



Reproductive Biology of *Varronia curassavica* Jacq. (Boraginaceae)

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ABSTRACT

Varronia curassavica, a subshrubby medicinal species associated with restinga in the Atlantic Forest, has been exploited by local people and the pharmaceutical industry. Indeed, restingas have experienced a continuous process of degradation, and thus, with species and ecosystem both at risk, efforts to support conservation actions are required. The present study aimed to evaluate aspects of *V. curassavica* reproductive biology. To accomplish this, morphological characterization was performed by monitoring flowering events. The availability of nectar and pollen, as well as the frequency and behavior of floral visitors and dispersers, was also evaluated. This species exhibits both heterostyly and protogyny. Anthesis is diurnal, and flowers last less than a day. The high number of flower and fruit abortions suggests that mechanisms, such as self-incompatibility intra-morphs and easily detached flowers, contribute to reduced fruit production. The high diversity of floral visitors indicate a generalist pollination syndrome. Diptera, Hymenoptera and Lepidoptera were the main pollinators, and nectar was the main resource sought by these insects. Fruits were dispersed by birds and ants. It can be concluded that the interaction of *V. curassavica* with several species is a key factor in its own survival and for maintaining the biological diversity of restinga.

Key words: dispersion, heterostyly, pollination, floral resources.

INTRODUCTION

The term restinga refers to the entire vegetation complex established in sandy soils of marine origin. Its diverse floristic composition and physiognomy result in a vegetation mosaic which is reflective of local gradients (Castro et al. 2007, Brasil 2016). At the same time, however, these vegetation formations are established in a soil type commonly leached and poor in nutrients, resulting in overall

fragility and susceptibility to different disturbances (Waechter 1985, Rocha et al. 2004).

In fact, restingas have experienced a continuous process of degradation since European settlement (Barcelos et al. 2012), which has only been exacerbated with increasing urbanization, resulting in further destruction and fragmentation (Rocha et al. 2003). Thus, with species, including both flora and fauna, and habitat at risk, efforts to support conservation actions are required.

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Varronia curassavica Jacq. (Boraginaceae) is a characteristic species of restinga vegetation. It is a perennial subshrubby species which occurs along most of the Brazilian coastline (Smith 1970, Judd et al. 2009). This species is used in folk medicine based on its anti-inflammatory, analgesic and cicatrizing properties (Lorenzi and Matos 2008). Apart from its popular medicinal use, the pharmaceutical industry has shown a growing interest in obtaining leaves as raw material for the manufacture of natural medicines.

Nevertheless, habitat fragility, combined with extractive collection practices, which is still regarded as the main way of obtaining medicinal plants of nature (Reis and Siminski 2011), can result in a significant reduction of natural populations or loss of genetic variability, compromising population sustainability (Ratnam et al. 2014).

Knowledge of reproductive biology in the context of floral morphology and interaction with biotic vectors is important for predicting species survivability (Faegri and Van der Pijl 1979, Rodríguez-Pérez 2005), understanding gene flow patterns and genetic differentiation of populations (O'Malley et al. 1988, Bawa 1992) and supporting conservation and sustainable management efforts (Mariot et al. 2014). Nevertheless, most *V. curassavica* studies have reported on its phytochemistry and pharmacology (Carvalho Jr. et al. 2004, Fernandes et al. 2007, Passos et al. 2007), while neglecting important questions of autoecology (Opler et al. 1975, Brandão et al. 2015). Therefore, the present study aimed to address the following issues specific to *V. curassavica*: 1) reproduction in relation to flowering, 2) resources provided to pollinators, 3) flower morphology in the context of specific pollination syndrome, 4) preservation of heterostyly or other floral arrangements contributing to the restriction or prevention of inbreeding, 5) floral visitors and potential pollinators, and 6) dispersers of fruits.

MATERIALS AND METHODS

STUDY AREA

This study was carried out in the herbaceous shrub vegetation located in a restinga (sandy dune) area of Joaquina Beach, Parque Municipal Dunas da Lagoa da Conceição (PMDLC) (27°37'46.19"S; 48°27'1.59"W), which is located east of Florianópolis, Santa Catarina, Brazil. PMDLC (Municipal Decree No. 231 of 16/09/1988) covers almost 563 hectares and is considered the largest sand dune area in Florianópolis (Caruso Jr. 1993, Cecca 1997). According to Köppen climate classification, this region is Cfa mesothermal humid (Köppen 1948) with hot summers and well-distributed rains throughout the year.

MORPHOLOGICAL CHARACTERIZATION

Based on species heterostyly, five flowers of each morph from each of ten individuals were collected. Length of the calyx and corolla together and length of calyx, corolla, tube, apocarps, and androecium were measured. Diameter of the opening of pollen tube was measured with a caliper, and the petals and stamens were counted. For data analysis, Student's t-test was used ($p < 0.05$) to detect differences between floral characteristics among morphotypes. The voucher specimen was deposited at the herbarium FLOR of the Universidade Federal de Santa Catarina (UFSC) with voucher number FLOR20081.

