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ANT-GARDEN EPIPHYTES ARE PROTECTED AGAINST DROUGHT IN A VENEZUELAN LOWLAND RAIN FOREST

Viviane Schmit-Neuerburg¹ & Nico Blüthgen²

¹Nees Institut für Biodiversität der Pflanzen, Universität Bonn, Meckenheimer Allee 170, D-53115 Bonn, Germany

²Lehrstuhl für Tierökologie und Tropenbiologie, Universität Würzburg, Biozentrum, Am Hubland, D-97074 Würzburg, Germany

Abstract. Neotropical ant gardens (AGs) represent a classic mutualism between ants and epiphytic plants. Previous studies showed that these plants benefit from effective fruit dispersal and improved nutrition provided by gardening ants. Here we show an additional positive impact of gardening ants and their substrate on the fitness and survival of the AG epiphyte *Peperomia macrostachya* (Piperaceae) and seedlings of other epiphyte species in a Venezuelan rainforest. AGs were inhabited by parabiotic *Crematogaster limata* and *Camponotus femoratus* as well as *Azteca* sp. During a dry period of two months following experimental exclusion of ants, the AG substrate became dry-porous and lost at least its outer layer after heavy rainfall. Plants wilted and large numbers of small epiphyte seedlings were lost from the AGs. When both ants and substrate were completely removed, adult *Peperomia macrostachya* were also affected and lost a significantly higher proportion of stems than unmanipulated AGs, while several remaining plants stopped flowering and failed to produce fruits. Since the absence of ants led to desiccation and subsequent losses of nest material, we suggest that ants contribute considerably to moisture and stability of the substrate. This protection may be essential for the successful performance of AG epiphytes, particularly during dry periods as in this study. Accepted 4 June 2007.

Key words: ant-plant interactions, canopy substrate, drought stress adaptation, mutualism, plant growth, Surumoni Crane Project, Venezuela.

INTRODUCTION

Ant-plant interactions play a major role in our understanding of symbiosis and mutualism in general (Bronstein 1998). A prominent example in Neotropical lowland rainforests are ant gardens (AGs), where carton and soil nest material is provided by ants and subsequently inhabited by characteristic epiphytes of various plant families (Madison 1979, Davidson 1988, Corbara *et al.* 1999). The question whether this interaction between ants and plants is mutualistic or commensalistic has been debated since the beginning of the twentieth century. Ule (1902), who proposed that ants ‘purposely’ place epiphyte seeds in their nests,

was heavily criticized by Wheeler (1921) and Weber (1943). Since then, many arguments have been found in favor of mutualism: ants may benefit from epiphytes through nutrition via extrafloral nectaries, fruit pulps or seed arils (Kleinfeldt 1986, Davidson 1988); ants profit from increased nest stability provided by epiphyte roots (Yu 1994), or nest site availability is often limiting for arboreal ants (Janzen 1974, Davidson & Epstein 1989, Fonseca 1999). Epiphyte roots can thus help ants in colonizing tree canopies by providing shelter and stabilizing structures for nest material. In return, the seeds or fruits of the epiphyte species involved are specifically attractive to AG ants (Davidson 1988, Davidson *et al.* 1990, Seidel *et al.* 1990, Orivel & Dejean 1999), perhaps due to specific chemical constituents mimicking an ant brood

* e-mail: s-neuerburg@gmx.de
bluehgen@biozentrum.uni-wuerzburg.de

(Seidel *et al.* 1990). Carried into the nest by ants, they are either placed into brood chambers (Seidel *et al.* 1990) or incorporated into carton walls (Orivel *et al.* 1998), where they finally germinate and grow. Kleinfeldt (1978) even documented that the AG epiphyte *Codonanthe crassifolia* (Gesneriaceae) stopped growing after germination when its roots were only surrounded by ground bark or cotton instead of detritus or ant carton. Apart from this beneficial positioning of seeds, ants have been suggested to contribute to the protection (Davidson & Epstein 1989) and nutrition of AG epiphytes (Kleinfeldt 1978, 1986; Longino 1986, Blüthgen *et al.* 2001). Compared with other canopy substrates, such as ant galleries, termite nests and galleries, AG nest material is highly enriched in nitrogen and phosphorous content, and also in other elements (Blüthgen *et al.* 2001). Presumably, cyanobacteria attached to epiphyte roots in AGs facilitate an additional nitrogen supply to epiphytes (Benzing 1990, Cedeño *et al.* 1999). In this study, we focused on the importance of ants for the maintenance of AG substrate and protection of epiphytes during a dry period.

