

# Flower and fruit development of *Parkia pendula* (Fabaceae, Mimosoideae)

Daniel Piechowski<sup>1,3</sup> and Gerhard Gottsberger<sup>2</sup>

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**RESUMO** – (Desenvolvimento de flores e frutos de *Parkia pendula* (Fabaceae, Mimosoideae)). *Parkia pendula* ocorre no Brasil, tanto na Amazônia como na Mata Atlântica nordestina. Seus botões, néctar e goma da vagem são recursos chave para a mastofauna da Mata Atlântica nordestina. Para aumentar o conhecimento sobre estes importantes recursos alimentares, este estudo teve como objetivo detectar e descrever as diferentes fases de desenvolvimento de flores e frutos. Este trabalho foi realizado em um fragmento de Mata Atlântica de 306 ha em Igarassu, Pernambuco, Nordeste do Brasil. Entre setembro de 2003 e janeiro de 2004, seis variáveis morfológicas foram medidas semanalmente em cinco inflorescências de dois indivíduos. Onze fases distintas de desenvolvimento puderam ser identificadas e descritas em detalhe nas 21 semanas desde o desenvolvimento das primeiras inflorescências até as vagens maduras. Essas fases são boas preditoras da fenologia de floração e frutificação de *P. pendula* porque são distinguíveis facilmente do solo da floresta. Além disto, a observação de abortos sincronizados de inflorescências, botões e vagens corrobora a estratégia de defesa previamente sugerida para *Parkia*, de saciedade de predadores.

**Palavras-chave:** aborto, mamíferos, Mata Atlântica, recursos chaves, saciedade de predadores

**ABSTRACT** – (Flower and fruit development of *Parkia pendula* (Fabaceae, Mimosoideae)). *Parkia pendula* occurs in Brazil in Amazonia and in the northeastern Atlantic Forest. In the latter, its buds, nectar, and seedpod gum are discussed to be keystone resources for the mammalian fauna. To enhance the knowledge about these important nourishment sources, the aim of this study was to detect and describe distinct phases in the flower and pod development. The study was conducted in a 306 ha forest fragment in Igarassu, Pernambuco, northeastern Brazil. Six morphometrical variables were measured weekly at five inflorescences of two individuals from September 2003 to January 2004. Eleven distinct developmental phases were identified in the 21 weeks lasting development from the very first inflorescences to mature pods and are described in detail. These phases are good predictors for the flowering and fruiting phenology of *P. pendula*, since they are easily distinguishable from the forest floor. Furthermore, highly synchronized abortions of inflorescences, buds, and pods were observed which support the previously assumed predator satiation defense strategy in *Parkia*.

**Key words:** abortion, Atlantic Forest, keystone resources, mammals, predator satiation

## Introduction

*Parkia pendula* (Willd.) Walp. (Fabaceae, Mimosoideae) is the most widely distributed Neotropical *Parkia* species (Hopkins 1986). In Brazil, it occurs in Amazonia as well as in the northeastern Atlantic Forest (Hopkins 1986). In the latter, it is a typical and abundant element of the flora with a much higher density than in the Amazonian forests (Ferraz *et al.* 2004, Guedes 1998, Piechowski & Gottsberger 2008, Siqueira *et al.* 2001).

*Parkia pendula* is pollinated by bats. Eleven phyllostomid bat species were recorded visiting *P. pendula* until now with *Phyllostomus discolor* Wagner being the main pollinator (Carvalho 1961, Hopkins 1984, Fischer 2000, Rodriguez-H. & Hopkins 2000, Piechowski *et al.* in press). Hundreds of bats can be encountered at a single flowering *P. pendula* tree (Hopkins 1984, Piechowski *et al.* in press). Beside bats, medium-sized non-flying mammals are attracted by the large nectar quantities of *P. pendula* (Hopkins 1984, Fischer 2000, Piechowski 2007a, b). The flowers are arranged in large capitula that are presented on long, stable axes underneath the flattened crowns, which therefore enables large bats like *P. discolor* to reach and pollinate the flowers. Two flower types occur at *P. pendula* capitula: fertile, hermaphrodite flowers as well as sterile, nectar-secreting ones (Piechowski *et al.* in press).

