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Does nectar production reduce herbivore pressure on *Passiflora* species (Passifloraceae) in a tropical rainforest in Costa Rica?

Puede la producción de néctar reducir la presión de herbivoría en especies de *Passiflora* (Passifloraceae) en un bosque tropical de Costa Rica?

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Abstract: Mutualistic ant-plant associations are common and important elements of tropical ecosystems. The most common ant-plant associations are loose mutualisms due to the presence of extrafloral nectaries (EFN). Such loose mutualisms are also found in the genus *Passiflora*. From some EFN-bearing *Passiflora* species, it is already known that ants help to significantly diminish herbivore pressure. It is not known (1) whether *Passiflora* plants react to herbivore damage with differences in nectar production to attract more ants, (2) if shoot growth depends on ant presence, and (3) to what extent *Passiflora* species with EFN rely on ants as defence against herbivores. To this end, observations were performed on eight different *Passiflora* species which differ in EFN number and size and in the quantity of nectar production. Exclusion experiments and observations of ant activity and nectar production with and without disturbance events were used to clarify the open questions. Results show that the presence of EFNs has an influence on the fitness of some *Passiflora* species and that nectar production and ant activity change after artificial injuries in most of the species observed. The results show further that EFN-bearing *Passiflora* species profit from the facultative relation with the ants present in a given habitat and have established a good balance between costs and benefits resulting from the mutualism.

Key words: *Passiflora*, mutualistic interactions, ants.

Resumen: Interacciones mutualistas entre hormigas y plantas son elementos comunes e importantes en los ecosistemas tropicales. La asociación más común entre hormiga-planta son mutualismos difusos debido a la presencia de nectarios extraflorales (NEF). Este tipo de mutualismo difuso también se encuentra en el género *Passiflora*. Se conoce de algunas especies de *Passiflora* que llevan NEF, que las hormigas ayudan a disminuir en un elevado porcentaje la presión de herbivoría. No se sabe si (1) las plantas reaccionan al daño por herbivoría con diferencias en la producción de néctar para atraer más hormigas, (2) el aumento de longitud depende de la presencia de las hormigas, y (3) hasta que punto las especies de *Passiflora* con NEF necesitan a las hormigas como defensa contra la herbivoría.

Para encontrar respuestas a estas preguntas se hicieron observaciones en ocho diferente especies de *Passiflora* que difieren en el tamaño, posición y número de NEF, en un bosque tropical en Costa Rica. Experimentos de exclusión y datos sobre la actividad de las hormigas y la producción de néctar con y sin interrupciones fueron utilizados para responder estas preguntas. Los resultados muestran que la presencia de NEF tiene una cierta influencia en la aptitud de algunas especies de *Passiflora*. y que la producción de nectar y la actividad de las hormigas cambia después de daños artificiales, aunque no está correlacionada positivamente en todas las especies observadas. Los resultados muestran que las especies de *Passiflora* relacionadas con NEFs se benefician de la relación facultativa con las hormigas presentes en un hábitat particular y han establecido un buen equilibrio entre costo y beneficio en el mutualismo.

Palabras clave: *Passiflora*, interacciones mutualistas, hormigas.

Introduction

In their natural environment, plants always suffer the stress of herbivory. During evolution, herbivore pressure has been the driving mechanism for plants to invest in defence strategies (Howe & Westley 1988). Those strategies include chemical and mechanical defence or combinations of them (Thomsen 1997, Brage et al. 2002). Ant partners are one strategy used by plants to reduce herbivore pressure. A number of studies have already shown the positive effects of ants on plants (Benson et al. 1976, Bentley 1976, 1977a, b; Koptur

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Fig. 1: (**a**) EFN of the leaf margin of *P. edulis* under the microscope. Note the clearly cup-shaped form. (**b**) Lower surface of a young leaf of *P. megacoriacea*. EFNs are embedded in the surface and high rates of nectar production could be observed most of the time. (**c**) Ants searching and sucking nectar from a fresh shoot of *P. coccinea*. The youngest shoots need the greatest protection, so nectar has to be produced continuously.

1979; STEPHENSON 1982; HORVITZ & SCHEMSKE 1984; KELLY 1986; KOPTUR et al. 1998; De la FUENTE & MARQUIS 1999), but interspecific interactions differ widely in such mutualisms (HOWE & WESTLEY 1988, CRONIN 1998). The intensity of protection depends on the local ant abundance and composition in the habitat (BENTLEY 1976, INOUYE & TAYLOR 1979, BARTON 1986, HORVITZ & SCHEMSKE 1990), and not every ant species provides the same level of protection. Some are highly protective, while others do not show any aggressiveness against herbivores (HORVITZ & SCHEMSKE 1984, RICO-GRAY & THIEN 1989, VANDERPLANK 1996).

