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Phenology and Reproductive Ecology of *Myrcia rostrata* and *M. tomentosa* (Myrtaceae) in Central Brazil

By

Helena Maura TOREZAN-SILINGARDI*)

& Paulo Eugênio Alves Macedo DE OLIVEIRA*)

With figures

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Summary

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We studied the reproductive ecology of two species from one of the largest Neotropical genera in Myrtaceae, *Myrcia rostrata* DC. and *M. tomentosa* (AUBL.) DC., which are commonly found in South American forests and cerrado. Their small hermaphrodite flowers are bee-pollinated, as usual for the species of *Myrtaceae*, and pollen is the sole reward offered to small social bees (*Trigona*, *Apis*, *Augochloropsis*). In both species the flowering period begins after the first spring rains, a common pattern in *Myrtaceae*. *M. rostrata* has a “multiple bang” flowering strategy while *M. tomentosa* has a “pulsed bang” one, which differ in duration and synchronization between individuals, with a blooming period of only three days in the latter species. Pollination experiments indicated these species are preferentially outcrossing, as many *Myrtaceae* studied, setting more fruits from cross than self-pollination. High natural fruit-sets observed for both species suggests adequate pollination at Panga Ecological Reserve. However, the reduced pre-emergent reproductive success values observed for *M. tomentosa*, due to larval herbivory inside floral buds, may limit its reproductive output.

*) MSc. Helena Maura TOREZAN-SILINGARDI, Prof. Dr. Paulo Eugênio Alves Macedo DE OLIVEIRA, Instituto de Biologia, Universidade Federal de Uberlândia, Caixa Postal 593, CEP 38.400-902, Uberlândia, MG, Brazil; e-mail hmtsilingardi@yahoo.com.br, poliveira@ufu.br

Zusammenfassung

TOREZAN-SILINGARDI H. M. & OLIVEIRA P. E. A. M. 2004. Phänologie und Reproduktions-Ökologie von *Myrcia rostrata* und *M. tomentosa* (Myrtaceae) in Zentral-Brasilien. – *Phyton* (Horn, Austria) 44 (1): 23–43, 3 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Zwei Arten aus einer der größten neotropischen *Myrtaceae*-Gattungen, *Myrcia rostrata* DC. und *M. tomentosa* (AUBL.) DC. wurden untersucht; beide finden sich häufig in südamerikanischen Wäldern und Cerrados. Die kleinen Zwitterblüten werden, wie für *Myrtaceae* üblich, von Bienen bestäubt. Pollen ist das einzige Angebot an kleine und mittelgroße, soziale Bienen (*Trigona*, *Apis*, *Augochloropsis*). Bei beiden Arten beginnt die Blühperiode nach den ersten Frühjahrsregen, ein häufiges Muster bei *Myrtaceae*. *M. rostrata* hat eine „multiple bang“-Blühstrategie während *M. tomentosa* dem „pulsed bang“-Muster folgt. Beide haben jährliche Blühperioden, differieren aber in Dauer und Synchronisation innerhalb der Population; letztere Art hat weniger und stärker synchrone Blühphasen. Bestäubungsversuche deuten bei beiden Arten – wie bei vielen *Myrtaceae* – auf vorherrschende Fremdbestäubung, wobei mehr Früchte angesetzt werden, als bei Selbstbestäubung. Hoher Fruchtansatz unter natürlichen Bedingungen in der Panga Ecological Reserve zeigt ausreichende Bestäubung an. Die geringeren Werte für den „pre-emergent“-Erfolg bei *M. tomentosa* sind durch Larvenfraß innerhalb der Knospen bedingt, was die Diasporen-Produktion begrenzen kann.

1. Introduction

Despite being the dominant family in some Neotropical plant formations, with many interesting species for conservation of natural areas (ARAÚJO & al. 1997, TABARELLI & al. 1999), *Myrtaceae* is still poorly studied, with a limited number of works on its reproductive biology (PROENÇA & GIBBS 1994, NIC-LUGHADHA & PROENÇA 1996, TOREZAN-SILINGARDI & DEL-CLARO 1998, NIC-LUGHADHA 1998).

The *Myrtaceae* has 132 genera with 3,675 species (NIC-LUGHADHA & PROENÇA 1996), and can be found all over the world, but especially in Australia and America (JOHNSON & BRIGGS 1984). Neotropical *Myrtaceae* belong mainly to the subfamily *Myrtoideae*, which comprises 60 genera and 2,375 species (NIC-LUGHADHA & PROENÇA 1996). They are ecologically very important in South American areas with temperate climates, constant water supply and nutrient-poor, lightly acidic soils. *Myrtoideae* species are trees or shrubs, with simple leaves punctuated with oil glands. Many of its species produce lots of small flowers per day on each tree, suggesting high levels of geitonogamy (NIC-LUGHADHA & PROENÇA 1996). Many observations suggest that facultative allogamy is wide-spread in the subfamily (NIC-LUGHADHA & PROENÇA 1996); self-incompatibility mechanisms (BEARDSSELL & al. 1993) and even late-acting self incompatibility occur in many of its species (PROENÇA & GIBBS 1994, NIC-LUGHADHA 1998). High outcrossing levels can be maintained even in self-compatible species through floral strategies that favor some pollinator foraging strategies

such as trap-lining. *Myrtoideae* reproductive systems vary from dioecy to hermaphroditic and from strict allogamy to autogamy; furthermore apomixis also occurs (NIC-LUGHADHA & PROENÇA 1996).

Reproductive ecology studies comprise different topics such as pollination biology, floral biology, breeding systems, incompatibility reactions and phenology (GIBBS 1990, KEARNS & INOUE 1993). Such studies, which include sympatric species sharing the same pollinator guild, can give us some insights into the phylogeny and evolution of floral characteristics (STILES 1985, SARAIVA & al. 1988, OLIVEIRA & al. 1992, PROENÇA & GIBBS 1994, ARMBRUSTER 1997).