Beside its flowers, *P. pendula* is also known for its unique seed-dispersal mechanism. The pods of *P. pendula* (together

with that of its close congener *Parkia paraensis* Ducke) secrete large quantities of a sticky amber-colored gum, into which the seeds are released after dehiscence of the pods (Hopkins & Hopkins 1983). Therefore, seed shedding is prolonged for several months and desynchronized between the trees (Oliveira *et al.* 2006). The gum is a source of protein, carbohydrates, calcium, and magnesium for parrots and primates, which act thereby as seed dispersers (Anderson & Pinto 1985, Peres 2000).

Due to the high attractiveness of nectar and seedpod gum, this tree species is discussed to be a keystone species for the mammalian fauna of northeastern Atlantic Forest fragments (Piechowski 2007b). The goal of the present study was to detect, describe, and quantify distinct phases in the flower and pod development, to enhance the knowledge about these important nourishment sources.

## Material and methods

**Study site** – The study was conducted in the 306 ha fragment of Atlantic Forest, locally known as Mata de Piedade (7°50'23''S, 34°59'54''W). This forest is located on the property of the sugarcane factory Usina São José S/A, Igarassu, PE, northeastern Brazil. The climate of this region is characterized by a rainy season from April to August and a dry period from November to December and is therefore noticeably seasonal (CPRH 2003). The annual precipitation is 1,520 mm but shows strong inter-annual and spatial variations (Schessl *et al.* 2008). The annual air temperature is relatively constant at approximately 25°C (CPRH 2003, Schessl *et al.* 2008). The bedrock is a Tertiary conglomerate on beach-ridged terraces of the Barreiras group with a sandy to loamy red-yellow podzolic topsoil (Dominguez *et al.* 1990, Schessl *et al.* 2008). The Piedade fragment is

<sup>1</sup> Institute of Systematic Botany and Ecology, Ulm University, Ulm, Germany

<sup>2</sup> Botanical Garden and Herbarium, Ulm University, Ulm, Germany

<sup>3</sup> Corresponding author: danielpiechowski@web.de

mainly located on a plain plateau at an altitude of 110 m, only the northern part and a flooded valley have an altitude of approximately 30 m.

The height of the close canopy is approximately 20 m; some emergent trees reach 35 m in height. Among tree species, there is a tendency towards deciduousness during the dry season, wherefore this forest may be characterized as a semi-evergreen rainforest (Schessl *et al.* 2008). The trees with the highest importance value indices (IVI) are *Tapirira guianensis* Aubl. (Anacardiaceae), *Pogonophora schomburgkiana* Miers ex Benth. (Euphorbiaceae), *Sclerolobium densiflorum* Benth. (Fabaceae), and *Parkia pendula* (Silva *et al.* 2008). The matrix surrounding the Piedade fragment consists of a uniform sugarcane monoculture.

Data collecting – Data were sampled weekly between September 2003 and January 2004 at five inflorescences of two adult *P. pendula* individuals (dbh: 58.3 and 58.2 cm; height: 16 and 19.5 m, respectively). Access to the inflorescences was achieved using the single rope technique (Barker 1997). To detect distinct developmental phases, the following six morphometrical variables were measured: a) length of the composed inflorescence, b) number of capitula per inflorescence, c) peduncle length, d) capitulum diameter, e) number of pods per capitulum, and f) mean pod length. Morphometrical variables were measured starting in the 6<sup>th</sup> week of inflorescence development due to the high rate of abortion during the first five weeks. The capitulum diameter was measured with a caliper to the nearest mm; all other variables were measured to the nearest cm using a tape measure. Additionally, the color of all generative structures was determined using the color-plates by Kornerup & Wanscher (1981). Morphological terms were used following Hopkins (1986). Specimens were deposited at the herbarium UFP of the Universidade Federal de Pernambuco (UFPE). Complementary studies on the pollination biology including nectar and scent chemistry were published elsewhere (Piechowski *et al.* in press).

## Results

Eleven distinct developmental phases could easily be identified in the 21 weeks lasting development of *Parkia pendula* from the very first inflorescence buds to mature pods (Fig. 1; Tab. 1) and are described in the following.

