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Epiphyte Orchid Establishment on Termite Carton Trails[1]

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ABSTRACT

In the coastal zone of central Veracruz, Mexico, we recorded the abundance of orchid plants growing on termite carton trails or directly on the peeling bark of *Bursera fagaroides*. Although only 19 percent of the surveyed trees contained termite carton trails, trees with termites hosted 92 percent of all orchid individuals. A disproportionate number of orchid seedlings occurred on termite cartons given the relative availability of carton and bark substrate. Our results show for the first time that orchids can establish on termite trails, and we discuss the potential for termite facilitation of orchid populations.

RESUMEN

En la zona costera de la región central de Veracruz, México, documentamos la abundancia de orquídeas sobre senderos de cartón de termitas y sobre la corteza exfoliante del árbol *Bursera fagaroides* Engl. (Burseraceae). Aunque solamente el 19 por ciento de los árboles investigados tenían senderos de termitas, estos albergaban el 92 por ciento de las orquídeas. Un número desproporcionado de plántulas de orquídea crecían sobre el cartón de las termitas a pesar de la abundancia relativa de cartón y corteza. Nuestros resultados demuestran, por primera vez, que las orquídeas pueden establecerse sobre senderos de termitas y discutimos la posible facilitación de las termitas en la población de orquídeas.

Key words: Bursera; Brassavola; *epiphytes; Mexico; Myrmecophila; Nasutitermes; safe sites; tropical dry forest.*

EPIPHYTES FACE A SPATIAL AND TEMPORAL MOSAIC OF SUBSTRATES on which they can establish, but substrate quality varies. Epiphyte population growth therefore depends on the abundance of safe sites (Bennett 1986, Ackerman *et al.* 1996). One strategy for dealing with this environmental variability is the development of seeds that have a high germination capacity on any substrate (Benzing 1990), causing the host species to be unimportant (Callaway *et al.* 2002). There are, however, host species (*e.g.*, trees with peeling bark) that have consistently fewer epiphytes, suggesting that their characteristics prevent epiphyte establishment (Johansson 1974).

Many epiphyte species establish directly on tree bark, and it has been shown that their success depends on several factors such as the presence or absence of alellochemicals, the water-holding capacity of bark, and bark stability (Frei 1974, Castro-Hernández *et al.* 1997, Callaway *et al.* 2002). Other epiphytes establish on trees due to the presence of facilitators such as fungi, lichens, or ant carton structures. Some epiphytes are dispersed by ants or in the fecal material of vertebrates and deposited within a pool of organic matter (Longino 1986, Davidson 1988, Catling 1997).

Some tropical epiphytes are facilitated by ant activity, and the interaction between ants and epiphytes has received much attention. This interaction is sometimes a mutualism: ants can disperse epiphyte seeds to safe sites where the epiphytes receive protection and nutrition, while the ants obtain food and use epiphytes as nests or to form part of their carton nest structure (Longino 1986, Rico-Gray *et al.* 1989, Yu 1994, Catling 1997). In Neotropical canopies, termites of the genus *Nasutitermes* (Isoptera: Termitidae) are also common. Like ants, they use epiphyte resources, and they may compete with ants for access to epiphyte domatia (*sensu* Huxley 1980) and for tree holes in which to make nests (Thorne *et al.* 1996a, 1996b; Dejean *et al.* 2003). However, epiphytes rarely use carton structures made by termites. Blüthgen *et al.* (2001) suggested that a termite carton has a lower nutrient content and is harder than an ant carton. We report here the first account of epiphytic orchid establishment on carton-covered foraging trails made by a nasutiform termite.

This study was conducted at "La Mancha" Coastal Research Center (CICOLMA, 19°35′12″N–19°36′18″N, 96°22′18″W–96°23′24″W, 0–150 m asl) in Veracruz, Mexico. The climate is warm and subhumid, with an average minimum temperature of 18°C and an average maximum of 34°C; total annual rainfall ranges from 1200 to 1500 mm and is concentrated in the summer (Castillo-Campos & Medina-Abreo 2003). There are eight different vegetation types at CICOLMA. This research was done in savannah-type vegetation (Castillo-Campos & Medina-Abreo 2003), an herbaceous community with abundant isolated dwarf trees. The trees are 3–7 m in height, and characteristic species are *Bursera fagaroides* Engl. var. *purpusii* (Brandegee) McVaugh & Rzed. (Burseraceae) (hereafter *B. fagaroides*), *Byrsonima crassifolia* (L.) HBK (Malpighiaceae), and *Coccoloba barbadensis* Jacq. (Polygonaceae). The most frequent epiphytes in savannah trees are bromeliads, but there are also orchid species, the most abundant being *Brassavola nodosa* (L.) Lindl. and *Myrmecophila grandiflora* (Lindl.) Carnevali,

