal flowers are hermaphrodite and do not produce nectar. Pollen grains are grouped in permanent indissoluble polyad. Anthesis is nocturnal and begins around 17:00 h. The main resource offered by flowers to visitors is the nectar produced by apical flowers. The unit of pollination is the capitulum visited by nectarivorous bats. Three species of bats were record visiting flowers: *Phyllostomus hastatus* (Phyllostominae) *Carolia perspicillata* (Carollinae) and *Glossophaga soricina* (Glossophaginae).

ACKNOWLEDGEMENTS

We thank to Fundação de Amparo à Pesquisa and the "Desenvolvimento Científico e Tecnológico do Maranhão (FAPEMA)" for financial support and we particularly thank Dr. Fernando Silveira (Universidade Federal de Minas Gerais, Brazil) for the Hymenoptera species identification. Adrian Barnett helped with English and Maurilene Souza Costa for the illustrations in figure 1.

REFERENCES

1. Alves AA, Sales RO, Neiva JNM, Medeiros AN, Braga AP, Azevedo AR. Degradabilidade ruminal in situ de vagens de faveira (Parkia platycephala Benth.) em diferentes tamanhos de partículas. Arquivo Brasileiro de Medicina Veterinária e Zootecnia. 2007 Apr; 59(4):1045-1051, doi: http://dx.doi.org/10.4025

2. Arroyo M.T.K. (1981) Breeding systems and pollination biology in Leguminosae. In: Polhill R.M., Raven P.H. (Ed.). Advances in Legume Systematic part 2. Kew: Royal Botanic Gardens. 1981; 723-769.

3. Baker HG, Harris BJ. The pollination of Parkia by bats and its attendant evolutionary problems. Evolution. 1957; 11: 449-460, doi: 10.1111/j.15585646.1957.tb02916.x

4. Baskin C.C., Baskin J.M. Seed: Ecology, Biogeography, and Evolution of Dormancy and Germination. London: Academic Press. 1998; 666p.

5. Bawa KS, Buckley DP. (1989) Seed: ovule ratios, selective seed abortion, and mating systems in Leguminosae. In: Stirton C.H., Zarucchi J.L. (Ed.). Advances in legume biology (Monographs in Systematic Botany). Kew: Missouri Botanical Gardens. 1989; 243-262.1

6. Bernhardt P., Kenrick J., Knox R.B. Pollination biology and the breeding system of Acacia retinodes (Leguminosae: Mimosoideae). Annals of Missouri Botanical Garden. 1984; 71:17-29.

7. Borges HBN. Biologia reprodutiva de Centrosema pubescens Benth. (Fabaceae). Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais. 2006 Apr; 1(1): 31-38.

8. Carvalho CT. Sobre os hábitos alimentares de Phillostomídeos (Mammalia, Chiroptera). Revista de Biologıa Tropical. 1961; 9(1): 53-60.

9. Cavada BS, Castellon RER, Vasconcelos GG, Rocha BAM, Bezerra GA, Debray H, Delatorre P, Nagano CS, Toyama M, Pinto VPT. Crystallization and preliminary X-ray diffraction analysis of a new chitin-binding protein from Parkia platycephala seeds. Acta Crystallographica. 2005 August; 61:841-843, doi: 10.1107/S1744309105024462

10. Cavada BS, Moreno FBB, da Rocha BAM, de Azevedo WFJr, Castello RER, Goersch GV, Nagano CS, de Souza EP, Nascimento KS, Baptista GR, Delatorre P, Leroy Y, Toyama MH, Vicente PT, Pinto AHS, Barettino D, Debray H, Calvete JJ, Sanz L. cDNA cloning and 1.75 Å crystal structure determination of PPL2, an endochitinase and N-acetylglucosamine-binding hemagglutinin from Parkia platycephala seeds. Federation of European Biochemical Societies Journal. 2006 Jun; 273:3962-3974, doi: 10.1111/j.1742-4658.2006.05400.x

11. Cavada BS, Santos CF, Grangeiro TB, Moreira da Silva LIM, Campos MJO, de Sousa FAM, Calvete JJ. Isolation and partial characterization of a lectin from Parkia platycephala Benth seeds. Physiology and Mololecular Biology of Plants. 1997; 3:109-115.:

12. Chaves S.R. Biologia floral e polinização de Parkia ulei (Harms) Kuhlm. e Parkia multijuga Benth. (Fabaceae-Mimosoideae) [dissertation]. Instituto Nacional de Pesquisas da Amazônia - INPA. 2015. 67 p.

13. Cowling RM, Lamont BB, Pierce SM. Seed bank dynamics of four co-occurring Banksia species. Journal of Ecology. 1987 Jun; 75(2):289-302.

14. Cruden R.W. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution. 1977; 31: 32-46.

15. Cruden RW. Pollinators in high elevation ecosystems: relative effectiveness of birds and bees. Science. 1972; 176:1439-1440.

