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Foraging preference of Atta cephalotes (Hymenoptera: Formicidae)

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ABSTRACT

Leaf cutter ants, *Atta cephalotes,* were found to make distinct tree species choices as herbivores in the premontane wet forest of Cerro Plano, Costa Rica. One trail from each of six nests was studied. Trail lengths varied, ranging from 3.30m to 40.40m. Trees were identified along the trail, as well as the host tree at the end of the trails. Three leaves were taken from each tree and tested for toughness, thickness, and percent water content. The results for each test for each tree along a trail were compared to those for the host tree. The ants selected for thinner leaves. A simple regression correlated leaf thickness and toughness. Because of the range of toughness per leaf thickness, however, the results for leaf selection based on toughness were not consistently significant with regards to being more or less tough than the host tree, suggesting that selection for toughness is secondary to selection to thickness. Selection for water content also yielded significant results, though; once again, not consistently significant with regards to having more or less water than the host. Our data suggests that other factors play a role in host selection of Atta, and further investigation of their selectivity would draw a more complete picture.

RESUMEN

Las zompopas, *Atta cephalotes*, descubrieron ser especialistas en el bosque lluvioso de Cerro Plano en Monteverde, Costa Rica. Estudiamos seis nidos, un sendero de cada nido. Las longitudes de cada nido fueron diferentes, entre 12.30 y 40 metros. Identificamos los árboles a lo largo de los senderos, y los árboles anfitriones a los términos de los senderos. Tomamos tres hojas de cada árbol y pusimos cada hoja a prueba de espesor, dureza y contenido de agua. Comparamos los resultados todos de cada árbol con los resultados del árbol anfitrión. Los árboles anfitriones tenían hojas menos el espesor de las hojas de los árboles de los senderos. Es posible que las zompopas escogieran las plantas sin savia y terpenoids.

INTRODUCTION

The fungus growers (Tribe Attini) are limited to the New World, most of the 11 genera, approximately 200 species, occurring in the tropical portions of México, Central and South America (Wilson, 1971). *Atta cephalotes*, leaf-cutting ants, are found below 2000 meters throughout Costa Rica. The nests of *Atta cephalotes* have been observed to have up to 5 million workers, including the small minimas, the large soldiers, and the most commonly noticed media. The nests of *A. cephalotes* can be seen as large bare areas with nest exits sometimes up to 50m apart. With the leaf material they collect, the ants grow a fungus, probably *Leucocoprinus gogogylophora*, a Basidiomycete (Martin, 1969 in Stevens, 1983). This fungus feeds the mature ants as well as the ant larvae (Stevens, 1983). The ants also feed on the sap of the leaves that they cut (Hölldobler and Wilson, 1990).

Leaf-cutters are considered the dominant herbivores in the Neotropics, cutting an estimated 12% to 17% of all leaves (Cherrett, 1986 in Hölldobler and Wilson, 1990). *A. cephalotes* is specialized to live in forest gaps, and thus thrives in plantations and farms (Cherret and Peregrine, 1976 in Hölldobler and Wilson, 1990). They have the ability to utilize a diverse array of plant species, leading them to have a considerable impact of agriculture in the Neotropics. In Santa Rosa National Park, more than 80 species of plants were taken by leaf cutters in one year (Stevens 1983). Annual damage by these ants has been estimated to be in the billions of dollars (Hölldobler and Wilson, 1990).

Plants have a variety of defenses from leaf-cutter ants. Reducing the nutritional quality of the leaves is one option. Lower levels of nitrogen and water have been shown to reduce herbivore preference. Leaf toughness has also been correlated with reduced herbivory. In addition, Howard (1988) has shown that selectivity is likely to be based on the presence of repellant substances in some plants, perhaps anti-fungal compounds. Tropical leaves often have high levels of anthocyanins which have been shown to have anti-fungal properties, making them inappropriate for leaf-cutters. Other repellent compounds include: terpenes, cyanogenic compounds, alkaloids, and saponins (Coley and Barone, 1996). A study in Costa Rica showed that a colony of *Paraponera clavata* defended their host tree by attacking a foraging column of *A. cephalotes* (Wetterer, 1994). Plants, therefore, can protect themselves by providing food for predators of the ants; in the case of *P. clavata* food is provided by extra-floral nectaries (Janzen and Carroll, 1983).

Leaf-cutting ants should not forage randomly. Instead, they should avoid well defended plants. A study done by Blanton and Ewel (1985) in Florencia Norte Forest of Costa Rica found that *A. cephalotes* attacked only 17 of 332 available plant species (in Hölldobler and Wilson, 1990). Leaf-cutter ants are known to avoid *Hymenaea courbaril*, which contains caryphyllene epoxide, a compound that has been shown to have anti-fungal properties (Howard and Wiemer 1986). *Inga punctata*, known for its extra-floral nectaries which attract ants, has been shown to be defended from leaf-cutters at low elevations where nectar feeding ants are abundant (Koptur, 1983). Leaf-cutter ants may also have nutritional requirements for their fungi; however, these requirements aren't well known (Hölldobler and Wilson, 1990).
In addition, Howard (1988) has shown that selectivity is likely to be based on the presence of repellant substances in some plants, perhaps anti-fungal compounds.

