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Floral biology of *Sesbania virgata*: an invasive species in the Agreste of Paraíba, northeastern Brazil[1]

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Abstract

Although reproduction seems to play an important role in the successful invasive strategy of *Sesbania virgata*, its floral biology is poorly known. We aimed at filling this gap by studying the floral biology of a population of *S. virgata* in the Agreste of Brazil. *Sesbania virgata* is a shrub that bears racemose inflorescences. Its flowers are zygomorphic, pedunculate, hermaphrodite, and have a pale yellow corolla, diadelphous androecium, anthers with longitudinal dehiscence, and inconspicuous stigma. *S. virgata* flowers display three different types of petals: banner (11.92 mm), wing (8.27 mm), and keel (9.3 mm). The flowering peak occurred from November to January. The average number of pollen grains per flower was 22,918, with a pollen viability of 99.93%. Its anthesis is diurnal and asynchronous. Although *S. virgata* is autogamous, its pollen/ovule ratio suggests that this plant has a mixed reproductive system (xenogamy + autogamy). Continuous flowering, flower morphology, and specialized breeding system are essential to assure the reproductive success of this species in the studied habitat. *Sesbania virgata* is a food source for flower visitors, due to its continuous flowering and large population. Therefore, it has an effective reproductive strategy that assures its invasion success.

Key words: breeding system, pollination, Fabaceae.

Resumo

A reprodução parece ser uma parte importante da estratégia de invasão bem-sucedida de *Sesbania virgata.* Apesar disso, a sua biologia floral é pouco estudada. O objetivo do nosso estudo foi preencher esta lacuna no conhecimento estudando a biologia floral de uma população de *S. virgata* no agreste brasileiro. *Sesbania virgata* é um arbusto que apresenta inflorescências racemosas. Suas flores são zigomorfas, pedunculadas e hermafroditas com corola amarelo-clara, androceu diadelfo, anteras com deiscência longitudinal, e estigma inconspícuo. As flores de *Sesbania virgata* apresentam três diferentes tipos de pétalas: o estandarte (11,92 mm), as alas (8,27 mm) e a quilha (9,3 mm). A maior intensidade do período de floração ocorreu entre novembro e janeiro. A média de grãos de pólen por flor foi de 22.918, com viabilidade polínica de 99,93%. A antese é diurna e assincrônica. Embora *S. virgata* seja autocompatível, a razão pólen/óvulo sugere a presença de um sistema reprodutivo misto (xenogamia + autogamia) nesta planta. A floração contínua, a morfologia floral, e o sistema reprodutivo especializado são indispensáveis para garantir o sucesso reprodutivo desta espécie no habitat estudado. A sua floração contínua e grande população faz de *S. virgata* uma fonte de recursos para os visitantes florais. Portanto, esta espécie apresenta uma efetiva estratégia reprodutiva que garante seu sucesso como espécie invasora.

Palavras-chave: sistema reprodutivo, polinização, Fabaceae.

Introduction

Fabaceae is the third largest and the second most economically important family of Angiosperms (Judd *et al*. 2009). In Brazil, the family is represented by ca. 190 genera and 2,100 species. It plays an important role as a floristic element in several vegetation types, mainly within the Atlantic Forest, where Fabaceae species stand out for their diversity and abundance (Lima 2000). Despite the richness and ecological

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importance of Fabaceae in Brazil, only a few studies have investigated the pollination biology and reproduction of this family (see Agostini *et al*. 2006; Nogueira & Arruda 2006; Guedes *et al*. 2009; Leite & Machado 2009). This situation is especially true for the invasive species of this family.

Sesbania virgata (Cav.) Pers. is commonly used in restoration programs due to its aggressiveness in terms of growth rate and ability to quickly cover up the soil. This species is native to several areas of Brazil. It occurs mainly in pioneer riparian vegetation of midwestern and southeastern regions (Carpanezzi & Fowler 1997; Braggio *et al.* 2002), in Brazilian Savanna (Cerrado) and Atlantic Forest areas (Braggio *et al.* 2002).

The biological traits of invasive plants influence their colonization success, and studying their reproductive system is particularly important for their management (Blanco 1972; Estes *et al*. 1983). However, Pyšek & Richardson (2007) stated that the role of plant traits in biological invasion is highly stage- and habitat-specific. When invasive species are able to set flowers and fruits in human-modified habitats, even in the absence of pollinators, in-depth studies are strongly needed. Self-fertilization assures the perpetuation of those species and thus also plays a role in biologic invasion.