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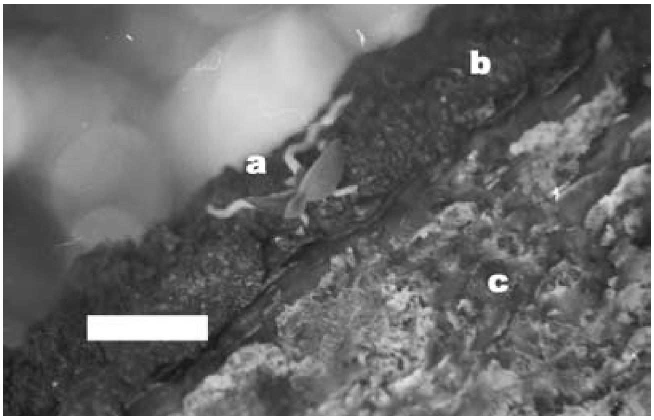

FIGURE 1. A seedling of the orchid *Myrmecophila grandiflora* (a) growing on the carton-covered foraging trails of *Nasutitermes nigriceps* (b). Note the peeling bark of *Bursera fagaroides* (c). Scale bar is 1.5 cm.

TABLE 1. *Orchid abundance on* B. fagaroides *trees with or without termite carton-covered foraging trails. For tree height, basal area, and orchid abundance the means (±SD) are shown.*

Tree group	Number of trees	Height (m)	Basal area (cm^2)	Number of orchid plants per tree
Without carton trails	282	1.71 ± 0.89	69.08 ± 76.69	0.07 ± 0.72
With carton trails	66	3.05 ± 1.26	171.74 ± 98.72	3.39 ± 7.26

Tapia-Muñoz & I. Ramírez [=*tibicinis* (Bateman) Rolfe] (García-Franco 1996, Martínez & García-Franco 2004).

Three termite species have been found in CICOLMA, but only one, *Nasutitermes nigriceps* Haldeman, develops nests and carton structures on trees (P. Rojas, pers. comm.). Species of this genus feed on wood, where they also make nests, later covering them with carton structures. Termite carton-structures are made with wood, saliva, and feces, and contain nutrients and fungi. Furthermore, termites use such structures to build a network of trails that extend across their foraging territory (Fig. 1). It has been suggested that the carton trails are long-lasting and that the termites defend this carton structure against ants and other termite species (Koford 1965, Adams & Levings 1987, Thorne *et al.* 1996b, Leponce *et al.* 1997) *Nasutitermes nigriceps* nests can measure up to 2 m in height and 1 m in width; they are among the largest made by arboreal termites (Thorne *et al.* 1996b).

In February and April of 1996, 348 *B. fagaroides* dwarf trees were marked on four 3500 m^2 plots, representing the study area's environmental variability (for further details see Ortíz-Pulido & Rico-Gray 2000). For each tree, we scored whether or not it had termite trails, and we measured the DBH, height, and the number of orchids growing on it. For each orchid individual we recorded species, growing substrate (bark, termite carton trail, or other), branch diameter, and, if the orchid was on a carton trail with well-defined borders, the width of the carton trail. Only juvenile orchid plants were assigned to a substrate, and only when all their pseudobulbs and roots were on a substrate; a juvenile was defined as a plant with a pseudobulb and leaf $\leq$ 3 cm in length (Fig. 1).

We performed a covariance analysis (GLIM 4; Francis *et al.* 1993) to compare orchid abundance on trees with and without termite carton trails. In this analysis the tree type (with and without termite carton trails) was a factor in the model, tree height was a covariable, and the number of orchid plants per tree was the response variable. We used tree height as the covariable instead of basal area, because tree height explained more of the deviance (53%) than basal area (32%). Since the response variable was a count, we used a Poisson Error Model. The final model was rescaled to overcome a weak overdispersion problem (*cf.* Crawley 1993).

We compared juvenile orchid abundance on termite carton trails and *B. fagaroides* bark. To estimate substrate abundance we calculated the average proportion of the branch circumference that was covered with termite carton trails. To do this we divided the termite carton trail width (including zero values) by the circumference of the trunk branch, for each branch on which a juvenile orchid was found. For each orchid species, we calculated expected orchid abundance values for the two substrates (termite carton and bark) based on the average proportion of branch circumference covered by termite carton, and used a χ^2 test (Zar 1996) with one degree of freedom to test for substrate preference.

We found 244 orchid plants growing on *B. fagaroides* trees: 150 *M. grandiflora* and 94 *B. nodosa*. Only 19 percent of trees had termite trails, yet they hosted 91.8 percent of the orchids (Table 1). Mean orchid abundance was different between tree groups (Table 2) and was positively related with tree height (Table 2), similar to other studies of epiphyte communities (*e.g.*, Yeaton & Gladstone 1982). The relationship of orchid abundance to tree height was different between tree groups, however (significant interaction term in Table 2). Orchid abundance increased more rapidly on trees with termite trails compared to those without.