Of particular interest to us were the trails on which *A. cephalotes* forage. These trails can stretch for more than 100m (Hölldobler and Wilson, 1990). The cost of transportation of leaves back to the nest should eventually offset the value of the leaves further down the trail (Covich, 1976). One hypothesis is that the leaf-cutters pass by suitable trees in order to preserve a back-up supply of leaves, although this has also been refuted (Hölldobler and Wilson, 1990). Previous studies have analyzed leaf-cutter selection by placing rye flakes or leaf pieces in their trail and measuring rates of pick-up (Howard, 1988; Howard and Wiemer, 1986). Our study compared the choices made by leaf-cutters in natural conditions. This way we were able to compare trees of the same species on the same trail. We hypothesized that *A. cephalotes* is a specialist herbivore. If so, the plants passed on the way to the host should have been measurably different. To test this we compared leaf toughness, thickness, and water content between trees that the ants pass and trees that host the ants. We also noted the presence of secondary compounds as reported by Raffauf and Schultes (1990), and Mabberley (1997).

MATERIALS AND METHODS

Data collection on plant preference were carried out during the wet season in the premontane wet forest of Cerro Plano (1440m) in Monteverde, Costa Rica. Collection occurred between October 16 and November 10, 2000.

We collected leaves from the trails of six colonies of *Atta cephalotes*. One trail was chosen for each of the six colonies. When possible, trails were chosen that went through a forested non-monocultured area and had between 10 and 20 trees along the trail. Five of the six nests (nests 1, 2, 4, 5, 6) were in forested areas, and their trails remained in the forest. Nest 3 was on the edge of an open field. The trail, however, went through a forested area. The length of each trail was measured (Table 1). We collected leaves from all trees with a diameter at breast height (DBH) greater than 10cm within 2.5 meters of the ant trail. Leaves were also collected for trees with DBH greater than 10cm that were touching the host tree.

Leaves were collected for identification and testing by breaking down small branches. Four methods were used in collecting specimens from the trees. If branches with leaves were low enough to reach, a branch was cut off with a knife. Otherwise, a rope was thrown over a branch and then the branch was pulled down. If the branches were too high to throw the rope over, then a fishing line was shot over a branch. Then, with the fishing line, a rope was reeled over the branch and the branch was pulled down. Leaves were shot down with a slingshot and rocks when they were too high to throw a rope over, or shoot fishing line over.

Twigs or small branches were collected and pressed in a plant press for identification. To aid in plant identification, we also took note of the presence or absence and quality of sap, odor of the leaves and the DBH. Three additional leaves were collected from each tree to be for leaf measurements. The leaves were labeled with the tree they were from and placed in a plastic bag to protect them until the tests could be performed later that afternoon. Leaves were chosen on the basis of appearing to be an average, mature leaf with zero to minimal damage.

Three leaf quality tests were performed: thickness, toughness, and water content. First, we measured the leaf toughness with a penetrometer, which measured the weight at which a leaf was punctured. The total mass, in grams, required to break the leaf's surface was recorded. The second test was a measurement of leaf thickness with Spi Vernier calipers. For both tests, one measurement was taken per leaf. The measurements were taken at the midway point on the leaf, avoiding the venation. For water content, we took an initial weight measurement after leaf toughness and thickness were measured. The leaves were then left in a dry box at 28.5°C overnight, and the final weight measurement was taken the next day. Leaves not completely desiccated the following day were left in the dry box until they were dry.

William Haber and Willow Zuchowski identified plants to species. The term "host tree" indicates the tree from which the ants were currently harvesting leaves. The terms "trail trees" or "trail leaves" indicate those trees and their leaves on the trail leading up to the host tree. We compared the host tree species to the species of the other trees along the trail (Tables 2, 3, 4, 5, 6, 7, and 8). The host was identified as common or rare, common meaning that the ants passed a tree of the same species along the trail, and rare meaning the host was a unique species to the trail.

For some trees, we were able to get samples, but unable to identify those trees. For those trees, we included the results for the leaf tests, but did not include the tree species in our data. We looked up possible deterrent compounds for each tree identified (Howard and Wiemer, 1986; Hölldobler and Wilson, 1990; Raffauf and Schultes, 1990; Mabberley, 1997).

Each trail was analyzed separately in Stat View using One Grouped t-tests. Trees along the trail and the touching tree(s) were compared using the host tree as the expected mean for thickness, toughness, and percent water content. We also performed a simple regression correlating the toughness to the thickness of the leaves.