Myrcia is a common forest genus well distributed in the cerrado biome, the Neotropical savannas of Central Brazil (LANDRUM & KAWASAKI 1997, MENDONÇA & al. 1998). In order to characterize the reproductive ecology and the floral visitors we studied two species of this genus, *Myrcia rostrata* DC. and *M. tomentosa* (AUBL.) DC., common in forests and open cerrado (savanna) formations of Minas Gerais state, Central Brazil.

2. Material and Methods

2.1. The Study Area

We observed both species from September 1999 to December 2001 at Panga Ecological Station, a natural area 30 km south of Uberlândia, comprising 403.85 hectares of well preserved cerrado vegetation, with many of the Central Brazilian phytophysionomies, including savanna and forest types (SCHIAVINI & ARAÚJO 1989). The reserve is located between 19°9'20" 19°11'10" S and 48°23'20" - 48°24'35" W, at an average altitude of 800 m (SCHIAVINI & ARAÚJO 1989). Mean annual temperature is 22° C, annual rainfall is ca. 1500 mm. Seasonality is marked, with a dry (May–September) and a wet period (October–April) (ROSA & al. 1991).

Climatological data were obtained from Geography Institute of the Federal University of Uberlândia for 2001 and the reproductive phenology data of 32 *Myrtaceae* species of the Panga Ecological Station were compiled from ARANTES & MONTEIRO 2002 (Figure 1).

2.2. The Species

Myrcia rostrata is widely distributed in tropical and sub-tropical South America, usually found in Brazil, south of the Amazonian hylaea, extending down to Santa Catarina state (LEGRAND & KLEIN 1969, LORENZI 1998). These fast growing trees can achieve 2 m in height within 2 years (LORENZI 1998) and individuals of this size already produce flowers and fruits (personal observation). *M. rostrata* is able to grow in degraded or modified environments and is interesting for urban arborization (LORENZI 1998). *M. rostrata* trees can grow up to 6 to 12 m and occur from cerrado (open savanna areas) to denser woodlands (locally cerrado), forest borders and gallery forests, as well as in forest gaps and disturbed areas inside the Panga Ecological Station (ARANTES & MONTEIRO 2002).

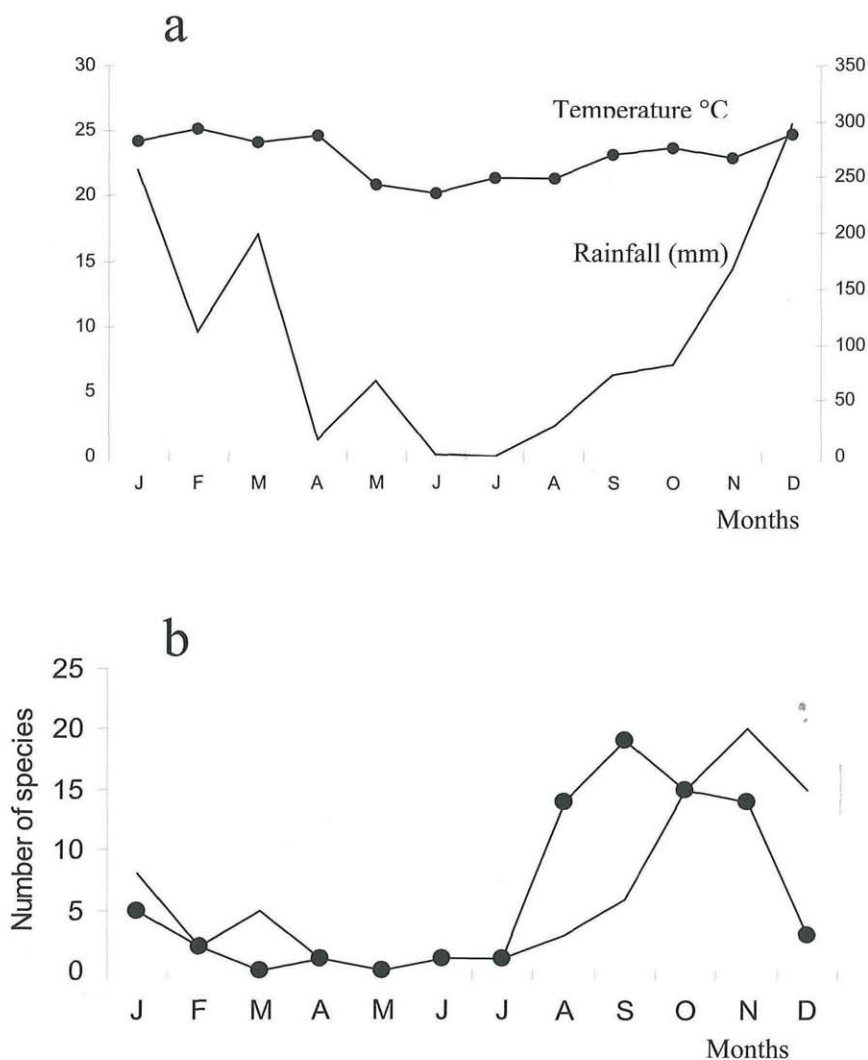


Fig. 1. a – Temperature and rainfall in the area of the Panga Ecological Station (S. of Uberlândia, Central Brazil) during the study period (2000). b – Flowering (marked line) and fruiting (continuous line) of 32 *Myrtaceae* species at Panga Ecological Station compiled from ARANTES & MONTEIRO 2002.

M. tomentosa is widely distributed in Neotropical America, from Panama to SE Brazil (LEGRAND & KLEIN 1969). Trees can grow up to 6 to 13 m from cerrado to denser woodlands and forest borders, as well as disturbed areas inside Panga Ecological Station (ARANTES & MONTEIRO 2002).

Samples of each species were included in the Herbarium Uberlandensis of the Uberlândia Federal University (HUFU 27.015 for *M. rostrata* and HUFU 17.309 for *M. tomentosa*).

