PLANTS IN THE DEVIL'S GARDEN: INTRUDERS IN AN ANT-PLANT MUTUALISM

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INTRODUCTION

Plant-animal mutualisms are exploited by other species of plants and animals, which harvest the benefits of these interactions without paying the costs, sometimes even harming the mutualists. This is well known in pollination mutualisms, where animals steal nectar and pollen without pollinating (e.g., Olesen 1997), and rewardless plants deceive pollinating animals (Pijl & Dodson 1966). Plant-fruit disperser mutualisms are also exploited by other plants (McKey 1975, Snow & Snow 1988) and frugivorous animals (Goulding 1985). Exploitation is much less studied in plant-ant mutualisms. Janzen (1975) mentions a *Pseudomyrmex* ant harvesting food resources of an *Acacia* without protecting it against herbivores. McKey (1984) describes a *Cataulacus* ant parasitizing a *Leonardoxa* plant-*Petalomyrmex* ant system, and Yu & Pierce (1998) a flower-castrating *Allomerus* ant in a *Cordia* plant-*Azteca* ant system. As far as we are aware, only one report refers explicitly to plants exploiting ant-plant mutualisms, viz. Janzen (1974). He describes qualitatively non-myrmecophytic plants in Malaysian ant gardens.

Here we describe the mutualism between the ant plant *Duroia hirsuta* (Poepp. et Endl.) K. Schumann (Rubiaceae) and its mutualistic ant *Myrmelachista* sp. (Formicinae) (Campbell *et al.* 1989). *Duroia hirsuta* is a medium-sized rainforest tree, widespread in low-

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land South America below 1000 m. It grows in small light gaps often lacking any further vegetation. The *Myrmelachista* ants are known to weed out other plants invading the gap of their host tree and to prune neighboring plants. Weeding or pruning of vegetation surrounding ant trees by ants is described by several authors, e.g., Janzen (1966, 1972). Locally, such an ant-made gap is known as a Jardín del Diablo (Devil's garden).

MATERIAL AND METHODS

This study was carried out in Yasuni National Park, Ecuador, during October-December 1995. The park consists of primary lowland rainforest. Other ant plants than *D. hirsuta* were observed in the study area, e.g., *Cordia nodosa, Tachigali paniculata, Triplaris americana*, various Melastomataceae species, and *Cecropia* and *Pourouma* species.

Along 1600 m of two established transects, positions of individuals of, and gaps between *D. hirsuta* were registered, and their densities calculated according to:

$$\text{Density} = \frac{(n-2) \cdot 10^4}{\sum_{i=2}^{n-1} [0.5 \cdot (t(i+1) - t(i-1))^2]} \text{ ha}^{-1}$$

where n is total number of trees or gaps along transects, and $t(i)$ is position (in meters) of the ith tree or gap along a transect. In order to describe size distributions of trees, tree height and distance from ground

and up to tree crown (bole height) were measured in order to get an estimate of crown volume (Fig. 1c). Since domatia are spread regularly all over the crown of the trees, crown volume was used as a rough measure of ant colony size. The crown had the shape of an ellipsoid the volume of which is $4/3\pi ab^2$, where 2a and 2b are the long and short axis of the ellipsoid respectively. Thus volume of crown becomes V = $4/3\pi$ (tree height − bole height) · (gap radius)^2 (Fig. 1a).

Two experiments were carried out to elucidate the behavior of ants against gap plants other than *D. hirsuta*. Firstly, a weeding experiment was set up. A pair of saplings of the palm *Iriartea deltoidea*, 10–20 cm in height, was planted into each of six gaps, halfway between *D. hirsuta* tree(s) and the margin of a gap.

