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Biotropica, Vol. 30, No. 2 (Jun., 1998), 324-327.

Stable URL:
http://links.jstor.org/sici?sici=0006-3606%28199806%2930%3A2%3C324%3AHAODAI%3E2.0.CO%3B2-9

Biotropica is currently published by Association for Tropical Biology.

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BIOTROPICA 30(2): 324–327 1998

Herbicidal Activity of Domatia-Inhabiting Ants in Patches of *Tococa guianensis* and *Clidemia heterophylla*[1]

Key words: Ant-plant mutualism; Clidemia heterophylla; *herbicide*; *Melastomataceae*; Myrmelachista; Tococa guianensis; T. chuivensis; T. occidentalis.

Morawetz et al. (1992) reported on an ant-plant interaction in the Sira Mountains of the Peruvian Amazon, in which ants of the genus *Myrmelachista* inhabiting leaf domatia of a species of *Tococa* (Melastomataceae) kill surrounding vegetation by first biting, and then spraying a poison, into leaves. This herbicidal activity by *Myrmelachista* clears a bare patch around the *Tococa* plant into which the individual spreads by vegetative reproduction to form a pure clonal patch up to 700 m^2 in area. In this note, we report on a similar situation involving a mixed stand of two melastome species, *Tococa guianensis* Aublet and *Clidemia heterophylla* (Desr.) Gleason, in Amazonian Ecuador. We show that woody plant density decreases toward the center of the patch, and that transplants of a variety of plant species are attacked by the ants and likely killed by them.

Most Ecuadorean material of *T. guianensis* is identified in herbaria as *T. chuivensis* Wurdack (if from Napo) or *T. occidentalis* Naud. (if from Pastaza or Zamora-Chinchipe). The species studied by Morawetz *et al.* in Peru was identified as *T.* occidentalis. During monographic work on *Tococa* [S. Renner, pers. obs.] it became clear that *T. chuivensis* and *T. occidentalis* are simply forms of the widespread and variable *T. guianensis* (see also Gleason 1931; Wurdack 1964: 424; 1973a: 399, 1973b: 556; 1980: 279–282). *Tococa guianensis* reproduces sexually (Renner 1989) as well as by runners and has large (about 2–3.5 × 1–2 cm) domatia in the leaf bases (illustrated in Wurdack 1980, pl. 28).

This study was carried out at the Jatun Sacha Biological Station, 8 km east of Misahuallí, Napo Province (1°4′ S, 77°36″ W) on 6–11 October 1995. In undisturbed forest on the station property, we discovered a 12 × 18 m patch of understory vegetation consisting of about four-fifths *T. guianensis* (voucher Renner 2175; deposited at the Herbario Nacional in Quito) and about one-fifth of *Clidemia heterophylla* (Renner 2169). The *Tococa* and *Clidemia* plants were inhabited by the same species of *Myrmelachista* (det. J. T. Longino). The *Tococa* shoots were connected by runners and believed to be a

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[1] Received 29 January 1996; revision accepted 21 January 1997.

single clone; the same was true of the *Clidemia* plants. The patch was surrounded by a zone 1 to 2 m wide and devoid of vegetation.

We estimated the area of the *Tococa-Clidemia* patch to be about 200 m^2. The center of the patch was virtually devoid of understory vegetation other than *T. guianensis* and *C. heterophylla.* Within the boundaries of the patch were 13 trees >10 cm DBH that reached to the canopy. This corresponds to a density of approximately 650 trees (>10 cm DBH) per hectare, which is typical of Amazonian rain forests (Valencia *et al.*, 1994). From the center of the patch, a 5 m radius circle (*ca* 80 m^2) included only one treelet of 4 cm DBH, with most of its crown dead. Closer to the periphery of the patch, and within the bare zone surrounding it, were several 1–10 cm DBH trees. These included nine tree ferns (3–5 cm DBH) and 16 saplings or treelets with an average DBH of 3.4 ± 1.9 SD cm (range 1–6). In the *ca* 120 m^2 included in this peripheral area of the *Tococa-Clidemia* patch, the average density of treeferns and treelets was 1.9 1–10 cm DBH individuals per 10 m^2, and 1.3 per 10 m^2 if tree ferns are excluded; the density was much lower (1 per 80 m^2, or 0.1 per 10 m^2) in the center of the patch. There were no woody plants <1 cm DBH in the patch, except for stems of *Tococa* and *Clidemia,* and no herbaceous ground-layer vegetation was found after a thorough search of the patch.