METHODS

Study site. The study site is located near the site of the Surumoni Crane Project on the upper Orinoco, Venezuela, in a gallery forest adjacent to the village of La Esmeralda at 3°9'–11' N, 65°31'–40' W and 105 m a.s.l (Morawetz 1998, Anhuf & Winkler 1999). The average annual temperature is 26°C, humidity is usually about 85–90%, and average annual rainfall 2700 mm, with a drier season between December and March (Anhuf *et al.* 1999, Anhuf & Winkler 1999). Field work was carried out during comparatively dry weather conditions in December 1999 to March 2000. The study site includes both *terra firme* forest and seasonally inundated forest, last flooded before this study in July 1999. The vegetation is formed by a tropical moist forest (*sensu* Holdridge *et al.* 1971) comprising the gallery forest along the Río Orinoco and the forest of the Surumoni Crane Project. The study area is especially poor in epiphytes, associated with a low abundance of suitable canopy substrates, but has a high density of ant-garden epiphytes in the nearby Surumoni Crane Plot (Cedeño *et al.* 1999, Engwald *et al.* 2000, Nieder *et al.* 2000).

Focal ant and epiphyte species. All ant species investigated, *Camponotus femoratus* Fab. (Formicinae), *Crematogaster limata parabiatica* Forel (Myrmicinae), and *Azteca* sp. (Myrmicinae), are known to initiate ant gardens (AGs) (Benzing 1991, Corbara *et al.* 1999,

Orivel & Dejean 1999). The former two ant species commonly live together in parabiosis (Wheeler 1921, Davidson 1988, Orivel *et al.* 1997). AGs of *Azteca* are less diverse in epiphytes and harbor epiphytes in lower densities (Davidson 1988), associated with a comparatively lower nutrient quality of the provided substrate (Blüthgen *et al.* 2001). AGs of *Azteca* are more abundant in sunnier areas such as orchards (Yu 1994, Catling 1997), whereas those of *Ca. femoratus* and *Cr. limata* are common in shadier environments such as old forest edges and forest understory. The latter AGs often harbor more shade-tolerant epiphytes (Corbara *et al.* 1999, Orivel & Dejean 1999). The epiphyte we mainly focused on, *Peperomia macrostachya*, commonly grows in AGs of *Ca. femoratus* and *Cr. limata* where seeds are transported and planted by the ants (Davidson 1988, Corbara *et al.* 1999, Orivel & Dejean 1999). *P. macrostachya* is comparatively shade-tolerant and common in the lower forest strata, where it is typically the first epiphyte to colonize newly established AGs in Peru (Davidson 1988).

Experimental treatment. Two types of AGs were treated separately in this study: (1) AGs built by the parabiotic ant species *Crematogaster limata parabiatica* and *Camponotus femoratus* ($n = 25$) and (2) AGs inhabited by *Azteca* sp. ($n = 14$). Each was studied in an area of a few hectares close to the Orinoco river, and some AGs may belong to the same polydomous colony. All investigated AGs occurred on trees and shrubs at 1.3–2.5 m above ground. For each AG the following data were recorded: epiphyte species and number of individuals, number of unidentified seedlings bearing fewer than four leaves, total length of plant shoots in each garden for each species, number of leaves, flowers and fruits. General water status of plants was evaluated visually. The diameter of the AG substrate was measured; for ovoid AGs, the average diameter (height + width + depth) / 3 was used. *Crematogaster* / *Camponotus*-AGs were allocated randomly to a control group ($n = 9$), treatment 1 ($n = 7$) and treatment 2 ($n = 9$). Because of the limited number of *Azteca* AGs, only a control group ($n = 7$) and a treatment group 1 ($n = 7$) were established. In treatment 1, ants were poisoned using a 20g/l aqueous solution of insecticide ("Neudorff Loxiran®-S-Ameisen Streu- und Gießmittel", active substance 10 g/kg chlorpyrifos). In treatment 2, both substrate and ants were carefully removed with spatula, brush and water. To prevent re-colonization of AGs after both treatments, we excluded ants by applying insect glue ("Neudorff Auro®-Insektenleim", consisting of *Ricinus* oil, waxes, and natural resins) on all phorophyte branches leading

TABLE 1. Epiphyte species growing in *Crematogaster* / *Camponotus* ant gardens: numbers of plant individuals (N) and ant gardens (AGs) where each species was found.

