SHORT COMMUNICATION

Ants as epiphyte gardeners: comparing the nutrient quality of ant and termite canopy substrates in a Venezuelan lowland rain forest

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The poor availability of suitable substrate and nutrients strongly limits the distribution and growth of vascular epiphytes in lowland rain forests (Benzing 1990, Nieder *et al.* 2000). In some epiphyte species nutrition may be assisted by adventitious roots that grow into animal debris in plant cavities such as domatia and bromeliad tanks (Huxley 1980). For epiphyte species lacking these modifications, animals may nevertheless play a substantial role by providing a large proportion of the limited substrate in lowland forests (Catling 1995, Longino 1986). Such associations between epiphytes and nutrient/substrate-providing animals may often be non-specific and commensalistic (Davidson & Epstein 1989, Longino 1986), while highly evolved mutualistic associations occur in the case of ant gardens which are very abundant in neotropical forests (Huxley 1980, Kleinfeldt 1986, Ule 1901). Ant gardens typically are densely inhabited by different epiphytes from various plant families whose seeds or fruits are attractive to the ants and carried into the nest (Davidson 1988). In addition, ants have been suggested to play a role in protection and nutrition of ant-garden epiphytes (Kleinfeldt 1978, 1986). Ants may benefit from epiphytes through increased nest stability (Yu 1994) or nutrition via extrafloral nectaries, fruit pulps or seed arils (Davidson 1988, Kleinfeldt 1986). In this study, we

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compare the nutrient quality of such ant gardens with other similar substrates rarely inhabited by epiphytes, namely nests and galleries of ants and termites.

The study site is on the Upper Orinoco in Venezuela at the Surumoni Crane Project (3°10′ N, 65°40′ W, 105 m asl). Average annual temperature is 26 °C, humidity usually 85–90% and average annual rainfall 2700 mm, dry season December–March (Anhuf & Winkler 2000). The site includes both terra firme and seasonally inundated forest. Soils are mainly arenolatosols and oxisols, highly acidic, nutrient-poor, and characterized by low cation exchange capacity, or entisols with high sand content, but soil heterogeneity of the study area is pronounced (Anhuf & Winkler 2000). Field work was carried out during dry and wet seasons of 1998 and 1999. Five different substrates were distinguished:

AG1: common ant gardens from an association of *Crematogaster* cf. *limata parabiotica* (Forel) and *Camponotus femoratus* Fab. (n = 10).

AG2: ant gardens inhabited by *Azteca* spp. (n = 14), including two *Azteca* nests without epiphytes and four nests with only a single epiphyte each, so that the status of true ant gardens was not clear for these nests at the time of sampling.

AR: ant runways (galleries) of *Pheidole biconstricta* Mayr on trees or shrubs (n = 16).

TR: termite runways (galleries) of *Nasutitermes* spp. on tree trunks (n = 7).

TN: termite nests of *Nasutitermes* spp. on trees (n = 6).

All substrates are constructed with carton material. AG1 and AG2 consist of various organic debris, plant fibres, bark, leaves, soil and sand, cemented with secretions (Davidson & Epstein 1989), AR from *Pheidole biconstricta* are made of relatively loose earthen material and debris that ants collected from the ground, while TR and TN basically represent termite excretions from ingested wood material (Wood & Sands 1978). Samples for AG2, AR, TR and TN were taken from localities in and around the crane plot. Additional samples for AG1 were from an island in the Orinoco and near the village of La Esmeralda. Substrate samples were collected from trees and shrubs at 1–4 m height above ground, and from the canopy accessed by the crane 10–15 m above ground. For plant tissue analysis, leaves from six plants of four AG1 were sampled (see Table 1; two *Anthurium gracile*, two *Peperomia* sp., one *Codonanthe calcarata*, and one *Philodendron deflexum*). Substrate and plant samples were collected in paper bags, remaining ants and plant material removed, dried in sunlight, and stored for several weeks prior to analysis. Samples were then dried at 60 °C, ground, and analysed in the Institute of Agricultural Chemistry in Bonn, Germany, in respect to per cent dry weight of carbon (C), nitrogen (N), calcium (Ca), magnesium (Mg), phosphorus (P) and potassium (K), using the following methods: C and N were analysed with a C-N analyser (NA1500, Carlo Erba Instruments). For analysis of minerals, 0.5 g of the sample was incinerated at 600 °C, and the ash was taken up with 5 ml HCl/H_2O (50/50). From this extract, total P concentration was determined colorimetrically using the molybdenum-blue

Table 1. Numbers of individuals (n) and frequency (freq.; number of nests and galleries that were inhabited by epiphytes / total number of nests and galleries examined) of epiphytic plant species in ant and termite substrates at the Surumoni project, Venezuela (see text for substrate codes).

