Reproductive biology of *Jacaranda ulei* Bureau & K. Schum. (Bignoniaceae)

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Abstract. Phenological events and floral biology of *Jacaranda ulei* were studied. After the first rains, new branches, leaves and flowers are produced. The flowering period lasts for almost three months; a great amount of flowers is produced; nectar is abundant. It was identified 15 species of bees visiting the plants, also ants, butterflies and hummingbirds. The flowers, fruits and seeds suffered from predatism and fungus parasitism, but the leaves remained intact. The species is strongly self-incompatible. 30% of the flowers from manually crossed pollination developed into fruits against only 10% of the naturally pollinated ones. In either case, seed germination was above 80%, requiring only humidity and room temperature. The necessity of having compatible individuals should be taken into consideration for cultivating this plant in gardens or herbalists.
Key words: Cerrado, conservation, medicinal plant, savannah, drought.

Resumo. Foram estudados eventos fenológicos e biologia floral de *Jacaranda ulei*. Após as primeiras chuvas, surgem novos ramos, folhas e flores. O período de floração dura quase três meses; produz-se uma grande quantidade de flores; o néctar é abundante. Foram identificadas 15 espécies de abelhas visitando as plantas, além de formigas, borboletas e beija-flores. As flores, frutos e sementes sofreram predatismo e parasitismo fúngico, mas as folhas permaneceram intactas. A espécie é fortemente autoincompatível. 30% das flores provenientes da polinização cruzada manual desenvolveram-se em frutos contra apenas 10% das polinizadas naturalmente. Em ambos os casos, a germinação das sementes foi superior a 80%, necessitando apenas de umidade e temperatura ambiente. A necessidade de indivíduos compatíveis deve ser levada em consideração no cultivo desta planta em jardins ou fitoterapeutas.
Palavras-chave: Cerrado, conservação, planta medicinal, cerrado, seca.

The genus *Jacaranda* Juss comprises of shrubs and big trees, being native to the Neotropical flora. In Cerrado biome, there are several shrubby species, such as *J. ulei* Bureau & K. Schum., *J. decurrens* Cham., *J. caroba* (Vell.) DC., *J. paucifoliolata* Mart. ex DC., *J. puberula* Cham., *J. racemosa* Cham., *J. rufa* Silva Manso. For morphological description and images of those species, consult Lohmann and Pirani 1996, Gentry 1992, Ribeiro 2003, Guimarães et al. 2008, Costa et al., 2011.

Due to the medicinal and ornamental interest of this common shrub (Duringan et al. 2002, Felfili and Fagg 2007, Fank-de-Carvalho et al. 2008, Silva and Felfili 2009, Gachet and Schühly 2009, Nunes et al. 2020), several studies have been carried out, aiming for botanical comprehension and cultivation: Miranda et al. (2018) studied the anatomy of wood and bark of stem, root and xylopodium; Silveira et al. (2013, 2018) developed techniques of micropropagation.

To be domesticated and cultivated in a broader scale, it is important to know the reproductive strategies, in order to produce viable seeds. Among *Jacaranda* species, the seeds often germinate at percentages above 65%, requiring only humidity and favorable temperature (Ribeiro and Borghetti 2014, Lunkes and Franco 2015). Germination data and pictures about *Jacaranda ulei* can be found at

Silveira et al. (2013). Anyway, obtainance of seeds may be complex, since the Bignoniaceae family is marked by floral self-incompatibility (Gandolphi and Bittencourt 2010). Regarding other species from *Jacaranda* genus, floral self-incompatibility was recorded for *J. racemosa* (Bittencourt and Semir 2006), *J. copaia* (Gurgel et al. 2006, Jones and Hubbell 2006, Maues et al. 2008), *J. rugosa* (Milet-Pinheiro & Schlindwen 2009), *J. mimosifolia* (Alves et al. 2010, Bittencourt 2019), *J. oxyphylla* (Guimarães et al. 2018), *J. rugosa* (Pontes et al. 2022), while *J. caroba* showed some floral self-compatibility at a range of about 3% of self-pollinated flowers growing into mature fruits (Yanagizawa 1983, Guimarães et al. 2008). The extension of floral self-incompatibility has not been recorded to *Jacaranda ulei*.

The present paper studies the breeding system of *J. ulei* as well the role and diversity of the visiting pollinators.