Facultative mutualisms are much more common than obligate ones in nature (HOWE & WESTLEY 1988). Plants and ants may have evolved in the same ecosystem, but each partner can survive without the other being present. Facultative ant-plant mutualisms very often involve guilds of ants. The anti-herbivorous effect of the different ant species can range from highly efficient to non-beneficial for the plant due to the low aggressiveness of the attracted ant partner. Plants which rely on the protection by ants must constantly invest in attraction, because ants also use other food resources, such as hymenopteran-derived liquids or other plant saps (HOWE & WESTLEY 1988). A common structure to attract ants is the development of so-called "extrafloral nectaries" (EFNs), specialised glands that can usually be found on the adaxial, abaxial or lateral parts of the leaf blade, the rachis, petiole, bracts, stipules, calyx or fruits (JOLIVET 1996). EFN-bearing plants are widespread and are known to occur in more than 90 families of flowering plants worldwide. The spectrum of EFN-bearing plant species found in a specific habitat has a great influence on the species composition of ants, their abundance and their interactions on the community scale (BLÜTHGEN et al. 2000, 2004). In turn, the community influences the evolution of EFNs (VANDERPLANK 1996, RUDGERS & GARDENER 2004). Ants that utilise extrafloral nectar may have the opportunity to discriminate among a wide variety of nectar sources, resulting in variation in the ant attention EFN plants receive (APPLE & FEENER 2001).

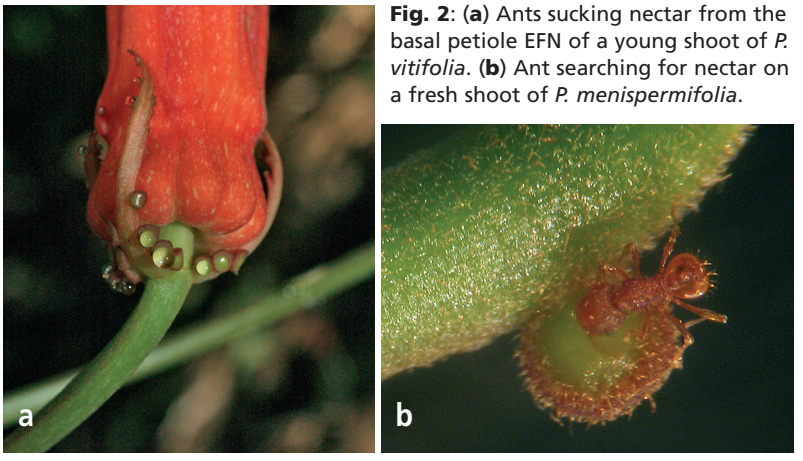


Fig. 2: (**a**) Ants sucking nectar from the basal petiole EFN of a young shoot of *P. vitifolia*. (**b**) Ant searching for nectar on a fresh shoot of *P. menispermifolia*.

Extrafloral nectaries with different structures and placements are found in *Passiflora* species (Passifloraceae) (Fig. 1 and 2). In Costa Rica, SMILEY (1986) found that *P. quadrangularis* was visited by 15 different ant species and *P. vitifolia* by 20 species. APPLE & FEENER (2001) found no mutual benefits between three EFN-bearing *Passiflora* species (*P. auriculata*, *P. biflora*, *P. oerstedii*) and the ants visiting them, whereas LABEYRIE et al. (2001) showed that herbivory increased significantly in *Passiflora glandulosa* when ants were excluded artificially. In the present study, we investigated eight different *Passiflora* species with morphologically different nectaries and different attractiveness to ants in a tropical lowland rainforest in Costa Rica. The effect of ants on leaf development and growth rates of the young

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shoots was examined in exclusion experiments. Ant attendance at day and night time, the ants' behaviour and nectar production after artificial injuries was observed in order to factor out the impact of the nectaries on the plants' fitness.

Material and Methods

The experiments and observations for this study were conducted at the "Estación Tropical La Gamba" in the Golfo Dulce region on the southern Pacific coast of Costa Rica. Eight *Passiflora* species (*P. coccinea*, *P. dispar*, *P. edulis*, *P. lobata*, *P. megacoriacea*, *P. menispermifolia*, *P. quadrangularis*, *P. vitifolia*) of the surrounding forest and the garden were included in the study.

Due to their common growth form as a liana, it is quite difficult to distinguish one *Passiflora* individual from another, because the lateral shoots have large extensions up into the canopy of the rainforest.Young shoots were therefore characterised as "patches" (defined as the part between the shoot tip and the fourth fully opened leaf) at the beginning of the experiment.

Herbivory and shoot increase

Herbivore pressure on leaves and the increase in shoot length were measured in "patches" of six *Passiflora* species (*P. coccinea*, *P. lobata*, *P. megacoriacea*, *P. menispermifolia*, *P. quadrangularis*, *P. vitifolia* – 6 to 40 patches per species). Every third to fourth day over a period of one month, the leaf surface area was monitored and the lengths of the shoots were measured in centimetres. To evaluate the impact of ant presence, a pairwise comparison was made including shoots accessible to ants and those from which ants were excluded with Tangle Trap (Tanglefoot company, USA). Previously existing connections with the surrounding vegetation were removed, along with possible new ones grown within the days between measurements because of the considerably high growth rates and movements of the tendrils. To determine exact information about leaf surface area for further calculations of leaf growth and herbivore pressure, the leaves were clamped under metal foil and the exact outline, damages and epiphylls growing on the leaf were plotted with a waterproof pencil. To be able to calculate the area of the leaves, quadrats of different sizes with defined areas were scanned as well. The number of pixels was calculated for the control areas and pixels to surface area calculated with linear regression between the values. Existing and assumed leaf areas were calculated with Adobe Photoshop 7.0 for Windows. Differences between existing and assumed area indicate the degree of herbivory and were stated in percent of assumed leaf area.

