

# Pollination Ecology of *Swartzia Apetala* Raddi Var. *Apetala* (Leguminosae-Papilionoideae).

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## ABSTRACT

The pollination ecology of *Swartzia apetala* Raddi var. *apetala* was studied in the restinga of Maricá, State of Rio de Janeiro, Brazil. *S. apetala* var. *apetala* is a shrub with asynchronic annual blooming, between the months of November and April (hot-rainy season). Each plant can exhibit more than one blooming episode in this period. Their flowers are hermaphrodites, apetalous, heterantherous, odoriferous, and the pollen represents the only reward offered to visitors. It is pollinized by species of *Centris* and *Xylocopa*, solitary and polylectic bees, which collect the pollen by means of vibratory movements. Other bees such as *Apis mellifera*, *Pseudaugochloropsis graminea* and *Trigona spinipes* are only pollen-thieves. In this variety of *Swartzia* vibrating is an efficient method to collect pollen from the anthers despite non-poricidal dehiscence. The flowering phenology and the behavior of visitors influence the rate of outcrossing.

**Key-words:** Leguminosae, Papilionoideae, *Swartzia*, buzz-pollination, pollen-flower.

## INTRODUCTION

The sandy coastal plains of Brazil are covered by very characteristic vegetation, usually called "restinga". Restinga vegetation is composed of different communities influenced by topography and environmental conditions. The variety of these factors favors the appearance of several habitats and, consequently, of a rich and diversified flora (Araújo, 1984), threatened by real estate projects and by the disordered development of coastal areas. There are many studies concerning different aspects of the biology of reproduction of the restinga species to understand the dynamics of this ecosystem (Correia, 1983; Pinheiro *et al.*, 1988; Lima *et al.*, 1989; Leite, 1991; Ormond *et al.*, 1991; Pimenta, 1992; Correia *et al.*, 1993; Costa *et al.*, 1993; Ormond *et al.*, 1993; Pinheiro *et al.*, 1994; Pinheiro *et al.*, 1995; Ormond, 1995; Pinheiro, 1995; Vieira, 1995; Correia *et al.*, 1996; Martins & Correia, 1996; Moço & Pinheiro, 1996; Santos & Lima, 1996). The study of the sexual displays and reproductive systems presented for the species of the restinga of Maricá revealed

that most of them depended on biotic vectors for pollination (Ormond *et al.*, 1991).

*Swartzia apetala* Raddi var. *apetala* is a shrub that occurs frequently in the restinga of Maricá and has pollen-only flowers. Pollen-flowers, particularly those with poricidal anthers, are noted for the great similarity in the pollination syndrome, being visited by bees that vibrate the anthers when collecting pollen ("buzz pollination"). In the genus *Swartzia*, the flowers present anthers with longitudinal dehiscence. However, pollen collection by buzzing bees, similar to the buzz-pollination that was described by Buchmann (1983) poricidal species, was registered to *S. pickelii* (Lopes & Machado, 1996). Other studies also mention the use of vibration in the pollination of other species with non-poricidal anthers (Buchmann, 1985; Oliveira & Sazima, 1990; Vogel, 1978).

In this work we aimed to study the pollination ecology of *Swartzia apetala* Raddi var. *apetala* emphasizing the efficiency of the vibration method to collect pollen from non-poricidal anthers.

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## MATERIAL AND METHODS

This study was performed during the period of March 1994 to February 1996 in the restinga located in the municipality of Maricá, including the Districts of Barra de Maricá and Itaipuaçu, State of Rio de Janeiro, Brazil (22° 56' 15'' to 22° 58' 12'' S and 42° 54' 08'' to 42° 47' 30'' W) (Louro & Santiago, 1984). The climate is tropical rainy, with a warm and rainy summer, in which December and January are the months with the highest pluviosity, and a winter with a non-severe drought (Dau, 1960). During the study period the mean temperature of the hottest month was 25.6° C and of the coldest month 20.8° C. The daily temperature ranged between 6° C and 7° C.

During this study, excursions were made throughout the flowering period. Flowers and buds were collected for morphological study and to perform laboratory tests. The floral visitors were also collected and dried for identification and analysis of the pollen location on their bodies.