The occurrence of *S. virgata* as invasive in the Brazilian Caatinga is somewhat recent, dating back to no longer than three decades (Andrade 2006). The preferential sites for the species within this biome are riparian forests around reservoirs (Andrade 2013). This species is also considered invasive in other regions of Brazil, and has a negative effect on the structure and diversity of native plant communities in all three study sites along riparian forests of the Paraiba River. In Area II, Salgado de São Félix, state of Paraíba, *S. virgata* had a higher value of importance for the shrub-arboreal layer (Souza 2012).

Studies on other invasive plants have associated invasion success with reproductive strategy, which is consistent with Williamson & Fitter (1996). For instance, characteristics such as independence of pollinators, large fruit set, and fast fruit ripening can facilitate the permanence of another plant species, *Ipomoea eriocalyx*, in invaded environments. Studies on floral biology, phenology, pollination mechanisms, and breeding systems in species of the Caatinga have been carried out since 1990 (Machado & Lopes 2002; Leite & Machado 2009). Such studies comprised mainly invasive species whose breeding systems take part in the invasion strategy. One example is *Raphiodon echinus*, typically found in the Sertão of Pernambuco, especially in temporarily flooded areas, road margins, and abandoned crops. Data available suggest that *R. echinus* is autogamous, but needs pollinators to secure its reproductive success (Dias & Kill 2007).

The breeding system of each species is crucial to assure the perpetuation of its descendants and enable the colonization of new habitats and the occurrence of natural evolutionary processes. Analyzing floral biology and pollination mechanisms is very important (Silva & Pinheiro 2007), especially in the case of species with invasive potential. In this sense, knowledge of floral morphology, pollination, and breeding mechanisms will contribute to set the ground for the control and management of this species. The present study, therefore, aimed at analyzing the floral biology of *S. virgata* in a population located in northeastern Brazil, to help understand how reproduction integrates the species invasion strategy.

Materials and Methods

Study area

The present study assessed a natural population of *Sesbania virgata* in the municipality of Areia, state of Paraíba, northeastern Brazil (06º58'04"S, 35º41'33"W, 527 m a.s.l.). The area is located in a region known as Brejo Paraibano (ca. 269,424 km^2) (IBGE 2011). The climate is mild, with average annual temperatures ranging from 22 to 26ºC. It has a rugged relief where open rainforests predominate (IBGE 1992), and highland swamps are also found.

Species description

Sesbania virgata is a shrub that reaches up to 6 m in height, 25 cm in diameter at breast height (DBH), and 5 m in crown width. It has a short lifespan (no longer than eight years) and a moderate ability to compete with grasses and resprout from stump after pruning or fire. It grows spontaneously on humid soils and can be associated with *Rhizobium* (Carpanezzi & Fowler 1997). Its fruits are nucoid, indehiscent, their color changes from green to opaque brown during the ripening, and they show a dry texture associated with rough skin. Their average values are 5.81 mm in length, 7.82 in width, and 5.81 in thickness. The seeds (ca.

4.44 per fruit) are reniform, light chestnut-brown with a smooth, glossy, and hard seed coat. Their average values are 6.87 mm in length, 4.4 mm in width, and 3.22 mm in thickness. The average weight of 1,000 seeds is 7.78 g. The germination is epigeal, and the seedling bears proto-leaves composed of 4–9 leaflets and a sub-woody, white or brown radicle (Araujo *et al.* 2004).

Data collection

Data collection and analysis were carried out from April to December 2010. We randomly sampled ten individual plants for analyzing their floral biology.

