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ASPECTS OF THE REPRODUCTIVE BIOLOGY OF *STENANONA FLAGELLIFLORA* (ANNONACEAE)

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Abstract

Stenanona flagelliflora was described in 2004. There are no studies on its biology. The goal of this study was to document some aspects of its reproductive biology. The particular objectives were to: i) describe the variation on vegetative and floral traits; ii) establish the composition of the community of floral visitors; iii) estimate the mating system and reproductive success; and, iv) establish the relationship between vegetative traits and reproductive success. The study was conducted within the Los Tuxtlas Biosphere Reserve, Veracruz, Mexico. We quantified several vegetative and floral traits; conducted observations and collected floral visitors; and determined the mating system and reproductive success. *Stenanona flagelliflora* has relatively few stamens and carpels, but a relatively high viability of pollen grains. The most abundant floral visitors were dipterans from the Phoridae Family. Mating system is between xenogamous and facultative xenogamous; thus, pollination depends upon pollen vectors. Fruit-set was relatively high; but seed-set was very low, because most monocarps did not contain seeds. Our results suggest that reproduction of *S. flagelliflora* is not limited by resource availability, but by pollinator frequency and effectiveness. To our knowledge, this is the first study on the reproductive biology of a species within the *Stenanona* genus.

Key words: Floral visitors; Fruit-set; Mating system; Pollen:ovule ratio; Reproductive success; Seed-set.

Introduction

Annonaceae is the largest family within the Magnoliales, containing between 120 and 135 genera and between 2000 and 2500 species (Cronquist, 1981; Gottsberger, 1989, 1999; Kelly, 2000; Stevens, 2001 onward). The knowledge on the reproductive biology of species within the family has received attention until the last few decades (Silberbauer-Gottsberger *et al*., 2003). Nowadays, there are numerous studies on the reproductive biology of Annonaceae, both in natural populations and in cultivars (Gottsberger, 1989; Norman *et al*., 1992; Webber & Gottsberger, 1995; Nagamitsu & Inoue, 1997; Küchmeister *et al*., 1998; Momose *et al*., 1998; Carvalho & Webber, 2000; Kiill & Costa, 2003; Ratnayake *et al*., 2006a, 2006b, 2007; Teichert *et al*., 2009, 2011, 2012; Gottsberger *et al*., 2011).

In general, it has been accepted that beetles are the main pollinators of Annonaceae (Gottsberger, 1989, 1999; Küchmeister *et al*., 1998; Silberbauer-Gottsberger *et al*., 2003; Ratnayake *et al*., 2006a; Gottsberger *et al*., 2011). However, pollination by thrips, bugs, cockroaches, bees, and flies has also been recorded within the family (Norman *et al*., 1992; Webber & Gottsberger ,1995; Nagamitsu & Inoue, 1997; Momose *et al*., 1998; Carvalho & Webber, 2000; Guirado *et al*., 2003; Silberbauer-Gottsberger *et al*., 2003; Teichert *et al*., 2009).

Annonaceae flowers attract their pollinators in diverse ways. The flowers of many Annonaceae species produce strong odours together with an increase of floral temperature; thus, favouring the attraction of visitors (Gottsberger, 1989, 1999; Küchmeister *et al*., 1998; Ratnayake *et al*., 2007; Gottsberger *et al*., 2011). Moreover, Annonaceae flowers have numerous reproductive organs (Gottsberger, 1989; Küchmeister *et al*., 1998; Kelly, 2000; Maas *et al*., 2007); which, together with stigmatic exudates, floral tissues, and pollen, are offered as rewards for their floral visitors (Norman & Clayton, 1986; Gottsberger, 1989; Küchmeister *et al*., 1998; Ratnayake *et al*., 2006a; Gottsberger *et al*., 2011).

Another important floral trait of Annonaceae is the formation of a floral chamber that encloses and protects the reproductive organs (Gottsberger, 1989; Webber & Gottsberger, 1995; Ratnayake *et al*., 2007; Teichert *et al*., 2011). Moreover, the opening of the floral chamber limits the access to the reproductive structures to those floral visitors whose body size is equal or less than the diameter of the opening (Gottsberger, 1999; Ratnayake *et al*., 2006a; Silva & Domingues, 2010). In addition, the floral chamber provides protection against predators as well as to adverse climatic conditions to those floral visitors able to enter into it (Gottsberger, 1989, 1999; Ratnayake *et al*., 2006a, 2007). Finally, the floral chamber might provide a mating site and/or a resting site for floral visitors (Gottsberger, 1989; Ratnayake *et al*., 2007; Gottsberger *et al*., 2011; Teichert *et al*., 2011).

As for their mating system, it is generally acknowledged that Annonaceae are outcrossers (Norman & Clayton, 1986; Norman *et al*., 1992; Andrade *et al*., 1996; Momose *et al*., 1998; Ratnayake *et al*., 2006b, 2007). Thus, Annonaceae species are protogineous (*i.e.* receptive stigmas before anther dehiscence) and show synchronized dichogamy (*i.e.* most flowers within a single individual are on the female phase or on the male one; Gottsberger, 1989; Küchmeister *et al*., 1998; Carvalho & Webber, 2000; Ratnayake *et al*., 2007). Therefore, outcrossing is favoured at the same time that geitonogamy is prevented (Carvalho & Webber, 2000).

In contrast with the great number of studies addressing the different aspects of reproductive biology of Annonaceae, fewer studies have recorded their reproductive success (*i.e*. seed-set and fruit-set) in natural populations (Norman & Clayton, 1986; Norman *et al*., 1992; Andrade *et al*., 1996; Nagamitsu & Inoue, 1997; Momose *et al*., 1998; Ratnayake *et al*., 2006b, 2007). In those studies, it has been shown that fruit-set is highly variable among species (1.7 % – 57 %; Norman & Clayton, 1986; Norman *et al*., 1992; Andrade *et al*., 1996; Nagamitsu & Inoue, 1997; Momose *et al*., 1998; Kiill & Costa, 2003; Ratnayake *et al*., 2006b, 2007). In addition, only one study has estimated seed-set in natural populations, showing that it is very low (2.3 %; Momose *et al*., 1998). The low reproductive success recorded in some of these studies has been attributed to the low effectiveness of pollinators, such that natural populations of Annonaceae are experiencing pollen limitation (Norman *et al*., 1992; Nagamitsu & Inoue, 1997; Momose *et al*., 1998; Ratnayake *et al*., 2007).