2.3. Phenology

Phenological observations were made every month for both species. *M. rostrata* was observed from August 2000 to October 2001, the number of monitored trees varied from 43 in the first to 76 in the last month. *M. tomentosa* was observed from September 2000 to October 2001, the number of observed trees varied from 20 in the first to 49 in the last month. The number of plants increased gradually during the time in order to substitute trees severely affected by a frost in July 2000 and prevent other losses. All sampled individuals were reproductive and apparently healthy trees. Both the species are evergreen. The phenological events (phenophases) observed were: the presence of new leaves, shedding of leaves, presence of floral buds, flowers and fruits. The intensity of each phenological event was scored for each tree as 0 if the event was absent, as 1 if the event was sporadic (from 1 to 25 % of the tree branches), as 2 if it was frequent (from 26 to 75 % of the tree branches), and as 3 if the event was observed in 76 to 100 % of the tree branches (adapted from FOURNIER 1974 and RIBEIRO & CASTRO 1986). We compared our data with those obtained by ARANTES & MONTEIRO 2002 for all the 32 *Myrtaceae* species from Panga Ecological Station in the period of September 1995 to August 1996. During the flowering period, non-quantitative phenological observations of individuals and populations were made on a weekly or daily basis to follow quick blooming episodes.

2.4. Floral Biology

Floral morphology was studied in fresh and fixed material. Pollen viability tests using acetic carmine (KEARNS & INOUE 1993) and pollen/ovule ratio analyses (CRUDEN 1977) were performed using pre-anthesis floral buds and flowers stored in 70% alcohol. Pollen grains from anthers (or half of an anther) of some flowers were stained, also with acetic carmine, and the total number of pollen grains (viable or not) counted under microscope. The results were used to estimate the number of pollen grains per flower. Stigma receptivity was tested on the first and second day after anthesis, with 3% hydrogen peroxide (FAEGRI & VAN DER PIJL 1979) in previously bagged flowers.

2.5. Floral visitors

Due to the brief flowering period in *M. tomentosa*, and in order to perform similar observation effort in both species, we carried out the observations of floral visitors during only two days in each species. Floral visitors were observed from 6:00 h to 16:00 h on the first day and from 6:00 h to 12:30 h on the second day. Observations were carried out on trees without any treatment and with many open flowers. Visitors were observed for 5 minutes every 30 minutes (MARTIN & BATESON 1994), in a total of 175 minutes of observation. The second day observations were reduced due to the absence of floral visitors during the afternoon of the first day. Floral visitors were collected and identified. Non-quantified observations of visitors done since then in-

dicating the spectrum of visitors and pollinators is not different from the observed during the limited study period presented here.

2.6. Breeding Systems

Breeding systems were tested on 37 trees of *M. rostrata* and 25 of *M. tomentosa* following PROENÇA & GIBBS 1994. Manual self and cross-pollinations (between trees at least 25 m apart) were performed on bagged flowers during first and second day of flower opening. Floral buds were bagged very early, when it became possible to individualize them in the inflorescence. Stamens were not removed for pollination due to the small flower size. Emasculated flowers were used only to test agamospermy, and the test was carried out in bagged pre-anthesis floral buds which had the stamens, part of the petals, part of the style and the stigma removed. Several dehiscing anthers were rubbed on the stigma during manual pollinations, and these flowers were tagged, bagged again and observed periodically. Inflorescences with floral buds only previously bagged and tagged, were observed to verify the occurrence of spontaneous self-pollinations. Natural pollinations were observed in tagged inflorescences.

The self-incompatibility index (ISI, sensu BULLOCK 1985) was calculated as the ratio between self and cross-pollination fruit-set. The pre-emergent reproductive success (PERS, sensu WIENS & al. 1987) which is the percentage of ovules that mature into seeds, was calculated as the seed:ovule ratio multiplied by the fruit:flower ratio. The reproductive efficacy index (REI, sensu RUIZ & ARROYO 1978) which indicates the relative efficacy of natural pollination was calculated as the ratio between fruit-set from natural pollinated and manually cross-pollinated flowers.

In order to verify seed predation, 20 fruits were collected in five trees each of *M. rostrata* and *M. tomentosa*. This analysis gives the percentage of fruits apparently perfect but containing destroyed seeds.

3. Results

3.1. Phenology

Flowering in *M. rostrata* and *M. tomentosa* was annual and regular during the observed period (Fig. 2). However, monthly based, quantitative phenology did not clearly detect fine flowering features and a single peak appeared for both species. Although these general flowering periods and peaks overlapped, flowers of *M. rostrata* and *M. tomentosa* did not open on the same day during the study period and they showed some differences in flowering dynamics which are described below:

The trees of *M. rostrata* and *M. tomentosa* had quiescent floral buds, some of them for up to three months during the dry season. Flowering occurred intensely after the first spring rains, from September to December. *M. rostrata* flowered in pulses during 13 weeks, from the end of September to the middle of December 2001. This species had the same flowering period and duration in the previous year, but began two weeks earlier. *M. tomentosa* flowered for a period of five weeks, from the end of August to the

end of September 2001, and had the same flowering period and duration in the previous year, but, as for *M. rostrata*, beginning two weeks earlier. Days with new flowers were separated by some days with no open flowers in either species. These species differed in the number of new flowers opened per day, the number of days with new flowers and the flowering synchronization of conspecific trees. The flowering dynamics of *M. rostrata* was characterized by a long period with many or few flowers opening on non-successive days and with less marked synchronization within the population. Flowering in *M. tomentosa*, in 2001, was restricted to just three highly synchronized flowering episodes separated by some days without flowers. Trees produced a large number of flowers during only two of such episodes. The second flowering day of most trees, when the remaining flower buds opened, coincided with the first flowering day of a few delayed individuals in the population, so that each one-day flowering episode involved different numbers of individuals and flowering intensities.

Fruits of *M. rostrata* and *M. tomentosa* matured irregularly from December to January (Figure 2). Leaves were produced all year round in *M. rostrata*, always with low intensity. *M. tomentosa* presented irregular leaf production during the study period. Shedding of leaves for both species was also irregular during the year and never intense (Fig. 2).