The observations of flower characteristics such as morphology, colour and nutritive resources, were performed on about 10 flowers from every 5 plants marked in the study areas. The phenological data was collected from 10 marked plants. Observations were made for the blooming period, and the number, duration and synchronization of the episodes. Additional observations in unmarked plants were performed periodically. The classification of the flowering pattern was done according to Newstrom *et al.* (1994).

The pollen grains from the two kinds of stamens were analysed separately. The viability of the pollen grains was tested with acetic carmine (Radford *et al.*, 1971), and the detection of lipids on the surface of the pollen grains ("pollenkitt") was done with Sudan III (Johansen, 1940). The stigma was examined under optical and stereoscopic microscopes and which was classified according to Heslop-Harrison & Shivanna (1977). The odour was detected and

classified from flower structures isolated in closed vessels. The odoriferous areas were seen in flowers plunged into the Neutral Red solution for about 10 min and after that washed in flowing water to check the colored areas (Vogel, 1963).

The foraging behavior of the floral visitors were followed during the period of anthesis throughout the flowering. Observations were made regarding the number of flowers visited per plant, time and mode of staying in the flower and the kind of resource collected.

## RESULTS

*S. apetala* var. *apetala* occurs behind sand dunes` belt, parallel to the sea, and at inland restinga. It may be present either inside of shrubs and at open spaces. The plants can reach 2,5m tall, and can be found isolated or aggregated.

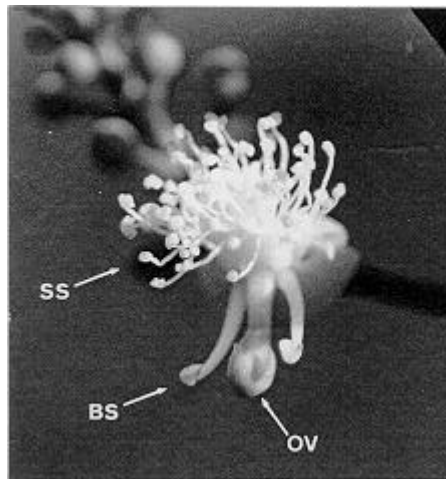
The flowering of *S. apetala* var. *apetala* was annual asynchronous in a populational level and occurred between the months of November and March (hot-rainy season). Intra-plant asynchronous blooming episodes were frequent, being marked by the blooming of a branch or a group of them in isolation. Each plant presented from 1 to 5 episodes, each one standing from 5 to 15 days, with an interval between them up to 15 days.

The inflorescence was racemose and varied in length from 1 to 18 cm, each one producing 1 to 40 flowers. The smallest inflorescences ( $\leq 9$  cm) presented 1 to 3 open flowers each day, and the largest ones, 6 to 8. The daily production of flowers per plant was around 80 flowers.

The flowers were hermaphrodites, zygomorphics, apetalous and odoriferous, ca. 1.50 cm long and the pollen represented the only reward to visitors. The calyx was glabrous, green-colored, and presented 4 or 5 lobes. The ovary was 4.5-6.0 mm long, glabrous, green-colored, unilocular, unilocular, superous, raised by a stipe 2.0-4.5 mm length, half-moon shaped, and presented 7-12 ovules. The style was lateral and short, with only 0.4 mm long, leaving the

stigma almost sessile. The stigmatic area was dry and papilous. The androecium was glabrous, white-colored, dimorphic, constituted by ca. 80 smaller stamens forming a brush at the upper end of the flower, and two bigger ones at the lower end, one on each side of the ovary. The former had anthers ca. 0.6-0.7 mm long and filaments 7.0-9.0 mm long. The anthers of both

stamen types had longitudinal dehiscence. Their pollen grains presented a viability index of about 90%. The grains from the big stamens formed small masses due to the high amount of lipids on their surfaces (“pollenkitt”), while the small ones were dry and powdery. Odour was released from the filaments of the small stamens, exhaling a strong sweet scent.