The inflorescence abortion rate was very high during the first five weeks of bud ripening. Nevertheless, there were clear differences between the inflorescence buds of the first two weeks compared with older ones. During the first two weeks (initial phase), the inflorescence bracts opened. The whole inflorescences were very compact (<5 cm total length) and all capitulum buds were still completely enclosed by capitular bracts (Fig. 1a). The elongating phase (weeks 3-7) was characterized by the elongating of the primary axes of the compound inflorescences whereas the peduncles were still relatively short. The number of capitulum buds (and peduncles) decreased dramatically (Tab. 1) during this five-week-lasting period. The capitular bracts of the remaining capitulum buds opened (Fig. 1b) and the final inflorescence and peduncle length as well as the final number of capitula per inflorescence (Tab. 1; Fig. 1c, d) was reached during the pre-flowering phase (weeks 8-10). The capitulum buds started emitting odor during the last week of this developmental phase. The following flowering phase (11<sup>th</sup> week) comprised the day before the one night of flowering as well as the following days until all unfertilized flowers were aborted (Fig. 1e-g). Due to the open flowers, the capitulum diameter increased significantly (Tab. 1). Opening started around noon of the day before the single flowering night of every capitulum (i.e., ca. 30 h before start of the nectar production) when the subtending bracts of the nectar-secreting flowers lifted slightly and the styles elongated, wherefore the capitula looked somehow linty (Fig. 1e). The fertile flowers opened 24 h later, i.e., around noon before the

Table 1. Morphometrical variables (mean  $\pm$  SD) and color of the buds, inflorescences, capitula, flowers, and pods during the different developmental phases of *Parkia pendula* (Willd.) Walp. Cap: capitulum; diam: diameter; Infl: inflorescence; Ped: peduncle; Wk: week.

Wk	Infl. length [cm]	Cap./Infl.	Ped. length [cm]	Cap diam. [cm]	Pods/Cap.	Pod length [cm]	Color	Phase
1	-	-	-	-	-	-	olive-green	Initial
2	-	-	-	-	-	-	olive-green	
3	-	-	-	-	-	-	olive-green	Elongating
4	-	-	-	-	-	-	olive-green	
5	-	-	-	-	-	-	olive-green	
6	32.6 $\pm$ 17.8	15.8 $\pm$ 6.2	-	-	-	-	olive-green	
7	58.6 $\pm$ 18.2	14.2 $\pm$ 3.1	-	-	-	-	olive-green	
8	93.2 $\pm$ 20.6	2.4 $\pm$ 1.1	41.7 $\pm$ 13.0	1.6 $\pm$ 0.3	-	-	olive-green	Pre-flowering
9	115.2 $\pm$ 13.5	1.8 $\pm$ 0.8	71.3 $\pm$ 12.7	2.3 $\pm$ 0.3	-	-	olive-green	
10	118.8 $\pm$ 10.8	1.6 $\pm$ 0.9	73.7 $\pm$ 12.1	3.2 $\pm$ 0.1	-	-	olive-green	
11	118.2 $\pm$ 10.4	1.6 $\pm$ 0.9	73.1 $\pm$ 12.3	4.1 $\pm$ 0.2	-	-	bright red	Flowering
12	117.6 $\pm$ 10.6	1.6 $\pm$ 0.9	73.0 $\pm$ 12.4	1.9 $\pm$ 0.1	35.7 $\pm$ 26.2	2.2 $\pm$ 1.3	olive-green	Reduction
13	117.2 $\pm$ 11.3	1.4 $\pm$ 0.9	72.7 $\pm$ 12.4	2.0 $\pm$ 0.2	21.9 $\pm$ 22.6	4.4 $\pm$ 2.0	olive-green	
14	117.8 $\pm$ 11.2	1.4 $\pm$ 0.9	72.9 $\pm$ 12.1	2.1 $\pm$ 0.2	5.4 $\pm$ 3.9	13.0 $\pm$ 4.8	reddish-brown	Growth
15	117.0 $\pm$ 11.0	1.4 $\pm$ 0.9	72.6 $\pm$ 12.2	2.0 $\pm$ 0.2	4.9 $\pm$ 2.9	18.1 $\pm$ 3.3	deep green	Unripe
16	117.8 $\pm$ 11.6	1.4 $\pm$ 0.9	72.9 $\pm$ 12.3	2.1 $\pm$ 0.2	4.4 $\pm$ 2.4	19.3 $\pm$ 1.8	deep green	
17	117.0 $\pm$ 11.5	1.4 $\pm$ 0.9	72.6 $\pm$ 12.2	2.0 $\pm$ 0.2	4.3 $\pm$ 2.3	19.4 $\pm$ 2.0	deep green	
18	117.6 $\pm$ 10.9	1.4 $\pm$ 0.9	72.6 $\pm$ 12.2	2.1 $\pm$ 0.2	4.3 $\pm$ 2.3	19.3 $\pm$ 2.3	deep green	
19	117.6 $\pm$ 11.8	1.4 $\pm$ 0.9	72.6 $\pm$ 11.7	2.0 $\pm$ 0.2	3.9 $\pm$ 2.2	19.5 $\pm$ 2.3	deep green	Gum-producing