3.2. Floral Biology

M. rostrata and *M. tomentosa* have hermaphrodite epigynous flowers presented in axillary panicle inflorescences (Fig. 3a, 3b). Symmetry is radial with floral diameter of 13–15 mm in *M. rostrata* ($n = 6$) and 7–10 mm in *M. tomentosa* ($n = 6$). The flowers have five green sepals, five white petals, and numerous stamens, as much as $109,07 \pm 13,3$ ($x \pm SD$, $n = 15$) for *M. rostrata* and $42,08 \pm 6,3$ ($x \pm SD$, $n = 12$) for *M. tomentosa*. Stamens are c. 4 mm long in *M. rostrata* and c. 3 mm long in *M. tomentosa*. Anthers are yellowish with longitudinal dehiscence and pollen shed as free grains. The white styles are c. 5 mm long in *M. rostrata* and 4 mm long in *M. tomentosa*. Stigmatic surface is minute and dry in both species. A short hypanthium tube is present in *M. tomentosa*, but lacking in *M. rostrata*. Nectar production was not observed in either species. The ovaries are bilocular and present four anatropous ovules per ovary in axile placentation in *M. rostrata* ($n = 25$) and *M. tomentosa* ($n = 12$). Embryo structure is of the myrcioid type (sensu CANDOLLE 1828 apud NIC-LUGHADHA & PROENÇA 1996) with leafy cotyledons that are much broader than the hypocotyl.

Anthesis started early in the morning, at 6:00 a.m. for both *M. rostrata* and *M. tomentosa*, and an intense and sweet odour could be quickly noted. Both species had floral anthesis of the 'Myrcia type' (Fig. 3c): all the filaments were curved hiding the anthers when petals opened, the style, in-

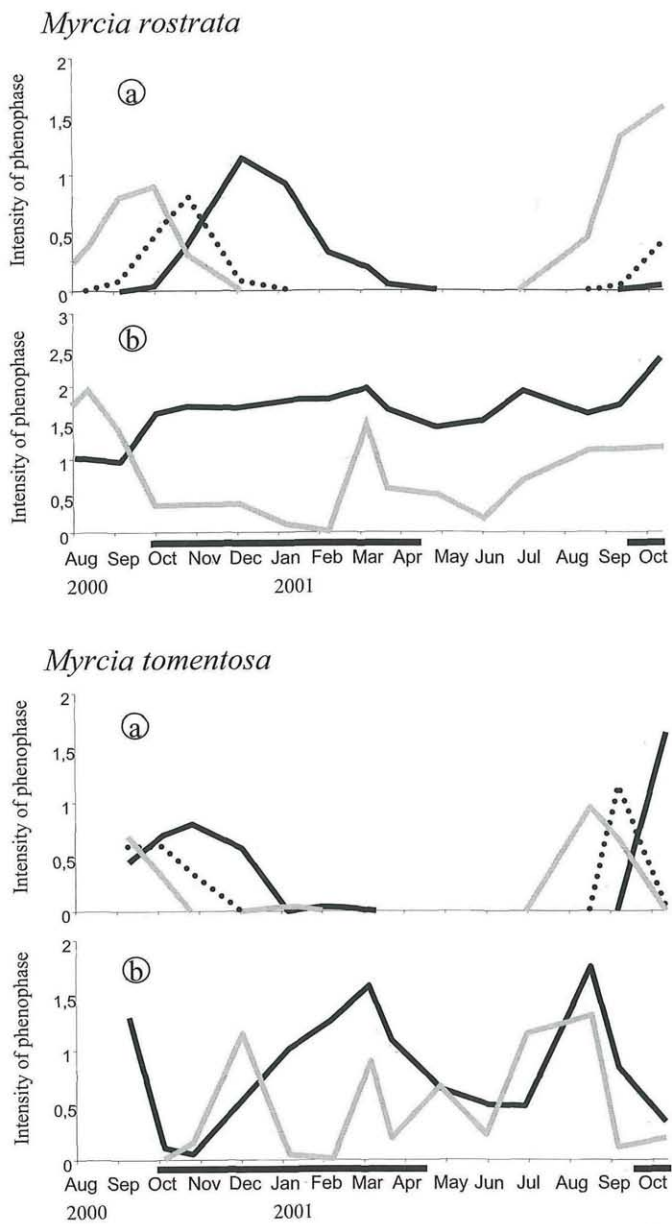


Fig. 2. Phenology of *Myrcia rostrata* and *M. tomentosa* at Panga Ecological Station in 2000 and 2001. a – Reproductive phenology: gray line indicates the presence of floral buds, dotted line indicates open flowers, black line indicates fruits. b – Vegetative phenology: black line indicates new leaves and gray line indicates leaf fall. The black bars below the graphics indicate the rainy period.

initially folded, was usually the first to straighten and protrude above the mass of filaments, which then began to uncurl starting with the outermost whorls (PROENÇA & GIBBS 1994). The unfolding process occurred faster in warmer than in cooler days.

M. rostrata and *M. tomentosa* flowers are functional for two days. The stigmatic surface is receptive for two days after start of anthesis. Petals dropped on the third or the fourth day for both species. *M. rostrata* stamens also dropped on the third or fourth day. However, anthers of *M. tomentosa* usually dropped during the first day of anthesis due to insect movements during the visits. Bagged flowers of these species lost their anthers only on the second day of anthesis. Unsuccessfully and not pollinated flowers dropped about a week after anthesis. Styles may remain until fruits start to develop and sepals are persistent on mature fruits of both species.

Pollen viability was high for *M. rostrata* (98.21 %) and for *M. tomentosa* (78.89 %). These values were used to calculate the average number of viable pollen grains per flower: 69,425 for *M. rostrata* (total pollen per flower: 70,690) and 71,505 for *M. tomentosa* (total pollen per flower: 90,650). Pollen/ovule ratios (sensu CRUDEN 1977) were 16×10^3 for *M. rostrata* and 22.6×10^3 for *M. tomentosa*.