Methods

Study site

The plants were sampled at the forest reserve of Embrapa Cerrado and the forest reserves of University of Brasília: Agua Limpa Farm (15° 56′ to 15°59′S and 47°55′ to 47°58′ W), Olympic Center (15°46′S – 47⁰ 50′W and 15° 45′S - 47° 51′W) and Biological Station. Floristic, edaphic and phytosociological studies of those regions can be found at Eiten 1984, Fiedler et al. 2004, Assunção and Felfili 2004, Silva and Felfili 2009. Agua Limpa Farm is a unity of conservation; the Cerrado areas of Olympic Center and of Biological Station are contiguous, placed on the margins of Lake Paranoa and are moderately anthropized, but they are close to the botanical laboratories, which facilitates some observations. Agua Limpa Farm is approximately 20 km distant hence being under the same climatic variations. Briefly, important features regarding the present study are: the soil is Red Latosoil, with deep (>1m depth) water reservoirs all year long; the climate is Cwa at Koppen´s classification: there is a rainy season from September to April with an annual rainfall of about 1,500 mm and a dry season from May to August. The temperatures lower down on May and June and from July to September the combination of hotter temperatures (mean of 35°C at midday) with drought brings common natural fires to the vegetation. In the open phytophysiognomies of

Cerrado where *Jacaranda ulei* commonly occurrs, glebes were marked, in which 810 plants were identified, from which the samples were taken.

Phenological monitoring

All marked plants were observed regarding phenophases and of parasite attack when it was the case. At Agua Limpa Farm, 148 plants were marked and used in the floral experiments. Additionally, 53 plants from the Biological Station and 30 plants from the Olympic Center were observed regarding phenological events, as to complement data published by Nunes et al. (2020). Voucher specimens were deposited at the Herbarium UB under the number of collector: Ribeiro (11.696 to 11.710) and Miranda TD (06 to 10).

The observations regarding phenology and the reproductive experiments were carried out for two consecutive years. The phenological events were weekly observed on 28 plants for the phenophase of: sprouting new shoots and leaves, of flowers, of fruits and finally leaf shedding, in a descriptive way of presence/absence of a given feature according Fournier (1974).

Floral biology

The anthesis was monitored in 165 flowers from 15 plants. The floral buds were bagged and then harvested throughout the day as the flower development occurred.

The volume of nectar was measured with a tiny needle in a syringe of 1 mL divided into 100 units. The concentration of sugars in the nectar was measured in a portable refractometer ATAGO N1®. In the total, 27 flowers were monitored regarding nectar, in between 07:00 and 07:30; 10:30 and 11:30; 13:30 and 14:30; 16:00 and 18:00. Nectar was harvested daily until the floral abscision.

Pollination tests were carried out for self and crossed pollination at Agua Limpa Farm. As control, 18 plants were marked. Manual crossed pollination was done in 16 plants of at least 90 m distant one from each other, totalling 2604 flowers. The floral buds were bagged in pre-anthesis and in the following day, with floral opening, the anthers were removed and stored in fridge and the flowers were bagged again. In the following day, the pollen grains were deposited in a model of web, that is, one plant could have given pollen to

many others and, inversely, one plant could have received pollen from more than one.

Manual self-pollination (geitonogamy) was carried out in 18 plants, totalling 304 flowers. The inflorescences were bagged in pre-anthesis and the next day, with flower opening, pollen from one flower was deposited in other flowers of the same individual. For spontaneous self-pollination, the inflorescences of 18 plants, totalling 1235 flowers, were bagged until the abscision of the corolla.

The growth of pollinic tubes were observed after 10, 24, 48, 72 and 96 hours from pollination in manually crossed or self-pollinated flowers. The floral samples were immersed in ethanol 70° GL, clarified in NaOH 8M solution for 15 min in a stove of 60 °C, stained with aniline blue 0.015% and observed under a microscope of fluorescence according Martin (1959). The stigmatic receptivity was observed in flower buds and after anthesis: the flowers (n=70) were kept in Petri dishes with agar-water. Pollen of the same flower and of different plants were deposited in the stigmatic responses were observerd in a magnifying glass.

Pollen viability and the number of pollen grains and ovules were measured in 10 flowers (20 anthers and 10 ovaries) from buds at pre-anthesis using Alexsander´s stain, clarification in NaOH 8M and observed under magnifying glass, according Martin (1959) and Cruden (1977).

After fruit ripening, 100 healthy seeds of each treatment (manual pollination and natural pollination) were sampled and put to germinate in Petri dishes with moist paper at a germination chamber with temperatures between 20 °C and 25 °C, with a photoperiod of 12/12 hours. Germination was documented daily until the 8th day, when then the observations were carried out on alternate days. After the appearance of the radicle, the germinated seeds were transferred for further cultivation.

Statistical tests with Student´s T-test were carried out with the aim of Excel® software.

Floral visitors

The floral visitors were followed at Agua Limpa Farm throughout all the flowering period from midnight to 19:30, being classified as: very frequent (6 to 8 visits per day); frequent (3 to 5 visits per day) or sporadic. In the total, 6 plants during the peak of the floral production, on October, were monitored regarding the visitors during 5 days at each year. The invertebrates were collected with an entomological net, bagged and conserved for identification (see acknowledgments). The vertebrates were photographed with common manual digital cameras at the moments they were seen.