To compare the density of plants in the *Tococa-Clidemia* patch with the density of such plants in other parts of the forest, we selected six 10-m^2 quadrats centered *ca*10 m from the edge of the *Tococa-Clidemia* patch in different directions. The stems of all woody plants were counted within each of these quadrats, with the following results: cover of herbaceous vegetation at ground level approximately 10 percent; stems less than 1 cm, 16.3 ± 5.9 SD per 10 m^2; stems 1–10 cm DBH, 5.0 ± 1.3 SD (size: $N = 30$, 4.0 ± 2.1 SD cm DBH, range 1–10 cm). The density of *Tococa* and *Clidemia* stems (all less than 1 cm DBH) was estimated within three 10-m^2 quadrats in the center of the *Tococa-Clidemia* patch. The number of stems of *Tococa* was 19, 21, and 28, and the number of *Clidemia* was 4, 9, and 3 in the same quadrats, respectively.

A second *Myrmelachista*-produced *Tococa-Clidemia* patch was located 10 m from the periphery of the big patch. It was about 2 × 3 m in size and consisted of about two-thirds *Clidemia* and one-third *Tococa* stems. This second patch was free of other vegetation and had up to 1 m of a bare zone around the perimeter, not so well defined as in the case of the larger patch. A third individual of *Tococa,* a shrub about 1.5 m in diameter, occupied by the same *Myrmelachista* ants and also surrounded by a conspicuous bare zone, was located in another area of the forest.

To determine the effectiveness of ants in keeping the *Tococa-Clidemia* patches free of other vegetation and in extending its boundaries, we transplanted 20–40 cm high individuals (generally with 4–6 leaves) of several species of understory shrubs and saplings, including *T. guianensis* and *C. heterophylla,* from the surrounding area into the center of the first, larger patch. Individuals of three species were also transplanted to the bare zone surrounding the patch (Table 1). Transplanting did not cause any of the plants to wilt. Within a few days, however, several of the plants had *Myrmelachista* ants on them and had suffered the characteristic damage described by Morawetz *et al.* (1992), which resulted from the ants having sprayed a toxin onto the leaf tissue. The pattern of damage in most leaves consisted of necrotic tissue concentrated along mid-veins at the leaf bases. The necrotic areas often would start as small spots, which gradually enlarged and coalesced with others. The breakdown of tissue within these necrotic areas soon caused the leaves to wilt. By October 30, all plants except the transplanted *T. guianensis* and *C. heterophylla* individuals and one Gesneriaceae in the bare zone surrounding the patch had died; by December 5, the gesneriad had expired too.

Our observations are consistent with the idea that one or several species of *Myrmelachista* kill vegetation growing near plant species they occupy, in this case *T. guianensis* and *C. heterophylla.* The presence of a bare zone at the edge of the big patch further indicates that the ants' herbicidal activities facilitate the spread of *Tococa* and *Clidemia* plants over time. *Tococa guianensis* occurs from southern Mexico and the West Indies (Tobago) all throughout northern South America to Bolivia. Its relationship with ants has been studied by a number of authors (Ule 1904, 1915; Couret 1966; Schnell 1967; Benson 1985; Herre *et al.* 1986), and the species is known to be inhabited by *Azteca, Allomerus, Dolichoderus, Pseudomyrmex, Crematogaster, Gnamptogenys,* and *Solenopsis* in addition to *Myrmelachista.* Apparently it is only in eastern Peru and Ecuador that *T. guianensis* is occupied by the particular species of *Myrmelachista* exhibiting the herbicidal activity observed by Morawetz *et al.* (1992) and us. In the vicinity of Manaus, where one of us studied the reproductive biology of *T. guianensis* (Renner 1989), it never formed mono-