16. del Sol FG, Gomez J, Hoos C, Nagano CS, Cavada BS, England P, Calvete JJ. Energetics of 5-bromo-4-chloro-3-indolyl-a-D-mannose binding to the Parkia platycephala seed lectin and its use for MAD phasing. Acta Crystallographica. 2005 Feb; 61:326-331, doi: 10.1107/S1744309105004835

17. Doyle JJ, Luckow M. The rest of the iceberg. Legume diversity and evolution in a phylogenetic context. Plant Physiology. 2003 March; 131:900-910, doi: 10.1104/pp.102.018150.

18. Eiten G. The Cerrado vegetation of Brazil. The Botanical Review. 1972 Jun; 38(2):201-341.

19. Endress P.K. Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge; 1994. 511 p.

20. Faegri K, Pijl L. The principles of pollination ecology. Oxford: Pergamon Press, 1979. 248 p.

21. Figueiredo PS, Girnos EC, Santos LS. Predação e parasitismo em sementes de duas populações de Parkia platycephala Benth., em áreas de cerrado no nordeste do Brasil. Revista Brasileira Botânica. 2008 Jun; 31(2): 245-251.

22. Gentry AH. Flowering phenology and diversity in tropical Bignoniaceae. Biotropica. 1974. 6:64-68.

23. Gould E. Foraging behavior of Malaysian nectar-feeding bats. Biotropica. 1978; 10:184-193, doi:10.2307/2387904

24. Gutterman Y. Delayed seed dispersal and rapid germination as survival mechanisms of the desert plant Blepharis persica (Burm) Kuntze. Oecologia. 1972; 10:145-149.

25. Heithaus, E.R. (1982) Coevolution between bats and plants. In: Kunz, T.H. (ed), Ecology of bats. Plenum Press: New York and London, 327-361.

26. Hopkins HC. Floral biology and pollination ecology of the neotropical species of Parkia. Journal of Ecology. 1984 March; 72 (1): 1-23, doi: 10.2307/2260003

27. Hopkins HCF. Parkia (Leguminosae: Mimosoideae). Flora Neotropica Monograph. 1986 Oct; 43:1-123.

28. Hopkins MJG, Hopkins HCF, Sothers CA. Nocturnal pollination of Parkia velutina by Megalopta bees in Amazonia and its possible significance in the evolution of chiropterophily. Journal of Tropical Ecology. 2000 Sept; 16:733-746.

29. http://pt.climate-data.org/location/44081/

30. INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA - IBGE. Manual técnico da vegetação brasileira: sistema fitogeográfico, inventário das formações florestais e campestres, técnicas e manejo de coleções botânicas, procedimentos para mapeamentos. Rio de janeiro: IBGE-Diretoria de Geociências, 2012. 271 p. (Manuais Técnicos de Geociências, 1).

31. Judd WS, Campbell CS, Kellogg EA, Stevens PF, Donoghue MJ. Sistemática vegetal. Um enfoque filogenético. 3ª ed. Artmed, Porto Alegre ; 2009. 632p.

32. Kearns CA, Ianouye DW. Techniques for pollination biologists. Niwot: University Press of Colorado; 1993. 586 p.

33. Kenrick J, Knox RB. Function of the polyad in the reproduction of Acacia. Annals of Botany. 1982; 50:721-727, doi: https://doi.org/10.1093/oxfordjournals.aob.a086414

34. Kenrick J, Knox RB. Quantitative analysis of self-incompatibility in trees of seven species of Acacia. Journal of Heredity. 1989; 80:240-245.

35. Kiill LHP, Drumond MA. Biologia floral e sistema reprodutivo de Gliricidia sepium (Jacq.) Steud. (Fabaceae-Papilionoidae) na região de Petrolina, Pernambuco. Ciência Rural. 2001 Dec; 31(4): 597-601.

36. Knudsen JT, Mori SA. Floral scents and pollination in neotropical Lecythidaceae. Biotropica. 1996; 28: 42-60.

37. Köppen W. Climatologia: con un estudio de los climas de la tierra. México: Fondo de Cultura Econômica; 1948. 478 p.

38. Koptur S. Outcrossing and pollinator limitation of fruit set: breeding systems of Neotropical Inga trees (Fabaceae: Mimosoideae). Evolution. 1984; 38:1130-1143.

39. Lamont B.B. Canopy seed storage and release: What's in a name? Oikos. 1991; 60:266-268.

40. Lewis G, Schrire B, Mackinder B, Lock M. Legumes of the world. Kew: Royal Botanic Gardens. 2005. 577 p.

41. Lorenzi H. Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Nova Odessa: Editora Plantarum ;1998. 384 p.

42. LPWG, Legume Phylogeny Working Group, 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. Taxon 66, 44–77. https://doi.org/10.12705/661.3.

43. Luckow M, Hopkins HCF. A cladistic analysis of Parkia (Leguminosae: Mimosoideae). American Journal of Botany. 1995; 82:1300-1320.