Results

Phenological events

Loss of leaves (deciduity) occurred around 2-3 weeks in the months of July and August, the drier period. Not all plants lost the leaves; some showed green leaves, some others just a few leaves and others showed complete deciduity. Therefore, the species is brevideciduous according the classification of Silva et al. (2021). However, all the branches that still beared fruits at that time lost all the leaves and did not re-sprout anymore. At the end of the dry season (end of August and beginning of September), new leaves sprouted, even before the first rains. In the burned places, new branches appeared right before and/or after the first rains of the rainy season. The new branches flowered only in the next year, that is, the branches produce flowers only after at least one year of growth (Table 1).

The inflorescences developed together with the increase in leaf density of the whole plant. The inflorescences developed in the apical bud, so that each branch flowered only once. Among the observed plants, flowers were seen from August to November, so that the flower period is long, of about 16 weeks. The peak of flowers occurred in October, when 90 plants (about 60% of the sample) were flowering.

The complete period of flowering lasted for 18 days on average, but some plants had flowered for about 40 days. The flowers were produced in a large amount, with daily opening of a significant number of flowers, in a sequence from the center to the extremities of each co-florescence. Taking the inflorescence as a whole, the co-florescences opened randomly, that is, apical co-florescences could open before the central ones. In the first 9 to 10 days, the opening of new flowers improved daily. After that, the daily production of new flowers decreased slowly. The flowers opened in both sunny and rainy days. Each plant produced from 1 to 7 inflorescences, in a total of 23 to 650 flowers per plant (average of 336 flowers). One plant produced only three flowers, visibly sick and attacked by parasites.

Fruitification occurred simultaneously to flowering. The first signs of fruitification (fall of the corolla and swelling of the ovary) appeared from 8 to 20 days after anthesis. After the fruits had reached their maximal size, it took about 20 to 40 days to mature and open, changing color from green to brown and dispersing the winged seeds. Most of the fruits opened at the end of the rainy season (April/May), but several plants still showed maturing fruits in the dry season (July/August). As the fruits get mature, the leaves of the fruiting branches start to show senescence, changing color to yellow and slowly falling. In the non-fruiting branches, the leaves remain green or, in some plants, are lost in the peak of the dry season. Table 1 summarizes the phenological events as observed.

Reproductive biology

The type of aestivation is of kind cochleate (Figure 1). Anthesis happened between 03:30 and 10:30, but mostly after dayrise, either on sunny and on rainy days. In a given plant, 90% of the daily opened flowers were sinchronic; the remnant 10% opened slowly throughout the morning. The flowers remained showy for about 48 h, but some continued for 4 days.

Nectar was not seen in flower buds, but started to be detected about 2 h after anthesis, with peak of production after between 4 to 5 hours of anthesis. Initially, nectar was just a moist over the basis of the corolla, but at the peak of the production it covered the nectary and part of the ovary. When the flowers had not been visited by pollinators, in the following day nectar flowed from the corolla.
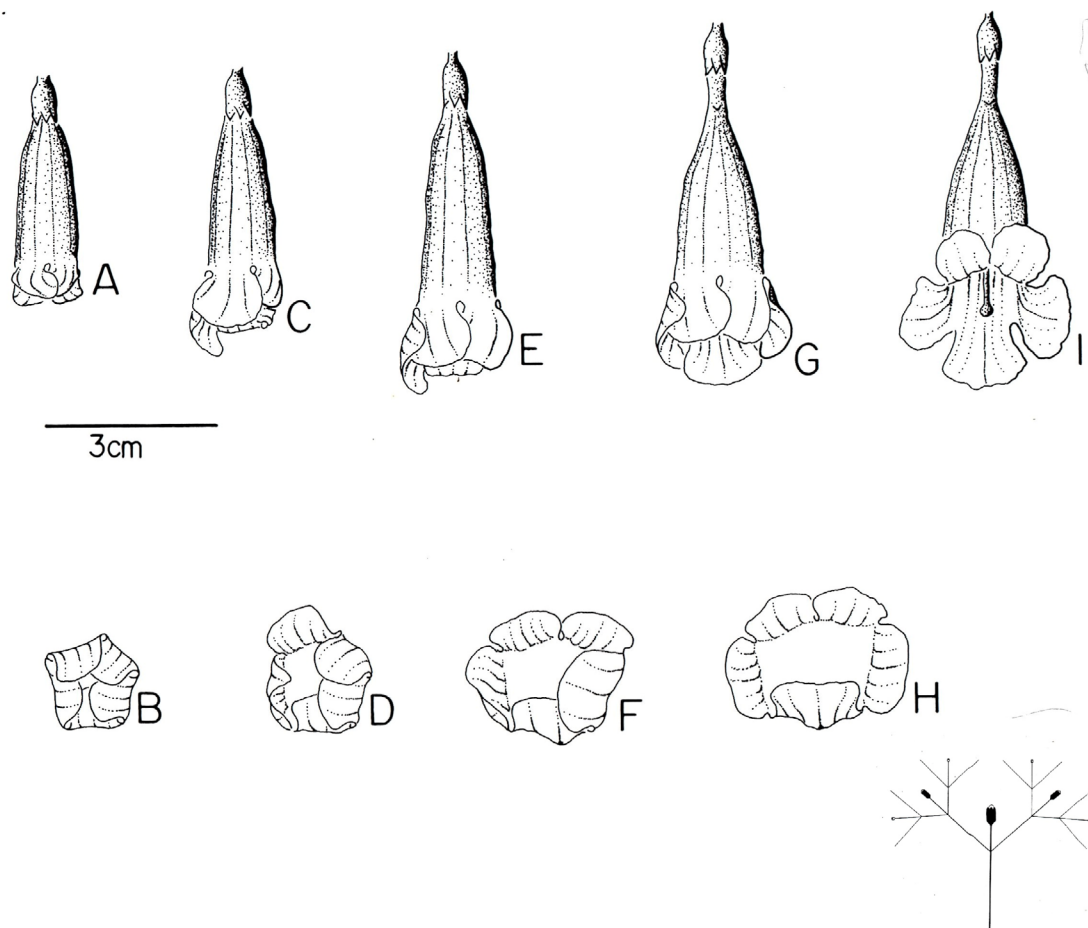

