Acta Zool. Mex. (n.s.) 78: 73-82 (1999)

DESCRIPTION AND SEASONALITY OF A HOMOPTERA-ANT-PLANT INTERACTION IN THE SEMIARID ZAPOTITLAN VALLEY, PUEBLA, MEXICO

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RESUMEN

Registramos la variación estacional de una interacción hormiga-homóptero-planta en el valle semiárido de Zapotitlán, Puebla, México. Los cóccidos estuvieron presentes en 35 (21.9%) de los individuos muestreados de *Agave kerchovei*. El ambrosía es forrajeado todo el año por hormigas (*Camponotus rubrithorax*), y el excedente se desplaza hoja abajo y es utilizado como sustrato por hongos, o es activamente forrajeado por insectos de diversos grupos (Diptera, Hymenoptera).

Las hormigas son significativamente más abundantes en la época más fresca y seca del año; también variaron de manera significativa con la precipitación y la densidad de homópteros. Las moscas, avispas y abejas fueron más abundantes durante el periodo más cálido y húmedo del año. El número de moscas se incrementa con la densidad de homópteros. El número de insectos voladores presentes en cualquier mes está asociado significativamente con la temperatura y el diámetro de las plantas. El número de hormigas y moscas depende en parte de la densidad de homópteros pero también de los factores ambientales. El ambrosía atrae a una variedad de insectos generando interacciones entre organismos que conformarían comunidades diferentes. La mayoría de los visitantes son depredadores, parásitos o parasitoides, quienes forrajean ambrosía, pero que están evidentemente atraídos por una gran cantidad de posibles hospederos o presas.

Palabras Clave: Homoptera, hormigas, variación de interacciones.

ABSTRACT

We report the seasonal variation of an ant-plant- coccid interaction in the semiarid highland Valle de Zapotitlán, Puebla, México. Coccids were present in 35 (21.9%, N= 160) of the *Agave kerchovei* individuals sampled. Honeydew is foraged year-around by ants (*Camponotus rubrithorax*), the surplus either moves down- leaf and is used as substrate by sooty moulds, or actively foraged by an assorted collection of insect species (Diptera, Hymenoptera). Ants are significantly more abundant in the drier and colder portion of the year, and they also varied in a significant way with precipitation and homopteran density. Flies, wasps, and bees were more abundant during the warmer and more humid period of the year. The number of flying insects occurring during any month was significantly associated with temperature and plant diameter. Flies were more abundant during the warmer months, and their numbers also increased with homopteran density. The number of ants and flies present on agave individuals depends in part on homopteran densities but also on environmental factors. Honeydew attracts a variety of insects generating interactions among organisms that would otherwise be a part of different component communities. Most visitors are predators, parasites or parasitoids, they forage for honeydew but are evidently attracted by a large quantity of possible prey or hosts.

Key Words: Homoptera, ants, variation of interactions,

INTRODUCTION

Thompson (1982) suggests that interactions between species evolve, grow (see below), and can become a focal point around which other species can also evolve and become part of it. Growth of interactions is basically the effect of the collection of unrelated species that take advantage of the resources available through an interaction. The latter is best developed over evolutionary time among mutualisms, because they often involve some easily exploitable resource (e.g., nectar, honeydew), and in general do not favor high levels of host and visitor specificity (Thompson, 1982, 1994; Boucher, 1985; Kawanabe *et al.* 1993). Mutualisms trigger development of related interactions that involve either exploiting these or diffusing the mutualism through more species in the community (Hacker and Bertness, 1966), forming an evolutionary unit of interaction (Thompson, 1982). The evolutionary result is that mutualisms can become a link to a wide variety of organisms that are otherwise part of very different component communities (Thompson, 1982, 1994). The interaction between ants and Homoptera is a good example, since honeydew, a side product and easily exploitable resource, is readily available. Honeydew is usually associated with interactions between Homoptera and ants (Addicott, 1979; Beattie, 1985; Buckley, 1987; Becerra and Venable, 1989, 1991; Rico-Gray and Thien, 1989), but a variety of other insects (*e.g.* wasps, bees, flies) are also attracted to it (Krombein, 1951; Zoebelein, 1956a, 1956b; Evans and Eberhard, 1970; Jirón and Salas, 1975; Vinson, 1976; Price *et al.* 1980; Downes and Dahlem, 1987; Moller and Tilley, 1989; Godfray, 1994). Moreover, honeydew can be the substrate for fungi (Jirón and Salas, 1975; Hughes, 1976; Borror *et al.* 1981; Greenberg *et al.* 1993; Cuautle *et al.* 1998), and even attract birds (Paton, 1980; Edward, 1982; Gaze and Clout, 1983; Greenberg *et al.* 1993). However, the climatic regime and seasonal pattern of the habitat can play an important role in promoting or diffusing an interaction by making honeydew either a constant or ephemeral resource (Rico-Gray, 1989, 1993; Greenberg *et al.* 1993; Rico-Gray and Castro, 1996; Rico-Gray *et al.* 1998a, 1998b). The purpose of this research was to describe and establish the seasonal variation of the interaction between *Agave kerchovei* Lem. (Agavaceae), *Camponotus rubrithorax* Forel (Hymenoptera: Formicidae), and an undetermined homopteran (Homoptera: Coccidae), in the semiarid highland of the Zapotitlán Valley, Puebla, México. In particular, we addressed the following questions: Are other insect species attracted to the ant-agave-coccid association?