MONITORING OF FLOWERING AND FLORAL RESOURCES

Fifty inflorescences (five inflorescences each from ten individuals) were marked, and measurements were taken of inflorescence length. Flower buds were counted for each inflorescence, as well as open and senescent flowers and the number of mature and immature fruits. Evaluations were performed every three days over the course of 49 days.

Floral studies, including the monitoring of anthesis, were conducted from the time of corolla opening until its shriveling. These studies were performed through continuous observations of flower buds in pre-anthesis, recording the opening time, duration of flowering, and changes in flower morphology. Stigma receptivity was tested from pre-anthesis to the time of flower shriveling using Sudan III staining in ten flowers of different individuals.

The release of pollen was evaluated in 50 flowers of 10 individuals during flowering through direct field observations by gently touching the anther with a glass microcapillary every two hours. To determine potential nectar secretion, 10 inflorescences were bagged with flowers in pre-anthesis from different individuals. After 24 hours, measurements were taken in 50 flowers (five per inflorescence). Nectar standing crop production was evaluated over the course of three days using 50 flowers from 10 individuals. Measurements began with flowers in pre-anthesis and were repeated every two hours during flowering. These measurements were done with microcapillaries (1µl), and quantification followed Dafni (1992).

FLORAL VISITORS AND DISPERSERS

Observations were performed at different times of the day during peak flowering in different individuals. These observations took place over the course of nine days between October of 2014 and March of 2015, from 5:00 am to 9:30 pm. For each visit, a record was made of the species, foraging behavior of visitors, i.e., floral resource collected, hour and frequency of visits, contact with floral parts and agonistic interactions, are defined as aggressive manifestations between the floral visitors in the competition for resources. The schedules presented in this paper do not take into account the Brazilian summer time.

Floral visitors were categorized as follows. A *pollinator* was considered any insect that touched reproductive structures, visited many flowers on different individuals, and exhibited the presence of pollen. An *eventual pollinator* was considered any insect that could pollinate, but showed low frequency of visitation and/or looked for other resources apart from pollen and nectar. A *potential pollinator* was considered a forager touching the reproductive structures and carrying pollen, but not visibly carrying pollen to other plants. A *visitor* was considered those insects that visited a flower, but did not touch reproductive structures.

When necessary, observed floral visitors were captured with an insect catching net and transferred to a test tube. To identify the presence of pollen on the body, insects were analyzed under stereomicroscope and photographed. Insects were then deposited in the collection held by the Entomology Laboratory, Universidade Federal de Santa Catarina. Species were identified by specialists following the classification of Triplehorn & Johnson (2011). Along with observations of floral visitors and floral monitoring, observations of daytime disperses were carried out at different times and in a random manner. Photography was used for record-keeping and identification. Specialists, as well as specialized literature, were consulted.

RESULTS AND DISCUSSION

FLORAL MORPHOLOGICAL CHARACTERIZATION

The studied population presented terminal spike inflorescence, which could reach eight cm in length (Figure 1). The rachis is cylindrical, slightly pubescent and furrowed on the base; greenish. The flowers are sessile, androgynous, gamopetalous, generally pentamerous, ranging between four to six petals; slightly zygomorphic. The calyx is gamosepalous, lobate, with sepals joined by two-thirds or more of their length; persistent in the