Figure 1. Stages of flower opening (anthesis) of *Jacaranda ulei*: (A and B) Flower bud in pre-anthesis (03:00); (C and D) beginning of anthesis with the superior lobes of the corolla semi-distended (03:35); (E and F) semi-distension of the lateral lobes of the corolla (03:55); (G and H) semi-distension of the inferior lobe of the corolla showing a funnel-like shape of the flower (04:20); (I) complete distention of all the lobes of the corolla, exposing the vegetative and reproductive structures (04:55). In the inferior-right detail: diagram of the inflorescence. Each co-florescence opens randomly, but inside it the inferior flowers open before the apical ones.

Figure 2. Inflorescences of J*acaranda ulei* attacked by fungus from the genus *Alternaria*. At the bottom: an overview of the whole plant attacked. At the top: detail of the flowers attacked. The leaves remained apparently healthy.

The mean concentrations of sugars were lower in the newly opened flowers on rainy days (15%), increasing at the first day (20%) and peaking at the se cond day (32%). In the flowers that remained opened after the second day, concentration of sugars was about 30%. In rainy days, the nectar from two-day old flowers tended to be diluted– mean of 25% of sugars. Each flower yielded about 4 µL of nectar during its life.

Some plants produced witish flowers, with corrugate and infertile corollas, indicating attack of pathogens. Predation signs were seen in flowers, buds, fruits and seeds. Fungus from the genus *Alternaria* were associated with floral malformation and signs of necrotic dots (Figure 2). Some flowers and fruits showed punctiform lesions, typically provoked by coleopters, but such insects could not be colected. Some fruits were strongly attacked, but complete predation of the fruit was not seen (Figure 3).

Each anther produced from 2,096 to 3,500 pollen grains (mean of 2,978; hence 8,384 to 14,000 pollen grains per flower), which changed in color from transparent to beige as the flowers opened. The pollen viability was estimated in more than 98%, as Alexsander´s staining showed them purple, while the inviable pollen grains remained witish. Each ovary showed 48 to 102 ovules, hence the mean ratio of 162 pollen grains to each ovule.

Either in crossed or self-pollination, after anthesis, as soon as pollen was deposited, the stigmas closed in between 30 to 180 seconds, being slower in the colder/rainier days. Also, the stigmas closed after a slight touch, which somehow had to be overcome for the pollination experiments. The application of pollen provoked such stigmatic reaction either in freshly opened or in senescent flowers, but did not provoke any reaction in the pre-anthesis floral buds. Either in crossed or self-pollination, there was growth and development of pollinic tubes, penetrating the ovule micropyle (Figure 4). The pollinic tubes reached the ovule micropyles within 24 hours after the deposition on the stigma.

No fruit was formed with manual or induced self-pollination. The species is strongly self-incompatible and xenogamic (Table 2). In the self-pollinated flowers, abscission of the ovaries occurred after 4 to 5 days. In the crossed-pollinated flowers there was also a massive abscission of the fruits, but that started later, around 10 to 15 days after pollination and lasted for about 45 days. After then, the fruits evolved to maturation, although suffered from predatism. In total, 30% of the manually crossed pollinated flowers evolved to mature fruits, while in the control group (naturally pollinated) only 10% of the flowers originated fruits. Each plant produced from zero to 16 fruits (mean of 10 fruits per plant). Some plants did not fruit in the first year of observation, but did in the second one and vice-versa.