Because trail two had two host trees, we separated the trail into 2A and 2B. For 2A, we compared the trees preceding host tree A to host tree A. For 2B, we compared trees preceding host tree B to host tree B. We exclude host tree A from our analysis of trail 2B.

RESULTS

For all six nests, significant results were found for at least one of the three tests performed on the leaves (Tables 2-9). Means and standard deviations are recorded in Tables 2-8.

TOUGHNESS

The host tree on trail 2A had a mean toughness in grams of 294.000 + 109.639. Trail 2A had trail leaves significantly less tough than the host tree's ($p = 0.0005$, mean = 243.433 $\pm$ 52.547). Four out of five of the trail trees had leaves less tough than the host's (Table 3). Trail 2B's host tree had leaves with a mean toughness of 362.367 $\pm$ 209.464. All six trail trees had leaves less tough than the host's leaves ($p = 0.004$, mean = 223.75 $\pm$ 67.332). Trails 4 and 6 had trail trees with tougher leaves than those of the host trees ($p = 0.014$ and $p = 0.0002$ respectively). Trail trees on trail 4 had a mean of 173.257 $\pm$ 65.495, nine of the ten trees were tougher than the host tree (mean = 106.5 $\pm$ 13.077). All 11 of the trees with toughness measurements on trail 6 had a mean toughness greater than the host tree's. The host tree on trail 6 had a mean toughness of 66.233 $\pm$ 27.863. Analysis of toughness on trails 1 and 5 yielded no significant results for differences in leaf toughness. Trails 1 and 5 had five out of 12 and nine out of 18 trees respectively with a mean toughness greater than their hosts.

THICKNESS

Analysis of leaf thickness on trails 1, 2A, 2B, 4, and 6 revealed that leaves along the trail were thicker than those of the host trees ($p = 0.0055$, 0.0384, 0.0212, 0.0156, 0.0006 respectively). Nine of 12 trees on trail 1 had leaves thicker than the host's. On trails 2A and 2B, five of five and five of six leaves, respectively, were thicker than their host trees'. There were eight out of ten and 11 of 12 leaves on trails 4 and 6 respectively that had thicker leaves than the host's. Trails 3 and 5 yielded no significant results with respect to leaf thickness. The host trees had thicker leaves than three of ten and five of 18 trees on trail 3 and trail 5 respectively. In total there were 46 of 73 trees whose thickness was greater than their host's thickness. Host trees 1 through 6 had mean thicknesses (in millimeters) of 0.233 ± 0.058, 0.317 ± 0.029, 0.167 ± 0.029, 0.317 ± 0.029, 0.113 ± 0.012, 0.233 ± 0.029, and 0.183 ± 0.029 respectively. The trail trees in sequential order had mean thicknesses of 0.293 ± .065, 0.39 ± 0.049, 0.342 ± 0.126, 0.24 ± 0.134, 0.195 ± 0.089, 0.219 ± 0.081, 0.281 ± 0.0748.

WATER CONTENT

The leaf-cutter ants preferred leaves with a lower percent water content than the trail trees on trails 2B (p = 0.0237, host mean = 0.445 ± 0.015, trail mean = 0.585 ± .107) and 4 (p=0.0086, host mean = 0.596 ± 0.008, trail mean = 0.664 ± .063). On trails 3 (p = 0.0377, host mean = 0.634 ± 0.018, trail mean = 0.568 ± 0.086), 5 (p = 0.0023, host mean = 0.683 ± 0.014, trail mean = 0.606 ± 0.091), and 6 (p = 0.002, host mean = 0.750 ± 0.020, trail mean = 0.645 ± 0.090), leaves with higher water content than the trail trees were preferred. Trails 1 and 2A yielded no significant results with respect to water content. In sequential order, 41.7%, 40%, 100%, 20%, 80%, 11.1%, and 8.3% of the trail trees on each trail had greater water content than the host tree did.

TRAIL TREES VS. HOST TREES

On the first five trails, the host trees were rare species, occurring only once on each trail. On trails 5 and 6 however, the host trees were common, occurring more than once on the trail. On trail 5, the ants both passed and harvested *Oreopanax xalapensis* (Araliaceae), while on trail 6, the common host species was *Alstomia pittieri* (Apocynaceae). Comparison of the trail *O. xalapensis* to the host *O. xalapensis* on trail 5 revealed a difference of 53.6% greater toughness, 49.8% more thickness, and 19.9% less water content in the host tree (Table 10). In comparing the trail *A. pittieri* to the host *A. pittieri* on trail 6, however, there was only a difference of 3.1% less toughness, 8.7% more thickness, and 2.7% greater water content in the host tree (Table 11). The thickness of the trail tree leaves in both trails was less than the thickness of the host tree leaves (trail trees = 0.117 ± 0.081, 0.167 ± 0.074; host trees = .233 ± 0.029, 0.183 ± 0.029). This opposes the trend in Table 9, where the mean thickness of the trail leaves is generally greater than that of the host tree's leaves.