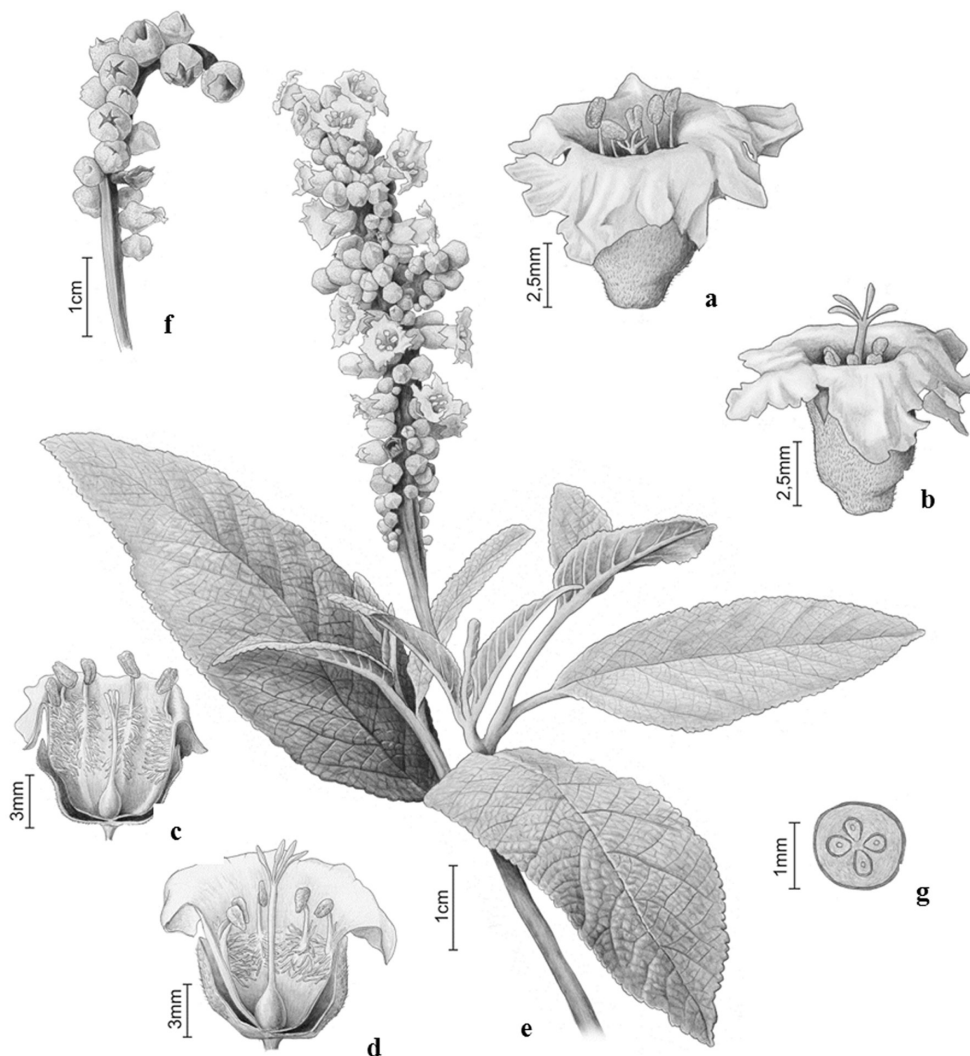


Figure 1 - a-g. *Varronia curassavica* Jacq.- **a.** Brevistylous flower; **b.** longistylous flower; **c.** brevistylous flower lateral section showing the reproductive structures; **d.** longistylous flower lateral section showing the reproductive structures; **e.** branch with inflorescence; **f.** infructescence; **g.** gynoecium. Illustration: Leandro Lopes de Souza.

axis of inflorescence, detaching only with the ripe fruit. The corolla is infundibuliform, obovate, dentate, white. Androecium generally consists of five stamens, ranging between four to six flowers, enclosed in longistylous flowers, epipetalous and inserted into the middle portion of the tube. Anthers are oblong, free, extrorse with longitudinal dehiscence; filaments are appendiculated at the base. Gynaecium is 4-locular, usually with four ovules. Styles are undivided; stigma is tetrafurcated and

clavate. The species exhibit intra-floral nectaries. The fruits are drupaceous, mucilaginous, red when they are ripe and usually contain one seed.

Morphological analysis exhibited two distinct morphs (Figure 1, Table I). Four of the nine evaluated measures presented statistical difference between morphs. Compared to longistylous flowers (one morph), brevistylous flowers (second morph) presented larger corolla ($t = 2.96, p < 0.05$), longer tube ($t = 2.64, p < 0.05$), and longer androecium

TABLE I
Average (mm) and standard deviation (S) of floral characters of *Varronia curassavica* Jacq. in a sandbank environment, Joaquina, Florianópolis, Santa Catarina, Brazil ($n = 50$).

Floral character	Brevistylous ($\bar{X} \pm S$)	Longistylous ($\bar{X} \pm S$)
Flower length	7.21 \pm 1.23	6.64 \pm 1.52
Calice length	4.44 \pm 0.49	4.16 \pm 0.53
Corolla length	5.65 \pm 0.62*	5.12 \pm 0.66*
Tube length	4.21 \pm 0.47*	3.84 \pm 0.51*
Diameter of tube opening	3.16 \pm 0.52	2.98 \pm 0.53
Number of petals	4.96 \pm 0.20	5.08 \pm 0.28
Pistil length	5.33 \pm 0.52*	7.16 \pm 0.69*
Androecium length	4.24 \pm 0.61*	3.48 \pm 1.32*
Number of stamens	4.96 \pm 0.35	5.04 \pm 0.35

* $p < 0.05$ for comparing between two floral morphotypes.

($t = 2.61$, $p < 0.05$). As expected, longistylous flowers exhibited a larger gynoecium ($t = -10.56$, $p < 0.05$). The number of anthers and petals ranged from four to six in both morphs, with five being the most frequent number.

The presence of heterostyly in *V. curassavica* is characterized by a self-incompatibility (SI) mechanism which is indicated by the existence of two distinct floral morphs differentiated by the spatial separation between the height of stigma and anthers (Barrett 1992). Heterostyly is common in Boraginaceae (Opler et al. 1975, Ganders 1979). Nevertheless, heterostylous variations may occur as a result of situations unfavorable to cross-pollination or by ineffectiveness or absence of

pollinators, or even by environmental disturbances (Sobrevila et al. 1983, Li and Johnston 2001). Therefore, it is the balance among pollinators that contributes to the maintenance of heterostyly and the population itself because viable offspring are generally only produced by crosses between different floral morphs (Barrett 2002, 2003).

