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Nectar Sugar Composition and Flower Visitors for the Naturalized Exotic *Lantana camara* (Verbenaceae) at Central Argentina

Carolina Torres & Leonardo Galetto[1]

Instituto Multidisciplinario de Biología Vegetal (UNC-CONICET), Casilla de Correo 495, 5000 Córdoba, Argentina.
Cátedra de Diversidad Vegetal II, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Argentina.

[1]**e-mail:** leo@imbiv.unc.edu.ar

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ABSTRACT

The aim of this work is to describe and quantify the flower visitors of the invasive *Lantana camara* L. (Verbenaceae) at the Chaco forest, and to analyze possible relations between nectar sugar composition and the main pollinators for this species. Volumes of nectar and sugar concentration were measured in six different populations of the naturalized exotic *L. camara* in Central Argentina. Quantitative nectar sugar composition was determined and compared between populations. In general, nectar sugar concentration ranged between 25-28% and volume per flower was very low (<1µL). Nectar sugars are glucose, fructose and sucrose for all populations, but hexoses clearly predominate over sucrose. Different insects were registered visiting the inflorescences. The more frequent pollinators were many species of diurnal butterflies, honeybees and bumblebees. A diverse insect assemblage visiting flowers of L. camara guarantees a high fruit production which can be related to the invasion process of this species in the Chaco region from Central Argentina.

Keywords: Nectar sugar composition, butterflies, bumblebees, honeybees, invasive species

INTRODUCTION

The probability of successful establishment by alien species and their spread through novel environments may be enhanced by ecological interactions as pollination and seed dispersal (Ghazoul 2002). Insects are usually involved in plant reproductive processes, mainly as pollinators. The woody shrub *Lantana camara* L. (Verbenaceae) is typically butterfly-pollinated (Barrows 1976, Andersson & Dobson 2003), which is native to tropical and subtropical America, and naturalized as an invasive species in other areas of America, Asia and Africa (e.g., Denton *et al.* 1991, Morton 1994, Baars & Neser 1999, Ghazoul 2005, Grilli & Galetto 2009). This species invades pasture, crops and native ecosystems, causing economic losses, environmental degradation, and the exclusion of native plants (Goulson & Derwent 2004). The leaves are toxic when ingested by most domestic livestock or native mammals, although toxicity varies greatly between strains (Johnson & Jensen 1998, Tokarnia *et al.* 1999). In tropical regions of the world, *L. camara* produces flowers and seeds almost year round (Barros *et al.* 2001, Ghazoul 2005). This species produces a high number of fruits per plant that are dispersed by animals (Kohli *et al.* 2006).

Lantana camara is a nectar plant for several tropical butterfly species and their flowers last three days and change colour from yellow newly-opened flowers to ageing orange, scarlet and magenta flowers in the same inflorescence (Barrows 1976, Ram & Mathur 1984). The shifts in petal colouration are caused because of the appearance of anthocyanin and pigment changes can be mediated by pollen addition on the stigma (Ram & Mathur 1984, Andersson & Dobson 2003 and references therein). Newly-opened, yellow flowers produce nectar

during the first day (Barrows 1976, Barros *et al.* 2001, Goulson & Derwent 2004). This species is self-incompatible (Barrows 1976, Barros *et al.* 2001, Goulson & Derwent 2004), and not capable of autonomous self-pollination (Hamm 2012). Available published data for *L. camara* nectar indicate that each flower produces less than 2µL (range 0.1 to 1.5 µL) in a concentration of 18-30% (Barros *et al.* 2001, Carrión-Tacuri *et al.* 2012). Nectar removal by floral visitors had a pronounced effect on the total amount of nectar secreted by *L. camara* but not on its sugar concentration (Carrión-Tacuri *et al.* 2012). As far as we know, no quantitative data on nectar sugar composition in *L. camara* are published (but see Bahadur *et al.* 1986 for qualitative sugar composition).