Family	Plant species	N	AGs
Araceae	<i>Anthurium gracile</i> (Rutge) Schott	8	5
Araceae	<i>Philodendron deflexum</i> Poepp. ex Schott	11	8
Bromeliaceae	<i>Aechmea tillandsioides</i> (Mart. ex Schult.& Schult.f.) Baker	2	2
Cactaceae	<i>Epiphyllum phyllanthus</i> (L.) Haw.	2	2
Gesneriaceae	<i>Codonanthe calcarata</i> (Miq.) Hanst.	4	3
Piperaceae	<i>Peperomia macrostachya</i> (Vahl) A.Dietr.	229	25
	Seedlings (indet.)	ca. 610	23

to the AGs. AGs in the control group remained unmanipulated, except that they were gently shaken for ca. five minutes in order to imitate the disturbance in treatments 1 and 2. The treatment was applied between December 1999 and January 2000, followed by a complete census four and eight weeks later. Weekly inspections were performed in order to control the general state of the AGs, and the effectiveness of ant exclusion and poisoning. Plant voucher specimens from previous studies were deposited at VEN (Caracas, Venezuela).

Data analysis. Net losses of epiphytes and changes in average shoot length and leaf numbers per epiphyte were subject to analysis of covariance (ANCOVA), where the values at the onset of the study (January) were employed as covariate, proportional changes until March as independent variable, and the treatments as categories. The covariate was included to ensure that results were unaffected by parameter variation among ant gardens before the study. Exclusion of the covariate did not affect any conclusion about significance. In addition, Fisher's exact test (two-tailed) was performed to test the heterogeneity of remaining versus lost epiphytes among treatments (ant gardens from each treatment pooled). While the former analysis uses one value for each AG (epiphytes pooled), the latter analysis is based on the total number of epiphytes (AGs pooled); the latter approach has greater statistical power, but may be biased by events in single AGs. Four *Crematogaster* / *Camponotus*-AGs and one *Azteca*-AG from the control group were deserted by ants during our study and were excluded from statistical comparisons. During substrate removal in treatment 2, the number seedlings was partly reduced, hence this treatment was not considered for analyses of seedling fates. Analyses were performed using Statistica 7.1 (StatSoft, Inc.).

RESULTS

AGs of parabiotic *Crematogaster* and *Camponotus*. The diameter of the AG substrate ranged from 5 to 23 cm, and supporting branches were 1–17 cm thick. Six epiphyte species were identified, among which *Peperomia macrostachya* (Piperaceae) was by far the most common (89.5% of the individuals, excluding small seedlings) (Tab. 1). *Peperomia macrostachya* in unmanipulated ant gardens showed almost no visible signs of drought stress, and leaves remained fresh during the course of the study (Fig. 1a). In contrast, in ant gardens from which ants had been excluded, substantial losses of substrate and epiphytes were notable just one month after treatment application. The formerly moist and firm substrate became dry and porous, and some AGs lost the outer layer of carton material during a rainy and windy week in late January (Fig. 1b). The process of deterioration continued until the end of our experiments after three months. Four AGs in the control group that had been deserted during the study were affected in a similar way as those where ants had been experimentally removed. In both treatment groups, all formerly fresh and fleshy plants of *P. macrostachya* wilted, with leaves and sometimes whole shoots being particularly limp in those AGs where substrate had been removed in addition to ants (treatment 2) (Fig. 1c).

