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Floral visitors of *Inga marginata* Willd. (Mimosaceae) in a coffee agroecosystem of Quindío, Colombia

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Abstract: Floral characteristics, nectar production and floral visitors were studied in three individuals of *Inga marginata* in a Colombian coffee agroecosystem. In October 2011, ten inflorescence buds per plant were marked and observed every two hours until the flowers senesced. Nectar standing crop was measured and focal observations of flower visiting insects were carried out. *Inga marginata* was a mass-flowering species and produced flowers twice a year, with a synchronic flowering period between trees. Nectar production was low, and no significant differences between day and night were found. 565 individuals in 23 species and four orders of insects were recorded with a higher frequency of nocturnal over diurnal visits. Beetles were the most frequent (56.6 %) and were represented by 15 species and seven families, but only 15 % were potential legitimate visitors. Our observations did not support pollination by bat species, which has been considered for *I. marginata* in previous studies.

Key words: Agroecosystems, flowering, *Inga*, insects, interactions, nectar production, phenology.

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Introduction

The genus *Inga* comprises about 300 exclusively Neotropical legume tree species, which have alternate, parapinnately compound leaves with extrafloral nectaries and large floral displays (Koptur 1983). The flowers are arranged in raceme-shaped inflorescences at the apices of the branches, they are composed of many brush-type flowers with reduced perianth parts, and numerous white stamens fused at the base. These stamens are the main mechanism of visual attraction and they form a tube within which nectar accumulates (Pennington 1997). *Inga* trees have a massive flowering pattern that attracts diverse visitors such as birds, insects and mammals (Greenberg *et al.* 1997; Koptur 1983, 1984; Marín-Gómez 2008; Marín-Gómez & García 2007; Stevenson 2000). These trees have a generalized pollination system with hummingbirds, bats, moths, bees, butterflies and beetles as the most important visitors and pollinators, but there are quantitative data only for a few species (Amorim *et al.* 2012; Koptur 1983;

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Marín-Gómez *et al.* 2011).

Inga marginata Willd. is a Neotropical tree species that can reach up 20 m in height. It is a common species from Mexico to Argentina, but with low population density (Pennington 1997). The species ranges from 0 to 1950 meters above sea level (masl) and inhabits disturbed primary forests, gallery forest, lowland and montane rainforest, and along riversides and roads. It is used for its edible fruits, wood, and is commonly planted as a shade tree in coffee plantations (Pennington 1997). Additionally, its fruits are consumed by the Blue Manakin in southeastern Brazil (Hasui *et al.* 2009), and evidence suggests they may also be eaten by primates (Stevenson 2000). The seedlings and fruit pulp are consumed by the rodent *Agouti paca* (Beck-King *et al.* 1999), and *Cebuella pygmaea* has been observed consuming its exudates in the Ecuadorian Amazon (Yépez *et al.* 2005). The flowers are consumed by *Didelphis albiventris* (Cantor *et al.* 2010) and they are also used by social and euglossine bees (Wilms *et al.* 2012). Furthermore, larvae of some butterflies eat young leaves of *I. marginata* (Kursar *et al.* 2009).

Despite its wide distribution and ecological importance, there are few recent studies concerning *I. marginata* and most of them are focused on herbivory (Kursar *et al.* 2009) and its effect on plant fitness (Bixenmann *et al.* 2012). Community studies include dispersal syndromes (Kinoshita *et al.* 2006), soil relationship and nitrogen inputs (Pereira-Silva *et al.* 2012) and ecophysiology (Matsubara *et al.* 2008; Palow *et al.* 2012). Concerning floral visitors, Wilms *et al.* (2012) found that pronounced mass-flowering of *I. marginata* attracted five species of bees. Although it has been considered that the species is pollinated by bats (Fleming *et al.* 2009), no studies have assessed floral phenology or pollinators of *I. marginata*, and so there is no evidence supporting this observation. Accordingly, the aim of this paper is to describe the floral biology, nectar production, and floral visitors of this *Inga* species.