3.3. Floral Visitors

M. rostrata flowers were visited by many bees, cited here in order of frequency. *Scaptotrigona depilis* (MOURE) and *Scaptotrigona polystica* (MOURE) arrived at the flowers just after opening (6:00–6:30 a.m.), with visiting peak from 8:00 to 10:30h and finishing at 11:00h. *Apis mellifera* (L.) was observed from 7:00 to 10:30h with visiting peak from 7:30 to 8:00h (Fig. 3e). *Anthodiocetes megachiloides* (HOLMBERG) was observed from 7:00 to 10:30h and *Augochloropsis* sp. (Fig. 3f), *Thectochlora alaris* (MOORE) and *Dialictus* sp. were rarely observed after 7:30h. Large or medium sized trees of *M. rostrata* with many open flowers received many visitors, while small isolated trees with a few flowers had just a few or no visitors at all. A few unidentified *Diptera* were observed on *M. rostrata* flowers on the first and second day of anthesis consuming pollen grains, in visits that could last for 1.5 minutes.

M. tomentosa flowers were visited and pollinated by bee species cited in order of frequency: individuals of *Trigona hyalinata* (LEPELETIER) (Fig. 3d) and *Scaptotrigona depilis* (MOURE) formed majority of the visitors, observed from start of anthesis (6:00–6:30 a.m.) to 11:00 h, with visiting peak from 8:00 h to 9:30 h. *Apis mellifera* (L.) was a frequent visitor from 7:00 h to 9:30 h. Members of *Megachilinae* visited rarely, after 7:30 h. *M. tomentosa* commonly received up to three *Meliponini* bees per flower at the same time, *Apis mellifera* individuals visited

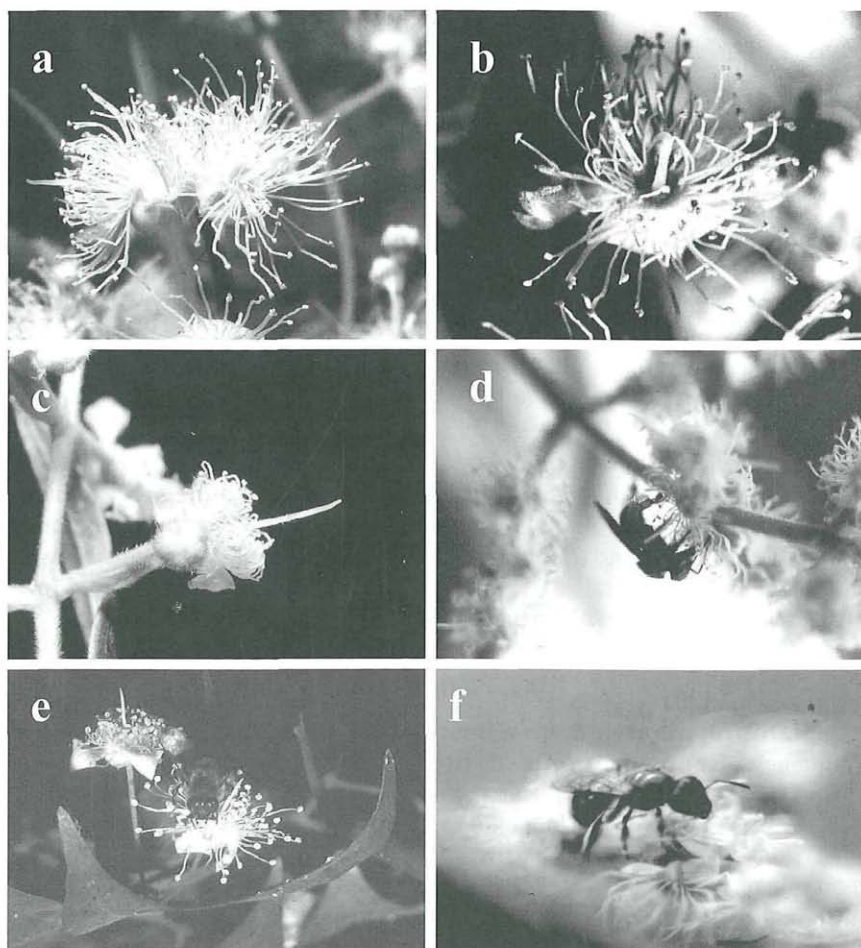


Fig. 3. a – *Myrcia rostrata* flower recently opened. b – *M. tomentosa* flower recently opened. c – *M. rostrata* flower at the beginning of the anthesis process. d – *Trigona hyalinata* collecting pollen in *M. tomentosa*. e – *Apis mellifera* collecting pollen in *M. rostrata* flower with a second day flower nearby. f – *Augochlorini* sp.1 collecting pollen in a *M. rostrata* flower.

these flowers together with Meliponini, but not with other *Apis*. There was no competitive behaviour between different bees at the same *M. tomentosa* flower. Every *M. tomentosa* tree observed, was intensively visited on the two flowering days, independent of the size or the distance of other conspecific flowering individuals.

Bees visiting flowers of *M. rostrata* and *M. tomentosa* collected pollen by gleaning the anthers while walking over the reproductive structures of

many flowers of a few close inflorescences. Individual bees visited some inflorescences on one tree and flew to another tree. Every time these flights could be observed, the bee flew to another conspecific flowering tree, despite of a few other species with possibly melittophilous flowers blooming nearby.

3.4. Breeding System

The controlled pollination treatments characterized *M. rostrata* (Table 1) and *M. tomentosa* (Table 2) as self-compatible species, capable of producing fruits with automatic self-pollination. However, fruit-set was increased by cross-pollination. The indices of self-incompatibility (ISI) calculated for *M. rostrata* (0.307) and for *M. tomentosa* (0.574) are characteristic of facultative autogamous species (sensu BULLOCK 1985). The reproductive efficacy calculated for *M. rostrata* and for *M. tomentosa* was 1.86 and 2.25 respectively.

Table 1.

Fruit-set of *Myrcia rostrata* after different controlled pollination treatments in 1999, 2000 and 2001.

Treatments	Flowers	Fruits	Fruit-set %
Manual self-pollination, 1° day	142	7	4.93
Manual self-pollination, 2° day	13	0	0
Automatic self-pollination	8,377	61	0.73
Manual cross pollination, 1° day	215	33	15.35
Manual cross pollination, 2° day	14	2	14.28
Natural pollination	12,682	3.622	28.56
Apomixis	182	0	0

Table 2.