Net losses of *P. macrostachya* shoots after two months varied significantly between ant gardens in different treatments (Fig. 2, Tab. 2). In control and poisoned AGs (treatment 1), only about one-fifth of the stems was lost, while more than half of the stems disappeared in AGs where both ants and substrate were removed (treatment 2). The number of remaining versus lost epiphyte shoots varied significantly between control and treatment 2 (Fisher's exact test, $p < 0.0001$, total $n = 164$ shoots) or treatment 1 and treatment 2 ($p < 0.0001$, $n = 154$), but not between



FIG. 1. *Crematogaster / Camponotus* ant gardens at the end of the study period from (a) the control group, (b) treatment 1 (ants poisoned), and (c) treatment 2 (ants poisoned and substrate removed).

control and treatment 1 ($p = 0.089$, $n = 140$), matching the results of post hoc comparisons across AGs (Fig. 2). Losses were not accompanied by detectable changes among remaining stems: the mean number of leaves per stem and mean length of stems did not differ significantly across treatments (Tab. 2).

In a total of 14 AGs from all treatments, individual *P. macrostachya* stems were flowering in January. The total number of inflorescences decreased, and the number of fruits increased until March (Tab. 3). However, in the control group and treatment 1, some plants flowering in January came to fruit before March, but none in treatment 2. All plants in the control group flowering in January continuously produced new flowers until March. Net changes of flow-

ers and fruits from January to March varied significantly between control and treatment 2 (Fisher's exact test, $p < 0.0006$, $n = 36$) and between treatment 1 and treatment 2 ($p < 0.016$, $n = 51$), but not between control and treatment 1 ($p = 0.11$, $n = 31$).

Losses of small seedlings were very pronounced in treatment 1 (Fig. 2). The number of remaining versus lost seedlings varied significantly between control and treatment 1 (Fisher's exact test, $p < 0.0001$, total $n = 493$ shoots). Treatment 2 was not considered here, since the removal of substrate directly caused losses of most seedlings. All effects were already apparent one month after treatment application (Fig. 2, similar significance values as in Tab. 2, not shown). The average net loss across poisoned AGs was only marginally

TABLE 2. ANCOVA results for treatment effects on changes among epiphytes in *Crematogaster* / *Camponotus* ant gardens. Values at the onset of the experiment used as covariate.

Variable	Treatment effect			Covariate	
	<i>F</i>	<i>df</i>	<i>p</i>	<i>F</i>	<i>p</i>
Net losses of shoots	6.4	2	0.0069	0.2	0.65
Net losses of seedlings ¹	4.7	1	0.052	1.8	0.20
Shoot length changes	0.9	2	0.44	1.1	0.30
Leaf number changes ¹	0.3	2	0.76	9.9	0.0052

¹ arcsin-transformed ($\chi = \arcsin(\sqrt{\chi})$) prior to analysis for variance homogeneity

significantly different from control AGs ($p = 0.052$) (Tab. 2). However, removal of an outlier from the analysis (one AG in the treatment group where no net loss was recorded, see Fig. 2) yielded a significant treatment effect ($p = 0.017$).

AGs of *Azteca*. The diameter of the substrate varied from 1.5 to 7 cm, and supporting stems were 0.5–2.5 cm thick. Only immature plants were found in *Azteca* AGs, mostly *Codonanthe calcarata* (Gesneriaceae). In the treatment group, one garden was completely de-