However, plant reproductive success might also be influenced by resource availability, such as it has been documented for diverse plant species (McIntosh, 2002; Asikainen & Mutikainen, 2005). Thus, plant reproduction might be strongly influenced by physiological and morphological traits associated with the capture of light, water, and nutriments (Coley *et al*., 1985; Bazzaz *et al*., 1987; Chapin *et al*., 1987; Saldaña & Lusk, 2003). Therefore, foliar damage and a limited interception of solar radiation might have a negative effect on plant reproductive success (Stephenson, 1981; Crawley, 1983; Marquis, 1984; Lehtila & Strauss, 1999; Hladun & Adler, 2009). For example, a reduction in leaf area causes a decrease in the amount of resources available for developing reproductive structures, thus, increasing the abortion rate (Stephenson, 1981; Crawley, 1983; Marquis, 1984). Therefore, it is possible that reproductive success of Annonaceae is not only limited by pollinator effectiveness but also by resource availability.

Although the knowledge on the biology of Annonaceae has increased in the last few decades, there is still a lack of studies for many species. For instance, there are not studies on the reproductive biology of species within the *Stenanona* genus. *Stenanona flagelliflora* was described in 2004 by Schatz & Wendt; this species produces the reproductive structures on long, thin, flexible, flagelliflorous branches; thus, representing the first report of flagelliflory within the mexican flora (Schatz & Wendt, 2004). *Stenanona flagelliflora* is an endemic species to Mexico (Schatz & Wendt, 2004), and it has been considered critically endangered (Anon., 2001). The objective of this study is to describe the reproductive biology of *S. flagelliflora* in Los Tuxtlas, Veracruz. Particularly, the study aimed at: i) describe the variation on vegetative and floral traits; ii) identifying the groups of floral visitors; iii) estimating the mating system and the reproductive success on a natural population of *S. flagelliflora*; and iv) establishing the relationship between vegetative traits and reproductive success as an attempt to infer the existence of resource limitation.

Materials and Methods

Study system: *Stenanona flagelliflora* was described by Schatz & Wendt in 2004. It is a small tree, 1–4.5 m tall that produces inflorescences on specialized flagelliflorous branches of up to 3 m in length that grow on the surface of the ground (Fig. 1). Flowers have three oval-ovate sepals; and six free, dark-red to purple-red petals in two slightly differentiated series. Each flower has 35 stamens, with connective tissue barely developed or prolonged into a horizontal to nearly vertical, deltoid, tuberculate appendage of up to 0.6 mm in length. Flowers have six free carpels, and ovules are solitary. Typically, one to three monocarps per flower complete their development. Mature monocarps are orange-red in colour. The species flowers from April to October. Fruits have been recorded from August to October. The species is distributed in the southern part of the Uxpanapa region of extreme southern Veracruz and the adjacent part of the Chimalapa region on eastern Oaxaca (Schatz & Wendt, 2004). It has also been recorded from Los Tuxtlas, Veracruz (A. Campos, *pers. obs.*), where the present study took place.

Study site: This study was conducted within the Los Tuxtlas Biosphere Reserve, in the Lic. Adolfo López Mateos locality (94^{o} 57’ 53.16” W y 18^{o} 26’ 19.60” N). Altitude of the study site is 219 m above sea level (Morteo, 2011), and vegetation is an evergreen rainforest (Miranda & Hernández, 1963). Climate is hot and humid, with an average annual temperature of 22–26 ^{o}C (Cruz, 2009), and a mean annual precipitation of 2000–2500 mm (Guevara *et al*., 1999; Cruz, 2009).

Vegetative traits: In order to know more about the biology of the species, some vegetative traits were measured on a total of 51 individuals. Number and length of flagelliflorous branches, plant height, stem diameter, total number of leaves, percentage of undamaged leaves and leaf coverage were estimated for each individual plant. Total length of ramified flagelliflorous branches was estimated as the sum of the length from each branch. Stem diameter was estimated at 10 cm in height in non-reproductive plants, and above the flagelliflorous branches in reproductive individuals. In order to determine the percentage of undamaged leaves, we established the total number of leaves per individual distinguishing between damaged (*i.e.* leaves with damage by herbivores and/or having foliicolous lichens growing on them) and undamaged leaves. Foliar coverage was estimated by measuring two perpendicular diameters; and then, entering them in the ellipse equation. All measured vegetative traits were reported as the mean ± standard error (s.e.).

Floral traits: On April 2011, floral buds in two different stages of development (starting to develop; and mature floral buds, right before floral anthesis) were marked and observed daily for up to 12 days. These observations were conducted in order to determine the number of days required for the maturation of a floral bud as well as the duration of anthesis. In floral buds starting to develop, basal diameter and bud length were estimated daily.

However, we were unable to stay in the field site to conduct daily observations for a longer period of time, and 12 days were not enough time for the completion of the phenological stage of bud. Thus, with data collected on bud dimensions throughout 12 days of observation, we estimated floral bud growth rate and then, the number of days required for a floral bud to reach the phenological stage of flower. Likewise, mature floral buds were marked and measured daily in order to determine floral size and days of flower anthesis. Flower basal diameter, flower length, and diameter of the floral chamber opening were estimated on each of these floral buds once the petals started to separate as the flower matured. A total of 36 floral buds starting to develop and 16 mature floral buds from 19 (1–5 floral buds per plant) and 12 individual plants (1–3 mature floral buds per plant), respectively; were used to conduct these observations.