Is honeydew foraged by other species besides ants and generating a multispecific association? Are environmental factors, such as precipitation and minimum temperature, associated with seasonal changes in the multispecific association?

MATERIALS AND METHODS

We established a permanent sampling site on a mountain side 3 km south of San Antonio Texcala in the Zapotitlán Valley, Puebla, México (18°20' N, 97°20' W; altitude 1500 m). The climate is dry with a rainy season occuring between May and August (sometimes September), total annual precipitation is ca. 310 mm, mean annual temperature is ca. 20°C, and the prevailing vegetation type is a dry xerophytic scrub, dominated in certain areas by *Neobuxbaumia tetetzo*, a giant columnar cactus (Zavala, 1982; Jaramillo and González-Medrano, 1983).

The site was surveyed monthly between August 1993 and February 1996. To assess the frequency of the ant-coccid association present on *A. kerchovei*, we randomly selected 160 agaves in the permanent sampling site, and also checked for the presence of any other associated insects and fungi (Cuautle, 1996; Cuautle *et al.* 1998).

Homopteran density was determined once in 30 plants, three leaves per plant (outer, inner and central shaft), and three sections per leaf (upper, central and lower). Homopterans were counted in 9 cm^2 areas in every leaf section (*i.e.* nine counts per plant), and pooled per section (Cuautle, 1996; Cuautle *et al.* 1998). We tested equal density between sections by means of a χ^2 goodness-of-fit test (Zar, 1996). To establish plant diameter, we measured five outer leaves per plant and established plant diameter size classes based on leaf length, as an indication of plant size. Monthly precipitation and temperature data were obtained from the nearest weather station (Zapotitlán). The month was considered the experimental unit. To assess between-month variation in the presence of insect visitors, we selected three agave individuals (from the 30 used above), and systematically sampled for one day (early morning to early afternoon) every month, and counted all the insects (ants, flies, wasps, bees) visiting them.

Log-linear models were fitted with the GLIM-4 statistical package (Francis *et al.* 1993) to test the hypothesis that insect abundance is related to the environmental factors, plant diameter (*e.g.* larger plants equal to more flying insects), and homopteran density (*e.g.* more coccids equal to more insects). Because we used "count data" (*i.e.* we counted how many times something happened, but we have no way of knowing how often it did not happen; Crawley, 1993), the goodness-of-fit was evaluated with a χ^2-test using the *G* statistic and a Poisson error distribution. With Poisson errors, the change in variance can be compared directly with χ^2 tables to assess its significance (Crawley, 1993).

RESULTS

Coccids were present on 21.9% of the 160 *Agave kerchovei* individuals sampled. The rate of homopteran colonization is relatively low, only 3.2% of 63 marked agaves without homopterans were colonized after 22 months. While the interaction is long-lasting (five marked agaves with homopterans remained unchanged after 22 months) even throughout the life of this semelparous species, as several *A. kerchovei* individuals with homopterans flowered during the study. The ant-agave-coccid association starts with the colonization by the coccid of the central-shaft leaves of an agave individual. Coccids are tended by ants (*Camponotus rubrithorax*), who feed on the produced honeydew, and a multispecific association is triggered. Honeydew is profusely produced, and even though it is foraged year-around by the ants, we observed that there is a surplus, which is readily available and becomes an easily exploitable resource. Honeydew either moves down-leaf and is used as substrate by fungi [*Ceratocystis* sp. (Ophiostomatales), *Capnodium* sp. (Dothideales)], or actively foraged by an assorted collection of insect species which have been reported to exhibit a variety of feeding habits, such as flies (Diptera: Bombyliidae, Calliphoridae, Muscidae, Syrphidae, and Tachinidae), wasps (Hymenoptera: Leucospidae, Mutillidae, Philantidae, Pompilidae, Sphecidae, and Vespidae), and bees (Hymenoptera: Megachilidae) (Table 1).