Variation in the number of petals and stamens is not mentioned in descriptive studies of the species (Smith 1970, Sánchez 1995, Melo and Lyra-Lemos 2008). Miller and Gottschling (2007), however, emphasize that the taxon has high morphological diversity, especially with respect to the architecture and size of the inflorescence (Sánchez 1995), but no reference is made to flowers.

FLOWERING AND FLORAL RESOURCES

Varronia curassavica flowers last less than a day, and its anthesis is diurnal. Figure 2 depicts the floral development and the time of day when changes occur. In windy and high temperature days the flowering time was shorter than the observed on colder days, anticipating the wilting of the corolla. The evaluated individuals showed stigma receptivity, even before floral anthesis, but pollen release occurred only after corolla opening. Such strategy (protogyny) can be considered as a mechanism promoting outcrossing.

About eight hours after the anthesis, the corolla begins to show the first signs of oxidation and wilting (Figure 2), yet the flower remains functional

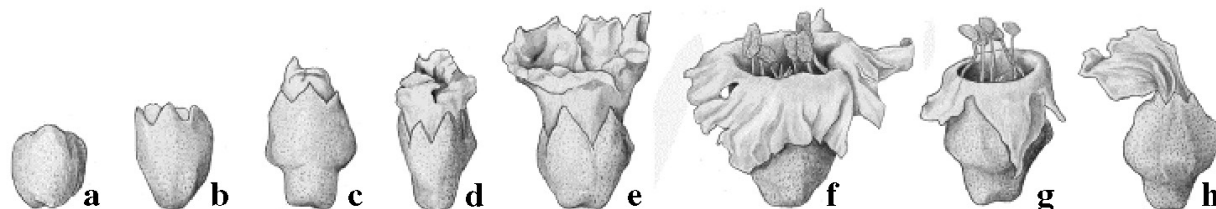


Figure 2 - Development of *Varronia curassavica* Jacq. flower bud **a**. flower bud; **b**. disruption of sepals (night before anthesis); **c**. start of anthesis, stigmas receptive (6:00 am); **d**. corolla exposed and lobes closed (start of pollen and nectar secretion (7:00 am); **e**. expansion and separation of lobes; **f**. flower completely open (9:00 am); **g**. beginning of wilting and floral oxidation (2:00 pm); **h**. flower completely oxidized (6:00 pm). Illustration: Leandro Lopes de Souza.

with receptive stigma, pollen availability and increase in the amount of nectar. After wilting, the corolla begins to detach itself easily. At nightfall, the corolla is very oxidized, but the reproductive structures remain functional, and the stigma remains receptive until the next morning.

Diurnal anthesis and short duration of *V. curassavica* flowers are commonly observed in Boraginaceae flowers (Opler et al. 1975, Machado and Loiola 2000). These features could restrict reproductive success in this species. However, the gradual opening of flowers, occurring on different days, tends to increase the time in which the floral resources are available to pollinators.

The development of inflorescences is summarized in Figure 3. Flower buds, flowers in anthesis, senescent flowers and unripe fruits in formation can be observed at the same time and in the same inflorescence. The flowers do not exhibit an opening pattern along the spike, and open flowers can be found anywhere in the inflorescence interspersed with flower buds in formation. After one month of evaluation, about 50% of the

inflorescences became senescent or broken (Figure 3a).

Increase in inflorescence growth continued for approximately seven weeks. Inflorescences reached an average length of 4.5 cm (± 0.29 cm). The average number of flower buds in each spike was 90 (± 43.15), decreasing at each evaluation. The number of open flowers per day and senescing flowers per inflorescence ranged from 0 to 12 and 0 to 13, respectively. The first unripe fruits were observed within three weeks of evaluation. In general, the species has a high investment in flower buds, but reduced fruit formation. Of the 50 evaluated inflorescences, only eight presented unripe fruits, with an average of 0.7 (± 0.3) per inflorescence. None of the evaluated inflorescences presented ripe fruits.

Abortion of flowers and immature fruits is considered a common phenomenon. Some of the most accepted hypotheses to explain these occurrences are related to the limitation of pollinators and resources, along with natural selection and paternity of the zygote (Bawa and Webb 1984).