In addition, we collected and stored mature floral buds (*i.e.* close to flower anthesis and undehiscent anthers) of *S. flagelliflora* in formaldehyde - acetic acid - ethyl alcohol for posterior processing in the laboratory. From each floral bud we quantified number of stamens and anthers per flower, and number and percentage of viability of pollen grains per anther and per flower as floral traits associated with the male function. Moreover, we also quantified the number of ovaries per flower, and the number of ovules per ovary and per flower as floral traits associated with the female function. A total of 48 mature floral buds from 29 different individuals were used to quantify number of stamens, anthers, ovaries and ovules per flower, and number of ovules per ovary.

Likewise, a total of 30 mature floral buds from 15 different individuals (two floral buds per individual) were used to determine number and viability of pollen grains per anther and per flower. In order to do this, a single theca from each floral bud was placed in a 0.5 ml microtube containing 200 µl of 1 % lactophenol aniline blue during at least 24 h. Then, each tube was vortexed during 1 min and the whole volume was placed on a clean slide under a stereoscopic microscope to determine the number and viability of pollen grains per theca. In order to estimate total number of pollen grains per anther; the number of pollen grains per theca was duplicated. Viability of pollen grains was determined as the percentage of viable pollen grains per theca divided by the total number of pollen grains in each theca. Viable pollen grains were spherical and strongly coloured in blue, whereas non viable pollen grains had a not well defined shape and showed a very light blue staining or not staining at all (Kearns & Inouye, 1993). The number and viability of pollen grains per flower was estimated by multiplying the values obtained per anther by the total number of anthers in each flower. All measured floral traits were reported as the mean ± s.e.

Although we were interested in describing other aspects of the reproductive biology of *S. flagelliflora*, such as stigma receptivity, anther dehiscence, and duration of each sexual phase during anthesis, it was impossible given the small size and the very low production of flowers. Attempts to conduct any of these observations would require at least a partial destruction of the flower, and thus, the results would probably being biased.

Fig. 1. *Stenanona flagelliflora* in "Los Tuxtlas", Veracruz, Mexico. a) Individual plant (Scale bar= 10cm). b) Flagelliflorous branch with a flower (Scale bar= 1cm). c) Flagelliflorous branches growing from the main stem of the tree, as indicated by the arrows (Scale bar= 1cm).

Floral visitors: We conducted observations and collects of the insects visiting the flowers of *S. flagelliflora* on 25–28 April 2011, as well as on 2 and 4 April 2012. Observations were conducted in 29–45 flowers in anthesis from 15 different individuals and in 25–70 flowers in anthesis from 17 individual plants in 2011 and 2012, respectively. Observations and collects of floral visitors were conducted from 0500–2200 hours during 15 min periods each hour, for a total of 540 min of observation (*i.e.* 9 h). Collects were conducted using fine paintbrushes and mouth aspirators. All insects collected were stored in 70 % ethanol and were identified by specialists.

Mating system: The mating system of *S. flagelliflora* was estimated in two ways. First, on 17–30 April 2011, we applied two pollination treatments on 33 individuals: i) spontaneous autogamy, and ii) open pollination. In the spontaneous autogamy treatment, floral buds were bagged with veil fabric (< 0.5 mm aperture) during the whole experiment; preventing the access of insects to the flowers. In the open pollination treatment, floral buds were kept available to all floral visitors and, right after flower senescence, the developing fruits were bagged with the same veil fabric used in the other treatment. Both spontaneous autogamy and open pollination treatments were applied in each experimental individual. Geitonogamy and allogamy hand-pollination treatments were also contemplated. However, due to the small size of the flowers, their protogineous nature, asynchronic anthesis within a single individual, and the difficulty to extract pollen grains from the anthers, we were not successful at applying these treatments.

The number of fruits obtained from each treatment (spontaneous autogamy and open pollination) was analyzed with a χ^2 test. If the species requires the service of pollinators (*i.e.* allogamy); then, the number of fruits obtained in the open pollination treatment was expected to be significantly greater than the one obtained in the spontaneous autogamy treatment. Conversely, if the species was mainly autogamous, a significantly greater number of fruits was expected under the spontaneous autogamy treatment.

Second, we determined the species mating system through the estimation of the pollen:ovule ratio (P/O), using the estimated number of pollen grains and ovules per flower obtained previously. The estimated P/O was then used to determine mating system according to the classification proposed by Cruden (1977).

Reproductive success: We determined the number of reproductive structures, fruit-set (*i.e.* number of flowers that produced fruits) and seed-set (*i.e.* number of ovules that produced seeds) as estimators of reproductive success.

The number of reproductive structures in each phenological stage (bud, flower, and fruit) was determined in a total of 51 individuals, every other week from April 17 to September 28, 2011. Thus, we were able to establish the maximum number of reproductive structures produced by each individual on a single date. Maximum number of reproductive structures (total, buds, flowers, and fruits) was reported as the mean ± s.e.

Then, in order to explore if reproductive success of *S. flagelliflora* is limited by resource availability, we conducted stepwise regression analyses. In these analyses, maximum production of reproductive structures of *S. flagelliflora* (buds + flowers + fruits), as well as maximum production of buds, flowers, and fruits, separately; were used as estimators of reproductive success. Likewise, plant height, stem diameter, total number of leaves, percentage of undamaged leaves and leaf coverage were used as rough estimators of the availability of resources. Data of total number of leaves, and maximum number of reproductive structures were transformed as $(x + 0.5)^{1/2}$, whereas the percentage of undamaged leaves was transformed as arcsen $(x)^{1/2}$ (Zar, 1999). Statistical analyses were conducted in SAS v. 9.0.

In order to estimate fruit-set, a total of 139 flowers from 57 different individuals were tagged and monitored every other week, from 20 April to 28 September 2011. Because *S. flagelliflora* has apocarpic flowers, fruit-set was estimated as the presence or absence of fruits per tagged flower, independently of the number of monocarps produced by each flower.

Seed-set was determined in 66 apocarpic fruits from 57 different individuals (one to eight fruits per individual). Then, we estimated seed-set by dividing the number of seeds per apocarpic fruit by the number of ovules per flower that was quantified previously (see the floral traits section above). Floral buds used for the estimation of number of ovules and apocarpic fruits used to quantify number of seeds were collected from the same individual plants.