For the analysis of floral morphology, we fixed the flowers in ethanol 70% and took them to the Laboratory of Plant Ecology at the Campus IV of the Federal University of Paraiba (UFPB) at Rio Tinto. The data recorded included: flower morphology, flower biometry, anthesis, breeding system, pollen viability, number of pollen grains, and flower visitors. We measured the size of the floral elements of 30 flowers (3 flowers per plant, ten plants) with a digital caliper. We collected

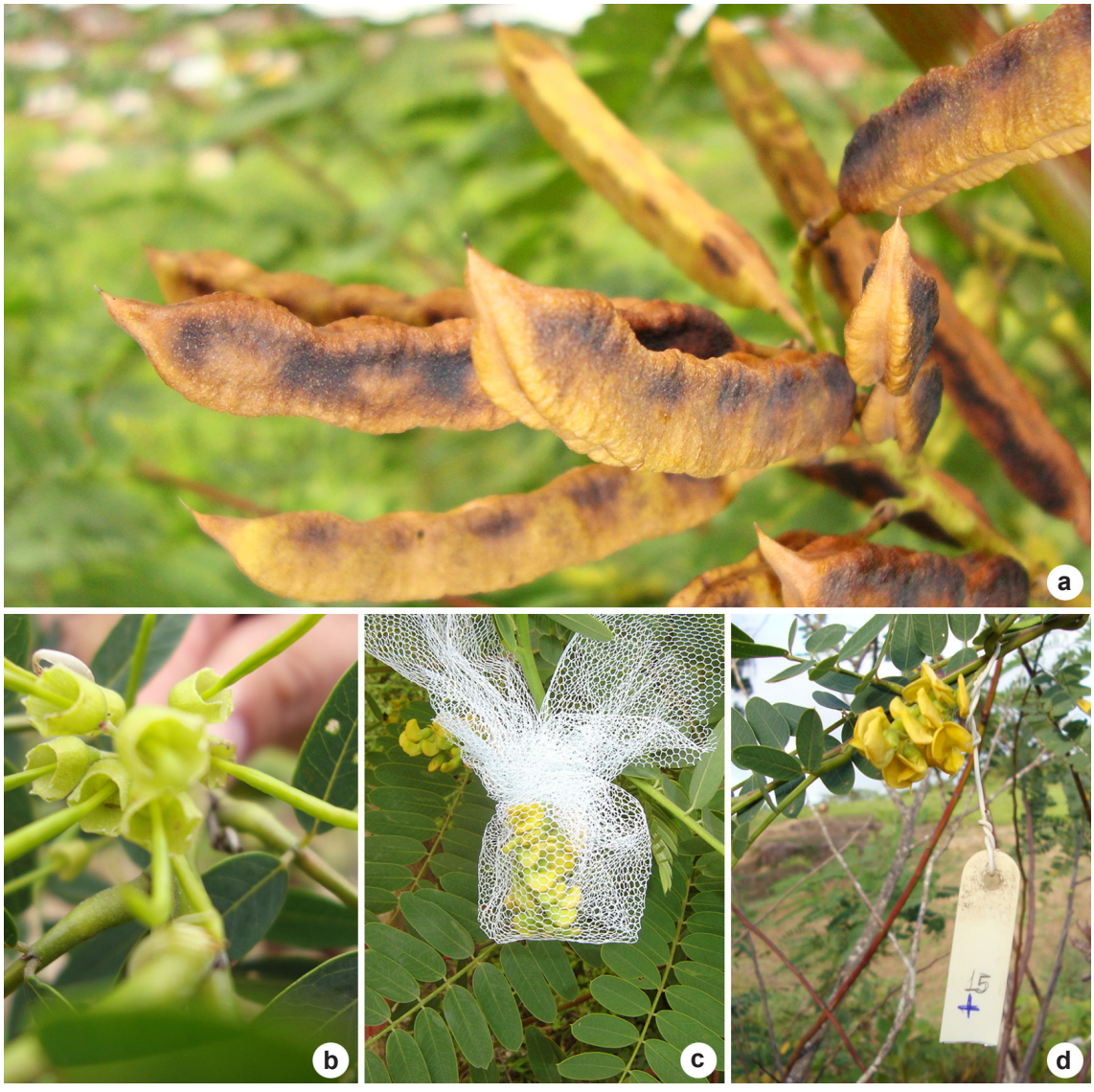

Figure 1 – Pollination experiments carried out in Areia, state of Paraíba, northeastern Brazil – a-b. fruit set; c. bagged flowers; d. flower marking.

inflorescences in the field. Next, we took the inflorescences to the Laboratory of Botany at the Agricultural Sciences Center, municipality of Areia, state of Paraíba, where we analyzed their flower morphology under a stereomicroscope.