Plants of *L. camara* produce high fruit crops at the Chaco forest from Central Argentina, and fruit removal is fast and complete after several weeks by birds as primary dispersal agents or ants as secondary ones (Grilli & Galetto 2009, Ponce *et al.* 2012). No data on pollination biology are available for this invasive species in the Chaco forests. Nectar traits as volume, concentration and sugar composition can be related to pollinators (Baker & Baker 1983, Galetto & Bernardello 2005). Although these nectar–pollinator associations are questioned (van Wyk 1993, Perret *et al.* 2001, Galetto & Bernardello 2003), more specialized, insect-pollinated flowers tend to show high sucrose nectars whereas non-specialized flowers, high-hexose nectars (Petanidou 2007 and references therein). The aim of this work is to describe and quantify the flower visitors of the invasive *L. camara* at the Chaco forest, and analyze possible relations between nectar sugar composition and the main pollinators for this species.

MATERIAL & METHODS

Samples of nectar and data on floral visitors were obtained from living plants of naturalized populations of *L. camara* at the Chaco forest from Argentina, Córdoba Province, Dept. Santa Maria: Los Aromos. Floral visitors were recorded on populations of several flowering individuals, totalizing 30 h of observations during December to March. Focal observations of animals visiting the flowers were carried out by observation from fixed points and, alternatively, by observations at random walks. Observation from a fixed point was characterized by the selection of 10 inflorescences of a focal individual during 15 min periods. During random observations, flower visitors were observed along tracks of approximately 200 m each. Visitors were considered as pollinators if they touched anthers and stigma when visiting the flowers. Two nectar variables were measured in the field: volume of nectar using graduated microcapillaries, and sugar concentration (percentage sucrose, w/w) with a pocket refractrometer (Atago®, Tokyo, Japan, 0-32%).

Nectar sugar composition was compared in nectar samples taken from flowers of one individual of each population. Nectar drops were placed on Whatman #1 chromatography paper and quickly dried; in the laboratory, nectar was re-dissolved and sugar separation was accomplished by gas chromatography. Nectar was lyophilized and silylated according to Sweeley *et al.* (1963). The derivatives were then injected into a Konik KNK 3000-HRGS gas chromatograph equipped with a Spectra-Physics SP 4290 data integrator, a flame ionization detector, and a SE 30 capillary column (30 m long, 0.25 mm diameter and 0.25 µm thickness of the inner pellicle). Nitrogen was the carrier gas (2 ml/min) and the following temperature program was conducted: 200ºC/1 min, 1ºC/min until 208ºC, 10ºC/min until 280ºC for 2 min. Carbohydrate standards (Sigma Chem.) were prepared using the same method.

RESULTS

Nectar volume per flower was very low (less than 1µL) and nectar concentration was ca. 27% (Table 1). Nectar sugars were glucose, fructose and sucrose for all the samples (Table 1). Hexoses clearly predominate over sucrose (Table 1).

Different insects were registered visiting the inflorescences of *L. camara* (Table 2). The more frequent pollinators were many species of diurnal butterflies, honeybees and bumblebees (Table 2, Fig 1). Usually, central yellow flowers were probed first by insects (Fig 1 A, B, D, E) but many pollinators then visited the other flowers of the inflorescence (Fig. 1 C, F).

DISCUSSION

Lantana camara is a preferred nectar plant for several tropical butterfly species (Barrows 1976, Ram & Mathur 1984, Andersson & Dobson 2003). Fuhro *et al.* (2010) have recorded 20 species of diurnal butterflies visiting *L. camara* in Southern Brazil, but *Agraulis vanillae* was the most frequent. In contrast, the main pollinator of *L. camara* throughout a substantial portion of its Australian range appears to be

Table 1 — Nectar volume, concentration, and sugar composition in different populations of *Lantana camara* from Central Argentina.

Populations	Volume per flower (µL)	Concentration (%)	Sugars (%) Sucrose	Fructose	Glucose
1	<1	27	12.2	36.7	51.1
2	<1	26	19.5	33.2	47.3
3	<1	28	19.6	34.3	46.1
4	<1	27	27.2	36.7	36.1
5	<1	27	24.7	38.9	36.4
6	<1	28	20.4	35.3	34.3
Overall	<1	27.2 ± 0.8	20.6 ± 4.6	35.8 ± 2.1	41.9 ± 7.1

Apis mellifera (Goulson & Derwent 2004). Lepidoptera and honeybees were registered for the Chaco region, as well as Diptera. In addition, *L. camara* is capable of utilizing different pollinators throughout its range, including hummingbirds and moths (Hamm 2012, Carrión-Tacuri *et al.* 2012). This species flowers during more than six months in the Chaco forests, during the rainy season (spring and summer). This

Table 2 — Number of recorded visits of flower visitors of *Lantana camara* at the Chaco forests from Central Argentina.