Finally, we estimated the percentage of monocarps aborted. In order to do this, we divided the number of monocarps per flower that started their development but never matured over the total number of carpels per flower. We also determined the time (in days) of monocarp maturation.

Results

Vegetative traits: On average, each individual of *S. flagelliflora* produces 1.41 ± s.e. 0.23 flagelliflorous branches (range: 0 – 6) with a mean length of 60.93 ± 16.32 cm (range: 2.1 – 449.5 cm). Individual plants had a mean of 90.85 ± 5.53 cm in height (range: 28 – 241 cm); 12.78 ± 0.58 mm in stem diameter (range: 4.85 – 22.96 mm); and 2,824.88 ± 333.53 cm^2 of foliar coverage (range: 270.96 – 14,306.85 cm^2).

Each individual had an average of 55.74 ± 5.85 leaves (range: 9 – 250). On average, 41.96 ± 4.36 leaves per individual were damaged (73.74 ± 1.93 %; range: 9 – 166 damaged leaves per individual). The highest percentage of damaged leaves per individual was 100 % (recorded in two individuals, with a total of nine and 41 leaves, each). On the contrary, the lowest percentage of damaged leaves was 40.74 % (one individual with 11 undamaged leaves out of a total of 27 leaves). In contrast, a mean of 13.78 ± 1.87 leaves per individual were undamaged (26.26 ± 1.93 %; range: 0 – 84 undamaged leaves per individual plant). Thus, the maximum and minimum percentage of undamaged leaves in *S. flagelliflora* individuals was 59.25 % (16 leaves out of a total of 27) and 0 %, respectively.

Floral traits: On average, floral buds grew up at a rate of 0.14 ± 0.02 mm/day and 0.12 ± 0.01 mm/day in length and basal diameter, respectively. During the 12 day period in which daily observations of the development of floral buds were conducted, only one bud completed its development and reached the phenological stage of flower.

Floral anthesis lasted 8.13 ± 0.53 days on average (range: 4 – 11 days). At the beginning of anthesis, flowers had 6.13 ± 0.22 mm, 8.04 ± 0.4 mm, and 1.89 ± 0.5 mm of basal diameter, length, and diameter of the floral chamber opening, respectively. Whereas at the end of the anthesis, these same floral traits were 8.71 ± 0.23 mm, 9.26 ± 0.38 mm, and 5.35 ± 0.48 mm, respectively. Out of these three floral traits, the opening of floral chamber had the fastest development rate (0.5 ± 0.07 mm/day), followed by basal diameter (0.33 ± 0.04 mm/day) and floral length (0.19 ± 0.04 mm/day). Based on the estimated growth rate of floral buds, as well as the average basal diameter and length of flowers at the beginning of anthesis, the estimated time required for a bud to complete its development was between 50.95 (estimated from basal diameter growth rate) and 57.17 (estimated from bud length growth rate) days.

Stenanona flagelliflora flowers had an average of 3.93 ± 0.17 carpels (between two and seven carpels per flower), and 1.01 ± 0.01 ovule per carpel; that is, an average of 3.98 ± 0.16 ovules per flower. The gynoecium is surrounded by an average of 32.15 ± 0.73 stamens (19–41 stamens per flower).

In average, each anther contained 486.06 ± 37.84 pollen grains; 385.33 ± 29.10 of them were viable and 100.73 ± 22.79 were non-viable. Therefore, a flower of *S. flagelliflora* produces an average of 16,168.7 ± 1,115.18 pollen grains (range: 7930 – 22847.5); from which 12,845.80 ± 877.45 (80.39 ± 3.75 %) are viable.

Floral visitors: A total of 94 arthropods belonging to 18 different species were recorded visiting the flowers of *S. flagelliflora* (Table 1). Floral visitors belonged to the orders Diptera, Thysanoptera, Hymenoptera (Formicidae), Hemiptera and Orthoptera, and to the classes Arachnida and Collembola (Table 1).

Floral visitors were observed visiting the flowers of *S. flagelliflora* throughout the day (Fig. 2a). The highest number of floral visitors was recorded at 1700 hours (21 individuals), whereas the lowest was observed at 0600 and 1400 hours (one floral visitor in each case).

Diptera was the most abundant group of floral visitors, accounting for 59.57 % (56 individuals) of the total visits. Dipterans were recorded during the whole period of observation, except at 0600 hours and after 2100 hours (Fig. 2b). Three genera of Diptera were recorded: *Borgmeieriphora*, *Megaselia*, and *Puliciphora* (Table 1). Among them, the last one was the most abundant (51 out of 56 individuals; Fig. 2b). In contrast, *Megaselia* and *Borgmeieriphora* dipterans were much less abundant (three and two out of 56 individuals, respectively; Fig. 2b).

The second most abundant group of visitors was Formicidae (Hymenoptera), with 19.15 % visits (18 individuals). Few ants were recorded throughout the whole time of observation (one to three individuals during each period of observation; Fig. 2a).

All other floral visitors were rather scarce (Fig. 2a). Thysanoptera, Collembola and Arachnida represented 6.38 % (six individuals) of visits each; whereas Orthoptera and Hemiptera had only 1.06 % (one individual) of visits each.

Mating system: Under the open pollination treatment, 29 out of 33 flowers produced fruits (87.88 %; Fig. 3). Meanwhile, only eight out of 33 flowers produced fruits under the spontaneous autogamy treatment (24.24 %; Fig. 3). There was a significant effect of pollination treatment on the production of fruits (χ^2= 11.91, gl=1, $P < 0.001$). Average P/O was 3,984.61 ± 310.75 (range: 1586 – 6,083.0).

Table 1. Arthropods collected visiting the flowers of *Stenanona flagelliflora* in "Los Tuxtlas", Veracruz. Unid.= unidentified.