The ants consistently passed up several species and families. *Sorocea trophoides* was passed a total of seven times on three trails. The *S. trophoides* were on average less tough, thicker, and contained more water (mean toughness = 148.248 ± 31.937, mean thickness = 0.264 ± 0.067, mean water content = 0.641 ± 0.0237) than the average of all the trees on all the trails (mean toughness = 193.387 ± 72.210, mean thickness = 0.250 ± 0.096, mean water content = 0.608 ± 0.092). *Cupania glabra* and *Exothea paniculata* of the family Sapindaceae were passed a total of 5 times on trails 1, 2A, 2B, and 3.

The ants passed *Inga punctata* eight times on trails; it was also a host tree on trail 2B, although no *I. punctata* was passed on trail 2B. The *I. punctata* that were passed were significantly different from the *I. punctata* host tree in all three tests (Table 12). The trail trees were 51.7% less tough (host mean = 362.367 ± 209.464, trail mean = 175.004 $\pm$ 36.765), 30% thicker (host mean = 0.167 $\pm$ 0.029, trail mean = 0.221 $\pm$ 0.039), and had 22.2% more water (host mean = 0.445 $\pm$ 0.015, trail mean = 0.544 $\pm$ 0.058) than the host *I. punctata*.

Results of the literature search for deterrent compounds are summarized in tables 14 and 15 (Howard and Wiemer, 1986; Hölldobler and Wilson, 1990; Raffauf and Schultes, 1990; Mabberley, 1997).

DISCUSSION

TOUGHNESS

Toughness showed significant differences within trails, but did not show a consistent trend across trails. Our simple regression correlated thickness and toughness (Figure 1), however, within that correlation; there is still a wide range of toughness per each leaf thickness. The ants appear to select for toughness secondary to thickness. It has been suggested that the forager size of leaf-cutter ants has evolved over time for the optimal cutting of tough leaves (Wilson 1980 in Howard 1988). Previous studies have shown that toughness is unrelated to palatability, and that the evolution of body size in leaf-cutters is a response to the challenges of leaf cutting, reducing the importance of tissue toughness in diet selection (Howard 1988). The importance of leaf toughness in our study is difficult to ascertain. A more clear trend starts to emerge when taking into account the presence of deterrent compounds.

THICKNESS

In the four cases in which the data were significant, the ants consistently showed a preference for thinner leaves. Thinner leaves may be easier for the ants to cut as well as carry. Previous studies have not looked at effects of leaf thickness in determining leaf selection (Howard and Wiemer 1986; Howard 1988). A further course of study could attempt to correlate leaf thickness and carrying efficiency.

WATER CONTENT

Water content also showed significant differences within trails, but did not show a consistent trend across trails. We believe this to be the result of different selection pressures for each nest. The moisture content of the leaves is a potentially important source of water for cultivating and maintaining proper humidity levels for their fungal gardens (Howard and Weimer 1986). One nest may require higher water content for optimal fungal growth at a particular point in time, and thus choose leaves with more water than a different nest.

TRAIL TREES VS. HOST TREES

Some of the trees that were consistently passed up by *A. cephalotes* may have had some characteristics to make them particularly unattractive to the ants. Alternatively, the ants may be attracted to specific plants for their nutritional qualities, although the nutritional requirements of leaf-cutters and their fungi are not well known. The family Moraceae is known for its thick latex, which may have been the repellent characteristic in *Sorocea trophoides*. When tested for sap, thick white sticky latex literally poured out of the tree. Latex has been known to adhere to the ants' mandibles, gluing them shut (Howard and Wiemer 1986). However, this does not explain the ants' choice of *Alstomia pittieri* (Apocynaceae) as a host tree.

The *I. punctata* host tree, on trail 2B, had leaves that were significantly thinner, contained less water, and were tougher than the *I. punctata* found along the trails. The ant's preference for thinner leaves is consistent with the overall trend noted earlier. Leaf thickness appears to be especially important because there should be little or no difference in leaf chemistry between the *Ingas*. We already noted that leaf toughness is not likely to be a major factor in the ants' choices, so the 51.7% change in toughness was surprising. The difference in water content was also relatively large and was not consistent with any trend we have yet observed. At high elevations, *Inga* is not protected from herbivory (Koptur, 1983). Therefore, this is not a factor that needs to be considered in the ants' choice of *Inga* as a host. Closer study of these *I. punctata* trees is required to understand the ants' choice. There may have been factors involved that we were not able to measure, for example age or nitrogen levels, that may have influenced the ants on trail 2B to choose *Inga* as a host, while on other trails the *Ingas* were repeatedly passed.