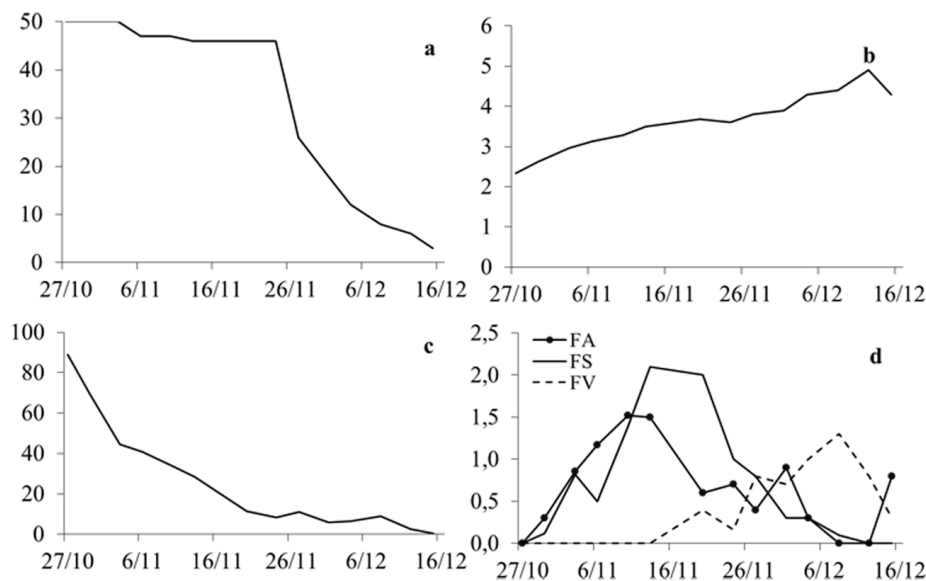


Figure 3 - Monitoring the development of inflorescence of *Varronia curassavica* Jacq. **a)** Number of monitored inflorescences; **b)** Length of inflorescence (cm); **c)** average number of flower buds; **d)** average number of open flowers (FA), average number of senescent flowers (FS); average number of immature fruits (FV).

The heterostyly of *Varronia curassavica* may also be an aspect contributing to the high levels of fruit abortion observed for the species. Another factor may be the easy detachment of flowers, especially toward the end of anthesis.

This species offers nectar and pollen throughout the day as resources for pollinators. Nectar production starts in the morning at anthesis and ends in the late afternoon when floral parts begin to wilt and oxidize (Figures 2 and 4). No nectar production occurred at night.

The average volume of standing crop nectar was 0.40 $\mu\text{L}/\text{flower}$ ($\pm 0.82 \mu\text{L}$), and the average volume of instant nectar was quite variable over the different measurement days (Figure 4). The first day of evaluation was overcast, with average temperature around 20 °C and winds not higher than 3 on Beaufort scale. On this day, average instant nectar of 0.093 $\mu\text{L}/\text{flower}$ ($\pm 0.2 \mu\text{L}$) was recorded. On the second and third day of evaluation, temperatures were between 28 and 32 °C with

winds reaching 6 on Beaufort scale and clear skies. On these days, instant nectar of 0.010 $\mu\text{L}/\text{flower}$ ($\pm 0.02 \mu\text{L}$) and 0.003 $\mu\text{L}/\text{flower}$ ($\pm 0.017 \mu\text{L}$) were recorded, respectively. These results suggest a lower nectar production on warmer and windy days. The average volume of potential nectar was about four times higher than the highest average of instant nectar, suggesting that produced nectar is quickly evaporated, thus reducing the observed levels in the measurements.

FLORAL VISITORS

Varronia curassavica flowers were visited between 6:00 am and 6:00 pm (Figure 5), practically the entire period of floral anthesis. Two visitation peaks were found: from 10:00 to 12:00 am and from 3:00 to 4:00 pm. The guilds of floral visitors expressed distinct behaviors. Hymenoptera and Diptera were more frequent in the late morning and between 3:00 and 4:00 pm. Lepidoptera concentrated most visits