Materials and methods

Study area

The study site was at *Finca El Oasis* Nature Reserve (4º 30´ N; 75º 36´ W), in the municipality of Córdoba (Quindío, Colombia), between 1600 and 1800 m. This reserve has an area of 60 ha, 20 ha of which are used for conservation of a native and a planted forest, respectively, and another 20 ha are planted with coffee shrubs shaded by tree species, among which *Inga, Erythrina*, *Ochroma*, *Cordia, Cecropia*, *Croton* and *Hamelia* are the most abundant genera.

Floral Biology

In October 2011, floral development and phenology were monitored for three individuals. We marked buds on 10 inflorescences per plant, which were subsequently observed every two hours until the flowers senesced, and changes in size, form and coloration were recorded. We measured the floral dimensions suggested by Koptur (1983) in 30 different flowers of the same trees. Nectar availability (standing crop) was evaluated by measuring the nectar volume from 120 randomly sampled flowers exposed to visitors, using 5 µl graduated microcapillary tubes. Ten flowers were sampled from two trees during the day (07:00 - 10:00 h and 15:00 - 18:00 h) and at night (19:00 - 20:00 h and 02:00 - 05:00 h). Voucher specimens were deposited in the *Herbario de la Universidad del Quindío* (HUQ).

Flower visitors

Focal observations of insects were carried out on two trees. A total of 60 inflorescences were sampled during the day (07:00 -10:00 h and 15:00 - 18:00 h) and night (19:00 - 20:00 h and 02:00 - 05:00 h). Each inflorescence was monitored only once for every observation period (one hour), checking five different inflorescences for 10 min each. For each observation period, we recorded the hour, insect morphospecies, number of flowers visited, resource consumed (nectar or pollen), and foraging behavior: potential legitimate visitors, thieves, and florivorous (Marín-Gómez & García 2007), and the movement between inflorescences.

Data analysis

The Kruskal-Wallis test was used to compare the nectar standing crop at different times over a 24 hour period. The number of insect visits between day and night was compared using the Mann-Whitney Wilcoxon test. The Spearman correlation coefficient was used to evaluate the association between the nectar standing crop and number of insect visits during the day and at night. Statistical analyses were processed in INFOSTAT package (Di Rienzo *et al.* 2012).

Table 1. Composition and number of insect visits on inflorescences of *I. marginata* in a Colombian shade coffee agroecosystem. Resources used: Pollen (Pol), Nectar (Nec), Reproductive structures (RS). Foraging strategies: Potential legitimate visitor (LV), Nectar thief (NT), Pollen thief (PT), Florivorous (Flo).

	07:00 - 18:00 h	19:00 - 05:00 h	Resource	Foraging strategy
Coleoptera				
Cantharidae				
Chauliognathus sp.		19	Pol	LV
Chrysomelidae				
Bruchinae		8	RS	Flo
Criocerinae		5	Pol	PT
Eumolpinae		11	Pol	PT
Diabrotica sp.1		45	Pol	PT
Diabrotica sp. 2		8	Pol	PT
Galerucinae sp. 1		15	Pol	PT
Lamprosomatinae sp. 1		18	Pol	PT
Lamprosomatinae sp. 2		5	Pol	PT
Scarabaeidae				
Callistethus caucanus		33	RS	Flo
Paranomala undulata		92	RS	Flo
Nitidulidae		5	Pol	PT
Staphylinidae				
Aleocharinae		2	Nec	LV
Quedius sp.		46	Pol -Nec	LV
DIPTERA				
Culicidae	4	4	Nec	NT
Drosophilidae	10		Nec	NT
HYMENOPTERA				
Apis mellifera	18		Nec	LV
Polistinae		13	Nec	NT
LEPIDOPTERA			Nec	
Astraptes sp.	3		Nec	LV
Arctiidae		16	Nec	LV
Gelechiidae		110	Nec	LV
Geometridae (larvae)		8	RS	Flo
Siproeta epaphus	67		Nec	LV
Total	102	463		

Results

Floral biology

Inga marginata was confirmed to be a mass-flowering species and produced flowers twice a year. A synchronic flowering period lasting 14 days was observed among the trees. The species exhibited a typical *Inga* brush-type inflorescence organized in erect racemes of 82 to 96 flower buds. The inflorescence development was acropetalous, with 18 to 26 flowers produced per day. Flowers were white, had a reduced perianth (12 ± 0.8 mm, N = 30), dark green tubular calyx (4.9 ± 0.6 mm, N = 30), with a single pistil and numerous stamens (92 ± 32.1 mm, N = 30) fused at the base forming a narrow tube (length: 6.9 ± 0.1mm; width: 0.8 ± 0.1 mm, N = 30). Pistil length, at 1.2 ± 0.7 mm (N = 30), was greater than that of the stamens.