Class	Order	Family	Species
Arachnida	Mesostigmata	Phytoseiidae	Unid.
	Sarcoptiformes	Scheloribatidae	*Scheloribates* sp.
	Trombidiformes	Trombididae	Unid.
	Unid.	Unid.	Unid.
Collembola	Entomobryomorpha	Paronellidae	*Cyphoderus*
			Unid.
	Unid.	Unid.	Unid.
Insecta	Diptera	Phoridae	*Puliciphora* sp.
			Megaselia sp.
			Borgmeieriphora sp.
	Hemiptera	Aphididae	Unid.
	Hymenoptera	Formicidae	*Linepithema humile* Mayr
			Tapinoma litorale Wheeler
			Brachymyrmex heeri Forel
			Brachymyrmex musculus Forel
			Pheidole sp.
	Orthoptera	Unid.	Unid.
	Thysanoptera	Thripidae	Unid.

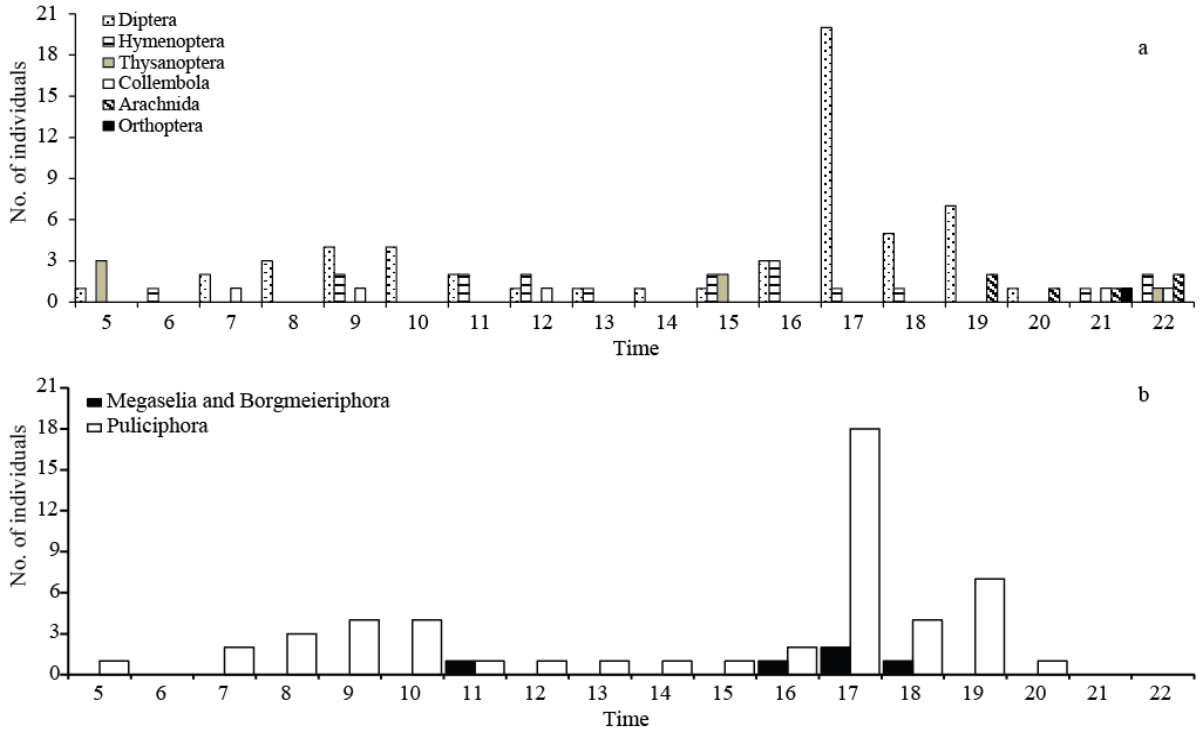

Fig. 2. Frequency of visits of arthropods collected on the flowers of *Stenanona flagelliflora* in "Los Tuxtlas", Veracruz. a) All groups of floral visitors. b) Diptera.

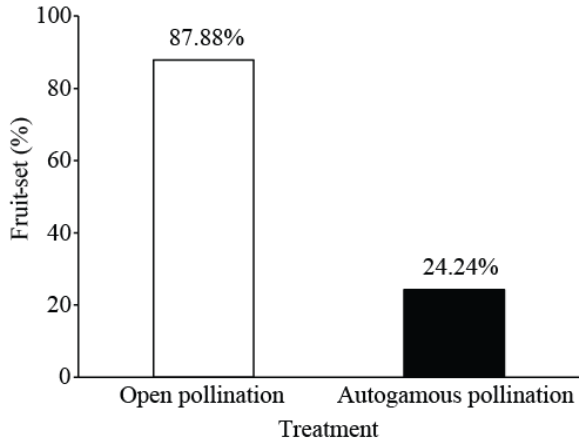

Fig. 3. Fruit-set of *Stenanona flagelliflora* flowers under open pollination (white bar) and spontaneous autogamic pollination (black bar).

Reproductive success: The maximum number of reproductive structures produced by an individual on a single date was 30 (22 buds, 0 flowers and 8 fruits). On the contrary, some plants (23 out of 51 individuals) did not produce a single reproductive structure. The average maximum number of reproductive structures per individual plant was 4.7 ± 0.92. The mean maximum number of buds, flowers and fruits per individual was 3.6 ± 0.7 (range: 0 – 22), 1.0 ± 0.22 (range: 0 – 6) and 1.25 ± 0.28 (range: 0 – 9), respectively. Total number of leaves was the variable that significantly explained the maximum production of reproductive structures ($F_{1, 49}$= 22.23, p< 0.0001, r^2= 0.31) and floral buds ($F_{1, 49}$= 19.94, P < 0.0001, r^2= 0.29; Fig. 4). Moreover, plant height was the variable that significantly explained the maximum production of flowers ($F_{1, 49}$= 20.62, P < 0.0001, r^2= 0.296) and fruits ($F_{1, 49}$= 12.22, P = 0.001, r^2= 0.20; Fig. 4).