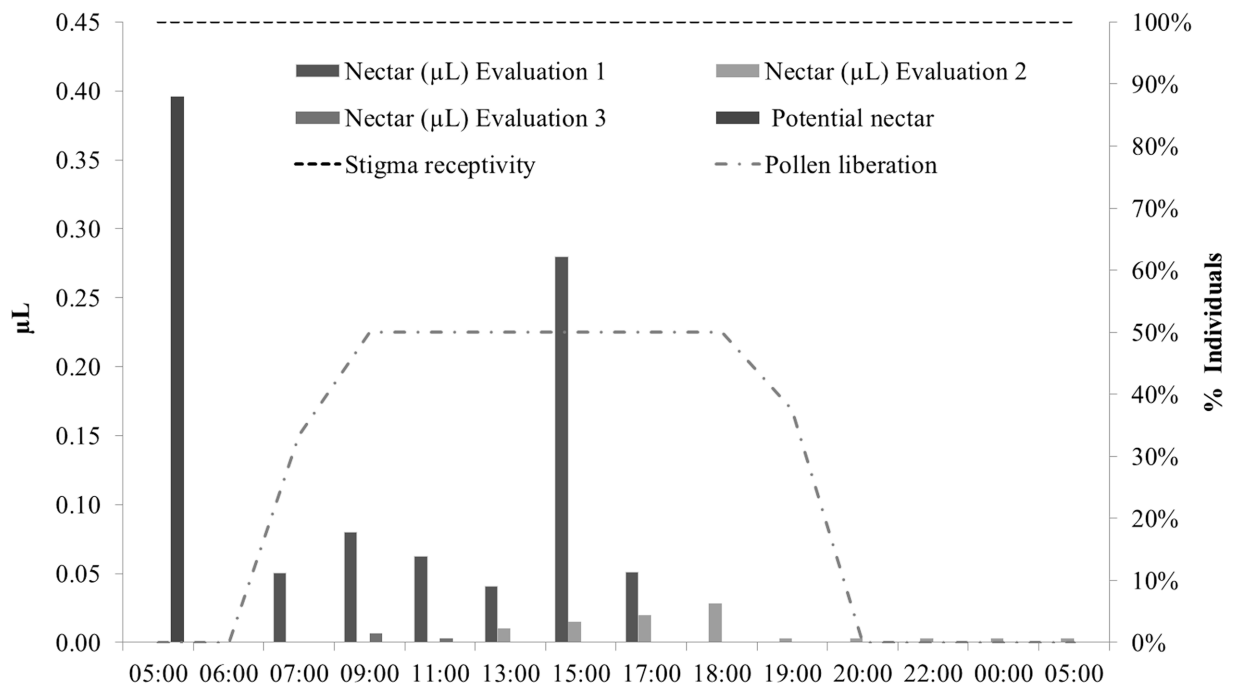


Figure 4 - Average volume of potential and instant nectar in μL per flower of *Varronia curassavica* Jacq. on different dates and at different hours of collection.

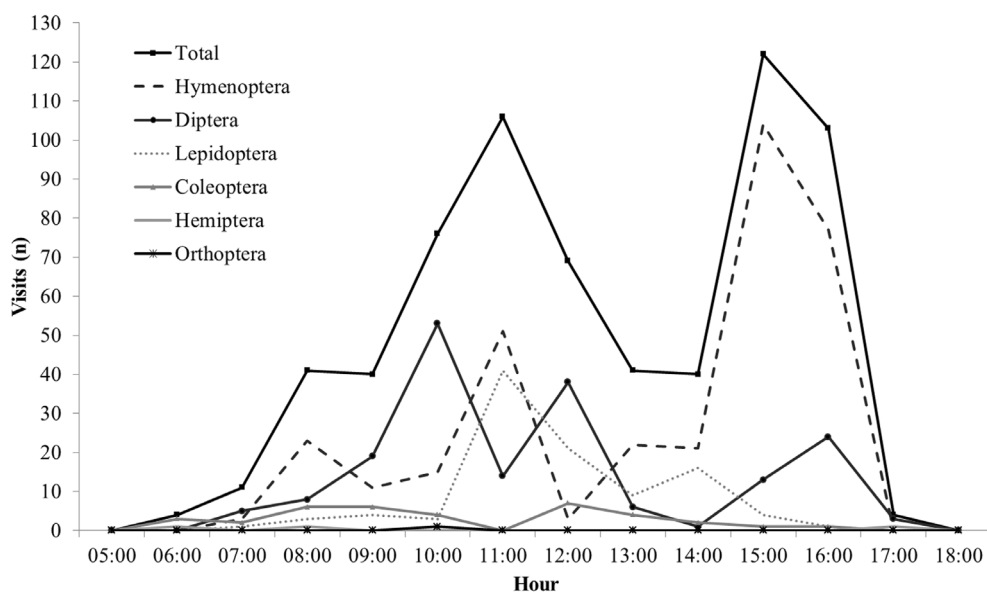


Figure 5 - Daily activity of *Varronia curassavica* Jacq. floral visitors between October of 2014 and March of 2015 in a sandbank environment, Joaquina, Florianópolis, Santa Catarina, Brazil.

between 11:00 am and 2:00 pm, while Coleoptera were more frequent in the morning.

Flowers were visited by 63 species (morphotypes) of the Insecta class, grouped into six orders and 24 families, totaling 655 visits (Table II). Diptera (30%), Hymenoptera (27%), and Lepidoptera (21%) were the orders with higher species richness, corresponding to 78% of all species. With 50% of visits, Hymenoptera constituted the most frequent order, followed by Diptera (29%) and Lepidoptera (16%) (Table II). *Apis mellifera* L. (Hymenoptera: Apidae) was the main visitor, responsible for 34% of all registered visits, followed by *Palpada* sp. (Diptera: Syrphidae) (15%).

The presence of ants (Hymenoptera), especially those of the genus *Camponotus*, was constant and was observed in inflorescences of all sampled individuals, as well the presence of nymphs and adults of Miridae (Hemiptera) within flowers, even before complete anthesis. Therefore, these insects were not considered in the analysis to prevent bias in the results.