Each mature fruit produced 18 to 92 seeds (mean of 60 seeds). About 60% of the seeds were apparently healthy; 5% were malformed and 35% showed signs of predatism and parasitism. There were no differences in the germination rate between healthy seeds obtained from natural or manually crossed pollination. In both groups, about 78% of germination was recorded. Germination started after 8 days of imbibition and after 34 days no more seeds germinated.

Floral visitors

The flowers were visited by 15 different species of insects of the orders Hymenoptera, Lepidoptera, Coleoptera and Mantodea (Table 3) and by hummingbirds, but spite the nocturnal monitoring, no bats were seen.

Visits to the flowers started around 08:30 and ended around 18:00, becoming more intense as the day went hotter, between 10:30 and 15:30. At sunset, very few visitors were seen. In the rainy or cloudy days, the visits were sporadic.

In a given plant, the presence of more than one individual of the same species of insect was registered, but not the visit by two different orders at the same time. The bee *Trigona spinipes* Fabr. was more frequently collected in the morning, while *Apis mellifera* L. could be seen all day long. The bees of the genus *Augochloropsis* Cockerell were more commonly collected between 11:20 and 15:30. The other insects were harvested either at dawn and/or twilight. The bees visited the flowers with nectar, either the recently opened ones or the older (3-4 day-old) ones, but they did not visit senescent flowers. Almost all of the bees flew in a clockwise sense as they approached to an inflorescence.

The bees of the genus *Trigona* Jurine, *Augochloropsis* Cockerell, *Apis* L., *Epicharis* Klug and *Bombus* Latreille were considered as pollinators because they systematically touched the anthers and the stigmas of the visited flowers. The bees from the tribe Eucerini and from the genus *Ceratina* Latreille, *Oxaea* Klug, *Paratrigona* Schwarz and *Scaptotrigona* Moure were considered as occasional pollinators because, although they searched for nectar in the outside, they often harvested pollen from inside the flower. The bee from the genus *Xylocopa* Latreille, the moth *Aguna albistria albistria* Plotz and the butterfly *Michaelus thordesa* were considered as cheaters because they only touched the flowers from the external side, never touching the anthers or stigmas. The role of the hummingbirds to the pollination was not clear because not all plants were visited by them during the observation period, so that the visits were only of some flowers of the same individual. The insect praying mantis (order Mantodea) was collected, but it eats other insects. Ants were seen walking by the whole plants and although visited the flowers (probably sipping nectar), they were not seen harvesting leaves nor floral parts.

Discussion

According to Stevens (1994), half of the aerial biomass of *J. ulei* is of flowers. At the same time the flowers attract many visitors, the leaves are very repulsive to them, as they are hard, densely hairy and with a great amount of glandular trichomes (Ogundipe and Wujek 2004). Indeed, larvae of lepidopters often eat leaves, and although lepidopters visited the flowers, no larvae were seen eating the leaves, on the contrary to other Cerrado species such as *Smilax goyazana* A. DC., whose leaves serve as food to insect larvae (Palhares et al. 2009). Moreover, Silva (2011) described larvae of butterfly Michaelus thordesa living in inflorescences of *J. ulei*, but not on the leaves.

Floral self-incompatibility has been described since Köelreuter (1761). Floral self-incompatibility has been understood as a strategy for a higher genetical diversity. Indeed, Jones et al. (2005); Jones and Hubbel (2006) have documented a high genetic variability in the wild population of *Jacaranda copaia*. However, the floral self-incompatibility requires that the species are present in a minimal frequency, below which crossed pollination is unlikely to occur. Also, that the flowers have to present strong mechanisms for attracting pollinators, hence the large production of flowers and nectar in *J. ulei*.

Table 1: summary of the phenological events.