A previous study done by Howard (1988) examined the influence of leaf chemistry on leaf selection. This study suggests that the ants avoid substrates containing tannins as well as other deterrent compounds. Perhaps, if we had the time and resources to test the trail trees and host trees for secondary compounds, we would be able to paint a more complete picture to explain the host selection of the ants. While we were able to consult literature (Howard and Wiemer, 1986; Hölldobler and Wilson, 1990; Raffauf and Schultes, 1990; Mabberley, 1997) on the presence or absence of secondary compounds (Tables 14 and 15) in each of the trees identified, we do not know the nutritional necessities of the ants (or their fungus). While we were able to identify some trees as having deterrent compounds, we still cannot definitively say that the ants would avoid these trees, as exhibited on trails 2A, 2B, and 6. Perhaps the concentrations of these compounds were so low that they did not affect the ants, or perhaps the particular compounds involved did not affect the ants. Also, the ants also discard leaves once they get to the nest. The ants may have been discarding these selections once they arrived at the nest.

Without further investigation, we can only say that the ants appear to be moderately selective. There are definite trends in their selection related to thickness. They especially preferred leaves that were thinner than the typical leaves found along the trail. Toughness, as mentioned previously, appears to be considered in the selection process secondary to thickness. There are so many factors involved in leaf selection (toughness, thickness, water content, secondary compounds), that the ants may have to decide on a tree per tree basis. Some factors may be more important than others. Some leaves may have a particular nutritional quality so important that it overrides the consideration of thickness, toughness, or water content. Not knowing the nutritional needs of the colony, we cannot say whether or not the ants are actually selecting specific trees, or avoiding trees. The ants may not be very selective, and only have a few characteristics they must select for to maintain their fungal gardens.

In some cases, trees that had been passed by were seen to host the ants at a later date. Some trees, which were passed on the trail, also showed signs of being host to leaf-cutters at an earlier time. We would have liked to have the opportunity to monitor the trails more closely to keep track of what trees were actually being used over a longer period of time along the trails. This might be especially helpful for the trails with a host of the same species as one of the trail trees. With these data, we would have a more comprehensive picture of why *A. cephalotes* in Cerro Plano choose the trees they do. Greater knowledge of leaf-cutters' nutritional requirements would help us to decide if the ants are choosing plants they want, or simply avoiding plants they don't want.

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Table 1. *Trail lengths and host trees.*

Trail	Length (m)	Host Tree
1	40.40	*Oreopanax panamensis*
2A	3.30	*Eugenia guatemalensis*
2B	13.60	*Inga punctata*
3	21.70	*Chionanthus panamensis*
4	22.10	*???*
5	31.00	*Oreopanax xalapensis*
6	36.30	*Alstomia pittieri*

Table 2. *Trail 1, means and standard deviations. Means greater than the host tree are bolded. Host tree values are italicized. P – values for One-group t-Test are in the sign column of the host tree's row, significant values are bolded.*

Species	Toughness mean (g)	Std dev	sign	Thickness mean (mm)	Std dev	sign	Water mean (% mass)	Std dev	sign
Myrcianthes undesc.	**327.233**	**7.681**	+	**0.320**	**0.069**	+	0.413	0.051	-
Meliosma idiopoda	**241.533**	**142.481**	+	**0.327**	**0.046**	+	**0.745**	**0.014**	+
Psychotria monteverdensis	204.000	82.194	-	0.207	0.012	-	0.458	0.139	-
Exothea peniculata	121.767	11.720	-	0.187	0.012	-	0.493	0.035	-
Sorocea trophoides	189.267	91.729	-	**0.313**	**0.101**	+	**0.609**	**0.022**	+
Sapium laurifolium	**299.133**	**147.846**	+	**0.393**	**0.012**	+	**0.625**	**0.331**	+
Hampea appendiculata	188.467	77.307	-	**0.367**	**0.083**	+	0.583	0.032	-
Hampea appendiculata	**244.900**	**109.546**	+	**0.300**	**0.000**	+	0.556	0.017	-
Ocotea flourbunda	173.700	49.109	-	0.200	0.000	-	0.563	0.002	-
Stauranthus perforatus	**264.200**	**98.201**	+	**0.280**	**0.020**	+	0.519	0.017	-
Sorocea trophoides	107.733	46.756	-	**0.313**	**0.012**	+	**0.618**	**0.139**	+
Sorocea trophoides	143.033	34.512	-	**0.307**	**0.012**	+	**0.654**	**0.047**	+
Oreopanax panamensis	*225.367*	*45.600*	*0.223*	*0.233*	*0.058*	***0.0055***	*0.603*	*0.006*	*0.230*

Table 3. *Trail 2A, means and standard deviations. Means greater than the host tree are bolded. Host tree values are italicized. P – values for One-group t-Test are in the sign column of the host tree's row, significant values are bolded.*