Another pair of saplings was used as controls and planted outside each gap (Fig. 1a). A control site with a light intensity as high as possible was chosen. The experiment was duplicated with 10–20 cm tall saplings of *Quararibea* sp. (Bombacaceae). All introduced plants of both species were planted in plastic bags and thus had no contact with soil in the gap. This procedure was followed in order to eliminate any effects from allelopathic agents, as discussed by Campbell *et al.* (1989). Both sets of plants were censused 1, 5 and, 8 weeks later. A second experiment was designed to demonstrate pruning behavior of ants. Although we did not observe any epiphytes on *Duroia* trees, we tied 20 epiphytes belonging to different species to ten *D. hirsuta* trunks just below the crown (Fig. 1a). Half
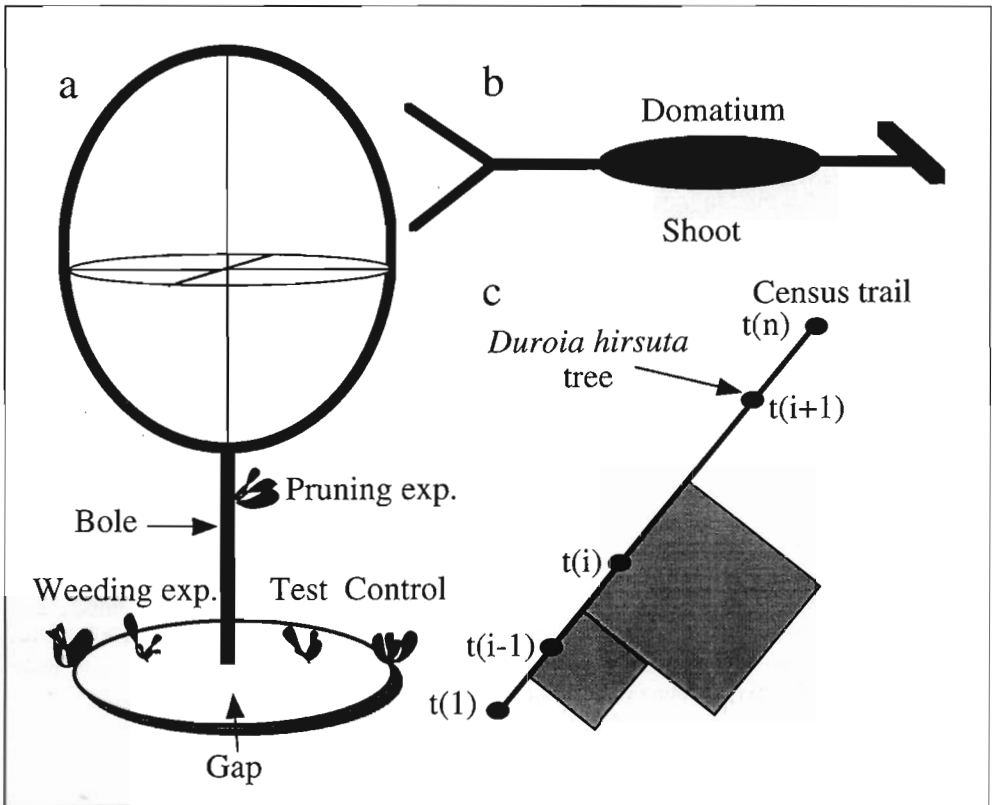

FIG. 1. (a). *Duroia hirsuta* and ant gap, showing the design of the weeding and pruning experiment; (b) shoot with a domatium; (c) census trail with trees showing how gap and tree densities were calculated. Each quadrat had one tree and the area of the quadrat was $(t[i+1] - t[i-1])^2$ m^2. The first and the last tree on the trail, $t(1)$ and $t(n)$, were not included in the calculation.

of the epiphytes had petiolated leaves and half sessile leaves, and each *D. hirsuta* trunk received a representative of each. The introduced plants were watered during the first week of the experiment. Later it proved unnecessary because of frequent showers in the area.

In some gaps we observed plant species other than *D. hirsuta*. The growth of these plants might have benefited from the improved light conditions in the gap. However, all plants were smaller than the *D. hirsuta* trees and thus assessed to have invaded after the gap was made. These plants seemed able to resist the weeding and pruning behavior of *Myrmelachista* ants. Species composition of the vegetation in 28 gaps was noted (see Table 2).

RESULTS

On its central part, each shoot had one domatium of a size of 4.5–5.0 x 0.5–0.6 cm with two entrance holes (Figs 1a, 2a). Only *Myrmelachista* sp. inhabited the domatia (Fig. 2d). In one gap the *D. hirsuta* tree had no ants. Some of its empty domatia contained debris from its former inhabitants. This gap without ants was overgrown by other plants, in particular by a large *Astrocaryum* palm. Its oldest leaves were withered and damaged, indicating former attacks by ants. Coccids (Homoptera) were observed in grooves inside 38% of the domatia (N = 200 domatia).

We censused 28 gaps with a total of 56 *D. hirsuta* trees (Fig. 2b). Gap boundaries were distinct, and

TABLE 1. Survival of plants planted in and outside *Duroia hirsuta* gaps.

	No. of survivors		
	Iriartea deltoidea	*Quararibea* sp.	Total
Test (N = 24) Inside gap	4	3	7
Control (N = 24) Outside gap	9	7	16

Fisher's exact test of independence (Sokal & Rohlf 1995, p. 734): *Iriartea*: $P = 0.10$; *Quararibea*: $P = 0.20$. Combining probabilities from these two independent tests of significance (Sokal & Rohlf 1995, p. 795): $\chi^2 = 7.85$, 4 degrees of freedom (two times the number of tests), $0.05 < P < 0.10$). One *Quararibea* test plant and one control plant were excluded because they died from drought.

single-tree gaps were almost circular in outline (Fig. 2c). Densities of trees and gaps were 23.3 and 11.6 per ha respectively. Average distance (± standard deviation) between neighboring gaps was 35.8 ± 43.6 m (range 0–150 m), and a gap had on average 2.2 ± 2.5 *D. hirsuta* trees. Average gap size was 58 ± 57 m². Average total height of a *D. hirsuta* tree was 5.1 ± 3.8 m and highly significantly correlated to its bole height (Pearson correlation test: ln(x+1)-transformed data: N = 48, correlation coefficient = 0.82, $P < 0.001$).