Ant activity and nectaries

24-hour activity: The ant activity was observed on 15 patches of four *Passiflora* species (*P. coccinea*, *P. dispar*, *P. quadrangularis*, *P. vitifolia*) for 24 hours. The total number of ants present on the patches was censused half-hourly and during three complete hours (12.00-13.00, 22.00-23.00, 03.00-04.00) every five minutes. During rainy periods, observations were stopped, because it is known that ant activity slows or ceases entirely during rainfall (SCHUPP 1986, WIRTH et al. 2001). Ants were not identified in the field because of difficulties in identification. Differences in the frequency of ant visitation, in the behaviour of the visiting ants, ant activity and nectar production on nectaries before/after artificial injury were observed.

Ant activity on nectaries: Differences in the frequency of ant visitation and in the behaviour of the visiting ants were observed for all petiole glands of the marked patches of five *Passiflora* species (*P. edulis*, *P. lobata*, *P. megacoriacea*, *P. quadrangularis*, *P. vitifolia;* all species with n = 2 plants except for *P. vitifolia* with n = 6). For 20 minutes, the number of ants present on the petiole and foliar glands (leaf blade and margin) and the type of ant activity was stated each minute. Hours with rain were excluded from the observation intervals. The choice of time depended on missing precipitation events and this condition was most probable between 10.00 and 13.00. For this period at least, moderate intensities of ant activity could be assumed. To guarantee similar moisture conditions for all observations, measurements were started no less than one hour after rainfall ceased.

Nectar production before/after artificial injury: In *P. edulis* and *P. lobata*, observations were performed both before and after artificial injury between 10.00 and 13.00. Wounds were made by scoring the surface of the stem with a razor blade. To avoid loss of nectar caused by ants visiting the nectaries, Tangle Trap was used to exclude ants from the "patches" included in this part of the study. Estimates were used to evaluate the amount of nectar produced. It was noted if the nectary was empty, partly filled with nectar (1/8, 1/4, 1/3, 1/2, 2/3 or 3/4 full) or totally filled.

Ant activity before/after artificial injury: For three *Passiflora* species (*P. coccinea*, *P. quadrangularis*, *P. vitifolia*, all n = 4), the ant activity on nectaries before/after artificial injury was documented. Three-hour observations were performed both before, and after the injury between 10.00 and 13.00. Damage comprised scoring the surface of the stem with a razor blade. The ant activity was documented every five minutes during the first hour after the injury was made and every 15th minute during the following two hours.

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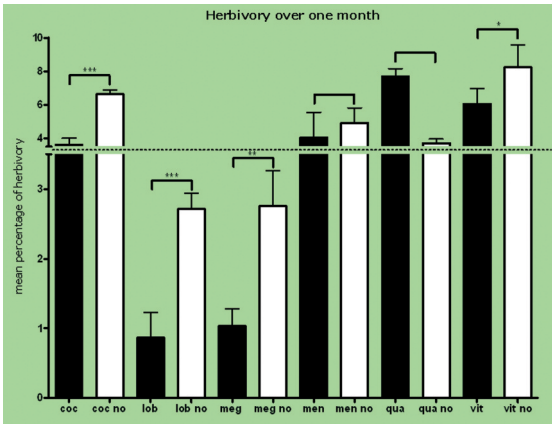


Fig. 3: Differences in herbivore pressure of *Passiflora* species kept with/without ants over a period of one month. All species except *P. quadrangularis* show increased herbivore pressure when ants were excluded, some of them significantly high . X: first letters of species, no = without ants. Y (two-segmented!): mean percentage of herbivory (given in % of leaf area loss) over the observation interval of one month. Error bars give standard deviation. (** P < 0.005; *** P < 0.0005).

Statistics

A paired t-test was used to test for significant differences in the shoot length increase between plants kept with ants and those where access was denied, and to test differences of ant behaviour towards nectaries, ant activity before/after injuries and nectar production before/after injuries. All statistical analyses, unless otherwise indicated, were performed using GraphPad Prism 4 for Windows.

Results

Herbivory

The experiments to test whether herbivore pressure and increase in shoot length showed differences between shoots accessible to ants and those where ants were excluded resulted in a clear trend towards enhanced herbivory on leaves with ant exclusion (Fig. 3). Four of the six *Passiflora* species (*P. coccinea* P = 0.0002, n = 25; *P. lobata* P = 0.0007, n = 13; *P. megacoriacea* P = 0.003, n = 6; *P. vitifolia* P = 0.025, n = 40) showed significantly increased herbivory over the observation period of one month when ants were excluded (Fig. 3). In *P. menispermifolia*, herbivory was increased but not significantly (P = 0.498, n = 11). In one species, *P. quadrangularis*, damage caused by herbivores was higher, despite the presence of ants.