We assessed the species' breeding system through pollination experiments (Fig.1) carried out in the field. We marked 20 individual plants and covered 23 inflorescences bearing pre-anthesis flower buds with voile bags to test for spontaneous self-pollination and fruit set. We left additional 23 inflorescences under natural conditions (control group), with flowers exposed to flower visitors. In both groups, we assessed pollination success through fruit yield. We monitored anthesis for five consecutive days. We marked pre-anthesis flower buds and recorded information on anthesis beginning and duration.

We carried out non-standardized observations of flower visitors during anthesis, and photographed the flowers whenever possible.

To compare the number of fruits formed between treatments, we calculated a t test in BioEstat 5.0.

Pollen viability and pollen/ovule ratio

To estimate the pollen viability, we removed the anthers of ten pre-anthesis flower buds and stained them with acetic carmine 2% (Radford *et al*. 1974). We considered viable the pollen grains stained in red. We performed pollen grain counting in a Neubauer chamber and determined pollen/ovule ratio following Cruden (1977). Although the pollen/ovule ratio per se does not prove that a species is autogamous, it corroborates this hypothesis.

Results and Discussion

Characteristics of the species

Sesbania virgata is a shrub that bears raceme inflorescences. Its flowers are zygomorphic, pedunculate, hermaphrodite, and show a pale yellow corolla, diadelphous androecium bearing anthers with longitudinal dehiscence, and inconspicuous stigma. In *S. virgata* flowers, three types of petals can be easily distinguishable: banner (11.92 mm), wings (8.27 mm), and keel petals (9.3 mm). The average number of pollen grains per flower was 22,918, which have high viability: 99.93% (Tab. 1). Brito *et al*. (2010) studied the reproductive biology of other Fabaceae species and also reported high pollen viability: 97% in *Sophora tomentosa* and 99% in *Crotalaria vitellina*. According to Etcheverry *et al*. (2008), the flowers of Fabaceae species show an intricate architecture. Therefore, pollen reception can only be achieved by highly specialized mechanisms. Although the population studied shows a continuous flowering pattern (Newstrom *et al*. 1994), a flowering peak occurred in the dry season, from November 2010 to January 2011.

Besides carrying male gametes, the pollen grains are also a protein source for flower visitors and paramount for the reproductive success of plants (Faegri & van der Pijl 1979). *Sesbania virgata* shows, on average, 22,918 pollen grains per flower, which makes the pollen one of the most important nutritional resources offered to pollinators.

Anthesis

The anthesis is diurnal and begins with the banner petal slowly unbending at ca. 10:00.

Table 1 – Floral traits of *Sesbania virgata* in a population studied in Areia, state of Paraíba, northeastern Brazil.

Traits	Measurements
Length (mm)	12.7 (15,29 ± 10,25)
Width (mm)	3.0 (7,94 ± 1,72)
Sepals (mm)	5.1 (5,96 ± 3,56)
Peduncle (mm)	3.8 (5,11 ± 2,36)
Stigma (mm)	8.8 (10,64 ± 7,09)
Pollen/ovule ratio	4,583.6
Pollen viability (%)	99.93%
Pollen grains (mean value)	22,918

This process is asynchronous: most flowers are completely open by 12:00, but some flowers begin anthesis only at 14:00. The increase in temperature probably favors anthesis, as its peak occurred around 12:00. The flowers remained open until the following day. Flower opening occurs from the base to the apex of the inflorescence. There are flowers and flower buds at different development stages on the same inflorescence. The extended flower opening favors pollinator activity throughout the day. This strategy may benefit cross-pollination, as it makes the pollen available as a resource in different plants and flowers simultaneously for flower visitors.

The asynchronous pattern seems to be common in some Fabaceae species. Usually, the anthesis is diurnal and lasts only one day (Primack 1985), but some species may show differences in flower duration, as observed in *Mucuna* sp. flowers (Agostini 2004). Guedes *et al*. (2009) classified the anthesis of *Canavalia brasiliensis* Mart. ex Benth (Fabaceae) as diurnal and asynchronous. Souza *et al*. (2012) classified the anthesis of *Senna cana* (Fabaceae) as diurnal and very slow. According to the same author, the reproductive success of *S. cana* and its subsequent establishment result not only from the morpho-structural characters of the flower, but also from the vegetative phenology and reproductive strategies.