TABLE 2. Plants growing in the gaps of the *Duroia hirsuta-Myrmelachista* mutualism. Only species present in at least three of the 28 studied gaps are included. Abundance of ferns could not be estimated accurately.

| Species	Presence of species in gaps (%)	Abundance (mean no. plants/gap)
Adiantum spp. (Pteridophyta)	39	–
Psychotria polyphlebia Smith (Rubiaceae)	36	0.43
Asplundia alata Harling (Cyclanthaceae)	32	0.61
Cordia nodosa Lam. (Boraginaceae)	29	0.54
Myrsinaceae sp.	25	0.68
Clidemia sp. (Melastomataceae)	21	0.21
Other ferns	21	–
Ischnosiphon sp. (Marantaceae)	18	0.21
Inga spp. (Mimosaceae)	14	0.18
Aiphanes ulei (Dammer) Burret (Arecaceae)	14	0.14
Aechmea sp. (Bromeliaceae)	11	0.11
Geonoma triglochin Burret (Arecaceae)	11	0.11
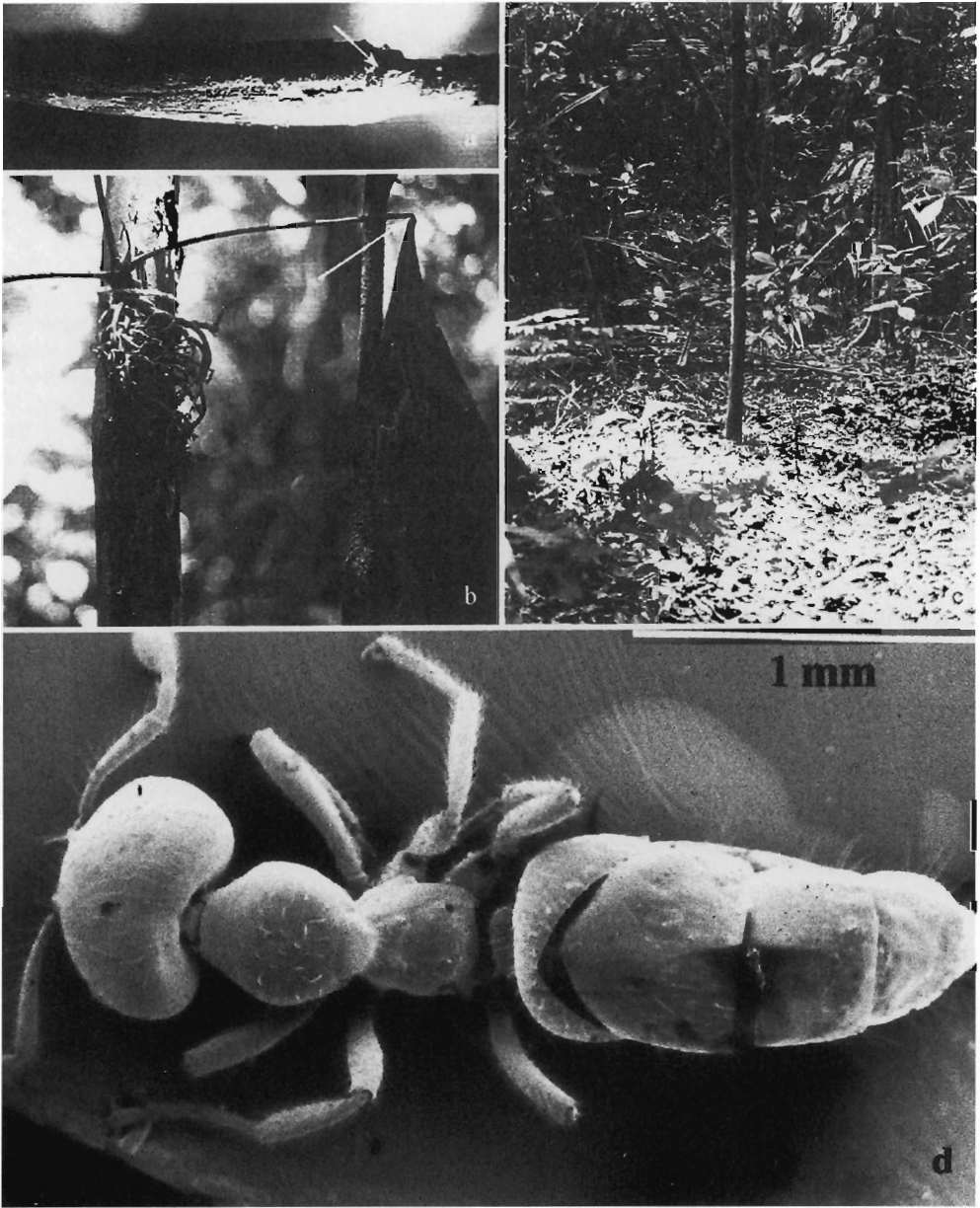
FIG. 2. (a) Domatium of *Duroia hirsuta* (arrow: one of the two entrance holes); (b) pruning experiment: damaged plant tied to the trunk of a *D. hirsuta* tree (leaf damaged at white arrow); (c) weeding experiment: *D. hirsuta* gap and an introduced plant (white arrow); (d) a worker ant of *Myrmelachista* sp. (Formicinae) (Scanning electron micrograph).