Of all visitors, 21% were classified as pollinators, belonging to the families Apidae, Halictidae, Scoliidae (Hymenoptera), Syrphidae, Muscoidea (Diptera), Danaidae, Hesperidae and Nymphalidae (Lepidoptera) (Table II). Moreover, 37% of visitors were classified as possible pollinators, 11% as potential pollinators, and 31% as floral visitors. The main resource sought by the insects was nectar (Table II).

For the genus *Cordia*, previous studies have indicated characteristically diverse floral visitors (Opler et al. 1975, Machado and Loiola 2000, Moura et al. 2007, Brandão et al. 2015), including a wide diversity of Lepidoptera, Hymenoptera, Coleoptera and Diptera, corroborating our results. Opler et al. (1975) also observed Lepidoptera and Hymenoptera as the most abundant orders visiting eight *Cordia* species. Machado and Loiola (2000) studied pollination by flies in *Cordia multispicata* Cham., whose flowers are similar to those of *V. curassavica*, and reported nine species of flies, as well as bees, such as *Apis mellifera*, *Trigona spinipes* and *Augochloropsis* sp., and butterflies.

TABLE II

Varronia curassavica Jacq. floral visitors in a sandbank environment, Joaquina, Florianópolis, Santa Catarina, Brazil. [Mo = number of morphotypes; N= number of visitors; Fr = relative frequency; P. Cl. = Predominant classification; C = Constant presence; AB = shelter; EX= excrement; NE = nectar; PO = pollen; SA = Salt; FW = floral whorl; NI = not identified; PO*= pollinator; PP = potential pollinator; PE = eventual pollinator; VF = visitor].

Order/Family	Mo	N	Fr (%)	Resource	P. Cl.	Order/Family	Mo	N	Fr (%)	Resource	P. Cl.
COLEOPTERA						DIPTERA					
Chrysomelidae	5	12	1.67	FW, PO, NI	PE	Diptera spp.	3	6	0.91	NI, SA, NE	VF
Coccinellidae	1	15	2.29	FW, PO	PE	Drosophilidae	4	13	1.99	SA, NE	PE
Dasytidae	1	1	0.15	PO	PE	Ephydriidae	1	1	0.15	NE	PE
Lampyridae	1	2	0.31	NI	VF	Muscoidae	7	59	9.01	NI, NE, SA	PO*
Scarabidae	2	2	0.30	NI, FW	PE	Syrphidae	4	108	16.49	NE	PO*
HYMENOPTERA						HEMIPTERA					
Hymenoptera spp.	3	9	1.37	NI, NE	VF	Miridae	2	C		NE, PO, AB	PP
Apidae	1	220	33.59	NE, PO	PO*	Pentatomidae	1	1	0.15	NE	PE
Formicidae	3	C		NI	PP	LEPIDOPTERA					
Halictidae	1	30	4.58	NE	PO*	Lepidoptera spp.	3	5	0.76	NE, SA	PE
Pepsidae	2	5	0.77	NI, PO	PE	Danaidae	1	5	0.76	NE	PO*
Scoliidae	2	34	5.19	NI, PO	PO*	Hesperiidae	4	72	10.98	NE, SA	PO*
Sphecidae	1	8	1.22	EX	VF	Lycaenidae	4	19	2.90	NE, SA	PE
Tiphiidae	1	6	0.92	NI	VF	Nymphalidae	1	3	0.46	NE	PO*
Vespidae	3	17	2.60	PO, EX	VF	ORTHOPTERA					
							1	1	0.1	FW	VF

For *C. verbenacea*, diptera (Syrphidae) (Souza-Silva et al. 2001) were reported.

Varronia curassavica is characterized by white and tubular flowers, diurnal anthesis, and exposed sexual organs. Nectar is available to all floral visitors, independent of the length of its mouthparts, as well the pollen from stamens projected above the corolla in brevistylous flowers. These attributes, together with the high number of flowers per inflorescence, can attract a large number of floral visitors, especially those with short mouthpieces, as commonly found in Diptera, Hemiptera, Coleoptera and some Hymenoptera species (Opler et al. 1975, Faegri and van der Pijl 1979, Proctor et al. 1996), demonstrating that the species presents a generalist pollination syndrome.

This characteristic may be advantageous for the species since the probability of outcrossing is

maximized. Furthermore, species with extended flowering throughout the year, as observed in *V. curassavica* (Guimarães 2006), make their resources predictable over time, increasing the number of fauna seeking nectar and pollen. Also, the gradual opening of flowers, occurring on different days, tends to extend the time during which resources are available to pollinators.

In terms of effectiveness of pollination, the butterflies that visited *V. curassavica* presented various proboscis sizes. While this characteristic was incompatible with the size of the floral tube, most species presented pollen on different parts of their body and were seen foraging various flowers and distinct individuals. On the other hand, most Diptera have proboscis ranging in size from 2 to 4 mm (Proctor et al. 1996), which is compatible with the length of floral tubes of the studied species.