TABLE 1. *Fate of 17 plants transplanted into the center of the* Tococa-Clidemia *patch or into the bare zone at its periphery (T = transplanted; N = necrosis; W = wilting as a result of ant damage; H = herbivore damage; D = dead; ++ = increase in effect from previous observation; — = no change from previous observation). It rained heavily the night of October 9–10, which seems to have influenced ant activity.*

	Oct 7 1400h	Oct 8 1400h	Oct 9 0800h	Oct 10 0900h	Oct 10 1700h	Oct 30	Dec 5
Center of patch							
Miconia punctata	T	N, W	—	—	N	D	
Tococa guianensis	T	—	—	—	—	—	—
Clidemia heterophylla	T	—	—	—	—	—	—
Leguminosae	T	N, W	—	—	D		
Sapindaceae	T	—	—	N, W	—	D	
Piper sp.	T	—	—	—	—	D	
Triolena obliqua		T	—	—	H	D	
Marantaceae		T	—	N, W	++	D	
Gesneriaceae		T	—	N, W	++	D	
Inga sp.		T	—	—	—	D	
Bauhinia sp.		T	—	N	N, W	D	
Pilea sp.		T	—	N	N, W	D	
Piper sp.		T	—	—	H	D	
Rubiaceae		T	—	N, W	—	D	
Bare zone							
Gesneriaceae		T	—	—	H	—	D
Rubiaceae		T	—	—	N	D	
Marantaceae		T	—	—	—	D	

specific stands. *Clidemia heterophylla* in Peru is sometimes occupied by *Pheidole* (Davidson *et al.* 1989) and then does not form monospecific patches; nor do *Maieta guianensis* Aublet and *Clidemia allardii* Wurdack, common understory shrubs at Jatun Sacha whose domatia are occupied by *Crematogaster* ants (pers. obs.; ants indentified by J. T. Longino). *Tococa guianensis* thus provides a further example of geographical variation in plant-ant interactions (cf. Davidson & McKey 1993). Central Amazonian *Myrmelachista* species also occupy *Duroia hirsuta* (Rubiaceae) and *Cordia nodosa* (Boraginaceae), and these plants then form monospecific or two-species patches because the ants kill surrounding vegetation by causing leaf necrosis in the same manner as described for *T. guianensis* (Davidson & McKey 1993).

Myrmelachista is a Neotropical formicine genus, all species of which are arboreal. Species apparently can only be told apart by queens (J. Longino, pers. comm.). In terms of nesting habits, species of *Myrmelachista* vary in specificity. Some are generalist dead-stem nesters; others always use live stems, but not of particular species of plants; still others are variously specialized on particular lineages of plants (J. Longino, pers. comm.).

The *T. guianensis-C. heterophylla-Myrmelachista* mutualism at Jatun Sacha is similar in most respects to the situation described by Morawetz *et al.* (1992) for eastern Peruvian *T. guianensis* (as *T.* occidentalis). The primary differences would seem to be: (1) that our patches consisted of two species of melastomes; and (2) that in Peru, *T. guianensis* was presumed to establish readily only in open clearings resulting from treefalls or landslides, or along ridgetops, whereas the patch we observed in Ecuador was located on flat land and included several canopy trees within it. This suggests that it became established under a closed forest canopy. Also, the absence of understory trees in the center of the patch suggests that the patch has existed for a very long time. The second, smaller *Tococa-Clidemia* patch and the isolated *Tococa* individual grew in fully shaded locations.

We are indebted to J. Longino for the identification of the ants and for comments on the manuscript and to C. Ott for finding the dead transplants after our departure from Jatun Sacha.

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