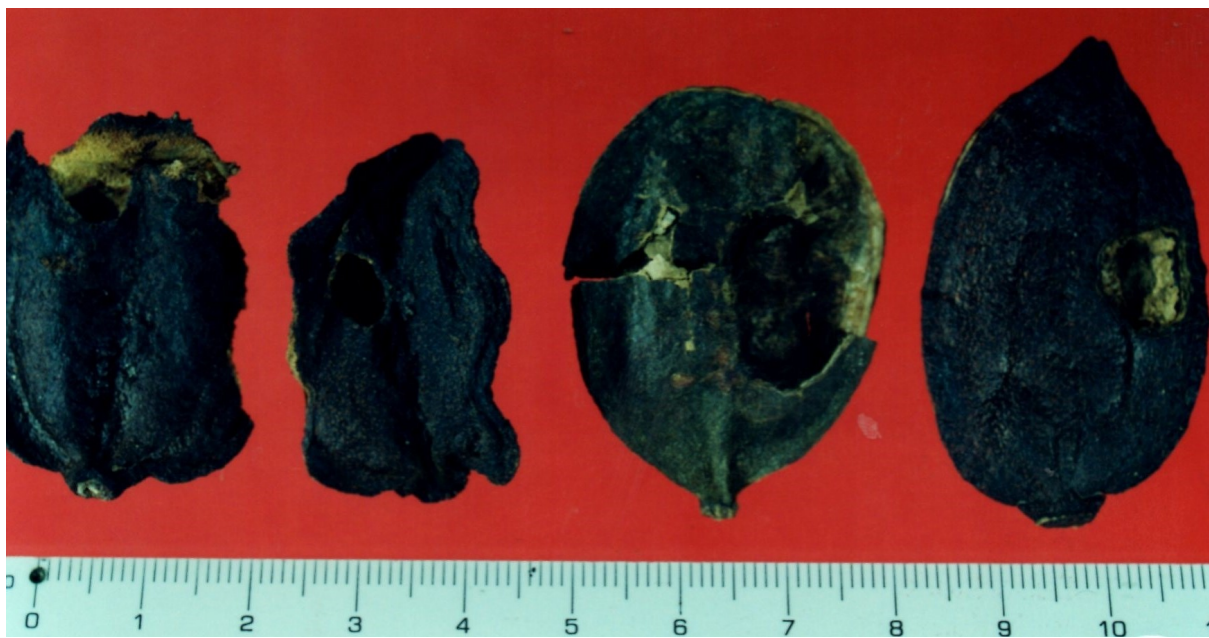|	September	October	November	December-March	April-June	July-August
Deciduity	-	-	-	-	+	+
Sprouting of new shoots	+	+	-	-	-	+/- (some)
Flowers	+	+	+	+/- (some)	-	+/- (some)
Fruits	+/- (some)	+	+	+/-(some)	+/-(some)	-
Seed dispersal	-	-	-	-	+	+/-(some)

Figure 3. Fruits of *Jacaranda ulei* strongly attacked by predators. The complete predation of the fruit was not observed.

Some degree of floral self-incompatibility has been described in almost half of the Angiosperm species (Gibbs 2014). Floral self-incompatibility may be precocious, when the growth of pollinic tube is inhibited (Sousa et al. 2016), or late, by the blockage of ovule fecundation, abscission of fruits or atrophy of the seeds (Gandolphi and Bittencourt 2010, Alves et al. 2019). In *J. racemosa*, self-pollination gives origin to embryo and endosperm, but it also induces the abscission of the fruit, being a model to what happens to other species of the genus (Bittencourt and Semir 2006). Also, sensitive stigmata, such as the ones of *J. ulei*, has been observed in the order Lamiales – families Bignoniaceae, Lentibulariaceae, Martyniaceae, Scrophulariaceae – and is related to floral self-incompatibility in the species presenting them (Milet-Pinheiro et al. 2009).

Notwithstanding, Lloyd (1979), Stephenson (1980), Webb and Lloyd (1986), Lloyd and Webb (1986) state that abscission of flowers and young fruits is common in all plants, but in species where fruit abscission is frequent, often the fruits grow slowly in the initial development and also require a relatively long time for maturation, such as observed in *J. ulei*.

The gap between fruit formation via controlled crossed pollination and natural pollination has been observed in other self-incompatible species (Maues et al. 2008, Gandolphi and Bittencourt 2010). It is possible that in natural pollination there may be some degree of self-pollination: the pollinator, when visiting the flowers, could provoke geitonogamy, which, in association with the fast stigmatic closure, would prevent that pollen from other individuals reach those flowers, hence inducing the abscission of young fruits.

In species with late self-incompatibility, it has been identified clusters of genetical loci of 4 to 20 alleles or more, in which there are systems of self-recognition. So, depending on the amount of homozigotic alleles, there is the expression of proteins that signalize to fruit abscission and/or seed atrophy (Scopece et al. 2010, Caruso et al. 2012). So, the high proportion of fruit abscission seen in *J. ulei* points out that it is necessary heterozigosis of several alleles as to allow fruit maturation. It is possible that the expression of those genes occur within 45 days, since after that period no fruit abscission was observed. Anyway, Chauan et al. (1987) succeeded in obtaining fruits in *J. mimosifolia* with daily application of gibberelic acid (GA3 50 ppm) on the flowers 5 days after anthesis, showing that this process may controlled by external phytoregulators.