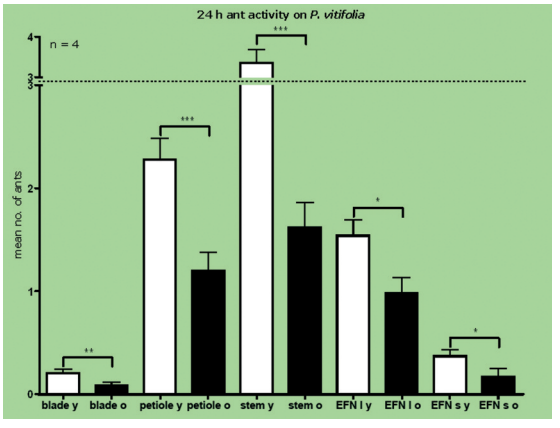


Fig. 4: 24-hour ant activity on different parts of the observed *P. vitifolia* patches. All young parts are attended significantly more by ants over the 24 hours than older parts. The petioles of young shoots showed a significant difference to older ones. X: location with additional letters (y = young, o = old, l = large, s = small). Y (two-segmented!): mean number of ants over the observation interval. Error bars give standard deviation. (** P < 0.005; *** P < 0.0005).

Growth rates of the shoots were significantly higher when ants were present in two species (*P. coccinea* P = 0.0003, n = 6; *P. quadrangularis* P = 0.002, n = 9), while in the other species (*P. megacoriacea* P = 0.55, n = 2; *P. menispermifolia* (P = 0.11, n = 3; *P. vitifolia* P = 0.17, n = 11) there was an obvious but not statistically significant trend towards increased fitness when ants were present. In contrast, *P. lobata* grew better when ants were absent (P = 0.001, n = 2), but as only two specimens were observed, this may be an artefact.

Ants and Nectaries

24-hour activity: In two of the four *Passiflora* species, a significant difference was found in the ant abundance on young parts compared with older parts of the shoots (*P. coccinea* P = 0.033, n = 3; *P. vitifolia* P = 0.0006, n = 4, Fig. 4). The maximum number was 18 ants in young shoots and 17 ants in older shoot parts of *P. coccinea*, and 23 in young and 15 in older shoot parts of *P. vitifolia*. In *P. dispar* (n = 4) and *P. quadrangularis* (n = 4), maximum ant abundance on young shoots was 1 and 3 ants, respectively, and 2 and 3 ants respectively in older parts; no part differed significantly in overall ant attendance from the other. The decrease of ant activity on *P. coccinea* between 14.00 and 17.00 and on *P. dispar* and *P. quadrangularis* between 15.30 and 16.30 was due to heavy rains. It is known that ant activity slows down or even stops during rain (Wirth & Leal 2001).

In *P. vitifolia*, we also investigated the exact position of ants on the shoot. Most significant of all were the differences between young and older petiole (P < 0.0001) and stem (P < 0.0001) followed by the leaf blade (P = 0.006). When examining the large basal EFNs (Fig. 6 a,b) and the small EFNs located in the middle of the petiole more closely, more ants were present on the large basal EFNs (EFN large P = 0.024; EFN small P = 0.04).

Ant activity on nectaries: It was observed that ants behave differently towards the EFNs of the five *Passiflora* species. Two types of behaviour have been distinguished – drinking and "searching" (only antennating the nectary). In three out of five species, the drinking activity was significantly higher than the searching activity (*P. edulis* P = 0.035, n = 2; *P. lobata* P < 0.0001, n = 2, *P. vitifolia* P < 0.0001, n = 6; Fig. 5). In *P. megacoriacea*, no significant difference could be found (P =

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0.079), while in *P. quadrangularis*, searching exceeded drinking activity (P = 0.4077).

Nectar production before/after artificial injury: Measurements of the amount of nectar produced within the hour before and the hour after injuries inflicted artificially with a razor blade were performed, in order to explain increased ant activity after artificial wounding. P. edulis (P = 0.03, n = 9) and P. lobata (P = 0.04, n = 10) showed significantly increased nectar production on petiole glands after injury. Glands on the leaf margin increased their nectar production significantly in P. edulis (P = 0.03). The other species did not (or only slightly) increase their nectar production.

Ant activity before/after injury: To observe possible changes in ant assemblage caused by injuries, ant activity was measured over a period of three hours before and after artificial injuries were made (Fig. 6). In the hour after the wounding, ant activity increased significantly in all three species investigated (*P. coccinea* P = 0.0033; *P. quadrangularis* P = 0.001; *P. vitifolia* P = 0.002; all n = 4). Three hours after the artificial injury, ant activity was still significantly higher in *P. quadrangularis* (P = 0.001) than on plants which suffered no damage. In the other two species (*P. coccinea* P = 0.23; *P. vitifolia* P = 0.16), ant activity decreased within this time interval. In *P. vitifolia*, ant presence was very high on the stem, followed by the petiole; in contrast, activity on the leaf blade and tendril was very low. In *P. quadrangularis*, ant activity on nectaries was generally low.

