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Associations Between Termites and Bromeliads in Two Dry Tropical Habitats[1]

Key words: British Virgin Islands; Bromeliaceae; fire protection; Guana Island; Isoptera; Minas Gerais, Brazil; Nasutitermes; *symbiosis;* Tillandsia.

THE ECOLOGICALLY AND NUMERICALLY PROMINENT TERMITE *Nasutitermes acajutlae* (Holmgren) occurs through the Caribbean from Puerto Rico south to Trinidad, possibly extending into South America (Thorne *et al.* 1994). This species builds arboreal nests that are among the largest known for any termite, measuring up to 2 m in height and 1 m in diameter (Thorne *et al.* 1994). Like other *Nasutitermes,* these termites build extensive networks of covered tunnels connecting the nest to distant foraging sites in the tree crown and ground below. Workers and soldiers, numbering well over a million individuals in mature colonies, travel within these "carton" tunnels which consist of partially digested wood, fecal material, soil, and water (Light 1933). We discovered an association between *N. acajutlae* termites and the bromeliad *Tillandsia utriculata* on Guana Island, British Virgin Islands (B.V.I.), during October 1994. *T. utriculata* is the largest of the local tank-forming or phytotelm bromeliads, that by definition impound water and litter as major sources of moisture and nutrients among inflated, tightly overlapping leaf bases.

Guana Island, a wildlife sanctuary which lies directly north of the eastern end of the island of Tortola, B.V.I., covers about 340 ha and rises to about 246 m at maximum elevation. Guana Island is volcanic and supports a rich diversity of flora and fauna due to habitat variation and a history of minimal disturbance (Lazell 1989). Dry lowland scrub forest predominates, while abundant cacti characterize scattered, drier sites. Wet areas are confined to the few ravines on the island. *T. utriculata* occurs abundantly in some of the drier woodlands, but they were not surveyed comprehensively.

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TABLE 1. *Transect survey of the association between active trails of the termite* Nasutiterines acajutlae *and the bromeliad* Tillandsia utriculata *in four locations on Guana Island, British Virgin Islands. Only trees (including cacti) that contained both termite trails and at least one bromeliad were included in the study.*

Location transect on Guana Island	Number of trees with termite trails intersecting the bromeliad	Number of trees with termite trails not intersecting the bromeliad
"Garden of Eden" nr. Guana Island Club	11	1
Trail to Longman's Point	75	2
White Bay Beach	17	0
Wei Ping Liao Trail	12	0
Total	115 (97.4%)	3 (2.6%)

The association between the termites and bromeliads on Guana Island was particularly easy to document because *N. acajutlae* builds distinctive and conspicuous trails, and *T. utriculata* often grows in relatively low canopies. We inspected every tree and large cactus that we could readily see along four transects in four locations on the island. Only trees and cacti that had both active termite foraging tunnels and at least one *T. utriculata* plant were examined.

Termite tunnels intersected a bromeliad in 97.4 percent of the 115 possibilities (Table 1; Fig. 1). Usually, *N. acajutlae* tunnels went to the root system or above to the water-filled leaf axils. Often tunnels continued into the shoots to cover impounded water. Some hung suspended for short distances (4–12 cm) between adjacent bark and the plant. A few tunnels led only to the moist area where the bromeliad rooted, but usually at least one leaf axil was accessed.

FIGURE 1. Photographs of tunnels built by the termite *Nasutitermes acajutlae* intersecting leaf base chambers of the bromeliad *Tillandsia utriculata* on Guana Island, British Virgin Islands. a. *N. acajutlae* trail built up to the moist root cluster and leaf base reservoirs of *T. utriculata.* b. *N. acajutlae* trail built over leaf bases of a *T. utriculata* plant.

Each tree was counted only once in a transect, but many trees hosted more than one *T. utriculata* plant, and termite trails intersected up to eight bromeliads on a single tree. We were unable to determine the extent of a complete network, *i.e.* how many bromeliads were tapped by a given *N. acajutlae* colony, in part because *N. acajutlae* foragers also travel within decayed wood. Quite likely, termites inconspicuously tap bromeliads from inside supporting trunks and branches. *N. acajutlae* may also tap *T. utriculata* rooted on the ground. Hence, our data probably present a conservative measure of the termite/bromeliad association.

Although diverse invertebrates occupy bromeliad tanks (*e.g.,* Picado 1911, Pittendrigh 1948, Laessle 1961, Fish 1983, Benzing 1990, Nadkarni & Longino 1990), this is the first report of an association with termites. Most likely the termites are visiting *T. utriculata* to obtain water, a scarce commodity given the xerophytic vegetation and porous soils of Guana Island. No formal weather records exist, but longtime residents and scientific researchers agree that the two years prior to our study were uncharacteristically dry in the Virgin Islands. Drought was particularly acute where aridity generally prevails as on Guana Island. Our related studies of termites on Guana Island (1989–1994), suggest diminished populations of *Nasutitermes* and other termites caused by abnormally low rainfall in 1993 and 1994, but more extensive records are needed to assess the magnitude and rarity of this presumed stress.

Organic matter suspended in the water impounded by *Tillandsia* shoots is a potential source of termite nutrients (Huxley 1980; Benzing 1981, 1990). However, preliminary bioassays ($N = 4$) using disks of saturated Whatman #1 filter paper and several hundred termite foragers indicated no preferences between bromeliad extracts and tap water. We do not know if termites feed on tank debris as the water level recedes.