Once reaching fruit maturity, in Bignoniaceae family it is common that the seeds present high germinability and without dormancy (Stephenson 1980, Bertin 1982, Gobatto-Rodrigues and Stort 1992, Barros 2001, Gurgel et al. 2006).
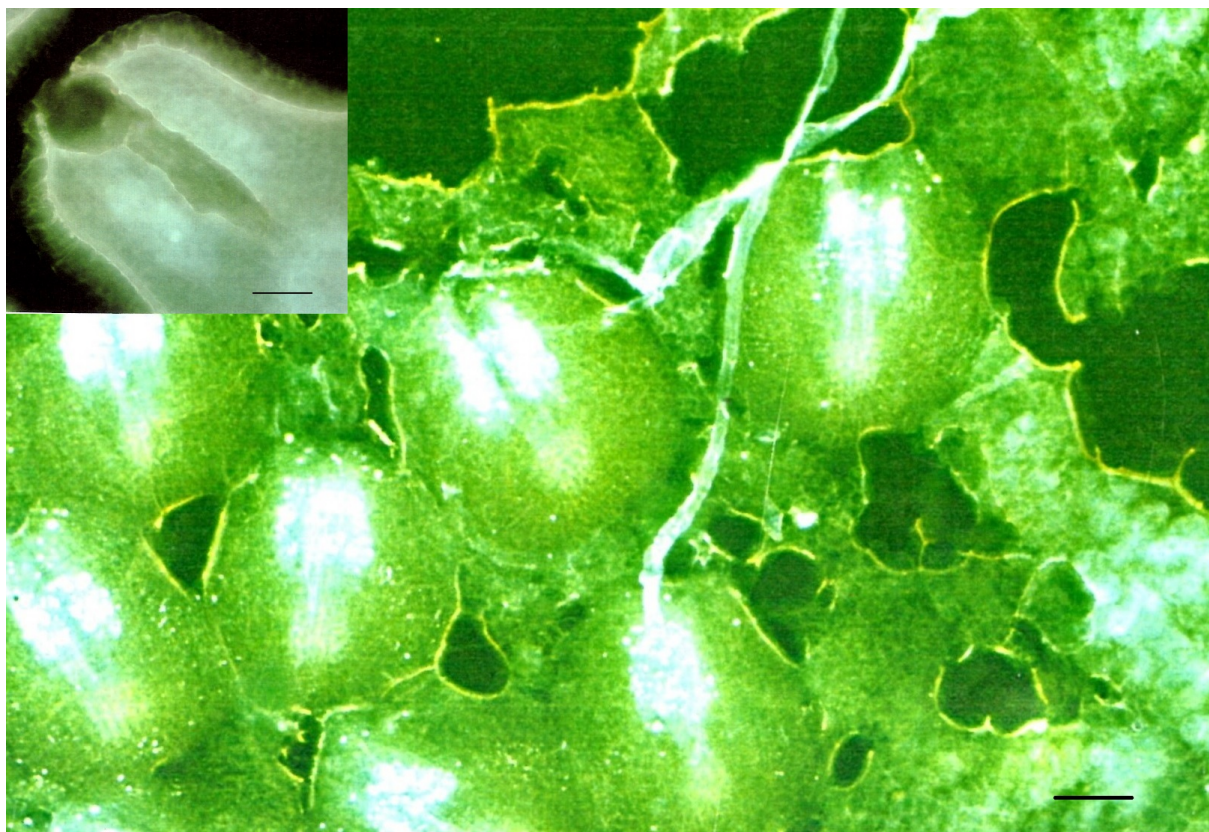
Figure 4. Microscopy of fluorescence in self-pollinated flowers after 24 hours from pollination, showing pollinic tubes entering the micropyle of the ovules. Scale bar = 100 µm. In the upper left detail: mature ovule under fluorescence showing the micropyle. Scale bar = 50 µm.

The anthesis and the time of visitation by the pollinators tend to be synchronic. Indeed, like in *J. ulei*, the flowers of *J. oxyphylla* (Guimaraes et al. 2008), *J. mimosifolia* (Alves et al. 2010) and *J. copaia* (Maues et al. 2008) open at dawn/early morning, which is the preferred time of the main pollinators. However, in the Caatinga species *J. rugosa*, the flowers open at the beginning of the night, although visitation occurs only in the next morning (Milet-Pinheiro and Schlindwen 2009). The diversity of floral visitors and the documentation of floral pathogens is in contrast with the reduced observation of predatism/ parasitism in the leaves. The flowers produce a great amount of nectar, hence attracting many visitors. As a comparison, 10 flowers of *Vismia guianensis* (Hyperidaceae) produces 6.7 µL of nectar (Santos and Machado 1998), while in the present study, *J. ulei* each one of the flowers yielded 4 µL of nectar. Stevens (1994) stated that the flowers of *J. ulei* may produce up to 12 µL of nectar in the three days of life.

Table 2: Fruiting success in controlled and naturally pollination carried out in *Jacaranda ulei*.

Treatment	Number of flowers	Number of mature fruits produced	Fuit/flower ratio	Germinability of healthy seeds
Natural pollination (control)	2,604	270*	11%*	79%
Manually crossed pollination	105	34*	32%*	78%
Geitonogamy	101	0	0	-
Forced self-pollination (bagged flowers)	1,235	0	0	-

* = Statistically significant difference (P<0.05) by Student´s T-test.