Anthesis lasted 20 h, and flower opening began at 12:00 h with a slow enlargement of the reproductive structures. Flowers fully opened in the afternoon, around 16:00 h, with the pistil and stamens then totally expanded. During anthesis, flowers gave off a slightly sweet scent. Individual flowers opened every day and remained open for 20 hours. Flower senescence was characterized by wilting of stamens, but the pistil remained erect. After 48 h, the flowers fell from the inflorescence. Nectar secretion started during pre-anthesis. Nectar secretion was variable and averaged 0.05 to 0.14 µl over time with production peaking from 20:00 to 03:00 h. Nectar production was generally low, and while it increased at night, no significant differences between periods were found (H: 0.15; gl = 11; P = 0.13) (Fig. 1). Despite the low nectar production, a positive correlation between standing crop and the number of nectar-consuming insects was found (rs = 0.74, P = 0.01, N = 12).

Flower-visiting insects of Inga marginata

During 12 h of observations, 565 insects were recorded, with a higher frequency of nocturnal over diurnal visits (H = 21, N = 36, P = < 0.01; Table 1). The average number of visits per inflorescence was 25 insects (± 23) at night, and seven (± 8.5) during the day. Insects belonged to 23 species of Coleoptera, Diptera, Hymenoptera, and Lepidoptera. Potential legitimate visitors showed two activity peaks during the morning between 08:00 and 10:00 h (butterflies), and at night between 02:00 and 03:00 h (beetles: Staphylininae, Aleocharinae, and Chauliognathinae). In contrast, nectar robbing and florivory only occurred at night (Fig. 2).

Beetles were the most frequent visitors (56.6 %) with 15 species and seven families. In this group, 42 % of the visits were from species consuming pollen (9 species); these were considered to be pollen thieves because they stayed on the same inflorescences and in some cases consumed anthers. Another 42.6 % of visitors (three species) were florivorous and consumed anthers, stamens, and styles. Only 15 % were potential legitimate visitors (Staphylinidae and Cantharidae) and they moved actively between nearby inflorescences, making contact with the stigma and stamens.

Moths comprised 22.3 % of the visitors; in this group, adults consumed the nectar and Geometridae larvae were florivorous of reproductive structures. By contrast, *Siproeta epaphus* and *Astraptes* sp., which represented 12.4 % of the visits, only consumed nectar. They are considered legitimate visitors because they not only contacted floral reproductive parts, but moved between inflorescences. Their visits were short, lasting from 1 s to 70 s per inflorescence, and they were most active between 08:00 to 10:00 h. Hymenopterans (*Apis mellifera* and Polistinae) were occasional visitors, accounting for 5.5 % of the visits. They fed on nectar, but only the honeybees were potential legitimate visitors. Dipterans (Culicidae and Drosophilidae) were rare visitors (3.2 %) and they fed on nectar in the morning.

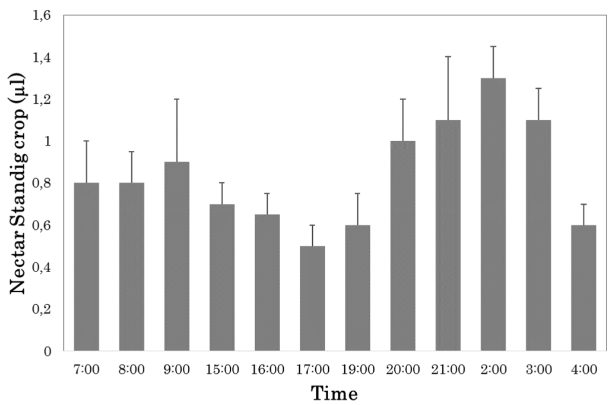

Fig. 1. *Inga marginata* nectar production in flowers exposed to visitors between observation periods in the morning and at night.