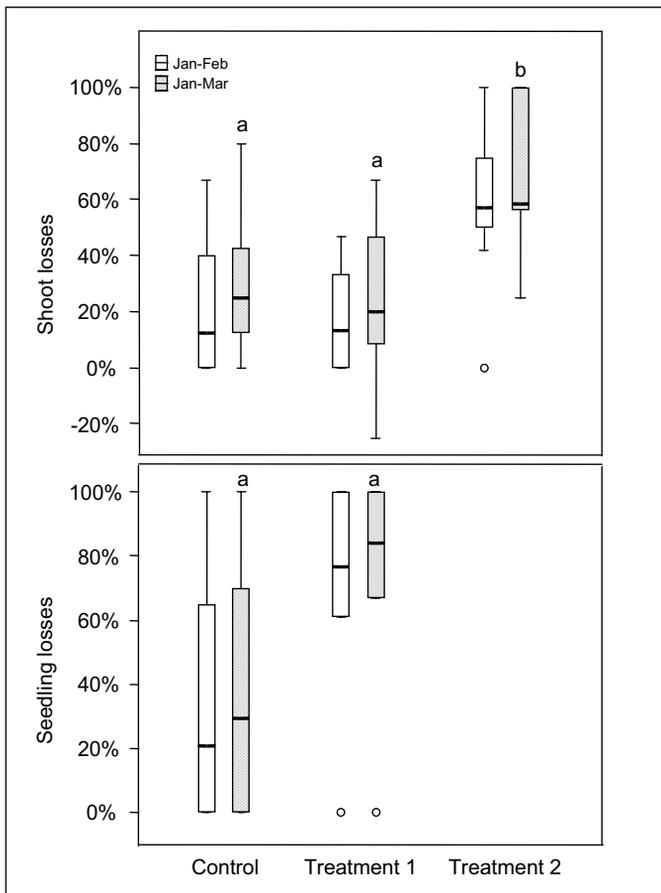


FIG. 2. Net losses of *Peperomia macrostachya* shoots and unidentified epiphyte seedlings in *Crematogaster* / *Camponotus* ant gardens after one month (white boxes) and two months (shaded boxes). Different letters indicate differences between treatments after two months (Tukey's HSD, all $p < 0.02$).

TABLE 3. Number of *Camponotus* / *Crematogaster* ant gardens with flowering or fruiting *Peperomia macrostachya* stems; total number of flowers and fruits produced in parentheses.

Group	January		February		March	
	flowering	fruiting	flowering	fruiting	flowering	fruiting
c	3 (8)	–	3 (6)	1 (1)	3 (6)	1 (1)
tr 1	6 (23)	–	6 (10)	2 (5)	3 (5)	3 (7)
tr 2	5 (28)	–	5 (11)	–	3 (5)	–

stroyed and the substrate of many other gardens was heavily damaged after a heavy rain in late January; plants were wilting. In contrast, all AGs in the control group remained intact and the plants stayed fresh, although one AG with only one seedling was deserted by ants before March. Numbers of plants in *Azteca* AGs decreased substantially during the experiment. In control AGs, 8% of the original epiphyte stems were missing after one month and 33% after two months (medians of 7 AGs), while losses were much more pronounced in AGs from which ants had been excluded (55% and 65% respectively, medians of 7 AGs). The treatment effect was significant for the first month across AGs (ANCOVA, $F_{1,11} = 5.1$, $p < 0.05$), but then partly compensated by large losses in control gardens so that effects across two months were not significant ($F_{1,11} = 2.2$, $p = 0.16$, mortality arcsin-transformed for variance homogeneity in both cases). However, the proportion of epiphytes remaining for two months (AGs pooled) varied significantly between control and treatment (Fisher's exact test, $p < 0.0001$, total $n = 225$ shoots).

DISCUSSION

In this study we found the activity of specific gardening ants to be important in maintaining ant garden (AG) substrate. Substrate deterioration was accompanied by rapid losses of seedlings after ants had been excluded. Ant activity did not immediately affect mortality and production of fruits among mature *Peperomia macrostachya* epiphytes, which were significantly reduced only when the substrate itself was completely removed. However, additional substrate losses may also translate into increased mortality and reproductive failure of mature plants in the long run, suggested by the severe effects in the treatment where substrate was removed. Moreover, roots of *P. macrostachya* were obviously unable to hold onto the phorophyte without support by substrate, supporting Da-

vidson's (1988) observation that this plant invests relatively little in supporting structures. Ants sometimes build AGs in tree forks, but also on steep and smooth bark, where they may be particularly affected. The fate of AGs after experimental ant exclusion is likely to reflect the natural development of AGs after ant colonies naturally abandon their nests, which we observed in five cases. Other authors also recorded deterioration of carton material shortly after AGs were abandoned, leading to disintegration of AGs and dropping or dying of epiphytes, which also happened when specific gardening ants were replaced by non-gardening species (Kleinfeldt 1978, Davidson 1988).