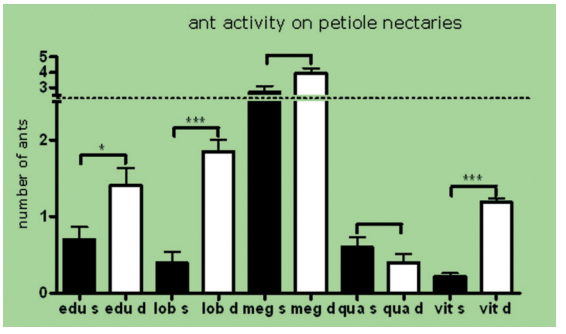


Fig. 5: Differences between drinking and searching activities of ants on petiole nectaries of five *Passiflora* species. X: first letters of species with additional letters (d = drinking, s = searching). Y (two-segmented!): mean number of ants over the observation interval. Error bars give standard deviation. (** P < 0.005; *** P < 0.0005).

Discussion

Herbivory

In facultative mutualisms, it has been demonstrated that the association of plants with ants reduces herbivore pressure, e.g. in *Leonardoxa africana* (Gaume et al. 1997), *Stryphnodendron microstachyum* (De la Fuente & Marquis 1999) and *Catalpa bignonioides* (Ness 2003). Another good example of facultative relationships between plants and ants is the genus *Passiflora*. Several *Passiflora* species have already been studied and some of them show adaptations that point towards facultative mutualisms with ants (Apple & Feener 2001, Labeyrie et al. 2001). Negative correlations between ant attendance and herbivore pressure or presence of herbivores have been verified in *P. incarnata* (McLain 1983), *P. glandulosa* (Labeyrie et al. 2001) and *P. coccinea* (Leal et al. 2006), and Apple & Feener (2001) investigated how the presence of nectaries may contribute to variation in ant visitation. Hairiness also seems to play a role in defence against herbivory for *Passiflora* species (Brage et al. 2002). In this study, the aim was to find out whether any connection exists between ant activity, herbivory, increases in shoot length, and nectar production in extrafloral nectaries (EFNs).

In all species investigated in this study except *P. quadrangularis*, herbivore pressure increased when ants had been excluded from the shoots. In *P. coccinea* and *P. lobata*, this effect was very significant. *P. coccinea* seemed to be especially well protected by ants, because ant activity increased significantly after artificial injury. Leal et al. (2006) stated that the attractiveness of *P. coccinea* to a wide spectrum of different ant species affords it good protection against herbivores. *P. megacoriacea* showed less herbivory and increased shoot length when access was given to the ants, but nectar production did not rise after artificial injury. Nectar production was generally high in this species and therefore the increase after injuries might not have been cost-effective. Surprisingly,

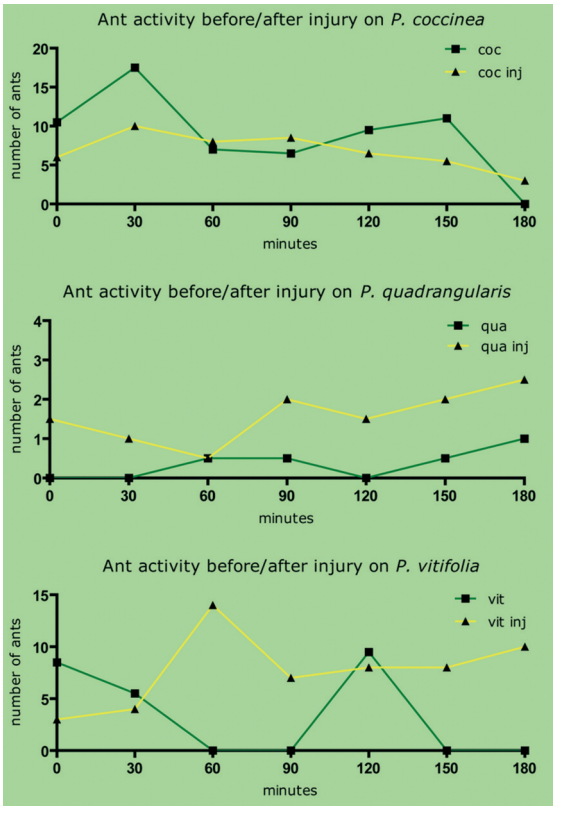


Fig. 6: Curves of ant activity three hours before/after artificial injury on three *Passiflora* species. On injured shoots (yellow), ant activity was slightly higher than on those without injury (green). Graphics: first letter of species, inj = with injury. Y (different maxima!): number of ants present.

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in *P. quadrangularis*, herbivory was even higher when ants had access to the shoot. This could be due to the fact that in the exclusion experiments with Tangle Trap, apart from ants, walking herbivores like caterpillars and leaf cutters were also excluded. In a study by BRAGE et al. (2002), *P. quadrangularis* was the species which was eaten the most among the five *Passiflora* species investigated. His explanation was the comparatively low level of ant visits that had also been observed by SMILEY (1986) and ourselves. We further observed that after artificial injury, the number of ants present on *P. quadrangularis* individuals remained very low, although nectar production increased slightly. On the other hand, shoot growth increased when ants were present. *P. quadrangularis* is the only species lacking EFN on the blade or margin, which could lead to a lack of protection in these parts and explain the increased herbivory on the leaf blade. Though not investigated experimentally, the morphologically different types of nectaries, varying amounts of nectar produced, differences in nectar composition and differences in the ants' preference (LANZA 1988, 1991) could be additional explanations for varying ant attendance on *Passiflora* species.