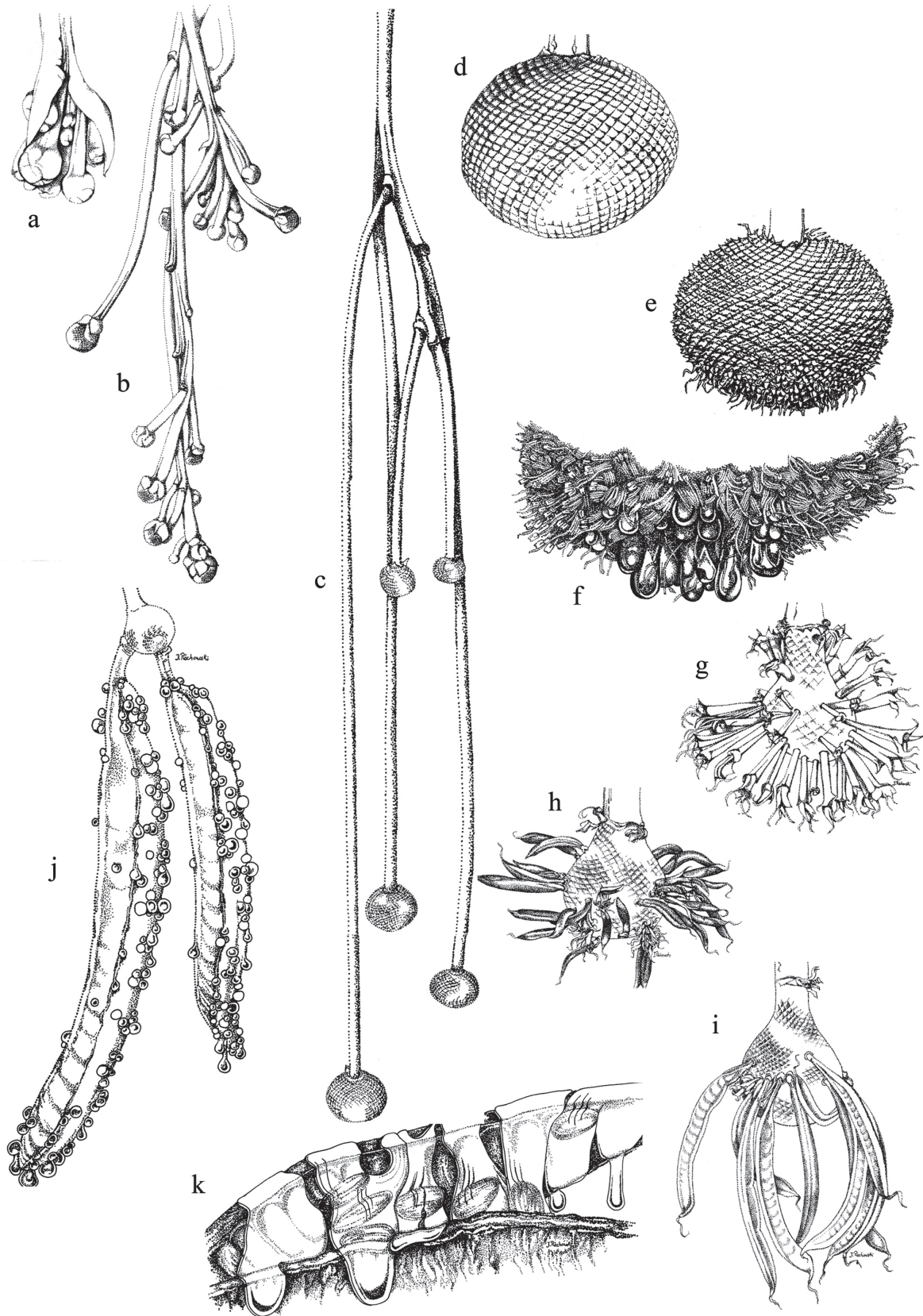


Figure 1. Phases in the development from buds to mature pods of *Parkia pendula* (Willd.) Walp. a. initial phase; b. elongating phase; c, d. pre-flowering phase; e. early flowering phase; f. detail of a flowering capitulum with nectar drops at the sterile flowers; g. post-flowering phase; h. reduction phase; i. growth phase; j. gum-producing phase; k. detail of an open mature pod (Illustrations by J. Piechowski after photographs).