Plant species	Family	AG1		AG2		AR		TR + TN	
		n	freq.	n	freq.	n	freq.	n	freq.
Aechmea tillandsioides L.B. Smith	Bromeliaceae	1	1/10	0	0/14	0	0/16	0	0/13
Anthurium gracile (Rudge) Schott	Araceae	5	3/10	3	3/14	0	0/16	0	0/13
Codonanthe calcarata Miq.	Gesneriaceae	5	4/10	3	3/14	0	0/16	0	0/13
Microgramma baldwinii Brade	Polypodiaceae	0	0/10	0	0/14	0	0/16	1	1/13
Peperomia sp.	Piperaceae	9	7/10	1	1/14	0	0/16	0	0/13
Philodendron deflexum Poepp. ex Schott	Araceae	2	2/10	0	0/14	0	0/16	0	0/13
seedlings (indet.)		0	0/10	c.110	8/14	1	1/16	0	0/13

Table 2. Nutrient concentration of epiphyte leaf tissues from *Crematogaster* / *Camponotus* ant gardens in per cent dry weight (median and range of six plants from four ant gardens).

	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
Median	2.11	0.44	0.30	0.66	0.18
(range)	(2.05 – 3.13)	(0.30 – 0.59)	(0.16 – 10.3)	(0.40 – 1.32)	(0.08 – 0.46)

method, K and Ca by flame photometry (Eppendorf), and Mg by flame spectroscopy (AAS, Perkin Elmer). pH was measured using an electronic pH-meter (Piccolo, Hanna instruments) on 5 g dried substrate wetted with 10 ml distilled water. Dry weight measurements were normalized by arcsine-square-root transformation.

Epiphytes were highly abundant in substrates provided by garden-building ants, but rare on other animal substrates (Table 1). While all ant-garden epiphyte species recorded were probably dispersed by ants (Davidson 1988), a single wind-dispersed fern (*Microgramma baldwinii*, a very common species in the study area) grew on a termite nest. Extensive studies in the surrounding forest by the authors confirmed that epiphytes occur only occasionally on ant and termite substrate other than ant gardens. The concentration of nitrogen (N), carbon (C) and minerals except for calcium (Ca) varied significantly between substrates (Figure 1). Dry weight of N and P was significantly higher in AG2 compared to non-garden substrates, and significantly higher in AG1 than in AG2 (Tukey test, Figure 1). A higher concentration of potassium (K) in ant gardens was only partly significant: $P < 0.05$ between AG2 and AR, and $P < 0.1$ between AG1 and AR. The mean concentration of N, P and K in ant gardens was two- or even three-fold higher than in other substrates, reaching or exceeding the respective levels that are considered as generalized minimum requirements for optimal growth of crop plants (Epstein 1965, see also Benzing & Davidson 1979) (arrows in Figure 1). In contrast, levels of Mg, Ca and C were similar between ant gardens and non-garden substrates with significantly lower concentrations in termite nests as a notable exception. Mean Mg and Ca concentrations were below critical levels for crops (Epstein 1965). The C/N ratio in ant gardens reached 14.9 (± 1.8 SD) in AG1, and 23.0 (± 7.4) in AG2, respectively. C/N ratios were similar in termite nests (19.6 ± 3.5), but higher in ant and termite runways (AR 25.1 ± 2.6; TR 47.1 ± 19.8). All substrates were moderately acidic; pH values – AG1 5.4 (5.0–5.8, n = 3 samples), AG2 4.6, AR 4.7, and TN 5.3 (each with n = 1). The same nutrients (N, P and K) that were significantly higher in ant garden substrate also occurred in high concentrations in tissues of ant garden plants (Table 2).