In the present study, no aggressive behaviour against herbivores could be observed although other studies have found differing degrees of ant aggression, ranging from disturbance of herbivores to direct attacks by the ants (SWIFT et al. 1994, APPLE & FEENER 2001, LEAL et al. 2006). It can therefore be assumed that the presence of ants on the leaf blade and petiole increases the disturbance of herbivores and acts as a deterrent to herbivores. During the 24-hour observations, a significant difference in ant presence between young and older plant parts could be seen in *P. coccinea* and *P. vitifolia*. These results show the better protection of the young, more vulnerable parts, which was also reported from other myrmecophytic plant species (HEIL et al. 2000). However, *P. lobata* did not seem to suffer increased herbivory or diminished length increase when ants were excluded. This indicates that in some species, ants may provide a certain protection, but other defence strategies, such as the combination of chemical and mechanical defence (AGRAWAL et al. 1998, 2006) may also exist. Habitat conditions, local ant composition, the rate of ant visitation and their preference for a certain food source may have a large influence on plant development (BRONSTEIN 1998, OLIVEIRA et al. 1999, APPLE & FEENER 2001).

Ants and Nectaries

In all eight *Passiflora* species investigated here, EFNs of the young leaves produced the highest amount of nectar. Nectaries of the petiole started to produce nectar before the corresponding leaf was unfolded. EFNs of the blade or margin started their nectar production a little later when the corresponding leaf was fully expanded and access for ants was easier. HEIL et al. (2000) interpreted this as an adaptive pattern, as the youngest, still unfolding leaves suffer most from herbivory and need the highest protection (MCKEY 1974, RHOADES 1979). Adult leaves are tougher, more fibrous and have incorporated more secondary compounds which are often toxic to herbivores (BEATTIE 1985). *Passiflora* species are known to incorporate saponins, alkaloids, and cyanogenic or phenolic substances (VANDERPLANK 1996) as one defence strategy and investment in nectar may therefore be useless. The fact that, during the 24-hour observation, the ant presence was higher on the younger plant parts than on older parts in three out of four species (*P. coccinea*, *P. dispar*, *P. quadrangularis*, *P. vitifolia*), also points towards this explanation. In all species studied, petiole glands were larger than those on the blade or margin, suggesting that the amount of nectar produced was higher on the petiole; this may be the reason why most of the observed ants were found on petiole glands, even if the nectaries of blade or margin were also producing nectar. In old EFNs, no nectar production could be observed because of damage (perhaps due to contact with the sharp mandibles which injure the smooth cells over time) and high fungal cover. When nectar was produced, the drinking activity of ants exceeded their searching activity. The only exception was *P. quadrangularis* – in this species, the searching activity exceeded drinking activity, probably due to the low volumes of secreted nectar. Nectaries of this species

Table 1: The relevance of different factors for the positive relationship between the experimentally used *Passiflora* species and the associated ants. (– negative/absent; ± neutral/more or less; + positive/present).

species	coc	dis	edu	lob	meg	men	qua	vit
Hairyness	–	–	–	+	–	+	–	±
petiole nectaries	+	+	+	+	+	+	+	+
nectaries on blade/margin	+	±	+	+	+	+	–	+
reduced herbivory (with ants)	±	/	/	+	+	±	–	±
increase in shoot length (with ants)	+	/	/	–	+	+	+	+
ant activity	/	/	±	+	+	/	–	+
nectar production (with injury)	/	/	±	±	+	/	+	+
average	**+**	**±**	**±**	**+**	**+**	**+**	**–**	**+**

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were held at most 15 % of their capacity. Because of the lack of sufficient nectar, ants were more likely to search.

The experiments with artificial injuries confirm the findings of SWIFT & LANZA (1993) and SWIFT et al. (1994) that extrafloral nectar production is an inducible defensive response in *Passiflora* species. In the present study, *P. megacoriacea* showed the highest secretion rates before the injuries, followed by *P. vitifolia* and *P. edulis*. After the artificial injuries on the stems, nectar production of the petiole glands doubled in *P. edulis* and *P. lobata*. In *P. quadrangularis*, nectar production did not increase greatly, and in *P. megacoriacea* and *P. vitifolia*, less nectar was produced after injury than uninjured plants. Surprisingly, in *P. vitifolia* and *P. megacoriacea*, ant activity increased, although the amount of nectar did not increase compared to undamaged shoots. This may be due to a change in the chemistry of the extrafloral nectar as a result of damage and therefore the attractiveness for ants might have risen. Changes in the volume or chemistry of extrafloral nectar in other plant species have been found by STEPHENSON (1982), KOPTUR (1989) and SMITH et al. (1990). In plants of the genus *Passiflora*, changes in nectar chemistry have not yet been demonstrated . Another explanation for the higher numbers of ants could be the attraction of ants by plant volatiles. Higher ant recruitment can follow abiotic disturbance events, the outflow of plant sap or the presence of green leaf volatiles (AGRAWAL & RUTTER 1998, BROUAT 2000, MAYER et al. 2008).

