



Floral biology of the velvetseed *Guettarda platypoda* DC. (Rubiaceae): Atypical distyly or style dimorphism?

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ABSTRACT

Distylous species have flowers with short styles and long stamens (thruns), and flowers with the inverse condition (pins) in different individuals. Studies suggested that style dimorphism (floral morphs that differ only in style height) is an intermediate stage in the evolution of distyly. We found populations of *Guettarda platypoda* DC. with apparent morphological variations of distyly and our objective was to assess stelar condition and other reproductive characteristics of *G. platypoda*. We analyzed the anthesis period, scent glands, nectar features, pollen number and viability, and measured lengths of corolla, anther and stigmatic lobes, heights of stigma and anther, and proportion of individuals of the floral morphs within the population. We characterized the species' reproductive system and investigated the behavior and frequency of its flower visitors. Two flower morphs were observed, one with a short style (thrum) and the other with a long style (pin); the anthers have similar height. Anthesis occurred between 1700 h and 1100 h. The volume of nectar, number of pollen grains and pollen viability did not differ between morphs, but the thrum showed more concentrated nectar. Both morphs had scent glands. The lengths of anthers and stigmas were similar among morphs, but the corolla was longer in the thrums. The influence of the corolla was the same on the different whorls in the pins, but stronger on stamen height than on stigma position in the thrums. The population is isoplethic and formed fruits in all treatments, with a partial incompatibility system for the thrums. Its visitors were three moth species, including two sphingids. The style dimorphism found in this sphingophilous species may indicate that *G. platypoda* represents an intermediate stage in the evolution towards distyly.

1. Introduction

Style dimorphism is a type of floral polymorphism characterized by individuals that have flowers with anthers arranged at the same height and stigmas at different heights (Ferreiro et al., 2011). Distyly, the most common type of heterostyly, is characterized by reciprocal herkogamy (RH), with the two morphs denominated thrum (short style and long stamens) and pin (long style and short stamens; Bahadur, 1968). Reciprocal herkogamy promotes cross-pollination between different individuals (morphs) and is believed to be evolved from style dimorphism (Lloyd and Webb, 1992a; Massinga et al., 2005).

The presence or absence of reciprocal herkogamy is used to classify a species as typical or atypical heterostylous, respectively (Richards and Koptur, 1993; Sánchez et al., 2013). However, as reciprocity can only be proven through precise morphometric measurements, typical heterostylous species are often erroneously described as being distylous.

Style dimorphism was correctly described for species of Rubiaceae, such as *Guettarda uruguensis*, *Mussaenda pubescens*, and *Morinda parviflora* (Bacigalupo 1957; Li et al., 2010; Liu et al., 2012), but it was mistakenly described for *Guettarda scabra* (Rubiaceae) (Richards and Koptur, 1993), *Anchusa officinalis* (Boraginaceae) (Philipp and Schou, 1981), and *Quinchamalium chilense* (Santalaceae) (Riveros et al., 1987).

Many species of Asteridae, including Rubiaceae, have flowers with epipetalous stamens, and this fusion of the androecium to the corolla plays a fundamental evolutionary role in the formation and maintenance of herkogamy, especially in species that show intermorph variation in the length of the corolla tube (Favre and McDade 2001; Santos-Gally et al., 2013). Mainly in polymorphic reproductive systems, epipetaly can have a double influence on the position of reproductive elements, because the stamens, especially the filaments, are fused to the corolla, and differences in corolla size determine the position of the anthers inside the flower and in relation to the stigma (herkogamy). In

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Guettarda scabra (Richards and Koptur, 1993), *Psychotria poeppigiana* (Faivre and McDade, 2001), and *Primula* (Primulaceae), whose family also has epipetalous stamens (Nishihira et al., 2000; Webster and Gilmartin, 2006; Kálmán et al., 2007), the height of sexual organs is related to the length of the corolla. Differences in corolla size between morphs are common. Typically, a longer corolla in the thrum morph promotes reciprocal positioning of its anthers to stigmas in the pin morph and vice-versa, favoring the intermorph pollen flow. In the genus *Narcissus* (Amaryllidaceae), the evolution of style polymorphism is correlated with a long and wide floral tube (Santos-Gally et al., 2013).

The genus *Guettarda* belongs to the subfamily Cinchonoideae and the monophyletic tribe Guettardeae (Bremer and Eriksson 2009). Distyly and dioecy were reported in this tribe (Achille et al., 2006; Zhou et al., 2012), but they are not considered as an ancestral and well-spread reproductive strategy. Studies on the reproduction of the genus are rare, and only available for *G. uruguensis* (Bacigalupo, 1957) and *G. scabra* (Richards and Koptur, 1993). The study on *G. scabra* focused on its reproductive biology and classified the species as atypical distylous. The study on *G. uruguensis* was part of a floristic inventory of the Rubiaceae of Argentina, and assigned the species as style dimorphic. In a recent study, Sánchez et al. (2010) stated that the attribution of distyly to *G. scabra* (Richards and Koptur, 1993) was a mistake and the species probably shows a typical case of style dimorphism, which reinforces the condition attributed to *G. uruguensis*.