Species	Toughness mean (g)	Std dev	sign	Thickness mean (mm)	Std dev	sign	Water mean (% mass)	Std dev	sign
Billia colombiana	**289.700**	**31.264**	+	**0.333**	**0.029**	+	0.522	0.010	-
Dendropanax arboreus	188.100	56.524	-	**0.467**	**0.058**	+	**0.637**	**0.036**	+
Cupania glabra	270.700	27.875	-	**0.367**	**0.058**	+	0.460	0.021	-
???	284.000	64.286	-	**0.383**	**0.029**	+	**0.623**	**0.060**	+
Cupania glabra	184.667	26.753	-	**0.400**	**0.100**	+	0.515	0.014	-
Eugenia guatemalensis	*294.000*	*109.639*	***0.0005***	*0.317*	*0.029*	***0.04***	*0.586*	*0.006*	*0.365*

Table 4. *Trail 2B, means and standard deviations. Means greater than the host tree are bolded. Host tree values are italicized. P – values for One-group t-Test are in the sign column of the host tree's row, significant values are bolded.*

Species	Toughness mean (g)	Std dev	sign	Thickness mean (mm)	Std dev	sign	Water mean (% mass)	Std dev	sign
Billia colombiana	289.700	31.264	-	**0.333**	**0.029**	+	**0.522**	**0.010**	+
Dendropanax arboreus	188.100	56.524	-	**0.467**	**0.058**	+	**0.367**	**0.036**	+
Cupania glabra	270.7000	27.875	-	**0.367**	**0.058**	+	**0.460**	**0.021**	+
???	284.000	64.286	-	**0.383**	**0.029**	+	**0.623**	**0.060**	+
Cupania glabra	184.667	26.753	-	**0.400**	**0.100**	+	**0.515**	**0.014**	+
Piper amalago	125.333	39.264	-	0.100	0.000	-	**0.754**	**0.025**	+
Inga punctata	*362.367*	*209.464*	***0.004***	*0.167*	*0.029*	*0.02*	*0.445*	*0.015*	***0.02***

Table 5. *Trail 3, means and standard deviations. Means greater than the host tree are bolded. Host tree values are italicized. P – values for One-group t-Test are in the sign column of the host tree's row, significant values are bolded.*

Species	Toughness mean (g)	Std dev	sign	Thickness mean (mm)	Std dev	sign	Water mean (% mass)	Std dev	sign
Cupania glabra	229.967	26.779	-	**0.383**	**0.076**	+	0.522	0.013	-
Cupania glabra	213.933	7.705	-	0.117	0.029	-	0.447	0.045	-
Panopsis suareolens	229.033	22.502	-	0.250	0.087	-	0.538	0.030	-
Citharexylum costaricensis	**284.300**	**37.222**	+	0.200	0.087	-	0.616	0.042	-
Ocotea whitei	217.800	49.368	-	0.100	0.000	-	0.573	0.015	-
Ocotea flouribunda	134.067	10.441	-	0.133	0.029	-	0.613	0.017	-
Trichilia havanensis	**254.967**	**16.224**	+	**0.517**	**0.029**	+	**0.665**	**0.008**	+
Prunus skutchii	203.567	16.393	-	**0.333**	**0.058**	+	0.499	0.006	-
Meliosma idiopoda	133.233	53.233	-	0.200	0.087	-	0.482	0.195	-
Meliosma idiopoda	162.500	14.290	-	0.167	0.029	-	**0.721**	**0.152**	+
Chionanthus panamensis	*247.333*	*32.234*	***0.028***	*0.317*	*0.029*	*0.09*	*0.634*	*0.018*	***0.04***

Table 6. *Trail 4, means and standard deviations. Means greater than the host tree are bolded. Host tree values are italicized. P – values for One-group t-Test are in the sign column of the host tree's row, significant values are bolded.*

Species	Toughness mean (g)	Std dev	sign	Thickness mean (mm)	Std dev	sign	Water mean (% mass)	Std dev	sign
Stauranthus perforatus	**293.133**	**57.013**	+	**0.417**	**0.029**	+	**0.629**	**0.037**	+
Meliosma idiopoda	**208.500**	**76.150**	+	**0.183**	**0.029**	+	**0.645**	**0.049**	+
Hasseltia flouribunda	**182.567**	**49.400**	+	**0.200**	**0.000**	+	**0.659**	**0.014**	+
Sorocea trophoides	**137.700**	**16.052**	+	**0.200**	**0.000**	+	**0.678**	**0.002**	+
Tabernaemonta longipes	41.100	8.741	-	**0.200**	**0.000**	+	**0.729**	**0.023**	+
Picrasma excelsa	**169.367**	**53.596**	+	**0.200**	**0.000**	+	**0.799**	**0.010**	+
Cassipourea elliptica	**185.133**	**39.176**	+	0.100	0.000	-	**0.674**	**0.027**	+
Casearia sylvestris	**223.300**	**52.514**	+	0.107	0.012	-	0.584	0.009	-
Sorocea trophoides	**148.967**	**31.970**	+	**0.217**	**0.029**	+	**0.653**	**0.015**	+
???	**142.800**	**18.784**	+	**0.120**	**0.020**	+	0.587	0.028	-
???	*106.500*	*13.077*	***0.010***	*0.113*	*0.012*	***0.015***	*0.596*	*0.013*	***0.0086***