Conclusions

In a concluding table, an overview of the different subjects investigated in this study and their importance for a positive relation between the experimentally used *Passiflora* species and the associated ants is given (Table 1). five out of eight *Passiflora* species profit from their association with ants. In *P. megacoriacea* and *P. vitifolia* the positive effect is specially clear. *P. dispar* and *P. edulis* are neutral in their relationship with ants, but data for herbivory and increase in length need to be added for more precise conclusions. Only *P. quadrangularis* does not seem to profit. Increase in length was slightly positively correlated with ant attendance, but the number of ants present was very low compared with the other *Passiflora* species included in the study.

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References

AGRAWAL A.A. & M.T. RUTTER (1998): Dynamic anti-herbivore defense in ant-plants: the role of induced response. — Oikos **83**: 227-236.

APPLE J.L. & D.H. FEENER Jr. (2001): Ant visitation of extrafloral nectaries of *Passiflora*: the effects of nectary attributes and ant behaviour on patterns in facultative ant-plant mutualisms. — Oecologia **127**: 409-416.

BARTON A.M. (1986): Spatial variation in the effects of ants on an extrafloral nectary plant. — Ecology **67**: 495-504.

BEATTIE A.J. (1985): The evolutionary ecology of ant-plant mutualisms. — Cambridge University Press, Cambridge UK.

BENSON W.W., BROWN K.S. & L.E. GILBERT (1976): Coevolution of plants and herbivores: Passion flower butterflies. — Evolution **29**: 659-680.

BENTLEY B.L. (1976): Plants bearing extrafloral nectaries and the associated ant community: interhabitat differences in the reduction of herbivore damage. — Ecology **57**: 815-820.

BENTLEY B.L. (1977a): The protective function of ants visiting extrafloral nectaries of *Bixa orellana* (Bixaceae). — Journal of Ecology **65**: 815-20.

BENTLEY B.L. (1977b): Extrafloral nectaries and protection by pugnacious bodyguards. — Annual Review of Ecology Evolution and Systematics **8**: 407-427.

BLÜTHGEN N., STORK N.E. & K. FIEDLER (2004): Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. — Oikos **106**: 344-58.

BLÜTHGEN N., VERHAAGH M., GOITIA W., JAFFE K., MORAWETZ W & W. BARTHLOTT (2000): How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. — Oecologia **125** (2): 229-40.

BRAGE M.J., KARLSSON H.B.E., LUNDH E.C.S., SANDKVIST M.L. & J.B. WÄRNBÄCK (2002): The role of trichomes and nectaries in the defence against insect herbivores in *Passiflora*. — Ecological methods, SLU, department of entomology.

BROUAT C., MCKEY, D., BESSIERE J.M., PASCAL L. & M. HOSSAERT-MCKEY (2000): Leaf volatile compounds and the distribution of ant patrolling in an ant-plant protection mutualism: preliminary results on *Leonardoxa* (Fabaceae: Caesalpinioideae) and *Petalomyrmex* (Formicidae: Formicinae). — Acta Oecologica, International Journal of Ecology **21**: 349-357.

BRONSTEIN J.L. (1998): The contribution of ant-plant protection studies to our understanding of mutualism. — Biotropica **30**: 150-161.

CRONIN G. (1998): Between-species and temporal variations in acacia-ant-herbivore interactions. — Biotropica **30**: 135-139.

De la FUENTE M.A.S. & R.J. MARQUIS (1999): The role of ant tended extrafloral nectaries in the protection and benefit of a neotropical rainforest tree. — Oecologia **118**: 192-202.

GAUME L., MCKEY D. & M-C. ANSTETT (1997): Benefits conferred by "timid" ants: active anti-herbivore protection of the rain-

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forest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. — Oecologia **112**: 209-216.

Heil M., Fiala B., Baumann B. & K.E. Linsenmair (2000): Temporal, spatial and biotic variations in extrafloral nectar secretion by *Macaranga tanarius*. — Functional Ecology **14**: 749-757.

Heil M., Koch T., Hilpert A., Fiala B., Boland W. & K.E. Linsenmair (2001): Extrafloral nectar production of the ant-associated plant *Macaranga tanarius* is an induced, indirect, defensive response elicited by jasmonic acid. — Proceedings of the National Academy of Sciences of the United States of America **98**: 1083-1088.

Horvitz C.C. & D.W. Schemske (1984): Effects of ants and an ant-tended herbivore on seed production of a neotropical herb. — Ecology **65**: 1369-1378.

Horvitz C.C. & D.W. Schemske (1990): Spatiotemporal variation in insect mutualists of a neotropical herb. — Ecology **71**: 1085-1097.