The abundance per month of ants, flies and the other flying insects differed throughout the study period. Figure 1 shows precipitation, minimum temperature, and number of insects per month visiting the *A. kerchovei* individuals studied. Table 2 shows the results of the significant associations among the factors considered; other combinations were nonsignificant. Ant abundance was significantly associated with the drier and cooler months. The number of ants varied also in a significant way with precipitation and homopteran density (Table 2a). Precipitation alone explained 10.7% and homopteran density 8.9% of the total deviance. In contrast, flying insects (flies, wasps, bees) were more abundant during the warmer and humid months. The number of flying insects occurring during any month was significantly associated with temperature and plant diameter, the generalized linear model explained 33.9% of the total deviance. Temperature alone explained 18.6% and plant diameter 7.2% of the total variance, the interaction between these variates explained an additional 8% (Table 2b). Flies were more abundant during the warmer months, and their numbers also increased with homopteran density, the generalized linear model explained 30.3% of the total deviance. Temperature alone explained 18% and homopteran density an additional 8.9% of the total deviance, finally, their interaction accounted for an additional 3% (Table 2c).

Table 1

Insects observed feeding on coccid honeydew and interacting with the agave-coccid-ant association studied. Feeding habits are based on Borror *et al.* (1981) and Goulet & Huber (1993).

Order / Family	Species	Reported feeding habits
DIPTERA		
Bombyliidae	unidentified	Liquids
Calliphoridae	*Cochliomyia* sp.	Parasite
Muscidae	unidentified	Insects
Syrphidae	unidentified	Predator
Tachinidae	unidentified	Parasitoid of other insects
HYMENOPTERA		
Leucospidae	*Lencospis affinis*	Parasite (bees, wasps)
Megachilidae	unidentified	Parasite
Mutillidae	*Dasymutilla* sp.	Parasite (bees, wasps, flies)
Philantidae	*Philanthus* sp.	Predator (bees, wasps, ants)
Pompilidae	unidentified	Predator (spiders)
Sphecidae	unidentified	Parasite, predator
Vespidae	*Brachygastra* sp.	Predator
Vespidae	*Leptochilus* sp.	Predator
Vespidae	*Polistes* sp.1	Predator
Vespidae	*Polistes* sp.2	Predator

Table 2

Significant results from the generalized linear models fitted to the number of insects (flying insects = bees, wasps and flies; flies = only flies), minimum temperature and precipitation per month data curves. df = degrees of freedom.

Organism	Source	χ^2	df	Explanation of variation (%)	Probability
a) Ants	Precipitation	39.75	1	10.7	< 0.0001
	Homoptera	33.22	1	8.9	< 0.0001
	Flies	31.84	1	8.6	< 0.0001
b) Flying insects	Temperature	89.83	1	18.6	< 0.0001
	Plant diameter	35.06	1	7.2	< 0.0001
	Interaction	39.50	1	8.2	< 0.0001
c) Flies	Temperature	52.33	1	18.0	< 0.0001
	Homoptera	25.71	1	8.9	< 0.0001
	Interaction	9.99	1	3.5	< 0.002