Table 7. *Trail 5, means and standard deviations. Means greater than the host tree are bolded. Host tree values are italicized. P – values for One-group t-Test are in the sign column of the host tree's row, significant values are bolded.*

Species	Toughness mean (g)	Std dev	sign	Thickness mean (mm)	Std dev	sign	Water mean (% mass)	Std dev	sign
Oreopanax xalapensis	86.600	0.900	-	0.117	0.029	-	**0.819**	**0.003**	+
Hampea appendiculata	126.500	42.686	-	**0.283**	**0.029**	+	0.634	0.015	-
Sorocea trophoides	**191.233**	**84.475**	+	0.167	0.058	-	0.629	0.062	-
Dendropanax arboreus	**206.100**	**78.825**	+	**0.300**	**0.000**	+	0.576	0.162	-
Sorocea trophoides	119.800	2.722	-	**0.333**	**0.029**	+	0.648	0.027	-
Nectandra salicina	**207.833**	**98.320**	+	0.133	0.058	-	0.484	0.069	-
Malvaviscus arboreus	131.200	38.074	-	**0.417**	**0.076**	+	0.665	0.007	-
Eugenia monticola	91.300	27.692	-	0.150	0.000	-	0.609	0.009	-
Stauranthus perforatus	**259.867**	**10.401**	+	**0.317**	**0.029**	+	**0.724**	**0.031**	+
Nectandra salicina	**362.100**	**107.400**	+	0.233	0.029	0	0.458	0.024	-
Styphnolobium montevirdensis	173.133	53.803	-	0.150	0.000	-	0.666	0.001	-
Meliosma idiopoda	**204.833**	**44.615**	+	0.183	0.029	-	0.621	0.004	-
Xylosma chlorantha	80.000	3.306	-	0.150	0.050	-	0.607	0.032	-
Ardisia compressa	**372.333**	**45.000**	+	0.217	0.029	-	0.681	0.023	-
Inga punctata	**223.033**	**121.006**	+	0.200	0.000	-	0.514	0.029	-
Inga punctata	155.967	55.975	-	0.167	0.029	-	0.519	0.095	-
Inga punctata	137.800	30.216	-	0.200	0.000	-	0.530	0.033	-
Inga punctata	**230.600**	**64.800**	+	0.233	0.029	0	0.525	0.023	-
Oreopanax xalapensis	*186.467*	*31.974*	*0.991*	*0.233*	*0.029*	*0.589*	*0.683*	*0.014*	***0.0023***

Table 8. *Trail 6, means and standard deviations. Means greater than the host tree are bolded. Host tree values are italicized. P – values for One-group t-Test are in the sign column of the host tree's row, significant values are bolded.*

Species	Toughness mean (g)	Std dev	sign	Thickness mean (mm)	Std dev	sign	Water mean (% mass)	Std dev	sign
Inga punctata	**160.300**	**29.858**	**+**	**0.217**	**0.029**	+	0.602	0.005	+
Inga punctata	**140.800**	**22.926**	**+**	**0.267**	**0.029**	+	0.659	0.001	+
Inga punctata	**197.333**	**13.727**	**+**	**0.283**	**0.029**	+	0.480	0.027	+
Lasiantheae fruticosa	No data	No data	0	**0.333**	**0.058**	+	**0.803**	**0.007**	+
Sapium macrocarpum	**212.333**	**49.631**	+	**0.267**	**0.029**	+	0.686	0.018	-
Sapium macrocarpum	**174.833**	**70.234**	+	**0.250**	**0.000**	+	0.737	0.008	-
Sapium macrocarpum	**152.800**	**49.234**	+	**0.300**	**0.000**	+	0.655	0.016	-
Psidium guajava	**124.200**	**20.055**	+	**0.350**	**0.050**	+	0.609	0.039	-
Psidium guajava	**131.367**	**23.881**	+	**0.283**	**0.058**	+	0.653	0.005	-
Alstomia pittieri	**68.333**	**14.123**	+	0.167	0.029	-	0.730	0.017	-
Clethra Ianata	**302.267**	**55.752**	+	**0.450**	**0.050**	+	0.605	0.039	-
Inga punctata	**154.200**	**7.908**	+	**0.200**	**0.000**	+	0.521	0.010	-
Alstomia pittieri	66.233	27.863	**0.0002**	0.183	0.029	**0.0006**	0.750	0.020	**0.002**