The observed wilting of plants or losses of leaf and shoots are typical water stress symptoms. Protection of epiphytes against drought may thus represent a major benefit of intact AGs. This may be most evident during the drier period when this study was performed. In their study of the water budget of the nearby Surumoni Crane Plot, Anhuf *et al.* (1999) documented a relatively high interception loss for the months of December to March, with a maximum of 56% in January 1998. Generally, drought stress is one of the most important factors controlling plant life and growth in the canopy (Benzing 1990, Nieder *et al.* 1999). Consequently, many epiphytes have developed adaptations to cope with drought stress (Sinclair 1983a,b; Goh & Kluge 1989, Benzing 1990, Zotz & Andrade 1997, Zotz & Ziegler 1997, Nieder *et al.* 1999). Such adaptations are obvious in two epiphytes that occur regularly in AGs elsewhere in the study area but were relatively uncommon in selected AGs here, i.e., the water-collecting tank bromeliad *Aechmea tillandsioides* and the succulent cactus *Epiphyllum phyllanthus*. Both species commonly grow without AG ants being present (Engwald 1999, Nieder *et al.* 2000). Their adaptations to drought stress might enable them to continue to grow, at least after successful germination and surmounting of the seedling stage, without the activity of gardening ants

and even when AG substrate is completely washed out. In contrast, the common ant-garden epiphyte we focused on, *P. macrostachya*, may be much less adapted to drought stress. It neither possesses a pronounced water-collecting architecture nor a velamen radicum. Compared with *Peperomia rotundifolia*, a common congeneric epiphyte in the study area (Engwald *et al.* 2000, Nieder *et al.* 2000), *P. macrostachya* has only slightly succulent, relatively broad leaves. Unlike several other epiphyte taxa, no crassulacean acid metabolism (CAM) or C4 photosynthetic pathway occurs in *P. macrostachya* or any other Piperaceae examined so far (Winter *et al.* 1983, Zotz & Ziegler 1997). Zotz and Ziegler (1997) found that water storage tissue only represents 20% of the leaf cross-sections in *P. macrostachya*, which is the second lowest value among seven *Peperomia* species analyzed (compared with 90% in *P. rotundifolia*). As a result, this species shows the highest chlorenchyma thickness among congeners, defined as total leaf thickness minus water storage tissue (Zotz & Ziegler 1997). Other epiphyte genera with similar or higher chlorenchyma thickness are typically CAM plants (Zotz & Ziegler 1997, see their Fig. 1). Seedlings of all observed AG epiphytes in our study do not display obvious drought stress adaptation, apart from adaptations occurring in mature individuals. Hence they should be particularly susceptible to desiccation during this early stage.

A previous study (Yu 1994) focused on the reciprocal effect in this mutualism: the importance of *P. macrostachya* in maintaining the AG substrate of parasitic *Camponotus-Crematogaster* associations. After experimentally pruning epiphyte leaves, Yu (1994) showed that AGs suffered from considerable substrate losses after heavy rainfall in his study, similar to the effect we observed following ant exclusion. He suggested that epiphytes protect the substrate by their function as living sump pumps by means of transpiration. However, as Yu did not replace the umbrella-like shelter of epiphyte leaves, his findings may also be explained by the epiphytes' function as mechanical shelter during rain. In our study we did not manipulate the transpiratory function of epiphytes nor the shelter of their leaves, but AGs suffered nevertheless from substrate loss. Hence the combination of both studies suggests that the interplay between the epiphytes' transpiration or mechanical shelter, the stabilization by epiphyte roots, and the activity of ants might be required to maintain AGs with *P. macrostachya* at least in the long term. While the benefit of ant activity was clear from our study, the mechanisms of this protection are not. Gardening ants may con-

tinuously repair the substrate and incorporate additional material, may evacuate excess water or actively add moisture during drought, but the contribution of such activities to the stability of the substrate remains hypothetical and merits further detailed observations.

In the study region, AGs are particularly abundant and harbor an important part of the local epiphyte flora (Cedeño *et al.* 1999, Engwald *et al.* 2000, Nieder *et al.* 2000). Since AGs may be viewed as an effective drought stress adaptation using the services of mutualistic ants, comparable to classical morphological or physiological adaptations, we suggest that such a high proportion of epiphyte individuals and species growing in AGs may partly reflect the pronounced dry seasons in this region compared with some other Neotropical forests (Anhuf *et al.* 1999, Anhuf & Winkler 1999). Further studies may reveal whether the proportion of epiphytes growing in AGs correlates with rainfall seasonality in general, and particularly with the extent of extreme conditions such as prolonged droughts in a region. Note that the importance of AGs for the epiphyte flora may be underestimated in floral surveys, since drought-insensitive mature plants might live longer than AG nests and not require protective substrate once they have reached a critical size, e.g., *Aechmea tillandsioides* or *Epiphyllum phyllanthus*.

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