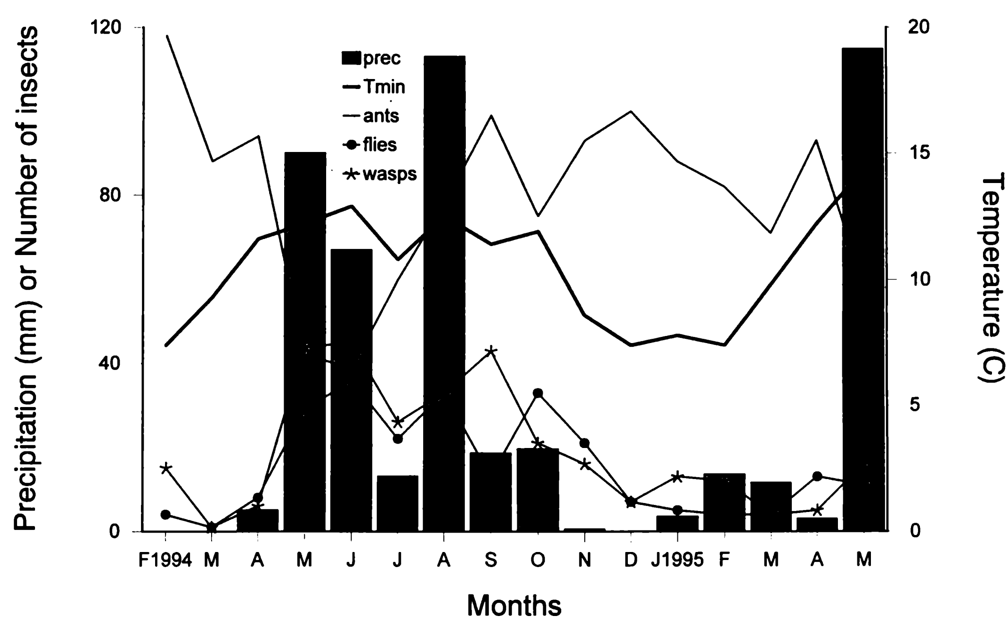

Figure 1

Precipitation, minimum temperature, and total number of insects (ants, flies, bees and wasps) visiting per month (February 1994 - May 1995) the *Agave kerchovei* individuals selected for this study.

DISCUSSION

Our results show that the animals utilizing honeydew created by homopterans are diverse and vary in relative abundance seasonally (see also Janzen, 1973; Smythe, 1982; Rico-Gray, 1993; Rico-Gray and Castro, 1996; Rico-Gray *et al.* 1998a, 1998b). The agave-ant-homopteran interaction serves as a focal point within communities, as honeydew attracts a variety of insects generating interactions among organisms that are otherwise part of different component communities (see also Krombein, 1951; Zoebelin, 1956a, 1956b; Jirón and Salas, 1975; Evans and Eberhard, 1970; Vinson, 1976; Price *et al.* 1980; Moller and Tilley, 1989; Godfray, 1994), diffusing the ant-homopteran mutualism through more species in the community. Even though most flying visitors to *Agave* *kerchovei* are predators, parasites or parasitoids, and are evidently attracted by a large quantity of possible prey or hosts, they actively forage for honeydew, but also vespids, pompilids and ants have been reported to forage on sooty moulds (Jirón and Salas, 1975). The above is not an isolated example for the study site; a larger group of insects with similar feeding habits (52 species, including all registered *A. kerchovei* visitors) visit the large inflorescences of *Beaucarnea gracilis* to forage for floral nectar but on different time periods (May-October for *A. kerchovei*, March-May for *B. gracilis*) (Cardel *et al.* 1997).

Liquid energy-rich food sources (*e.g.* honeydew, nectar) are at times the only food resource for insects in dry seasonal environments (Rico-Gray, 1989, 1993), forcing them to shift resources (Rico-Gray and Sternberg, 1991), which does not favor high levels of host and visitor specificity. Also, homopteran honeydew has been suggested as a key in the evolution of Diptera (Downes and Dahlem, 1987). The latter supports the idea that resources which are central to a mutualistic interaction for other purposes (*i.e.* rewards in exchange for pollination or defense), become the focal point around which interactions grow through the collection of unrelated species (Thompson, 1982, 1994; Kawanabe *et al.* 1993). On the other hand, since ant-Homoptera associations are among the most facultative, opportunistic and variable mutualistic interactions (McNeil *et al.* 1977; Addicott, 1978; Bristow, 1984, 1991a 1991b; Cushman and Addicott, 1989, 1991; Cushman and Whitham, 1989; Rico-Gray and Castro, 1996), and since the seasonal nature of the environment and of food availability forces insects to move between food sources, decreasing the chance to form specific interactions, it seems difficult to establish and predict the effect of these interactions throughout the community, the evolutionary potential for their future growth, or their potential for coevolution.

ACKNOWLEDGEMENTS

We appreciate the help during field work of M. Palacios-Rios, S. Koptur, Y. Cardel and D. García-Suárez. The fungi were identified by G. Carrión, and the insects in the Museo de Entomología, Universidad Autónoma de Yucatán. The study was supported by CONACYT 1259 and 0137 to VRG, Instituto de Ecología 902-16 to VRG, JGGF, JLP, and Tulane University graduate program to LBT.

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Recibido: 12 de enero 1998
Aceptado: 15 de febrero 1999