



Food source quality and ant dominance hierarchy influence the outcomes of ant-plant interactions in an arid environment



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ABSTRACT

In this study, we conducted a series of experiments in a population of *Vachellia constricta* (Fabaceae) in the arid Tehuacan-Cuicatlán valley, Mexico, in order to evaluate if the food source quality and ant dominance hierarchy influence the outcomes of ant-plant interactions. Using an experiment with artificial nectaries, we observed that ants foraging on food sources with higher concentration of sugar are quicker in finding and attacking potential herbivorous insects. More specifically, we found that the same ant species may increase their defence effectiveness according to the quality of food available. These findings indicate that ant effectiveness in plant protection is context-dependent and may vary according to specific individual characteristics of plants. In addition, we showed that competitively superior ant species tend to dominate plants in periods with high nectar activity, emphasizing the role of the dominance hierarchy structuring ant-plant interactions. However, when high sugar food sources were experimentally available *ad libitum*, the nocturnal and competitively superior ant species, *Camponotus atriceps*, did not dominate the artificial nectaries during the day possibly due to limitation of its thermal tolerance. Therefore, temporal niche partitioning may be allowing the coexistence of two dominant ant species (*Camponotus rubritorax* during the day and *C. atriceps* at night) on *V. constricta*. Our findings indicate that the quality of the food source, and temporal shifts in ant dominance are key factors which structure the biotic plant defences in an arid environment.

1. Introduction

Within the wide variety of ecological interactions between ants and plants in the tropics, the most well-documented associations are those involving plants with extrafloral nectaries (EFN-bearing plants) (Rico-Gray and Oliveira, 2007). In this type of association, ants obtain a sugary food source from plants in exchange for protection against potential herbivores, which is recognized as a biotic defense (Heil and McKey, 2003; Rico-Gray and Oliveira, 2007). Extrafloral nectar (EFN) is a highly nutritious resource documented in more than 3000 species of tropical plants (Aguirre et al., 2013; Weber and Keeler, 2013) and consists basically of water, glucose, fructose, sucrose and small amounts of amino acids (González-Teuber and Heil, 2009; Wäckers, 2001). Although the basic composition of nectar sugars does not change in most plant species (González-Teuber and Heil, 2009; Heil, 2015; Del-Claro

et al., 2016), the quality (e.g., proportion of sugars) and quantity (e.g., rate of nectar production) of EFNs may vary due to different biotic and abiotic factors, such as: period of the day (Anjos et al., 2016; Dáttilo et al., 2015; Falcão et al., 2014; Heil et al., 2000), intensity of herbivory (Heil et al., 2001; Ness, 2003), availability of soil water and nutrients (Pringle et al., 2013), genotypic differences (Wooley et al., 2007) and plant ontogeny and phenology (Miller, 2014; Queiroz et al., 2013; Quintero et al., 2013). Therefore, once EFNs are considered as a highly nutritious resource for ants, it is expected that any changes in their quantity and composition may affect the outcome of ant-plant mutualisms (Rico-Gray and Oliveira, 2007).

In arid and semi-arid environments, the marked contrast in temperature and humidity between day and night (Fitzpatrick et al., 2014) and between seasons (Aranda-Rickert et al., 2014) seems to strongly affect the quality and quantity of EFNs and the outcomes of ant-plant

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interactions (Oliveira and Brandão, 1991; Oliveira et al., 1999; Fitzpatrick et al., 2014; Rico-Gray and Oliveira, 2007). Such variation in the characteristics of nectar occurs mainly due to the high rates of evapotranspiration in dry environments which makes the production and secretion of EFN metabolically more costly for plants and therefore more variable over time (Fitzpatrick et al., 2014). As a result, an increase in the quality and quantity of extrafloral nectar (Radhika et al., 2008) seems to be restricted to periods when herbivore pressure is higher (usually overnight) and in more palatable tissue (e.g. immature leaves) (Dáttilo et al., 2015; Falcão et al., 2014; Millán-Cañongo et al., 2014), according to “Optimal Defense Theory” (McKey, 1979, 1974).

Foraging activity of ants on EFN-bearing plants depends mainly on the quality and quantity of nectar available (Blüthgen and Fiedler, 2004a; Lange et al., 2017), as well as the specific nutritional and physiological needs of each ant colony (Byk and Del-Claro, 2011; Díaz-Castelazo et al., 2004). Moreover, the effective protection against potential herbivores offered by ants largely depends on their intrinsic aggressiveness (Campos and Camacho, 2014; Ness et al., 2010). Additionally, it is known that the activity and aggressiveness of ants foraging on plants may decrease in sugarless food sources (Fitzpatrick et al., 2014; Grover et al., 2007). Therefore, the protection efficiency offered by ants and their foraging activity (in terms of abundance and richness) on plants seems to be context-dependent and directly related to the quality of the food source provided (Fitzpatrick et al., 2014; Grover et al., 2007; Lange et al., 2017).