Order	Family	Species	Frequency (30 h of observations)
Diptera	Syrphidae	sp. 1	4
	Tachinidae	sp. 1	7
Hymenoptera	Apidae	Apis mellifera	234
		Bombus morio	26
	Halictidae	Augochloropsis sp.	6
	Vespidae	Brachygastra lecheguana	4
		Polystes sp.	9
Lepidoptera	Hesperiidae	Hesperiinae:	
		Hylephila sp.	11
		Eudaminae:	
		Chioides sp.,	23
		Erynnis sp.	15
	Lycaenidae	Thecla sp.	26
	Nymphalidae	Agraulis vanillae	17
		Dione sp.,	8
		Hypanartia bella	4
		Phyciodes sp. 1	7
		Phyciodes sp. 2	9
	Noctuidae	sp. 1	5
	Papilionidae	Papilio thoas	7
	Pieridae	Colias lesbia	11
	Pyralidae	Hypsipyla sp.	6
	Riodinidae	Calospila sp.	26
	Zygaenidae	Zygaena sp.	3

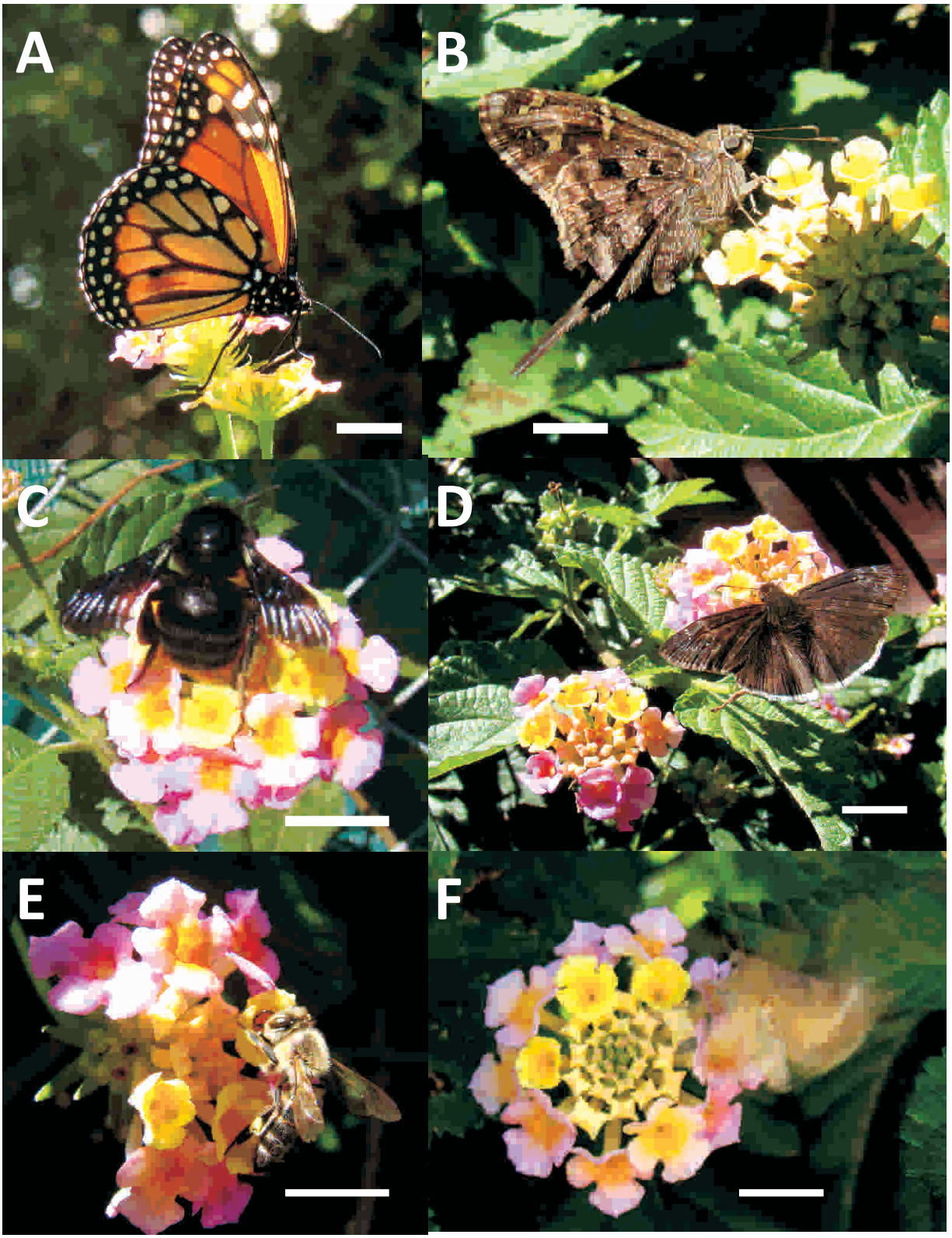

Fig. 1 — Pollinators of *Lantana camara* registered in Central Argentina. A. *Agraulis vanillae*, B. *Chioides* sp., C. *Erynnis* sp., D. *Bombus morio*, E. *Apis mellifera*, E. *Noctuidae* sp. 1. Bars = 1 cm.

species can be considered as a pollinator generalist within the Chaco region, trait that may contribute to its success as an invasive species.

Flower adaptions to their pollinators have been found in nectar chemistry (Baker & Baker 1983, 1990); for example, some correlations between nectar sugar proportions and different types of pollinators. As regards for some species of butterflies, experimental data showed that females preferred nectar with higher amino acid concentrations (e.g. Alm *et al.* 1990, Erhardt & Rusterholz 1998, Mevi-Schütz & Erhardt 2002), and male and female *Ornithoptera priamus* butterflies clearly preferred a sucrose over a glucose solution of an equal concentration of 25% (Erhardt 1992). Nevertheless, *L. camara* received most visits from different species of butterflies but showed predominance of hexoses over sucrose in its nectar sugar composition. It is important to note that experimental data was obtained for a limited number of butterfly species and preferences for nectar with sucrose predominance cannot be generalized. The generalist *Apis mellifera* can collect nectar of very different sugar compositions