**Figure 1.** Flower structure of *Swartzia apetala* var. *apetala*: SS = small stamen, BS = big stamen, OV = ovary.



**Figure 2.** Pollination of *Swartzia apetala* var. *apetala* by *Centris flavifrons*. Note the area where the bee abdomen comes in contact with the stigma and the big stamens.

Anthesis began at 5.30 am. There was a complete exposure of the pollen grains in the anthers of the big stamens, caused by the total retraction of the thecae. In the small stamens, the pollen grains remained inside of the thecae that had tiny longitudinal apertures. There was a spatial separation between the gynoecium and the stamens in the flower; therefore the pollen grains never came in contact with the stigma (Fig. 1). Around 12 noon, the scent exhalation ceased, the small stamens faded and the large ones fell off, characterizing the end of anthesis. The group of small stamens only falls from the floral receptacle at the end of the day.

The flowers of *S. apetala* var. *apetala* were visited by *Xylocopa ordinaria* (Smith), *Xylocopa frontalis* (Olivier), *Centris flavifrons*

(Fabricius), *Centris varia* (Erichson), *Centris lutea* (Friese), *Apis mellifera* (Linneus), *Trigona spinipes* (Fabricius), and *Pseudaugochloropsis graminea* (Fabricius). The visits began around 5.30 am, at which time the flowers are attractive and the floral reward is available. They occurred more frequently from 5.30 am to 9.30 am. Approximately from 10 am the visits became scarce and the anthers of the flowers were practically without pollen.

The *Centris* and *Xylocopa* species were pollinators, *X. ordinaria* and *C. flavifrons* being the most frequent in populations studied (Table 1). All these species of bees were solitary and polylectic, ranging from medium to large size, and only the females collected the pollen grains to feed their larvae. The intra-floral visits of

these bees were fast, with a mean time of 29 seconds for *Xylocopa* and 12 seconds for *Centris*. The bees visited few flowers per plant, never exceeding 20 in a foraging flight.

During the visits, the pollinating bees landed on a flower, held the group of small stamens with the first and second pair of legs, put the wings back, bent the abdomen and vibrated. These vibratory movements allowed the cloud-like

departure of the pollen grains from the small stamens, and deposition on the ventral surface of the bee. During the vibratile behavior, the dorsal portion of their abdomen came in contact with the stigma and the big stamens (Fig. 2). After visiting several flowers, the bees flew over the inflorescence and cleaned the ventral surface of the abdomen, transferring the pollen derived from the anthers of the small stamens to their third pair of legs.

**Table 1:** Relative activity and frequency of the visiting bees *Swartzia apetala* var. *apetala* observed during the study in the restinga of Barra de Maricá/ Itaipuaçu - RJ.

| SPECIES                             | ACTIVITY     | FREQUENCY (*) |
|-------------------------------------|--------------|---------------|
| Anthophoridae                       |              |               |
| <i>Xylocopa ordinaria</i>           | pollinator   | high          |
| <i>Xylocopa frontalis</i>           | pollinator   | low           |
| <i>Centris flavifrons</i>           | pollinator   | high          |
| <i>Centris lutea</i>                | pollinator   | low           |
| <i>Centris varia</i>                | pollinator   | low           |
| Halictidae                          |              |               |
| <i>Pseudaugochloropsis graminea</i> | pollen-thief | low           |
| Apidae                              |              |               |
| <i>Apis mellifera</i>               | pollen-thief | medium        |
| <i>Trigona spinipes</i>             | pollen-thief | medium        |

(\*) **low frequency:** less than 5 visits per plant/day; **medium:** 5 to 10 visits per plant/day; **high:** more than 10 visits per plant/day .

The grains of the big stamens remained on the dorsal surface of the abdomen and were not removed during this cleaning process.

*Apis mellifera* (a medium-sized bee), *Trigona spinipes* and *Pseudaugochloropsis graminea* (both small- sized bees), acted only as pollen-thieves (Table 1). *A. mellifera* and *T. spinipes* foraged in a similar way and their intra-floral visits took a long time, varying from 2-15 min. They landed on the small stamens and with their front legs and mouth parts collected pollen from each anther in a single step, and used up the floral reward. Manipulation of the large anthers rarely occurred. In these species of bees, the pollen deposition was diffuse. They collected pollen from several flowers of the same plant, making short flights.