Ant dominance hierarchy plays a remarkable role in structuring species turnover and resource monopolization by ants on EFN-bearing plants (Blüthgen and Fiedler, 2004b; Cerdá et al., 2013; Dáttilo et al., 2014). Generally it is expected that dominant ant species (i.e., both numeric and behavioural dominance) (reviewed by Cerdá et al., 2013), tend to monopolize and aggressively defend the best quality resources from other dominant, subdominant or submissive ant species, which is especially important in the effectiveness of ant-plant protection against herbivores (Blüthgen and Fiedler, 2004b). Despite the monopolization of the best quality resources by dominant ant species, we know that EFN does not retain the same characteristics throughout the day and the night (Anjos et al., 2016; Falcão et al., 2014; Heil et al., 2000). For instance, Dáttilo et al. (2015) showed that there is a high day/night turnover of ant species foraging on EFN-bearing plants in an arid environment and that some ant species monopolize plants exactly at the moment when there is a greater secretion of nectar and a higher activity of herbivores (i.e., at night). In this way, based on the co-evolution of biotic defenses provided by ants on plants (Heil and McKey, 2003), it would be expected that the foraging time of dominant ant species would be similar to the secretion of high-quality nectar from plants. Unfortunately, and to our knowledge, no study has already tested this hypothesis. Related to this as well, it is specifically still unknown how the quality and availability of the EFN food source affects the efficacy of ants in plant protection against herbivores in arid environments (but see Fagundes et al., 2017).

In this study, we conducted a series of experiments within a population of *Vachellia constricta* (Fabaceae) in the arid Tehuacan-Cuicatlán valley, Mexico, in order to evaluate if the quality of an EFN food source influences the plant protection and resource dominance by ants. Specifically, the following questions were addressed: i) Do ants better protect plants with a higher quality of EFN? ii) Does the ant dominance of EFN and the effective protection of host plants change between day and night? iii) Are the foraging times of the most dominant ant species similar to the periods of secretion of high-quality nectar in the plants? iv) Could the most dominant ant species change its foraging time according to the availability of a high-quality food source in plants?

2. Material and methods

2.1. Study area

The study was carried out in July 2015 at the Botanical Garden Helia Bravo Hollis (18°19'54" N and 97°27'21" O, 1507 m a.s.l.), which is located in the municipality of Zapotitlán Salinas, state of Puebla, Mexico. The study area is located in the Tehuacán-Cuicatlán Biosphere reserve, where different plant associations are recognized with a large percentage (~20%) of endemic species (Valiente-Banuet et al., 2009, 2000). The annual average temperature of the region oscillates between 18 and 22 °C, but during the same day, it can vary from 10 to 39 °C (Servicio Meteorológico Nacional, 2016). The average annual rainfall is about 400 mm (Dávila et al., 2002). The region is characterized by a dry season, which runs from November to May, and a rainy season, which runs from June to October (Valiente-Banuet, 1991).

2.2. Species studied

Vachellia constricta (Fabaceae) Benth. Siegler & Ebinder is a thorny shrub that grows up to 4 m in height, with bipinnate leaves, and presents one extrafloral nectary (0.4–0.7 mm in diameter) located between or just below the first pair of pinnate leaves (Clarke et al., 1990; Rico-Arce, 2007). Despite *V. constricta* is a non-mycetophytic plant species, it is extremely common to observe different ant species foraging on their branches mainly due to the presence of EFN (unique reward offer to ants) (Rico-Gray et al., 1998). Based on this *V. constricta* could be considered as a myrmecophilous plant (Heil and McKey, 2003). Finally, in our area of study, we did not find any association between *V. constricta* and hemipteran trophobionts or myrmecophilous Lycaenidae caterpillars, which secrete honeydew and that, could potentially attract ants. This plant species has been mainly recorded in arid and semi-arid zones (Gómez-Acevedo et al., 2010), and is widely distributed from the southern United States of America to southern Mexico (Clarke et al., 1990). However, despite its wide geographic distribution, *V. constricta* is a species with low population densities in the Tehuacán-Cuicatlán Biosphere Reserve (Guzmán-Mendoza and Castaño-Meneses, 2007; Valiente-Banuet et al., 2009).

2.3. Activity and concentration of extrafloral nectar of *Vachellia constricta*

To determine the number of active nectaries of *V. constricta* during the day and night, as well as to quantify the natural concentration of their extrafloral nectar, we selected 15 plants, and in each plant, we chose five branches (10 apical nectaries). We restricted access to the nectaries by winged and non-winged visitors for 5 h using a mesh bag and a non-toxic resin (Tanglefoot®, MI, USA). Then, we counted the number of active and inactive nectaries between 11:00 h (day) and 23:00 h (night), according to the method proposed by Dáttilo et al. (2015). In this method, is clearly possible to see the nectar production based on turgor and nectar accumulation on EFNs and, therefore, useful to monitoring nectar production in plants where is difficult to measure nectar volume using microcapillaries. Therefore, the number of active nectaries is positively related to nectar production of *V. constricta* in our study area. We chose these two times to sampling ants just because they are the highest (23:00 h) and lowest (11:00 h) peak of nectar activity of EFN-bearing plants in dry environments (Falcão et al., 2014; Lange et al., 2017). We used Wilcoxon paired tests (paired by plant individual) to evaluate if there were differences in the percent of active nectaries per plant between day and night.

To quantify the sugar concentration of *V. constricta*, we collected the nectar of 30 different NEFs (two nectaries per plant) with a microcapillary tube (1 µl) and quantified the sugar concentration with a portable refractometer (ATAGO® with automatic correction of temperature, concentration range: 0–85° BRIX scale). The extrafloral nectar of *V. constricta* was extracted from all the plants together to obtain a

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