Soils from many tropical forests are generally characterized by low concentrations of various nutrients (Vitousek & Sanford 1986). Nutrient availability in canopy substrates, however, typically is much higher than in soil (Benzing 1990, Putz & Holbrook 1989). Trees in montane cloud forests are typically
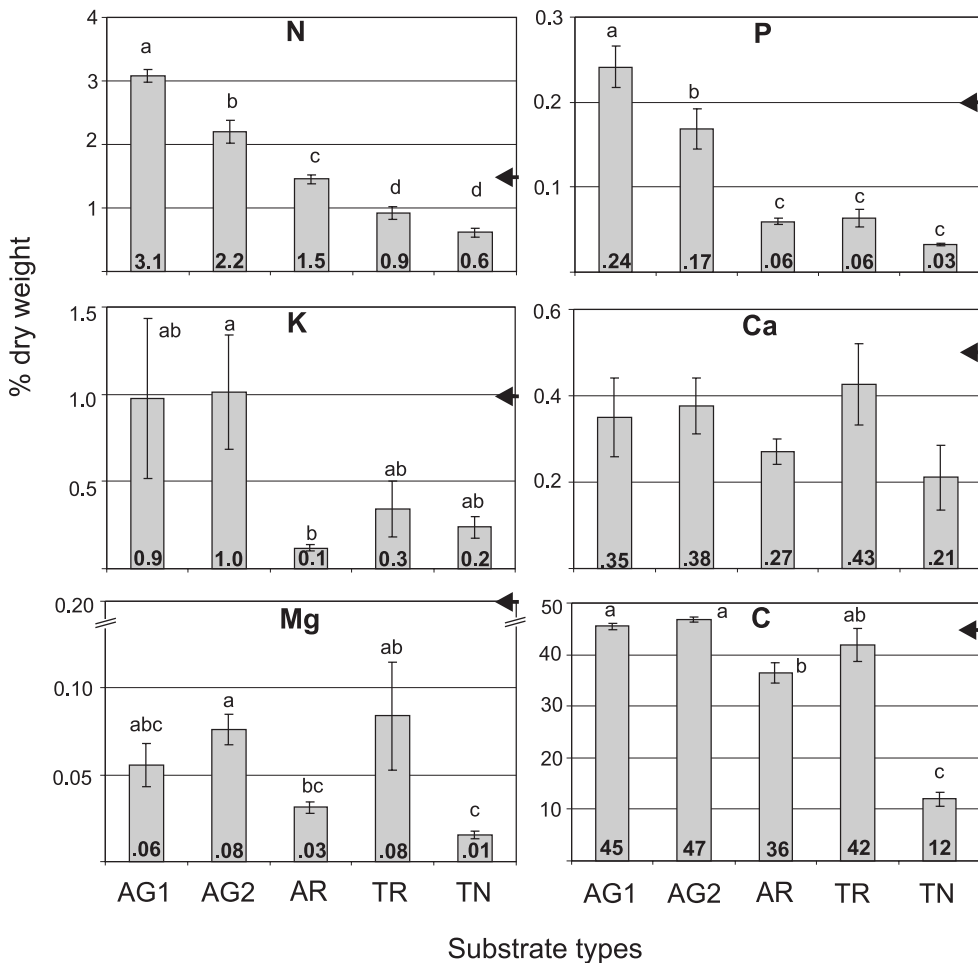
Figure 1. Nitrogen, minerals and carbon (means of per cent total dry weight) in five types of substrate provided by ants and termites at the Surumoni project, Venezuela. For details of substrate types and nutrients see text. Error bars show standard error of mean. For each element, means sharing the same letters do not differ significantly at $P < 0.05$ (Tukey's HSD for unequal N). In Ca, effects in the ANOVA were not significant. Arrows indicate adequate levels for optimal growth of crops (Epstein 1965).

covered with thick layers of substrate suitable for abundant epiphyte growth, but lowland rain forests lack such accumulations of substrate. At the study site, epiphytes outside ant gardens grew on a mean substrate layer of only 3.7 mm (mainly lichens or debris in bark crevices), compared to 67 mm in a cloud forest site in Venezuela (Engwald 1999). Considerable amounts of canopy substrates in lowland forests are provided by ants and termites. Of various potential rooting media, only ant gardens are commonly used by epiphytes, while termite structures and ant runways are rarely used, epiphyte occurrence corresponding with differences in the nutritional quality of these substrates. The

concentrations of N, P and K in ant gardens are higher than other epiphytic substrates (Benzing 1991, Coxson & Nadkarni 1995, Hofstede *et al*. 1993, Nadkarni 1984), and comparable to those levels for growth of crop plants in eutrophic soils (Epstein 1965). In non-garden substrate, levels of N, P and K were much lower, while Mg and Ca were relatively poor in both ant-garden and non-garden substrates. Furthermore, the C/N ratios in ant gardens and termite nests were close to or within the optimal range between 8 and 15 for cultivated soils (Brady & Weil 1996).