Hossaert-McKey M., Orivel J., Labeyrie E., Pascal L., Delabie J.H.C. & A. Dejean (2001): Differential associations with ants of three co-occurring extrafloral nectary-bearing plants. — Ecoscience **8**: 325-335.

Howe H.F. & L.C. Westley (1988): Ecological Relationships of Plants and Animals. — Oxford University Press, New York, Oxford.

Inouye D.W. & O.R. Taylor Jr. (1979): A temperate region ant-plant-seed predator system: consequences of extra floral nectar secretion by *Helianthella quinquenervis*. — Ecology **60**: 1-7.

Jolivet P. (1996): Ants and plants – an example of coevolution. — Backhuyus Publishers, Leiden, The Netherlands.

Kelly C.A. (1986): Extrafloral nectaries: ants, herbivores and fecundity in *Cassia fasciculata*. — Oecologia **69**: 600-605.

Koptur S. (1979): Facultative mutualism between weedy vetches bearing extrafloral nectaries and weedy ant in California. — American Journal of Botany **66**: 1016-1020.

Koptur S. (1984): Experimental evidence for defense of *Inga* (Mimosoideae) saplings by ants. — Ecology **65**: 1787-1793.

Koptur S., Rico-Gray V. & M. Palacios (1998): Ant protection of the nectaried fern *Polypodium plebeium* in Central Mexico. — American Journal of Botany **85**: 736-739.

Labeyrie E., Pascal L., Delabie J., Orivel J., Dejean A. & M. Hossaert-McKey (2001): Protection of *Passiflora* glandulosa (*Passifloraceae*) against herbivory: Impact of ants exploiting extrafloral nectaries. — Sociobiology **38**: 317-321.

Leal I.R., Fischer E., Kost C., Tabarelli M. & R. Wirth (2006): Ant protection against herbivores and nectar thieves in *Passiflora* coccinea flowers. — Ecoscience **13**: 431-438.

Lanza J. (1988): Ant Preference for *Passiflora* Nectar Mimics that contain Amino Acids. — Biotropica **20** (4): 341-344.

Lanza J. (1991): Response of fire ants (Formicidae: *Solenopsis invicta* and *S. germinata*) to artificial nectars wit amino acids. — Ecological Entomology **16**: 203-210.

Mayer V. Schaber D. & F. Hadacek (2008): Volatiles of myrmecophytic *Piper* plants signal stem tissue damage to inhabiting *Pheidole* ant-partners. — Journal of Ecology (doi: 10.1111/j.1365-2745.2008.01390.x) online first.

McKey D. (1974): Adaptive patterns in alkaloid physiology. — American Naturalist **108**: 228-230.

McLain K.D. (1983): Ants, Extrafloral Nectaries and Herbivory on the Passion Vine, *Passiflora incarnata*. — American Midland Naturalist **110**: 433-439.

Ness J.H. (2003): *Catalpa bignonioides* alters extrafloral nectar production after herbivory and attracts ant bodyguards. — Oecologia **134**: 210-218.

Oliveira P.S., Rico-Gray V., Díaz-Castelazo C. & C. Castillo-Guevara (1999): Interactions between ants, extrafloral nectaries and insect herbivores in neotropical costal sand dunes: herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). — Functional Ecology **13**: 623-631.

Rhoades D.F. (1979): Evolution of plant chemical defense against herbivores. Herbivores: Their interaction with secondary plant metabolites. — In: Risenthal G.S. & D.H. Janzen (eds), Academic Press, New York, London: 4-53.

Rico-Gray V. & L.B. Thien (1989): Effect of different ant species on reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae). — Oecologia **25**: 301-315.

Rudgers J.A. & M.C. Gardener (2004): Extrafloral nectar as a resource mediating multispecies interactions. — Ecology **85**: 1495-1502.

Schupp E.W. (1986): *Azteca* protection of *Cecropia*: Ant occupation benefits juvenile trees. — Oecologia **70**: 379-385.

Smiley J.T. (1986): Ant constancy at *Passiflora* extrafloral nectaries: effects on caterpillar survival. — Ecology **67**: 516-521.

Smith L.L., Lanza J. & G.S. Smith (1990): Amino acid concentrations in extrafloral nectar of *Impatiens sultani* increase after simulated herbivory. — Ecology **71**: 107-115.

Stephenson A.G. (1982): The role of extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increase in fruit production. — Ecology **63**: 663-669.

Swift S. & J. Lanza (1993): How do *Passiflora* vines produce more extrafloral nectar after simulated herbivory? — Bulletin of the Ecological Society of America **74**: 451.

Swift S., Bryant J. & J. Lanza (1994): Simulated herbivory on *Passiflora incarnata* causes increased ant attendance. — Bulletin of the Ecological Society of America **75**: 225.

Thomsen K. (1997): Cyanogenic constituents in woody plants in natural lowland rainforest in Costa Rica. — Botanical Journal of Linnean Society **124**: 273-294.

Vanderplank J. (1996): Passionflowers. Revised and enlarged edition. — Cassel Publisher, London.

Wirth R. & I.R. Leal (2001): Does rainfall affect temporal variability of ant protection in *Passiflora coccinea*? — Ecoscience **8**: 450-453.

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