In the weeding experiment, plants on the ground in the gap were killed by ants. More plants survived outside the gap than inside (Table 1). The difference was, however, not significant. Two saplings died from drought. Plants outside the gap were also attacked by ants. Thus control plants might have been too close to the gap and probably were placed in a border zone between the gap and the surrounding vegetation. In the pruning experiment, all ten epiphytes with petiolated leaves were fatally damaged during the first two days of the experiment (Fig. 2b), whereas all ten plants with sessile leaves survived throughout the entire 8-week experimental period. *Myrmelachista* ants always attacked where the petiole joined the blade.

The 12 most abundant plant taxa growing in the gaps are listed in Table 2. Average numbers of taxa and individuals per gap were 4.0 ± 2.5 and 6.0 ± 6.0 respectively. Two were myrmecophytes themselves: *Cordia nodosa* and *Clidemia* sp. *Inga* plants had extrafloral nectaries visited by various ants. Ferns and the *Aechmea* had no leaf petiole and were thus not harmed by *Myrmelachista* ants. *Asplundia alata*, *Aiphanes ulei*, and *Geonoma triglochin* grew only at the border of the gap. The total number of species in a gap was affected neither by gap size nor ant colony size (Spearman correlation analysis: $n = 28$, correlation coefficient = 0.36, $P > 0.05$ [no. of plant spp. in a gap *vs.* gap size]; correlation coefficient = 0.15, $P > 0.10$; [no. of plant spp. in a gap vs. colony size]).

DISCUSSION

Campbell *et al.* (1989) also found no or very few plants surviving in *D. hirsuta* gaps. They attributed this to an allelopathic agent produced by *D. hirsuta* and absorbed through the roots of intruding plants. However, they also suggested that the effect might be related to formic acid from ants. Based on our experiment, we suggest that other plants in gaps were mainly damaged by ants, because roots of introduced plants did not come into contact with gap soil. Plants introduced near Melastomataceae species also guarded by ants gave similar results (e.g., Morawetz *et al.* 1992).

The behavior of *Myrmelachista* ants improved light conditions for *D. hirsuta* trees considerably. This was beneficial to the ants, because it secured a continuous supply of new domatia, allowing the colony to expand. Leaves of *D. hirsuta* were almost without any herbivory damage (pers. obs.). Thus, the benefits

to the tree were an improved light regime enhancing growth, probably less competition for soil nutrients with other species, and perhaps also reduced leaf herbivory, whereas the costs were production of domatia, which was probably low since the extra mass of wood needed for a domatium was minimal, and finally the effects of coccids. Likewise, benefits to ants were domatia and excretions from coccids, while costs were weeding/pruning around host trees.

We suggest that, through various adaptations, a set of plant species survive in ant-made gaps and benefit from relaxed competition without paying the costs of the mutualism. We cannot confirm that gap-intruding plants are harmful to the mutualism. However, several pieces of evidence suggest that this may be the case: an observation of a *D. hirsuta* tree abandoned by ants and overgrown by other plants; the observed high intensity of weeding and pruning by ants; the presence of gaps, and the obvious relationship between the growths of tree and ant colony. Traits allowing other plants to live in a Devil's garden may not be the result of selection for gap use; they may be traits present for other reasons (exaptations) incidentally allowing them to survive in *Duroia* gaps. Thus we do not suggest any coevolutionary history between intruding plants and *Myrmelachista* ants. However, intruders may certainly have a harmful impact on *Duroia* trees, suggested by the behavior of their ants. We conclude that plant-ant mutualisms, like other mutualisms, suffer from exploitation by other plants.

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