Flies, which have known importance to pollination in Boraginaceae (Machado and Loiola 2000), can be important pollinators because they are present throughout the year without displaying restricted periods of activity (Faegri and Van der Pijl 1979).

Hymenopterans were the most frequent visitors, and half of the visits of this order were carried out by *A. mellifera*. Although *A. mellifera* is an exotic species recently introduced to the North American continent (Oliveira and Cunha 2005), they are efficient pollen collectors and carriers. This species was also the main visitor and pollinator of *C. globosa* in the Caatinga area (Machado et al. 2010), highlighting its importance for the Boraginaceae family.

The relationship between ants and *V. curassavica* has provoked some attention (Belo et al. 2011, Brandão et al. 2015); however, its effectiveness as a pollinator is questioned by such limiting factors as absence of wings, frequent foraging in the same plant (Hölldobler and Wilson 1990) and production of lipophilic substances that may inactivate pollen (Beattie 1985, Dutton and Frederickson 2012). However, by the high frequency of visits (Gómez and Zamora 1992, Rico-Gray and Oliveira 2007), foraging behavior, and pollen grains attached to their body (Oriani et al. 2009, Galitzki et al. 2013), ants could be suggested as efficient pollinators. Since their foraging commonly occurred in the same plant, our results suggest the ants may be occasional pollinators.

Mirids were observed in high frequency, but they do not present evident structure that would contribute to pollen transfer. Still, the presence of pollen grains on their body and their constant foraging make these insects potential pollinators. Mirids were also observed to frequently change flowers. Beyond the food supply, the massive presence of these insects in *V. curassavica* may also suggest that the inside of the corolla could be a shelter for these species.

The wide variety of floral visitors and different guilds of pollinators could be crucial for the reproductive success of *V. curassavica*. The species presents known mechanisms for the prevention of self-pollination (heterostyly and protogyny), inhabits an inhospitable environment, with highly variable temperature and wind, high salinity, low soil fertility and constant changes between flooding and drought. These are factors that may limit the development and establishment of several species.

Furthermore, the species provides resources for several important pollen vectors. Their continued flowering (Guimarães 2006) allows visitors a greater predictability in the provision of resources and, therefore, the maintenance of pollinators in the area throughout the year (Newstrom et al. 1994), many of which are common in restinga areas and are pollinators of several other species in this environment (Silva and Pinheiro 2007, Schmid et al. 2011, Lopes et al. 2015). Thus, the maintenance of these interactions is essential for both *V. curassavica* populations and restingas.

DISPERSERS

During 20 hours of random observation, five species of birds, all omnivorous, were recorded feeding on *V. curassavica* fruits: *Turdus amaurochalinus* (Muscicapidae), *Mimus saturninus* (Mimidae), *Pitangus sulphuratus* (Tyrannidae), *Passer domesticus* (Passeridae) and *Zonotrichia capensis* (Passerellidae). Birds are considered efficient dispersers of seeds as a consequence of their mobility, diet and retention time of the ingested seeds (Ortiz-Pullido et al. 2000). Thus, they are able to disperse seeds well away from the parent plant (Francisco and Galetti 2002), contributing to the gene flow between populations. Although their foraging behavior has not been evaluated, the bird families Tyrannidae, Muscicapidae and Mimidae are usually swallows and are therefore considered the best dispersers (Moermond and Denslow 1985),

increasing the possibility of carrying seeds away from the parent plant. The species *Acromyrmex striatus* (Formicidae) was also observed dispersing the fruits of *V. curassavica*. Moreover, birds typically occupy open and disturbed areas (Francisco and Galetti 2002), thus facilitating the movement of seeds in fragmented habitats (Silva 2010). Consequently, the relationship between *V. curassavica* and their dispersers can affect both bird and plant populations, as well as the richness of bird species in restinga areas.

Even ants can carry seeds, albeit by shorter distances when compared to birds or mammals (Bond and Slingsby 1984), and their behavior as dispersers can contribute to the reduction in seedling competition near the parent plant (O'Dowd and Hay 1980) in addition to seed deposition in soils rich in nutrients and favorable to germination, such as anthills (Rissing 1986). Barroso et al. (2009) studied the morphology and germination of *Cordia sellowiana* and *C. myxa* seeds and observed ants feeding on fruit of these two species. Thus, ants can alter the deposition of seeds, influencing the reproductive success of *V. curassavica* and the spatial structure of its populations. Even in the absence of abundant fruit production, this resource, as well the flowering, is extended throughout the year, serving as a complement to the diet of different omnivorous species.

In conclusion, based on its floral characteristics, gradual and prolonged flowering, and resources, *V. curassavica* presents interaction with a wide variety of insects and birds. This level of interaction has significant importance in the maintenance of the species, securing its reproductive success and helping to counteract the limitations of the environment and the fragility of their flowers. In addition, by supplying forage and refuge, such interactions maintain the biological diversity of restinga fauna.

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