Although termites probably visit *T. utriculata* primarily to exploit moisture, effects on plants more likely vary with local circumstances. Absorbant termite carton tunnels wick moisture away from shoots. Up to 35-cm lengths of termite tunnel were saturated with moisture siphoned from leaf axils or areas of seepage around roots. *Tillandsia utriculata* tolerates considerable drought, but any tank bromeliad fails if leaf axils dry out for extended intervals (Madison 1977; Benzing 1981, 1990). Conversely, overhanging portions of termite carton should reduce losses from a plant's supply of moisture.

Termites are ill-suited to match certain ants as plant mutualists. Termites typically remain confined to tunnels and are therefore unavailable, even if disposed, to deter plant predators. Some ants deposit nutritive materials in bromeliad shoots, thus contributing to plant welfare (reviewed in Huxley 1980, Benzing 1990). An occasional termite may die or drown in a leaf axil, but probably not often enough to significantly promote plant nutrition. Termite tunnel carton that ends up in the tanks is also unlikely to constitute much of a nutritional supplement for the bromeliad.

The termite diet precludes bromeliad seed dispersal, a phenomenon known from several ant/epiphyte relationships (reviewed in Huxley 1980, Benzing 1990, Yu 1994). Only once did we observe a juvenile *T. utriculata* rooted in a termite tunnel or a bromeliad growing adjacent to a termite nest. Furthermore, a number of the termite trails turned toward a bromeliad, suggesting that the plant had arrived first and had been subsequently located by exploring termites. Thus, the relationship between termites and plant probably pivots on moisture rather than predator deterence, nutrition, or seed dispersal. The dynamic may shift according to circumstance from weakly mutualistic through commensalistic to parasitic if plants become water-stressed.

A heavy rain in October 1994, the first following a prolonged drought, provided an opportunity to observe termite trail construction. As is typical for arid-land *Nasutitermes,* trail building escalated because workers need moisture to masticate and manipulate materials used for tunnel construction. Trails were rapidly laid down on four trees which supported bromeliads that *N. acajutlae* had only recently discovered. In each case, the termites first lay a trail of fecal deposits and secretions on the tree bark, typical of their normal building behavior (Jones 1980). Tunnel construction then began at the junction with the bromeliad, proceeding down the tree. By working from the bromeliad down instead of from the base of the tree up, the termites had ample moisture for their work.

Do termites use trees with bromeliads for *both* food and water, or are they exploring some supports only to obtain moisture from the attached epiphytes? Host trees we examined were generally mature with apparent or probable zones of dead wood. In addition to the tunnels leading to the bromeliad, usually one or more of the trails led to a feeding site through a knothole or dead branch. However, young trees with no dead wood would, because of their age, also be the trees least likely to support

epiphytes. If one found a case in which the termites appeared to be occupying the tree only for access to the bromeliad, the carton tunnels should be scraped away to confirm presence or absence of any covered access holes into the tree wood.

Although *N. acajutlae* appears to be remarkably drought tolerant, probably more so than other *Nasutitermes* species in the Caribbean, bromeliads may at least occasionally provide essential moisture. *N. acajutlae* workers possess comparatively large water sacks, sufficient to store enough water for prolonged dry weather (M. S. Collins, pers. comm.). *N. acajutlae* is clearly not a specialist on trees with bromeliads, but linking to one or more tank reservoirs may enable these termites to thrive or survive in an otherwise inhospitable season or habitat. To further understand the ecological dynamics of this association, we plan to seek comparative data on intersections between *N. acajutlae* foraging trails and *T. utriculata* plants on wetter islands in the Virgin Islands cluster, and on Guana Island in times of heavier rainfall.

Preliminary observations in the rocky, semiarid "campos rupestres" of Minas Gerais state in southeastern Brazil indicate that associations between termites and water-impounding bromeliads occur beyond Guana Island. A brief foray into the field near the city of Diamantina revealed covered termite trails leading from the soil up along the precipitous faces of large rocks to the bases of several large, lithophytic and water-impounding *Aechmea phanerophlebia.* Unlike *Tillandsia utriculata, Achmea phanerophlebia* produces an urn-shaped shoot that intercepts no litter, but often houses ant colonies. In all other respects, the relationship appeared to be equivalent to that observed on the Caribbean island.

Several more locally abundant terrestrial Bromeliaceae representing *Dyckia* and *Encholirium* also attracted unidentified termites at the Brazilian site, as did some companion flora (*e.g.,* Cyperaceae, Vellosiaceae) of similar low stature. Virtually every mature plant contacted mounds of termite carton. Inspection indicated no damage from the insects. Root systems located in soil rather than in adjacent termite construction indicated that termites build around established plants as in the case of *Tillandsia utriculata* in the British Virgin Islands.

Drought may render bromeliad phytotelmata an important termite resource in the high rocky grasslands of southern Brazil as on Guana Island. A broader variety of terrestrial herbs, including Bromeliaceae, could provide similar assistance, not as liquid water but as vapor to humidify termite galleries. A variety of benefits may accrue in turn to the flora. Abundant, charred vegetation and extraordinary insulation on endemic flora (thick bark, persistent leaf bases on herbs) reflect frequent natural fires in the campos rupestres. Recent fires had seriously burned some of the few exposed bromeliads, but none of those plants embedded in termite carton (similar findings elsewhere noted by Morison *et al.* 1948, Harris 1961). The survivorship and fecundity of bromeliads among other low-growing vegetation would also be improved if these insects promote plant nutrition or deter herbivores. Additionally, spiny-leafed *Dyckia* and *Encholirium* may discourage large, local ant-eaters seeking termites as food.

Termites constitute prominent components in diverse ecosystems, particularly in the tropics, where they substantially enhance nutrient cycles. Observations reported here indicate that termite colonies in some dry habitats may establish long-term relationships with bromeliads to access water. Consequences probably vary for the plants. Some of these relationships seem pervasive enough to warrant further inquiry.

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