flowering night. The well-exserted bright red colored anthers and the apical part of the filaments caused the red color of the capitula. The time of anther opening corresponded always with the starting of the nectar production around dusk. After anther opening, the red color became a yellowish tone due to the openly presented yellow-colored polyads. Additionally, large nectar drops accumulated at the styles of the nectar-secreting flowers soon after dusk (Fig 1f). The pale styles of the fertile flowers elongated between 20:00 h and 21:00 h and exceeded the anthers. The anthers were getting darker with proceeding time. Therefore, the color and brightness of the capitula changed from bright red via red with a yellowish tone to dark purple-red during the one night of anthesis.

Most flowers were aborted during the next three to four days; only 50 to 100 flowers remained at the olive-green receptacle (Fig. 1g). A small fraction of these flowers developed into small, olive-green pods (reduction phase, weeks 12 and 13; Fig. 1h), and just every seventh of these latter proceeded its development (Tab. 1). These pods grew strongly during the following 14<sup>th</sup> week (growth phase; Fig. 1i). The color of the pods changed to reddish-brown (Tab. 1) during the growth phase and turned into deep green thereafter (unripe phase). The fruits reached their final length and final number per capitulum in the unripe phase (weeks 15-17; Tab. 1). After these three weeks, they entered the gum-producing phase, during which they produced a very sticky exudate, especially at the thickened ventral sutures (Fig. 1j). This gum-producing phase lasted two weeks (weeks 18 and 19) before gum production stopped and the pods began to dry out. The pre-dispersal phase lasted for two weeks (weeks 20 and 21). The pods were dry and dark and the gum was still attached. The following dispersal phase lasted for several weeks, depending on the strength of precipitation since heavy rainfall washes off the water-soluble gum. Although the pods were open, a huge number of seeds remained on the pods glued to the very sticky exudate (Fig. 1k) or was still being connected with the pod by their funicles. The pods often remained for several months still attached on the tree after releasing all the seeds (post-dispersal phase).

## Discussion

The described phases in the development of flowers and buds of *Parkia pendula* were very distinct and were clearly distinguishable with binoculars. Together with the observed temporal pattern, they are therefore good predictors of flowering and fruiting of *P. pendula*. Furthermore, observations on *Parkia platycephala* Benth. (D. Piechowski, unpubl. data) suggest that these phases and their temporal pattern may also hold true for the development of other *Parkia* species, at least for the section *Platyparkia*. The short flowering period of individual trees (Piechowski 2007b) as well as the fruiting time may therefore be estimated long in advance.

Additionally, the data clearly showed a three times repeated temporally correlated pattern of an enormous abortion of reproductive organs followed by a very fast development of the remaining ones. These highly synchronized events occurred on three morphological levels: the inflorescence-level, the capitulum-level, and the pod-level. The reduction on capitulum-level is also described by Hopkins (1986) but she did not observe the high synchronization within the whole reproduction process: capitulum buds were aborted only in the short time between the growth of the primary axes and peduncle elongation and not during all bud phases. This kind of highly synchronized abortion during the early developmental stages of reproductive organs is well documented for the fruit abscission in several species (Stephenson 1981). Reallocation of limited resources is generally suspected to be the proximate reason for these abortions since resources are usually translocated out of the aborted organ before abscission and the remaining fruits benefit from these 'surplus resources' (Stephenson 1981). A possible ultimate reason for the overproduction and later abscission might be predator satiation (Janzen 1971), which for *Parkia* was already hypothesized earlier by Hopkins & Hopkins (1983) to be a defense strategy against the high seed-beetle diversity at *Parkia* in the Amazon basin (Hopkins 1983). Besides invertebrates, the Brazilian porcupine (*Coendou prehensilis* L.) was identified as a common herbivore of *P. pendula* buds (Piechowski 2007b).

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