*Pseudaugochloropsis graminea* collected pollen by means of vibration. The intra-floral visit was long, up to 5min. During the visits, the bee

landed on the small group of stamens (five), holds some of them with its first and second pair of legs and vibrated. This vibration released a pollen cloud and the grains were deposited over the whole ventral surface of the bee. Then it walked over the small stamens and repeated this movement up to five times on each flower, foraging different groups of stamens in a circular route. The bees of this species rarely foraged the big stamens. Pollinating and pollen-thief bees were frequently observed foraging together on the same plant, with no aggressive behavior.

## DISCUSSION

The maintenance of the populations of all bee species in a given ecosystem is related to the continuous offer of different floral rewards, especially nectar and pollen. *S. apetala* var. *apetala* flowers intensely in the hot-rainy season and their pollen contributes to the feeding of the

larvae of *Xylocopa frontalis*, *X. ordinaria*, *Centris flavifrons*, *C. varia*, *C. lutea*, *Apis mellifera*, *Pseudaugochloropsis graminea* and *Trigona spinipes*. Among these species, *Centris flavifrons* and *Xylocopa ordinaria* stand out as the effective pollinators of this plant, collecting pollen by means of vibratory movements (“buzz pollination”), despite the non-poricidal anthers. Bees of the genus *Eulaema* present the same behavior when visiting the flowers of *Swartzia pickelli* (Lopes & Machado, 1996).

The use of the floral vibration method to collect pollen in species with non-poricidal anthers has been recorded in several families (Buchmann, 1985; Macior, 1964 e 1968; Oliveira & Sazima, 1990; Vogel & Machado, 1991). In spite of being initially regarded as rare and occasional (Buchmann, 1985), this collecting method has now proven to be efficient for the species with non-poricidal anthers as for those with poricidal anthers (Oliveira & Sazima, 1990). In poricidal species the pollen transfer is more precise, preventing great losses (Buchmann, 1985).

In *S. apetala* var. *apetala*, heteranthery has an important role in pollination dynamics. Pollen grains with different functions are deposited in distinct areas on the body of the pollinator. This spatial difference in pollen grain deposition on the body of the pollinator, enables only the grains from the big anthers to be deposited in the stigma of another flower. The consequence is the reduction of interference between food and fertilizing pollen grains, favoring pollination and the reduction of pollen waste. In this regard, the different amount of pollenkitt present on the surface of the grains has an important role in *Swartzia* pollination and signifies a highly adaptive character. Undoubtedly, the adherence of the fertilizing pollen during the transport on the body of the bee and their capture for the dry and tiny stigma are favored by the great amount of this substance, while the production of dry grains for the small stamens allows the release of this pollen in the form of a cloud. *Apis mellifera* and *Trigona spinipes*, not being able to vibrate, make long visits, manipulating each anther individually. It could be concluded that in *S. apetala* var. *apetala* pollen collection by

vibration, performed by pollinating bees, might be the most efficient foraging pattern, since the pollen grains were collected simultaneously from all feeding anthers in a short period of time.

In the restinga of Maricá, *Centris* spp. and *Xylocopa* spp. were the main pollinators of many poricidal species that flowers in the same season, belonging to the Leguminosae, Melastomataceae and Ochnaceae families (Correia *et al*, 1996; Costa *et al*, 1993; Pinheiro, 1995; Pinheiro *et al*, 1988). The use of several sources of pollen by bees has been advantageous in order to assure different nutritional requirements for the offspring (Haydak, 1970). On the other hand, the frequency of outcrossing should decrease according to the number of species in flowering at the same time (Heirich & Raven, 1972).