Considering the scarcity of studies on *Guettarda* and the diversity of reproductive systems attributed to species of the genus, the objective of the present study was to assess the reproductive biology of *Guettarda platypoda* in a *restinga* of northeastern Brazil. In addition to basic aspects of floral biology and pollination ecology, the results found in the present study allowed us to answer the following questions: (1) Are the flowers of *G. platypoda* functionally unisexual or hermaphrodite? (2) Which type of reproductive strategy is present in the species: distyly, style dimorphism, or dioecy? (3) Is there a balance in the ratio of thrum and pin individuals? (4) Does the corolla play an important role in the arrangement of the reproductive whorls? (5) Is there reciprocity between the reproductive whorls of the morphs? And (6) Do the flowers of *G. platypoda* have an incompatibility system?

2. Material and methods

2.1. Study area

The study was carried out from July 2008 to July 2009 in Nossa Senhora do Oiteiro de Maracaípe, a Private Natural Heritage Reserve located in the municipality of Ipojuca (08°31'48"S and 35°01'05"W), Pernambuco, northeastern Brazil (Ibama, 2000). The reserve has an area of 76.2 ha and is characterized by a *restinga* vegetation (coastal, sandy shrubland, a subtype of Atlantic Forest) and strong human influence through monocultures. The climate is classified as AS' (sensu Köppen, 1948), which is defined as a tropical rainy climate with dry summer, rainfall in the driest month below 60 mm, and annual rainfall of approximately 2500 mm (INMET, 2010). The rainy season occurs from April to September, with the highest rainfall between May and July. The dry season occurs from October to March, with a peak between October and December (INMET, 2010).

2.2. Study species

Guettarda platypoda is a shrubby species endemic to Brazil, abundant in *restingas*, whose distribution comprises from northern to northeastern regions of the country (Zickel et al., 2007; Barbosa, 2013). It flowers all over the year, with a peak between January and June (Medeiros et al., 2006). Preliminary observations showed the existence of two floral morphs produced by distinct individuals, which were previously classified as pins and thrums during preliminary

observations.

2.3. Floral biology

We established the beginning of anthesis as the separation of the corolla lobes and the flower lifespan comprising from the opening of flower buds to the fall of petals. We estimated pollen production from 30 anthers, one per flower, collected from ten individuals of each morph type (three flowers per individual). To assess pollen viability, we used the cytoplasmic staining technique by acetic carmine (Dafni et al., 2005) and counted the first 500 pollen grains collected from 80 anthers, four per flower bud, collected from ten individuals of each morph type. We checked stigmatic receptivity using peroxidase reaction (Dafni et al., 2005) and assessed the presence of scent-emitting regions using neutral red staining (Dafni et al., 2005). For these tests, we used 25 pre-anthesis flower buds, five per individual, collected from five individual plants of each morph.

We measured sugar concentration with a handheld refractometer and nectar volume with a graduated microsyringe (Microliter[®] 10 µl) from 0700 h to 0800 h, using 28 previously bagged thrum and 34 pin flowers of ten individuals of each morph (around three flowers per individual). We calculated means of nectar concentration and volume per individual, and compared the results per morph with the Mann-Whitney test (Sokal and Rohlf, 1995).

We calculated the pollen/ovule ratio (P:O) by counting the pollen grains of one anther per flower bud, using 30 buds collected from ten individual plants per morph (three flowers per individual). We also calculated the total number of ovules present in the ovary, using 30 buds collected from ten individuals (Cruden, 1977). We calculated mean values of pollen and ovule number per individual and used the Mann-Whitney test to compare the average production of pollen grain per morph (Sokal and Rohlf, 1995).

2.4. Floral polymorphism and morph ratio

To characterize the reproductive strategy of *G. platypoda*, we analyzed its flowers following Ferrero et al. (2009) and Ferrero et al. (2011a) for distyly and style dimorphism.

We collected and fixed in alcohol (70%) 100 flowers per morph, collected from 10 individual plants. We measured corolla total length, anther height and length, stigma height, and stigmatic lobe length using a digital caliper (Starrett 727, precision 0.01 mm) and a stereomicroscope (Bel-photronics XTL series). We checked for morphometric differences between morphs using the generalized linear mixed model with Inverse Gaussian and Gaussian distribution. The response variable was the floral organ, the fixed factor was the morph, and the random factor was the individual plant.

We carried out the morphometric analysis with standardized data, as flower morphs differed from each other in the size of the corolla tube. Because floral morphs have different corolla lengths and epipetalous stamens, the variation in stamen length could be a result of the variation of corolla length. We standardized the corolla length to isolate or 'cancel' its effect on stamen length.

We tested for dependence between height of floral whorls and corolla length with a generalized linear mixed model in which the slopes that differed significantly from zero indicate a relationship (Faivre and MacDade 2001; Sá et al., 2016). The height of the organ was the response variable, the fixed factor was the type of structure (anther and stigma height), corolla tube length was included as covariate, and individual plant was included as a random factor. The statistical analysis was carried out in the package Vegan (Oksanen et al., 2013) for R (R Development Core Team, 2009).

We tested for reciprocity between reproductive whorls of floral morphs with the Sánchez index (Sánchez et al., 2013), which is based on the comparison of the relative position of the reproductive whorls (stigma and anther height) of each flower. For this calculation, we

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