44. Luckow M, Miller JT, Murphy DJ, Livshultz T. A phylogenetic analysis of the Mimosoideae (Leguminosae) based on chloroplast DNA sequence data. In: B.B. Klitgaard and A. Bruneau (editors). Advances in Legume Systematics, part 10, Higher Level Systematics, Royal Botanic Gardens, Kew, Jan 2003 197-220.

45. Machado FA, Alves AA, Moura JWS, Bezerra AME. Valor Nutritivo da Vagem de Faveira (Parkia platycephala Benth) para Ruminantes. Revista científica de produção animal. 1999; 1(1): 39-43.

46. Machado, ICS, Lopes AV. A polinização em ecossistema de Pernambuco: uma revisão do estado atual do conhecimento. In: Tabarelli, M., Silva, J.M.C. (Eds). Diagnóstico da Biodiversidade de Pernambuco. Secretaria de Ciência e Tecnologia e Meio Ambiente, Fundação Joaquim Nabuco e Editora Massangana, Recife, Pernambuco. 2002; 583-596.

47. Mann K, Farias CM, del Sol FG, Santos CF, Grangeiro TB, Nagano CS, Cavada BS, Calvete JJ. The amino-acid sequence of the glucose⁄mannose-specific lectin isolated from Parkia platycephala seeds reveals three tandemly arranged jacalin-related domains. Eurpean Journal of Biochemistry. 2001; 268:4414-4422.

48. Ohashi K, Thomson JD. Trapline foraging by pollinators: its ontogeny, economics and possible consequences for plants. Annal of Botany. 2009 Apr; 103: 1365-1378, doi: 10.1093/aob/mcp088.

49. Pagano M, Gauvreau K. Princípios de Bioestatística. São Paulo: Pioneira Thomson Learning; 2004. 522 p.

50. Piechowski D, Dötterl S, Gottsberger G. Pollination biology and floral scent chemistry of the Neotropical chiropterophilous Parkia pendula. Plant Biology. 2010 March; 12:172-182, doi:10.1111/j.1438-8677.2009.00215.x

51. Pio Correia M. Dicionário das plantas uteis do Brasil. Rio de Janeiro: IBDF: 1969. 710 p.

52. Ribeiro JELS, Hopkins MJG, Vicentini A, Sothers CA, Costa MAS, Brito JM, Souza MAD, Martins LHP, Lohmann LG, Assunção PACL, Pereira EC, Silva CF, Mesquita MR, Procópio LC. (1999) Flora da Reserva Ducke: Guia de Identificação das Plantas Vasculares de uma Floresta de Terra Firme na Amazônia Central. Instituto Nacional de Pesquisas da Amazônia/DFID, Manaus. 1999. 816 p.

53. Schrire, B.D., Lavin, M., Lewis, G.P., 2005. Global distribution patterns of the Leguminosae: Insights from recent phylogenies. Biol. Skr. 55, 375–42

54. Simmons NB. Order Chiroptera. In: Wilson D.E., Reeder, D.M. (Ed.). Mammal species of the world: a taxonomic and geographic reference. Baltimore: Johns Hopkins University Press. 2005; 312-529.

55. Sornsathapornkul P, Owens JN. Pollination biology in a tropical Acacia hybrid (A. mangium Willd. x A. auriculiformis A. Cunn. ex Benth). Annals of Botany. 1998; 81:631-645.

56. Stone GN, Raine NE, Prescott M, Willmer PW. Pollination ecology of acacias (Fabaceae, Mimosoideae). Australian Systematic Botany. 2003; 16:103-118.

57. Taddei VA. Sistemática de quirópteros. Boletim do Instituto Pasteur. 1996; 1:3-15.

58. Tschapka M, Dressler S. Chiropterophily: On bat-flowers and flower bats. Curtis’s Botanical Magazine. 2002; 19:114-125.

59. Tybirk K. Flowering, pollination and seed production of Acacia nilotica. Nordic Journal of Botany. 1989; 9:375-381.

60. Tybirk K. Pollination, breeding system and seed abortion in some African acacias. Botanical Journal of the Linnean Society. 1993; 112:107-137.

61. Tybirk K. Reproductive biology and evolution of the genus Acacia. Bulletin of the International Group for the Study of Mimosoideae. 1997; 20:45-53.

62. Vieira RE, Kotaka CS, Mitsui MH, Taniguchi VAAT, Ruvolotakasusuki MCC, Terada Y, Sofia SH, Costa FM. Biologia floral e polinização por abelhas em siratro (Macroptilium atropurpureum Urb.). Acta Scientiarum. 2002; 24(4):857-861.:

63. Vogel S, Lopes AV, Machado IC. Bat pollination in the NE Brazilian endemic Mimosa lewisii: an unusual case and first report for the genus. Taxon. 2005; 54: 693-700, doi: 10.2307/25065426

64. Vogel S. Chiropterophilie in der neotropischen flora. Neue Mitteilungen I. Flora. 1968; 157:562-602, doi: 10.1016/S0367-1801(17)30097-2

65. Wiens D, Calvin CL, Wilson CA, Davern CI, Frank D, Seavey SR. Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. Oecologia. 1987 mês; 71:501-509.