because this species can modify sugars by hydrolysis during the conversion of nectar to honey (von der Ohe 1994). Thus, the high frequency of honeybees observed on *L. camara* flowers in the Chaco region is not surprising and coincides with data from Australia (Goulson & Derwent 2004). In the context of the invasion theory, nectar sugar composition can be one of the important traits that the exotic plant would be using to attract a wide array of pollinators. Sugar composition of *L. camara* seems to be in accordance with preferences of many pollinator species and this trait may be favoring fruit and seed production.

Lantana camara is considered to be among the world's 10 worst weeds but the consequences of the invasion process at the ecosystem level are little understood (Sharma *et al.* 2005). The success of *Lantana* as an invader species in the Chaco region is related to ecological interactions as pollination and seed dispersal (Grilli & Galetto 2009, this work). Animal-plant interaction webs across Chaco region will be irreversibly related to the spread of flowering and fruiting plants such as *L. camara*, because this species interacts with many animal species and displays extended flowering and fruiting periods. Predicting *L. camara* invasion is complicated but the development of some tools, as the management of honeybee hives suggested by Goulson & Derwent (2004) for Australian plant populations, may provide an important tool for control *L. camara* fruit and seed production. This plant species is considered to be a weed of international significance because of its widespread distribution and substantial impact on agriculture, forestry, and biodiversity (Sharma *et al.* 2005). New studies are urgent and necessary to better understand the functional pathways or mechanisms that underlie the invasion process and its impacts on the ecosystem. This knowledge may contribute to the eradication or the control of *L. camara* populations in the Chaco region.

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