Fruit-set of *Myrcia tomentosa* after different controlled pollination treatments in 2001. All fruits resulting from the apomixis tests were seedless and probably due to galling process.

Treatments	Flowers	Fruits	Fruit-set %
Manual self-pollination, 1° day	217	20	9.22
Manual self-pollination, 2° day	106	1	0.94
Automatic self-pollination	8,902	493	5.54
Manual cross pollination, 1° day	193	31	16.06
Manual cross pollination, 2° day	102	10	9.80
Natural pollination	11,644	4.219	36.23
Apomixis	150	6	4.00

The pre-emergent reproductive success (PERS) was 7.3 % for *M. rostrata* and 12.7 % for *M. tomentosa* which are within the range found by WIENS & al. 1987 for outbreeding species. PERS and some other reproductive characteristics of the studied species were compared with other *Myrtaceae* from the cerrado biome (Table 3).

Table 3.
Breeding system information for 17 species of *Myrtaceae* in Central Brazil

Species	Plants	Flowers	Fruits	Fruit-set %	SR*	ISI**	PERS***
<i>Eugenia disenterica</i> ¹	2	325	22	6.8	SC	0.83	0.6-4.6
<i>Siphoneugena densiflora</i> ¹	2	244	31	12.7	SI	0	0.8-4.7
<i>Blepharocalyx salicifolius</i> ¹	2	126	9	7.1	SI	0	0.7-7.1
<i>Campomanesia pubescens</i> ¹	6	81	15	18.5	SI	0.09	4.7
<i>Campomanesia velutina</i> ¹	1	122	10	8.2	SI	0	0.3-4.1
<i>Psidium firmum</i> ¹	10	152	67	44.1	SC	1.29	4.6-12.7
<i>Myrcia linearifolia</i> ¹	1	125	17	13.6	SI	0.12	2.3-6.8
<i>Myrcia rhodosepala</i> ¹	5	212	31	14.6	SC	1.24	2.5-7.3
<i>Eugenia ligustrina</i> ²	—	57	27	47.37	SC	0.38	—
<i>Calycorectes psidiiflorus</i> ²	—	53	5	9.43	SC	0.30	—
<i>Eugenia aurata</i> ³	3	50	47	94.0	SC	—	—
<i>Eugenia involucrata</i> ³	8	181	105	58.01	SC	1.687	—
<i>Eugenia punicifolia</i> ³	5	20	14	70.0	SC	0.555	—
<i>Myrcia uveravensis</i> ³	5	205	48	23.41	SC	0.395	—
<i>Myrcia</i> sp. 1 ³	5	86	20	23.25	SC	—	—
<i>Myrcia rostrata</i> ⁴	37	12,682	3,622	28.56	SC	0.307 ^a	7.3
<i>Myrcia tomentosa</i> ⁴	24	11,644	4,219	36.23	SC	0.574	12.7

SR*— reproductive system (SC: self-compatible, SI: self-incompatible); ISI*— index of self-incompatibility (BULLOCK 1985); PERS***— pre-emergent reproductive success (WIENS 1984); ¹ Data from PROENÇA & GIBBS 1994. ² Unpublished data from G. OLIVEIRA. ³ Data from Barbosa 1997. ⁴ This study.

Some seemingly cleistogamous floral buds, which did not open their petals but had an enlarged ovary, occurred in *M. rostrata* (2.07 %; n = 2,802) and *M. tomentosa* (3.62 %; n = 4,809). This false cleistogamy resulted from herbivorous larvae developing inside the pistil (galls) which destroyed the ovary contents completely. This would also explain the few fruits resulting from the apomixis tests for *M. tomentosa* (Table 2).

3.5. Fruits and Seeds of *Myrcia rostrata* and *M. tomentosa*

Mature fruits in *M. rostrata* were black, cylindrical berries of 14 mm length and with a sweetish pulp. Each fruit usually had only one seed (97 %), rarely two (n = 100 fruits from natural pollination, and from different trees). Natural fruit-set was high, an average 28.56 % in 1999, 2000

and 2001. The fruits formed after natural pollination had 18 % of seed herbivory or predation, forming 85 perfect seeds in 100 fruits (20 per tree counted).

M. tomentosa fruits were pubescent, black, globular berries, 9 mm diameter, with a sweetish pulp. Each fruit usually had a single seed (96%), rarely two (2%), three (1%) or four seeds (1%) ($n = 100$ fruits from naturally pollinated flowers and different trees). The fruits formed after natural pollination had 98 % of ovary- or seed-predation, forming only 4 viable seeds in 100 fruits formed after natural pollination (20 per tree counted). Seed or ovary predation also occurred in fruits from previously bagged, manually pollinated flowers (Table 4).

Table 4.

Herbivory in *Myrcia tomentosa* fruits after different controlled pollination treatments. (* floral buds bagged during initial development) .

	Natural pollination N (%)	Cross pollina- tion *	Manual self- pollina- tion *	Automatic self-pollina- tion *	Apomixis *	Herbivored ovaries from floral buds without anthesis
Fruits with larvae	87 (83%)	5 (16%)	3 (30%)	73 (69.5%)	3 (100%)	17 (100%)
Fruits without lar- vae	18 (17%)	26 (84%)	7 (70%)	32 (30.5%)	0	0
Herbivored seeds or ovaries	106 (72%)	5 (12%)	3 (30%)	86 (70%)	3 (100%)	17 (100%)
Perfect seeds	41 (28%)	36 (88%)	7 (70%)	37 (30%)	0	0

The PERS values calculated considering only the number of viable seeds was of 6.1 % for *M. rostrata* and of 3.5 % for *M. tomentosa*. Both species showed, on the same branch, small immature fruits together with fruits that were mature enough to attract frugivorous birds and be dispersed. The seeds of *M. rostrata* and *M. tomentosa* are embedded in a succulent pulp and dispersed mainly by birds. *Tangara cayana*, a frugivorous bird present in the area, was observed eating fruits of *M. tomentosa*.