The inter-specific competition for pollinators might favor the selection of reproductive strategies that benefited the attraction of pollinators, increased the frequency of visits and reduced the interference of foreign pollen (Bawa, 1983). In *S. apetala* var. *apetala* the plant display, odor concentration and the amount of available rewards to the visitors, resulting from intense daily flower production, were the important factors that reinforced attraction. According to Jansen (1971) massive flower production was an efficient strategy used to enhance the visitors attraction and to assure a higher number of legitimate visits. The flower attraction function was performed only by the group of small stamens, since the flowers did not have petals and the calyx was inconspicuous during the anthesis. These stamens, besides being showy, were responsible for odour emission and the production of the nutritional reward. In this variety, the scent was very strong, which was not common in other mellitophilous pollen-flowers which, in general, produced a weak sweet fragrance (Batra, 1984; Faegri & Pijl, 1971; Pinheiro, 1995).

It was observed that *S. apetala* var. *apetala* presented a peak in the visiting frequency of pollinating bees from 8 am to 9.30 am. Pinheiro (1995) noted that seven species of

Melastomataceae from the restinga, that bloom in the same season and offer pollen to the same bee species, have their visits restricted to the early morning hours, 100% of their flowers being pollinated from 7 am to 8 am. Levin & Anderson (1970) sustained that the flowers of a species ignored in a such foraging flight might be the target in the next one. In order to show the bees efficiency as pollinators, Batra (1984) pointed out that they have the tendency to visit a sequence of flowers from the same species in succession. However, the fertilizing pollen deposition in an area of the body of the bee that was not coincidental with the area of deposition of any other poricidal species in the restinga of Maricá, even with other species of heterandric Leguminosae, like *Senna* spp., showed the specialization in the pollination of *S. apetala* var. *apetala*.

*S. apetala* var. *apetala* was self-incompatible and showed a low reproductive success and the movement of the pollinating bees between plant populations was essential to the deposition of compatible pollen on the stigma, in order to increase fruit production (Moço, 1996). Frankie & Baker (1974) and Bawa (1983) stated that the asynchronism between flowering episodes in the same plant could decrease the interference of incompatible pollen and to improve crossings. This could be expected to happen in the present case also. Opportunistic pollen-thief visitors, such as *A. mellifera*, *P. graminea* and *T. spinipes*, actively collected pollen from the small stamens and finish them off. This reward was limited, on the contrary of nectar and oil, that in many species might be continuously secreted during anthesis (Percival, 1965; Simpson & Neff, 1983; Vieira, 1995). Therefore, the pollinating bees increased inter-plant foraging flight to obtain the optimum amount of food for their offspring. In this way, the plundering activity enabled a higher pollen flow increasing the outcrossing rates.

*C. flavifrons* and *X. ordinaria* exhibited long foraging flights with short intra-plant visits favoring cross-pollinations. The same behavior

was also recorded in other species with mass blooming, such as *Marcetia taxifolia* in the restinga of Maricá (Pinheiro, 1995) all visited by solitary bees. Heinrich (1972) remarks that the vibratory movements caused an increase in the temperature of the thoracic flight muscles, therefore it could be assumed that the use of vibration to collect pollen and need to alternate the visiting periods with long flights to keep their body temperature stable. Some doubts still remain as to the reasons that lead the bees to forage few flowers per plant in species with great reward availability (Frankie et al., 1976; Augspurger, 1980; Frankie & Harper, 1983), but at any rate, this behavior favors cross-pollinations.

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#### RESUMO

A ecologia da polinização de *Swartzia apetala* Raddi var. *apetala* foi estudada na restinga de Maricá, Estado do Rio de Janeiro, Brasil. *S. apetala* var. *apetala* é um arbusto com floração do tipo anual assincrônica, entre os meses de novembro e abril (estação quente-chuvosa). Cada planta pode apresentar mais de um episódio de floração neste período. As flores são hermafroditas, apétalas, heterândricas, odoríferas e o pólen constitui a única recompensa oferecida aos visitantes. É polinizada por espécies de *Centris* e *Xylocopa*, abelhas solitárias e poliléticas, que coletam o pólen através do método de vibração. Nesta variedade de *Swartzia* a vibração é um método eficiente de coleta de pólen apesar das anteras apresentarem deiscência rimosa. Outras abelhas, como *Apis mellifera*,

*Pseudaugochloropsis graminea* e *Trigona spinipes*, são pilhadoras de pólen. A fenologia da floração e o comportamento dos visitantes florais influenciam a taxa de fertilização cruzada.

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