Of the 244 orchid plants, 218 (69 *B. nodosa* and 149 *M. grandiflora*) were juveniles that grew only on carton trails or on bark. The remaining 26 were adult plants of *B. nodosa* or juvenile plants growing on another substrate (two *B. nodosa* seedlings

TABLE 2. *Analysis of covariance testing the effect of termite presence (tree group) and tree size (tree height) on the number of orchid plants growing on* B. fagaroides *trees.*

Source of variation	*F*/deviance	df	*P*	Explained deviance (%)
Tree group	136.7	1	<0.0001	13.1
Tree height	550.0	1	<0.0001	52.7
Interaction	8.9	1	0.0031	0.9
Error	348.0	344		33.3
Total	1043.6	347		

TABLE 3. *Number of juvenile orchid plants found on termite carton trails and on the peeling bark of* B. fagaroides. *Figures in parenthesis are the expected number of plants according to substrate abundance. For both species the observed abundances were different from the expected ones (χ^2 test,* $P < 0.0001$*).*

	Number of orchid plants	
Orchid species	Bark	Carton trails
B. nodosa	34	35
	(66)	(3)
M. grandiflora	43	106
	(143)	(6)

on lichens, another two on *Tillandsia ionantha* Planchon roots, and one *M. gradiflora* seedling on orchid roots). No adult plants of *M. grandiflora* were found. Termite carton trails averaged 14.4 ± 5.0 mm in width (mean ± SD, $N = 77$) and covered 4.3 ± 6.0 percent ($N = 155$) of the branch circumference where orchids were found. Both for *B. nodosa* ($\chi^2 = 366.1$, 1 df, $P < 0.00001$) and *M. grandiflora* ($\chi^2 = 1637.9$, df = 1, $P < 0.00001$) the abundance of juveniles was different between substrates (Table 3). In both orchid species, juvenile abundance was lower than expected on bark and higher than expected on carton trails (Table 3).

The orchid abundance that we found on *B. fagaroides* was low compared to that of epiphytic bromeliads on the same host. On ten *B. fagaroides* measuring over 2.5 m in height, López-Villalobos (2002) found 411 *Tillandsia palmasoloana* Matuda plants and 782 *T. paucifolia* Baker (Bromeliaceae) plants. Most bromeliads were on small diameter (<2 cm) branches, while the orchids we found were on trunks and branches measuring over 6 cm in diameter (7.98 ± 6.50 cm, $N = 216$; mean ± SD). Bark peeling occurs almost three times faster on large branches and trunks compared to twigs: peeling rate was 0.32 percent per day on large branches, 0.13 percent per day on twigs (López-Villalobos 2002). It is unknown what causes bromeliads to preferentially establish on small branches while orchids preferentially establish on larger branches and trunks. But the high peeling rate on large branches and trunks must inhibit the establishment of large orchid populations. On substrates with high peeling rates, termite trails could increase rates of orchid establishment.

Blüthgen *et al.* (2001) suggested that nutrient levels in a termite carton are too low for epiphyte establishment, but our results show that in at least some situations epiphytic orchids can establish on termite carton. Termite carton may facilitate orchid establishment because it consists of wood and bark that has been stabilized, enriched (Koford 1965, Peaking & Josens 1975, Wood & Sands 1978, Eggleton *et al.* 1995, Thorne *et al.* 1996b), and may contain mycorrhizal fungi. It has been shown that termites produce antifungal compounds in their fecal pellets as well in the defensive glands of soldiers (Rosengaus *et al.* 1998, 2000). However, orchid seeds depend on mycorrhizal fungi during the early stages of germination (Benzing 1981, Arditti & Ghani 2000). Mycorrhizal fungi may occur in termite carton trails and it is possible that the termite antifungal compounds do not kill them.

Our results show that epiphytic orchids can establish on termite trails, but does this imply that termites facilitate orchids at the population level? Facilitation is a direct positive interaction in which the fitness of at least one of the interacting species increases, without affecting the fitness of the other species (Hacker & Gaines 1997). The facilitators improve the fitness of the other species in one of two ways, by creating or maintaining habitats (as germination areas) or by increasing their survival in response to environmental stress (Hacker & Gaines 1997). Although mature orchid plants were rare at our study site, we observed a few large individuals in *B. fagaroides* trees adjacent to our study plots, and a few flowering individuals growing on the ground. In the coastal zone of Yucatan, Mexico, Rico-Gray (1987) observed *M. christinae* Carnevalli & Gómez-Juárez (=*tibicinis*) growing on the ground and suggested that the plants first establish on trees and then fall to the ground. It is possible that the higher establishment rate on termite carton has no population-level consequence for the orchids at our study site, and the population of mature plants is limited by other factors. On the other hand, termites could be true facilitators, enhancing the recruitment of reproductive individuals both in trees and on the ground.

There are two main mortality factors in epiphytic plants: desiccation (Zotz & Tyree 1996, Zotz & Andrade 1998) and dislodgement from the anchorage position (Martínez & García-Franco 2004, Mondragon *et al.* 2004, Zotz 2004). Carton trails of *Nasutitermes nigriceps* may mitigate both of these mortality factors. Carton trails may retain greater moisture levels for longer compared to the bark, and the trails may be a more durable and longer-lasting substrate compared to the peeling bark of *B. fagaroides*.

It has been suggested that epiphytes make generalized use of carton structures (Longino 1986) but until now the emphasis has been entirely on the carton constructed by ants (Longino 1986, Yu 1994, Catling 1997). Our data show for the first time that epiphytes can establish on termite carton and that this interaction could facilitate orchid establishment on a peeling-bark tree species.

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