A total of 66 out of 139 flowers produced fruits; thus, fruit-set was 47.48 %. Within a single individual, the average fruit-set was 65.88 ± 5.70 %. Out of 139 flowers, 157 monocarps started their development. However, only 93 of them reached maturity; thus, the average percentage of monocarp abortion was 40.76 %. Within a single individual, the average percentage of monocarp abortion was 33.3 ± 5.11 %. At the flower level, from one to five monocarps started their development, but only one to four reached maturity.

Only ten out of the 93 monocarps produced contained seeds (10.75 %). A single seed was recorded within each monocarp. The average seed-set per flower was 4.38 ± 1.55 %.

In average, each monocarp matured in 64.07 ± 4.27 days (range: 15 – 154 days). In those flowers in which more than a single monocarp matured, the second monocarp matured in 36.41 ± 3.0 days after the maturation of the first one. Maturation of a third monocarp required 28.0 ± 0.0 more days in average.

Discussion

Vegetative and floral traits: Vegetative traits of *S. flagelliflora* at Los Tuxtlas are similar to those reported by Schatz & Wendt (2004) from the Uxpanapa population of the species.

Number and viability of pollen grains of *S. flagelliflora* are within the ranges recorded for other Annonaceae species. For instance, species within the genus *Duguetia* have similar number and viability of pollen grains (Silva & Domingues, 2010; Teichert *et al*., 2012) than *S. flagelliflora.* We quantified a single ovule per carpel, and around 32 stamens and four carpels per flower of *S. flagelliflora*. Stamen and carpel number are slightly different from those recorded by Schatz and Wendt (2004; 35 stamens, six carpels); thus, it seems that some among-population variation in floral traits exists. Stamen and carpel number is relatively low when comparing with other species within the family. Actually, flowers from plants within the Annonaceae commonly have numerous stamens and carpels (Küchmeister *et al*., 1998; Kelly, 2000; Maas *et al*., 2007). However, other *Stenanona* species and *Oxandra euneura* are the Annonnaceae species with the fewest number of stamens (12 – 75) and carpels (2 – 30; Webber & Gottsberger, 1995; Schatz & Maas, 2010). Now, *S. flagelliflora* can also be included within the Annonaceae species with fewer stamens and carpels.

It has been suggested that the large number of stamens and carpels in Annonaceae species is associated with the groups of insects that visit their flowers. The most common floral visitors of Annonaceae species are beetles; which usually chew the floral parts. Thus, beetles visit the flowers searching for connective tissue from the stamens, pollen grains and/or stigmatic exudates and are considered voracious floral visitors (Norman & Clayton, 1986; Gottsberger, 1989, 1999; Andrade *et al*., 1996; Küchmeister *et al*., 1998; Carvalho & Webber, 2000; Ratnayake *et al*., 2006a; Gottsberger *et al*., 2011). Therefore, Annonaceae species that are pollinated by beetles usually have large flowers with thick, fleshy petals and numerous reproductive organs (stamens and carpels; Gottsberger, 1989, 1999; Webber & Gottsberger, 1995; Silberbauer-Gottsberger *et al*., 2003). In contrast, Annonaceae species that are pollinated by other groups of insects have flowers of smaller size and with fewer reproductive organs (Norman *et al*., 1992; Webber & Gottsberger, 1995). The most frequent visitor to the flowers of *S. flagelliflora* are Diptera, which have sucking mouthparts (Ollerton, 1999) and visit the flowers searching for nectar, mating sites and/or oviposition sites (Disney & Sakai, 2001; Sakai, 2002; Albores-Ortiz & Sosa, 2006). Adult Diptera do not chew on floral parts (Nagamitsu & Inoue, 1997; Silberbauer-Gottsberger *et al*., 2003; Gottsberger *et al*., 2011); thus, they do not damage the reproductive structures, except when larvae develop within the floral chamber (Disney & Sakai, 2001; Sakai, 2002). Therefore, the small number of stamens and carpels recorded in the flowers of *S. flagelliflora* might be determined by the lack of floral visitors with chewing mouthparts.

Most studies on the reproductive biology of Annonaceae species lack information on the time of maturation of floral buds. We estimated that bud development is completed in around 50 days. A similar period of time is required for bud development in *Anaxagorea prinoides* (Teichert *et al*., 2011). Thus, long bud development is not exclusive of *S. flagelliflora*. Floral anthesis in Annonaceae species is short (2 – 3 days; Gottsberger, 1989; Momose *et al*., 1998; Carvalho & Webber, 2000; Jürgens *et al*., 2000; Ratnayake *et al*., 2006a, 2007; Teichert *et al*., 2011). In contrast, flower anthesis in *S. flagelliflora* lasted between 4 and 11 days. A similar duration of floral anthesis has been recorded in *Asimina parviflora*, another Annonaceae species pollinated by flies (Norman *et al*., 1992). In other families of plants, duration of floral anthesis has been associated with pollinator frequency and effectiveness (Ashman & Schoen, 1994; Schoen & Ashman, 1995). Thus, flowers experiencing fast removal and delivery of pollen last shorter than flowers that are visited less frequently (Proctor & Harder, 1995; Schoen & Ashman, 1995; Clayton & Aizen, 1996). Then, the long anthesis observed in *S. flagelliflora* might be associated with the low frequency of visits (between 0.08 – 0.24 individuals per hour per flower) and pollination effectiveness of its main floral visitors (4.38 % seed set).

Reproductive success, mating system and floral visitors: Mean daily production of flowers in *S. flagelliflora* was very low (1.0 ± 0.22 flowers per day; range: 0 – 6). A similar result has been recorded in *Duguetia cadaverica* (2.5 flowers/individual/day; Teichert, 2008) and *Xylopia* spp. (1 – 8 flowers/individual/day; Webber & Gottsberger, 1999). In contrast, other Annonaceae species produce up to 50 flowers per day (Armstrong & Marsh, 1997; Kiill & Costa, 2003; Teichert *et al*., 2011). Thus, it seems that daily flower production is highly variable among Annonaceae species.