Nutrient data in the present study are similar to those found elsewhere: similar high concentrations of C and N were measured in ant gardens from French Guyana (Belin-Depoux 1991), while nutrient levels of different termite nests are very similar to those for termite substrate in the present study (arboreal *Nasutitermes ethratae* nests in Venezuelan savannas, Putz & Holbrook 1989; terrestrial termite mounds in forests at the Rio Negro, Salick *et al*. 1983; various terrestrial termite mounds worldwide, Wood & Sands 1978). The high concentrations of N, P, and K observed here in epiphyte tissue from ant gardens exceed the typical levels reported for epiphytes on other substrates (Richardson *et al*. 2000, see also Benzing & Davidson 1979), indicating that ant gardens provide an exceptionally suitable substrate in respect to these particular nutrients. Benzing & Davidson (1979) found that the demand for N, P and K by a bromeliad species was higher than for other nutrients. High nutritional quality may correspond with the observation that ant garden plants typically have higher growth rates than many other epiphytes in the study site (V. Schmit-Neuerburg, unpubl. data). Kleinfeldt (1978) observed that *Codonanthe crassifolia* exhibits higher growth rates when rooted in ant gardens than elsewhere. The continuous input of these critical nutrients through the activity of nesting ant colonies throughout the year may be particularly effective for the productivity and success of ant garden plants.

Several factors other than nutrient quality could potentially influence the establishment of epiphytes: (1) Physical properties of substrates are likely to be important, such as softness, moisture holding capacity, porosity, stability and longevity. For instance, *Nasutitermes* nests are characterized by a hard surface and fine texture which may be unsuitable for germination of most epiphytes, at least as long as these nests are actively maintained. The substrate provided by *Pheidole biconstricta* runways is relatively porous and might be too short-lived to play an important role for epiphytes. (2) Chemical ingredients of animal excretions other than nutrients may promote or inhibit plant growth (Davidson & Epstein 1989). (3) The microflora of ant and termite substrates may be generally abundant, as shown for cyanobacteria on ant gardens (Cedeño *et al*. 1999) and for bacteria and fungi on termite mounds (Petal 1978), which might have an impact on plant growth. (4) Ants and termites may actively prune or remove epiphytes (e.g. in domatia-bearing ant-plants, Janzen 1966). (5) The dispersal mechanism of the epiphytes is important, most obviously in ant gardens, where epiphyte fruits or seeds are specifically planted by

gardening ants (Davidson 1988). Seeds might also be taken by non-gardening ants and simply left in the nest substrate or trash pile (Davidson & Epstein 1989, Longino 1986). This may be true for many *Azteca* nests with only single epiphyte seedlings in the nest carton. Evidence for accidental seed transport by *Azteca* was found on shrubs of *Tococa guianensis* (Melastomataceae), where *Peperomia* seedlings grew in debris chambers of ant domatia inhabited by *Azteca* (N. Blüthgen, pers. obs.).

In ant gardens, it seems clear that both ants and plants benefit from the association (Davidson 1988, Kleinfeldt 1986, Yu 1994), although some aspects of this mutualism have not been studied. Two possible explanations for the high concentration of N, P and K in ant gardens are considered further:

(1) High concentrations of nutrients are a general feature of ant nests irrespective of any mutualism with epiphytes. N, P and K are also typically increased in terrestrial ant nests compared to surrounding soil (Beattie 1985, Petal 1978). Enhanced levels of N and P may be regarded as an effect of concentrated detritus, carcasses and metabolic products typical for omnivorous ants. In termite substrate, the lack of a predatory habit may be responsible for a lower P content compared to ant nests. Nevertheless, the content of N, P and K in terrestrial nests may be much lower than in canopy substrates, due to lower contents of organic material (less than 10%: Beattie 1985, Petal 1978).

(2) High concentrations of nutrients result from the behaviour of gardening ants to meet specific plant requirements. The significant difference in N and P between *Crematogaster–Camponotus* and *Azteca* ant gardens in our analysis shows a species-specific component and may be seen as evidence for this hypothesis. Davidson (1988) reported that mammalian faeces are collected and incorporated into the garden by gardening ants (including *Azteca*), which might specifically raise the nitrogen and mineral concentration. To assess the specific role of gardening ants, future studies need to compare carton nests from non-gardening ants with true ant gardens.

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