4. Discussion

4.1. Phenology

Both species had annual and regular flowering periods (cf. NEWSTROM & FRANKIE 1994), blooming every year and roughly at the same period of the year, but their phenological dynamics were different in many aspects.

Reproductive phenology of *M. rostrata* may be characterized as “multiple bang” type (sensu GENTRY 1974) and that of *M. tomentosa* as “pulsed bang” type (sensu PROENÇA & GIBBS 1994). Both terms were used to describe annual, episodic flowering, but PROENÇA & GIBBS 1994 used “pulsed bang” to emphasize a highly synchronized blooming pattern, as observed here for *M. tomentosa*, in contrast to less synchronized and longer episodes usually described for some tropical *Bignoniaceae* and similar to the observed here for *M. rostrata*.

“Multiple bang” flowering (GENTRY 1974), originally defined for *Bignoniaceae* species, has been cited as particularly common in tropical plants. Such plants make use of conspicuous visual and olfactory stimuli to attract pollinators and usually offer no reward. But other species have frequent visitors looking for pollen (GENTRY 1974). Other *Myrtaceae*, such as *Eugenia oerstediana* and *Psidium guineense* (SUAREZ & ESQUIVEL 1987) also show “multiple bang” flowering dynamics.

The “pulsed bang” flowering strategy was described by PROENÇA & GIBBS 1994 to a few other *Myrtaceae*, such as *Myrcia rhodosepala*, *Blepharocalyx salicifolius* and *Eugenia parnahybensis*, all of them with the shorter flowering periods and precise synchronization between individuals of the same population found here for *M. tomentosa*.

Both “multiple bang” and “pulsed bang” flowering dynamics promote visits of opportunistic social and eusocial bees, which are able to recruit many individuals quickly to exploit a very rich food source of short duration. *Vellozia squamata* (*Velloziaceae*), for example, a species with more or less synchronized flowering pulses scattered during the dry season, has large flowers with lots of pollen but was visited and pollinated only by small social bees, which suggests that the large solitary bees, common in the area, were unable to accommodate to the pulsed flowering phenology in this species (OLIVEIRA & al. 1991).

Floral dynamics of *M. rostrata* and *M. tomentosa*, with overlapping flowering periods, but unsynchronized flowering days, may promote a better use of common pollinator service. The existence of some different plant species offering alternative food sources to a guild of visitors, can facilitate their maintenance in the area (NEWSTROM & FRANKIE 1994).

The flowering period of *M. rostrata* and *M. tomentosa* after the first spring rains is similar to that observed by ARANTES & MONTEIRO 2002 for the *Myrtaceae* species of the Panga Ecological Station. The same rain triggering flowering phenology was observed for the *Myrtaceae* in other sites in Central Brazil (KAWASAKI 1989; MORELLATO & al. 1989; PROENÇA & GIBBS 1994). There is some evidence that rainy periods with its associated changing temperatures, followed by some days without rain, can interrupt the water stress and meristematic dormancy (FRANKIE & al. 1974). These rains are considered as important triggers of synchronized flowering in

tropical plants of seasonal areas in general (FRANKIE & al. 1974, OPLER & al. 1976) and for many woody plants in the cerrado biome (OLIVEIRA & GIBBS 2000). The flowering periods of *Myrtaceae* species in the Panga Ecological Station can be characterized as aggregated. Similar aggregated flowering was observed in the forest of Chiloé island (Chile), where the *Myrtaceae* flowering dynamics indicated the use of the same pollination guild on alternating days of the same period (SMITH-RAMÍREZ & al. 1998). KOCHMER & HANDEL 1986 used the term “phylogenetical inertia” to identify a group of genetically determined physiological mechanisms, found in phylogenetically related species within a family. This hypothesis is consistent with the fact that there are overlapping flowering periods in many species of *Myrtaceae* (SMITH-RAMÍREZ & al. 1998). The synchronization of flowering periods permits to offer a continuous food source to floral visitors, which can improve visiting and pollinization rates (OPLER & al. 1976). Non-coincidental days of anthesis for each species indicate an adaptation to avoid interspecific pollination (RATHCKE 1983, WASER 1978). Less overlapping sequential flowering periods, as observed in *Myrtaceae* family, can be considered as a consequence of evolutionary selective pressures to reduce species competition for pollinator services in a guild of plants (OPLER & al. 1976, STILES 1985). Differential sensibility to changes of climate conditions due to the first spring rains and different time interval from quiescent buds to anthesis, may explain overlapping flowering periods which avoid same day flowering in the two species.

The fruit-set period is less aggregated than the flowering one in the *Myrtaceae* species. The extended fructification pattern of *Myrtaceae* may be a consequence of indirect variables in morphology, size and ripening time from many species and from interactions with disperser animals during the year (SMITH-RAMÍREZ & al. 1998). Vegetative phenology in both species was typical of evergreen species (OLIVEIRA 1998), with continuous leaf production throughout the year occurring only to *M. rostrata*, and *M. tomentosa* presenting irregular peaks of leaf production.

4.2. Floral Biology and Pollinators

M. rostrata and *M. tomentosa* have short-lived, small, hermaphrodite flowers, with radial symmetry, a punctiform stigma, onset of anthesis in the early morning, a sweetish odour, and pollen as the sole reward, characteristics that are common in the melittophilous species of the subfamily *Myrtoideae* (NIC-LUGHADHA & PROENÇA 1996, LANDRUM & KAWASAKI 1997).

Bee pollination is predominant in the cerrado biome and Neotropical forests (OLIVEIRA & GIBBS 2000). But in the cerrado there are few specific plant-pollinator relationships, most of them are between plant guilds, with flowers which are morphologically and functionally able to offer resources to a group of pollinators (OLIVEIRA & GIBBS 2000). OLIVEIRA & GIBBS 2000

observed that plants with small, unspecialized flowers were pollinated by a guild formed by bees, wasps and Diptera (flies). This group of pollinators is similar to that observed on *M. rostrata* and *M. tomentosa* at Panga Ecological Station.