Fruit-set in *S. flagelliflora* was intermediate (47.28 %) in comparison with other Annonaceae species. For instance, species within the genera *Asimina*, *Popowia*, *Unonopsis*, *Xylopia*, and *Uvaria*, have a fruit-set of 1.7 – 8 % (Norman & Clayton, 1986; Nagamitsu & Inoue, 1997; Momose *et al*., 1998; Ratnayake *et al*., 2007; Teichert *et al*., 2009). In contrast, *Annona squamosa* has a fruit-set of 70 % (Kiill & Costa, 2003). Although fruit-set in *S. flagelliflora* was intermediate, seed-set was very low (4.38 %). Likewise, a low seed-set has been recorded in *Popowia pisocarpa* and *Polyalthia littoralis* (2.3 % and 2.5 %, respectively; Okada, 1990; Momose *et al*., 1998). Thus, results from these three species suggest that Annonaceae seem to have a low seed-set. However, there is a lack of studies estimating seed-set in natural populations of Annonaceae; thus, more research is needed in order to state that low seed-set is typical of Annonaceae species.

As for the relationship between resource availability and reproductive success, plant height and total number of leaves had a positive relationship with the production of reproductive structures in *S. flagelliflora*. A positive relationship between plant size and reproductive success has also been recorded in many other plant species (Willson & Schemske, 1980; Escobar *et al*., 1986; Freitas & Kvist, 2000; Susko & Lovett-Doust, 2000; Griffin & Barrett, 2002; Horvitz & Schemske, 2002; McIntosh, 2002; Kolb, 2005).

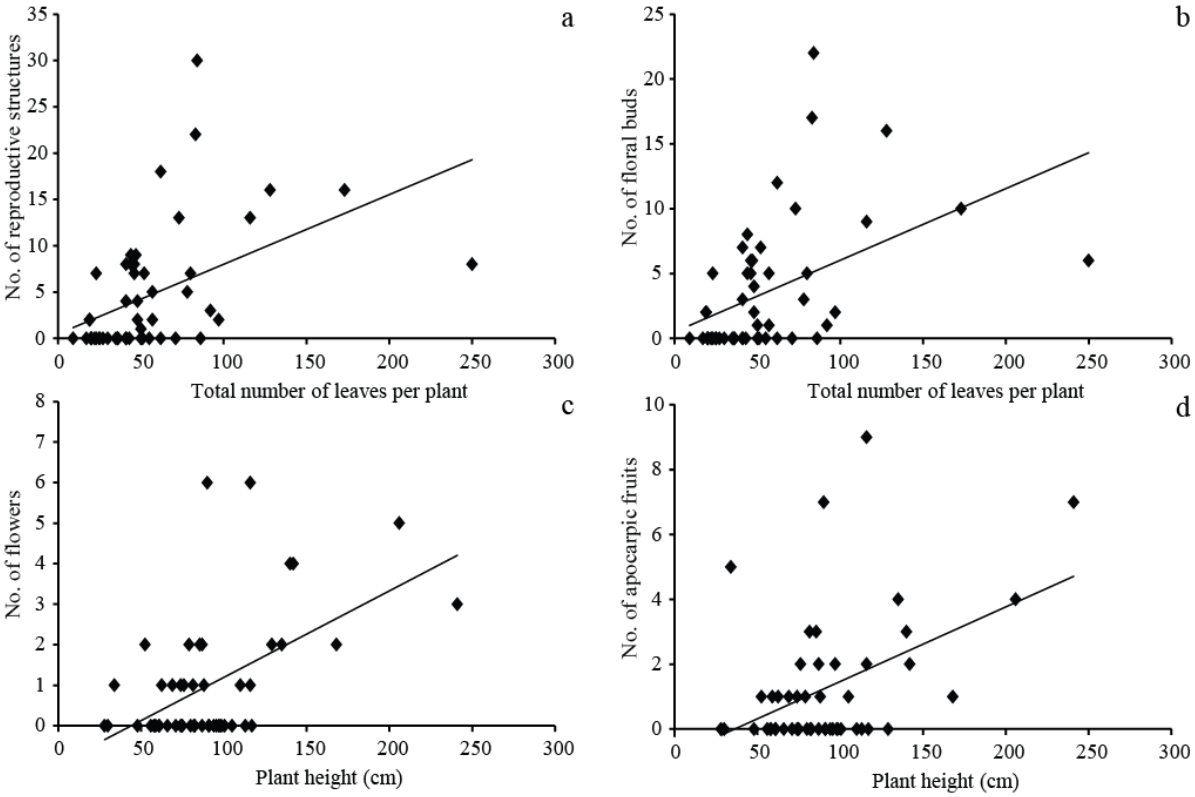

Fig. 4. Regression analyses between variables associated with the reproductive success of *S. flagelliflora* and measures of resource availability (a and b, total number of leaves per plant; c and d, plant height).

The positive relationship between maximum number of reproductive structures and leaf number is particularly interesting for two reasons. First, leaf number is associated with a plant's photosynthetic rate. Thus, it is expected that the higher the number of leaves, the greater the amount of resources available for reproduction; and, consequently, higher reproductive success. In other plant species, leaf number has been found positively correlated with number of fruits, inflorescences, and flowers (Lovett-Doust & Lovett-Doust, 1988; Puentes & Ågren, 2012). Second, leaf damage decreases the photosynthetic area; and, consequently, the amount of resources that can be allocated towards reproduction. Thus, a negative effect of leaf damage on plant reproductive success is expected, as it has been recorded in other studies (Stephenson, 1981; Coley *et al*., 1993; Strauss, 1997; Lethila & Strauss, 1999; Hladun & Adler, 2009; Puentes & Ågren, 2012). Contrary to our expectations, we found a positive relationship between leaf number and production of reproductive structures in *S. flagelliflora*, even when most leaves (74 %) within a single individual were damaged by herbivores, lichens, or both. Actually, it is also surprising to find that individual plants with high percentages of damage (52.63 – 95.12 %) have a 100 % fruit-set, although very low seed-set (0 – 25 %). Therefore, it seems that reproductive success of *S. flagelliflora* is not completely influenced by the availability of resources; instead, it seems to be strongly determined by pollen limitation.