Table 3: Floral visitors of *Jacaranda ulei*

Visitor	Category	Frequency of visitation
Hymenoptera		
1. Anthophoridae		
Xylocopa virescens Lepeletier	cheater	+
Ceratina sp.	occasional	++
Epicharis schrottkyi (Friese)	occasional	++
Eucerini sp.	occasional	++
2. Apidae		
Bombus atratus Franklin	effective	+++
Apis mellifera Linnaeus	effective	+++
Trigona spinipes Fabricius	effective	+++
Scaptotrigona postica Latrielle	occasional	++
Paratrigona lineata Lepeletier	occasional	++
3. Halictidae		
Augochloropsis smithiana (Schrottky)	effective	+++
Augochloropsis sp.	occasional	++
Augochlora sp.	occasional	++
4. Oxaeidae		
Oxaea flavescens Klug	cheater	+
Lepidoptera		
1. Hesperiidae		
Aguna albistria albistria	cheater	+
2. Lycoenidae		
Michaelus thordesa	cheater	+

Obs:
(+) sporadic visitation
(++) occasional visitation (3 to 4 visitations per day) and/or weekly visitation
(+++) daily visitor (6 to 8 daily visits or more)

Regarding nectar sugars, other Bignoniaceae such as *Pyrostegia venusta* (Gobatto-Rodrigues and Stort 1992), *Campsis radicans* (Bertin 1982), *Zeyheria montana* (Bittencourt and Semir 2004) produce nectar with about 25% of sugars, similar to observed in this study on *J. ulei*. In contrast, Alves et al. (2010) documented that *J. mimosifolia* produces a higher volume of nectar (7 to 20 µL of nectar per flower), but more diluted (12% of sugars). As comparison, flowers of the genus *Passiflora* L. (Passifloraceae), pollinated by big bees, offer sweeter nectars, with about 30-40% of sugar concentration (Koschnitzke and Sazima 1997).

In Cerrado, bees are the main pollinators, since most (85%) of the plants have flowers that produce nectar to attract them (Silberbauer-Gottsberger and Gottsberger 1998). No only in *J. ulei*, but also in Cerrado plants with very different floral structures, such as *Byrsonima* (Barros 1992), *Vochysia* (Oliveira and Gibbs 1994), *Eugenia dysenterica* (Proença and Gibbs 1994), *Jacquemontia multiflora* (Kiill and Ranga 1996), *Kielmeyera* (Barros 2002) have in common the production of nectar as to attract bees. Such differences in floral structures with a convergent ecophysiological feature are related to the great diversity of bees in Cerrado, as shown in the present study. Yanagizawa and Maimoni-Rodella (2007) consider that true cheaters are not common; instead, most bees are pollinators, some being more efficient than others. Since bees harvest both nectar and pollen, the fact of a given bee species has not been seen touching the anthers does not mean it never does. The bee may sometimes search for pollen, so that it transfers pollen from one flower to another one.

Indeed, Quinalha et al. (2016) documented in *J. caroba* that the flowers visited by small bees, apparently cheaters, produced seeds, although less frequently compared to other bees. Also, Souza et al. (2019) observed that the nectar consumption of small bees did not prevent bigger bees from visiting and pollinating the flowers of *J. caroba.* Regarding vertebrates, tubular flowers tend to attract hummingbirds, which explains the visitation of them to *J. ulei*.

In Cerrado, there are flowers all year long, but most of the flowers appear at the onset of the rainy season (Barros and Caldas 1980, Barros 1992, Barros 2002). Stevens (1994) registers that *J. ulei, J. rufa* and *J. caroba* produce flowers at about the same time, but *J. simplicifolia* starts flowering around December, that is, after the peak of flowering of the other *Jacaranda* species. This may be interpreted as a strategy to face the competition for pollinators (Boaventura 1998).

Cornucopy-type inflorescences sensu Gentry (1974) such as of *J. ulei* represent to the visiting fauna an abundant source of food, since nectar and pollen are available at a considerable amount and for a relatively long period. So, the cultivation of *J. ulei* in urban gardens might help to sustain a micro-ecosystem, especially regarding the biodiversity of bees. Moreover, Silberbauer-Gottsberger and Gottsberger (1988) describe that most Cerrado flowers are white, beige and yellow, so that the red, blue and violet flowers (such as those of *J. ulei*) present an additional ornamental value.

Conclusions

In conclusion, *J. ulei* follows the pattern previously observed to other species from the genus *Jacaranda*, being strongly self-incompatible, and with seeds easy to germinate. This should be taken into consideration when producing seedlings of this plant of ornamental and medicinal interest. To the invertebrate fauna, the flowers of *J. ulei* seem to be an important source of food, hence being indicated to be cultivated in urban gardens and ecological parks.

Acknowledgments

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