Breeding system

Sesbania virgata is autogamous, as fruits were formed in both treatments: control and spontaneous self-pollination (Tab. 2). This result provides evidence that *S. virgata* does not depend on pollinators to transfer pollen grains from the anthers to the stigmatic surface. The pollen grains were already available when the flower bud was closed.

There was a significant difference in fruit set between the control and the treatment of spontaneous self-pollination ($t = 3.0720$, $p = 0.0018$). This result suggests that pollinators increased fruit set in this species. The reproductive success was 55.67% in the control (pollination free from visitors) and 27.34% in the treatment of spontaneous self-pollination. Aguiar *et al*. (2012) reported a mixed reproductive system in *Oeceoclades maculate* composed of cross-pollination and autogamy. Similarly to our study species, this system is probably related to its success in colonizing new and isolated habitats.

The population studied showed a continuous flowering pattern. Therefore, a given number of flowers per day on each plant, in a large amount at the peak of the phenophase, could restrict the movement of pollinators. Indeed, we observed few pollinators visiting several flowers per plant, as well as several different plants. Some pollinators were bees (*Xylocopa* sp.), and we collected them. We bagged flowers after the first visit of pollinators to reduce the pollen flow and avoid additional visits of other pollinators. However, those flowers set fruits. According to Stephenson (1981), this could reduce the pollen flow among plants, which would favor self-pollination.

Autogamy is a reproductive characteristic of invasive and pioneer species that occupy clearings and forest edges (Williamson 1996; Holsinger 2000). In the present study, *S. virgata* individuals occurred in areas similar to clearings, *i.e.*, high-light environments. Repeated cycles of colonization and low density may favor this kind of reproduction to assure the perpetuation of the species (Barret *et al*. 2008). Although several Fabaceae species are autogamous (Arroyo 1981), there is evidence that cross-fertilization also takes place (Borges 2006).

This strategy assures the maintenance of genetic variability, which is necessary for the permanence of the species in the habitat in the face of environmental pressures that are common in tropical areas. The mesquite tree (*Prosopis juliflora*), a legume (Fabaceae) of the subfamily Mimosoidae, is another invasive species with a reproductive biology similar to that of *S. virgata*. It has invaded extensive river margins and degraded areas, which resulted in high population density (Andrade *et al*. 2009; Leão *et al*. 2011).

Table 2 – Pollination and fruit set in flowers of *Sesbania virgata* (in each treatment) in Areia, state of Paraíba, northeastern Brazil.

Treatments	Flowers/Fruits (Fr/Fl)	Success %
Spontaneous self-pollination	12.69/3.47	27.34
Open pollination (control)	12.95/7.21	55.67

In spite of the fruit set observed in autogamy experiments, the pollen/ovule ratio also suggests *S. virgata* as a preferentially xenogamous plant. However, in self-pollination experiments, we observed the formation of fruits. Therefore, this classification may not be suitable for *S. virgata*, as spontaneous self-pollination also occurs. According to Baker (1974), a certain balance between self-compatibility and cross-pollination is beneficial to weeds. The author states that once a seed is dispersed to a distant place, the formation of a new population will depend on the self-pollination capacity of the species. *Sesbania virgata* is autogamous, which seems to be a good strategy combined with the ability of this species to invade degraded areas, such as the study site.

Autogamy would work as a safety mechanism to assure reproduction when pollinators are scarce (Endress 1994). Hence, autogamy might contribute to increasing seed set and the species' fitness.

Results indicate that, despite the high pollination efficiency, populations of this rewarding orchid species (*Epipactis palustris*) were strongly pollen limited. On the other hand, costs of early inbreeding depression were high, which may prevent rapid evolution of complete selfing (Jacquemyn & Brys 2015).

According to Raven (1996), the appearance of the hermaphrodite flower was an important evolutionary development in Angiosperms. The presence of carpels and stamens in the same flower allows the pollinator to remove and deposit pollen simultaneously. This process increases the efficiency of the pollinator at each visit and, thus, gives a selective advantage to the plant.

Conclusions

Sesbania virgata is autogamous, which is an important mechanism to assure colonization. The reproductive success and establishment of the species is a result of its reproductive strategy, as well as of its production of flowers/pollen, mainly during the dry season. This strategy is advantageous for the studied species in the marshes ("Brejo") of Paraíba, where the climate is favorable and with no heavy rains that might harm flowers.

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