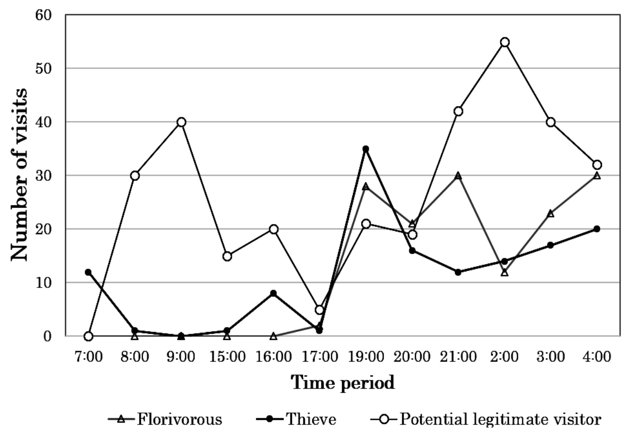

Fig. 2. Distribution of number of insect visits to *I. marginata* inflorescences over time, according to foraging behavior.

Discussion

Mass-flowering in *I. marginata* may be advantageous in attracting pollinators (Engel & Martins 2005; Gentry 1974) principally because of the species' low population density and short bloom periods (Koptur 1984). However, after some flowering periods, no fruits were found to be forming in any sampled tree. Low fruit set seen here is similar to that observed in other *Inga* species, which despite flowering continuously throughout the year and blooming massively during the flowering peaks, produce few fruits (Amorim *et al.* 2012; Barros *et al.* 2013; Koptur 1984). In spite of the high visit frequency of insect visits on some *Inga* species (Cruz-Neto *et al.* 2011), self-pollination is likely to be a common occurrence for most flowers (Amorim *et al.* 2012), because although insects move pollen between flowers or even between inflorescences (geitonogamy), pollen of another tree is required to achieve pollination (Barros *et al.* 2013). Therefore, non-production of fruits in this case would not be explained by the pollinator limitation hypothesis (Koptur 1983, 1984), as a high frequency of insect visits was observed. By contrast, other mechanisms as self-compatibility (Amorim *et al.* 2012), geitonogamy (Barros *et al.* 2013), pollen limitation (Koptur 1984), flower predation (Marín-Gómez 2011), or even distance between trees may be negatively affecting fruit production.

Insect visitation in our study was positively related to nectar production, indicating that changes in nectar quantity may affect patterns of visitation activity. Similarly, Amorim *et al.* (2012) observed this relationship between nectar secretion and frequency of pollinator visits in the congener *I. sessilis*, and Cruz-Neto *et al.* (2011) found the same between hawkmoth abundance and flowering of three *Inga* species. Some *Inga* species are susceptible to flower visitor activity both during the day and at night (Amorim *et al.* 2012). However, *I. marginata* showed higher insect activity at night, in contrast to *I. edulis* and *I. ornata,* on which most visitors were diurnal (Marín-Gómez & García 2007; Marín-Gómez *et al.* 2011). Wilms *et al.* (2012) found *Melipona rufiventris, Partamona helleri* and three more species as frequent visitors and potential pollinators of *I. marginata*, but no bee species other than *Apis mellifera* were found in this study. Rather, Coleoptera was the most abundant and diverse group with nocturnal activity. Although beetles are pollinators of some plant species (Beath 1996); they may be also thieves and florivorous in others, as has been reported in *Inga* (Marín-Gómez & García 2007) and observed in this study.

Although we observed bats visiting inflorescences of *I. marginata*, those observations did not support pollination by bat species, as has been previously reported (Fleming *et al.* 2009). Bats were not seen consuming nectar in our sample. It can also be noted that the morphology, size and rewards of *I. marginata* flowers are all inconsistent with the chiropterophyly syndrome. *Inga marginata* produces very low nectar quantities, its flowers are too small and its tube too narrow for a bat to insert its tongue to get nectar. To be effective, pollination depends on the match between particular characteristics of flowers and pollinator morphology and behavior (Amorim *et al.* 2012). Moreover, it is necessary to understand the reproductive system of the plant and other aspects of its floral biology such as the relationship between pollen and ovule production (Barros *et al.* 2013). Finally, although this study was based on observations of only three trees, the results obtained here constitute a first approximation to the study of the floral biology of *I. marginata*, and a baseline of quantitative data from which to infer the role of insects in its pollination.

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