In the *Myrtaceae*, pollination is effected mainly by bees (PROENÇA & GIBBS 1994, NIC-LUGHADHA & PROENÇA 1996, TOREZAN-SILINGARDI & DEL-CLARO 1998), but in a number of other species the pollinators can be birds (CROME & IRVINE 1986, HOPPER 1980), lizards (WHITAKER 1987) or bats (CROME & IRVINE 1986, HOPPER 1980).

The behaviour of *M. rostrata* and *M. tomentosa* floral visitors while collecting pollen consecutively on flowers of the same inflorescence, and on other inflorescences of the same tree, promotes mainly geitonogamy. Outcrossing is favored by the large number of anthers and pollen grains. Pollen/ovule ratios (cf. CRUDEN 1977) of *M. rostrata* and *M. tomentosa* are typical for strictly allogamous species. Bees such as Halictidae, Apis, Scaptotrigona and Trigona, pollinators of *M. rostrata* and *M. tomentosa* (except Halictidae bees for *M. tomentosa*), also pollinate some other gallery forest species. All the cited bees walk over the reproductive parts of the flower. *Myrciaria dubia* also was pollinated by Meliponini bees (PETERS & VASQUEZ 1987). Trigona bees visited *Blepharocalyx salicifolius*, *Eugenia dysenterica*, *Myrcia linearifolia* and *M. rhodosepala* in cerrado, but PROENÇA & GIBBS 1994 suggested detailed observations to define which of them were the pollinators. In the same cerrado area near Brasília, OLIVEIRA & GIBBS 2000 observed Trigona cupira, T. branneri, T. postica, Bombus atratus and B. morio visiting *Blepharocalyx salicifolius* and noted that small social bees had homogenous pollen loads with just one type of pollen. This suggest that small bees visit just one plant species each time, and may be much more faithful pollinators than large and medium sized bees.

M. tomentosa presents a hypanthium tube or hypanthial cup (sensu NIC-LUGHADHA & PROENÇA 1996) prolonged beyond the ovary, and longitudinally dehiscent anthers. Some *Myrtaceae* species like *Myrcia rhodosepala*, *Siphoneugena densiflora* and *Blepharocalyx salicifolius* which have the hypanthial cup and "staminal display", are buzz pollinated (PROENÇA 1992). However, the main visitors of *M. tomentosa* are eusocial bees as Apis and Trigona, which usually are unable to vibrate flowers, collecting pollen mainly by gleaning the anthers (PROENÇA 1992).

4.3. Breeding Systems

M. rostrata and *M. tomentosa* are self-compatible species, with higher fruit production after cross pollination, a characteristic of facultative allogamy. The auto-incompatibility index (sensu BULLOCK 1985) from *M. rostrata* (0.307) and from *M. tomentosa* (0.574) indicate facultative auto-

gamy and are near to that found for many other cerrado *Myrtaceae* (PROENÇA & GIBBS 1994, BARBOSA 1997, TOREZAN-SILINGARDI & DEL-CLARO 1998). Although some authors consider that there are more xenogamous species in the *Myrtaceae* (BEARDSELL & al 1993), the extensive surveys by NIC-LUGHADHA & PROENÇA 1996 showed that there are as many facultatively autogamous as allogamous species in the subfamily *Myrtoideae*.

Although carmine staining overestimates pollen viability, the quantity of viable pollen grains per flower was very high (69.425 pollen grains in *M. rostrata* and 71.505 pollen grains in *M. tomentosa*). The great number of pollen grains and the very few ovules of *M. rostrata* and *M. tomentosa* (just 4 ovules) resulted in high values of pollen/ovule ratios (CRUDEN 1977) (16,000 and 22,600 pollen grains per ovule respectively), indicating preferential outbreeding.

The fact that fruit-set following natural pollination is higher than fruit-set after manual cross-pollination indicates that *M. rostrata* and *M. tomentosa* are being adequately pollinated at Panga Ecological Station. The mean reproductive efficacy of Cerrado woody species is 0.51 (OLIVEIRA & GIBBS 2000). The values calculated for the studied species (respectively 1.86 and 2.25) may also suggest that hand cross-pollination of small flowers with a single, minute stigma, is not as efficient as bee pollination, and can also damage the flowers.

The pre-emergent reproductive success of *M. rostrata* and *M. tomentosa* (7.3 and 12.7 respectively) is similar to the values found by PROENÇA & GIBBS 1994 in some *Myrtaceae* from cerrado, and characterize them as obligatory outbreeding species. PERS defined by WIENS & al. 1987 suggests values near 22 % for outbreeding species and 90 % for inbreeding species. These authors conceive PERS as a measure of the selective forces acting on embryo's phenotype during its development. Allogamous species lose proportionally more genetically heterozygotic offspring during the pre-emerging phase of life cycle than in the post-emerging phase (NIC-LUGHADHA 1998).

Both species had fruit predation due to larval development inside the pistil, but it was more intense in *M. tomentosa*, even in floral buds bagged early, during their initial development, suggesting that oviposition occurred on very young floral buds. The PERS values calculated with non-predated fruits of *M. rostrata* and *M. tomentosa* (6.1 and 3.5 respectively), were lower than the PERS values calculated considering the total number of fruits (7.3 and 12.7 respectively) and indicate that predation of pistils in *M. tomentosa* affects the fruit-set seriously.

The *Myrtaceae* subfamily *Myrtoideae* has a great number of species well distributed all over tropical America, in environments with varied climatic, edaphic and other local conditions. The generalist flowers of *M. rostrata* and *M. tomentosa* can be visited by a guild of generalist visitors

and pollinators and are capable of inbreeding. Their zoochoric fruits are food sources for not only birds and mammals, but also for insects. *M. ros-trata* and *M. tomentosa* individuals can grow in several plant formations as cerrado s. str., cerradão, forests and forest borders (ARANTES & MONTEIRO 2002). This ability and their generalist reproductive features suggest they may be interesting species for the regeneration of disturbed areas but the intense fruit predation in *M. tomentosa* indicates that seed production and use may be problematic in this species.

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Eugenio Alves Macedo

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