Pollen limitation in *S. flagelliflora* might be attributed to the low efficiency, foraging behavior, and frequency of its most abundant floral visitors. Phoridae and Formicidae had a frequency of visits of almost 60 % (56 individuals) and 19 % (18 individuals), respectively. Phoridae are apterous flies that usually visit the flowers in search of nectar, yeasts, carrion fluids, pollen grains and fungal spores (Brown, 2010). Although these flies are apterous, flagella from different individual plants growth intermixed, favoring the delivery of pollen grains among plants. On the other hand, it has been documented that ants visit flowers to feed from the perianth (Escobar *et al*., 1986; Silva & Domingues, 2010); pollen grains (Ratnayake *et al*., 2006a); small insects; and, other invertebrates (Beattie, 1985). Unfortunately; due to the small size of the flowers (8 – 9 mm in length), the diameter of the floral chamber opening (2 – 5 mm), and the size of both flies (0.5 – 5.5 mm in length; Brown, 2010) and ants (1.25 – 3.5 mm in length; Wheeler, 1905; Naves, 1985; Collingwood *et al*., 1997; Quirán, 2005); we were unable to conduct detailed observations on the behaviour of these two groups of insects while they were inside the flowers. However, most flies were observed among the anthers, on the basal part of the flower; and they were never observed touching the stigmas. Likewise, ants were observed foraging on the apical part of the perianth and did not seem to contact the reproductive organs. Therefore, *S. flagelliflora* might be experiencing pollen limitation since flies and ants seem to be very poor pollinators. Pollen limitation has been recorded in other Annonaceae species with a xenogamous to facultatively xenogamous mating system (Norman & Clayton, 1986;

Norman *et al*., 1992; Momose *et al*., 1998; Ratnayake *et al*., 2006b, 2007); such as the one suggested for *S. flagelliflora* according with its P/O ratio (Cruden, 1977). A consequence of pollen limitation is the decrease in seed production (Norman *et al*., 1992; Nagamitsu & Inoue, 1997; Momose *et al*., 1998); which might be the cause of the low reproductive success of *S. flagelliflora*.

Although other groups of insects were observed (Thysanoptera, Collembola, Arachnidae, Orhoptera and Hemiptera) visiting the flowers of *S. flagelliflora*, their frequency was very low (1 – 6 %). Moreover, most of these groups of insects are not known as pollinators (Proctor & Yeo, 1973; Proctor *et al*., 1996; Ollerton, 1999; Silva & Domingues, 2010). Furthermore, although the flowers of *S. flagelliflora* were visited by several groups of insects, such as it has been recorded in other Annonaceae species (Nagamitsu & Inoue, 1997; Küchmeister *et al*., 1998; Carvalho & Webber, 2000; Silberbauer-Gottsberger *et al*., 2003; Ratnayake *et al*., 2006a, 2007); they have several traits that are associated with fly pollination (Norman *et al*., 1992; Gottsberger, 1999; Silberbauer-Gottsberger *et al*., 2003; Su *et al*., 2005; Gottsberger *et al*., 2011). For instance, the flowers of *S. flagelliflora* are dark purple - red in colour, grow on the surface of the ground (Schatz & Wendt, 2004); produce stigmatic exudates (Corona, 2012) and pollen grains (Endress & Doyle, 2009) as rewards for their pollinators; and form a floral chamber (Gottsberger, 1989, 1999; Silberbauer-Gottsberger *et al*., 2003; Gottsberger *et al*., 2011; Teichert *et al*., 2011). The presence of these traits in *S. flagelliflora* suggests the existence of a fly pollination syndrome, as it has been recorded in other Annonaceae species (Norman *et al*., 1992; Silberbauer-Gottsberger *et al*., 2003).

Finally, two phenomena observed in *S. flagelliflora* seem to be associated with the low reproductive success of the species. First, most monocarps lacked seeds, suggesting the formation of parthenocarpic fruits; as it has been recorded in other plant families (Jordano, 1988; Sato *et al*., 2001; Ramos-Ordoñez *et al*., 2008). Parthenocarpic fruits might form as a consequence of resource limitation, abortion of embryos, pollen limitation, failure of pollen tubes to grow after pollination, thermic stress, and hormonal changes (Gillaspy *et al*., 1993; Ercan & Akilli, 1996; Sato *et al*., 2001). In *S. flagelliflora*, the formation of parthenocarpic fruits and the poor reproductive success might be explained by the existence of pollen limitation caused by the low frequency of visits and effectiveness of its pollinators, as it was discussed above.

Second, sexual reproduction in *S. flagelliflora* is poor; thus, one might expect that some strategy of asexual reproduction exists. In the studied population of *S. flagelliflora*, roots and leaves growing from the distal part of the flagelliflorous branches were observed (Campos-Villanueva, Figueroa-Castro, Xicohténcatl-Lara, *pers. obs.*). This suggests that flagelliflorous branches might have an important role on vegetative growth, such as some authors have indicated (Schatz & Wendt, 2004; Teichert, 2008; Schatz & Maas, 2010). It is possible that *S. flagelliflora* might reproduce asexually in order to compensate its limited success through sexual reproduction. However, more studies are needed in order to corroborate any of these ideas.

In conclusion, our results suggest that *S. flagelliflora* has a xenogamic mating system, meaning that the production of fruits and seeds depends upon pollen vectors. Although fruit-set was not very low, most fruits lacked seeds; suggesting that floral visitors are not effective pollinators. Because sexual reproduction of *S. flagelliflora* is poor, it is possible that the species might have developed some mechanisms of asexual reproduction. Moreover, our results suggest that reproduction in *S. flagelliflora* is not limited by the availability of resources. Instead, it seems that the low effectiveness of pollinators is the main factor determining the poor reproductive success of *S. flagelliflora*.

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