Table 9. *Trends relative to the host. Positive signs indicate trail means greater than host mean. Insignificant results are reported as a zero.*

	Leaf Characteristics		
Nest	Toughness	Thickness	Water Content
1	0	+	0
2a	-	+	0
2b	-	+	+
3	-	0	-
4	+	+	+
5	0	0	-
6	+	+	-

Table 10. *A comparison of average values for the two Oreopanax xalapensis trees on trail 5. Thickness of the trail tree leaves is less than that of the host tree's, opposing the trend across all trails in Table 9.*

	Toughness (g)	Thickness (mm)	Water Content (% mass)
P-value	.9916	.5891	**.0023**
Trail mean	86.600	0.117	81.9
Std. dev.	84.088	.081	.091
Host mean	186.467	0.233	68.3
Percent Difference	-53.5%	-49.8%	+19.9%

Table 11. *A comparison of average values for the two Alstomia pitteri trees on trail 6. Thickness of the trail tree leaves is less than that of the host tree's, opposing the trend across all trails in Table 9. Positive percent difference values indicate trail mean greater than host.*

	Toughness (g)	Thickness (mm)	Water Content (% mass)
P-value	**.0002**	**.0006**	**.002**
Trail mean	68.333	0.167	73.0
Std. dev.	59.360	.074	.090
Host mean	66.233	0.183	75.0
Percent Difference	+3.1%	-8.7%	-2.7%

Table 12. *Results of One group t-Test comparing Inga punctata found on the trail to the I. punctata host tree. We gave p-values a negative sign if the mean value of the trail trees was less than the host tree's value. Positive percent difference values indicate trail mean greater than host*.

	Toughness (g)	Thickness (mm)	Water Content (% mass)
P-value	**0.0001**	**0.0062**	**0.0019**
Trail mean	175.004	0.221	0.544
Std. dev.	36.765	0.039	0.058
Host mean	362.367	0.17	0.445
Percent Difference	-51.7%	+30%	+22.2%

Table 14. Presence of deterrent compounds for trails 1, 2A, 2B, and 3. Host trees are in bold.

Trail 1	?	Trail 2A	?	Trail 2B	?	Trail 3	?
Myrcianthes undesc.	0	Billia colombiana	0	Billia colombiana	0	Cupania glabra	+
Meliosma idiopoda	0	Dendropanax arboreus	0	Dendropanax arboreus	0	Cupania glabra	+
Psychotria monteverdensis	+	Cupania glabra	+	Cupania glabra	+	Panopsis suareolens	0
Exothea peniculata	0	Cupania glabra	+	Cupania glabra	+	Citharexylum costaricensis	0
Sorocea trophoides	0	**Eugenia guatemalensis**	**+**	Piper amalago	0	Ocotea whitei	+
Sapium laurifolium	+			**Inga punctata**	**+**	Ocotea flouribunda	+
Hampea appendiculata	0					Trichilia havanensis	+
Hampea appendiculata	0					Prunus skutchii	+
Ocotea flouribunda	+					Meliosma idiopoda	0
Stauranthus perforatus	0					Meliosma idiopoda	0
Sorocea trophoides	0					**Chionanthus panamensis**	**0**
Sorocea trophoidea	0						
Oreopanax panamensis	**0**						

Table 15. *Presence of deterrent compounds for trails 4, 5, and 6. Host trees are in bold*.

Trail 4	?	Trail 5	?	Trail 6	?
Stauraundanthus perforatus	0	Oreopanax xalapensis	0	Inga punctata	+
Meliosma idiopoda	0	Hampea appendiculata	0	Inga punctata	+
Hasseltia flouribunda	0	Sorocea trophides	0	Inga punctata	+
Sorocea trophoides	0	Dendropanax arboreus	0	Lasiantheae fruticosa	0
Tabernaemonta longipes	+	Sorocea trophides	0	Sapium macrocarpum	+
Picrasma excelsa	+	Nectandra salicina	+	Sapium macrocarpum	+
Cassipourea elliptica	+	Malvaviscus arboreus	0	Sapium macrocarpum	+
Casearia sylvestris	0	Eugenia monticola	+	Psidium guajava	0
Sorocea trophoides	0	Stauranthus perforatus	0	Psidium guajava	0
???	?	Nectandra salicina	+	Alstomia pitteri	+
???	**?**	Styphnolobium montevirdensis	+	Clethra lanata	0
		Meliosma idiopoda	0	Inga punctata	+
		Xylosma chlorantha	+	**Alstomia pitteri**	**+**
		Ardisia compressa	0		
		Inga punctata	+		
		Inga punctata	+		
		Inga punctata	+		
		Inga punctata	+		
		Oreopanax xalapensis	**0**		

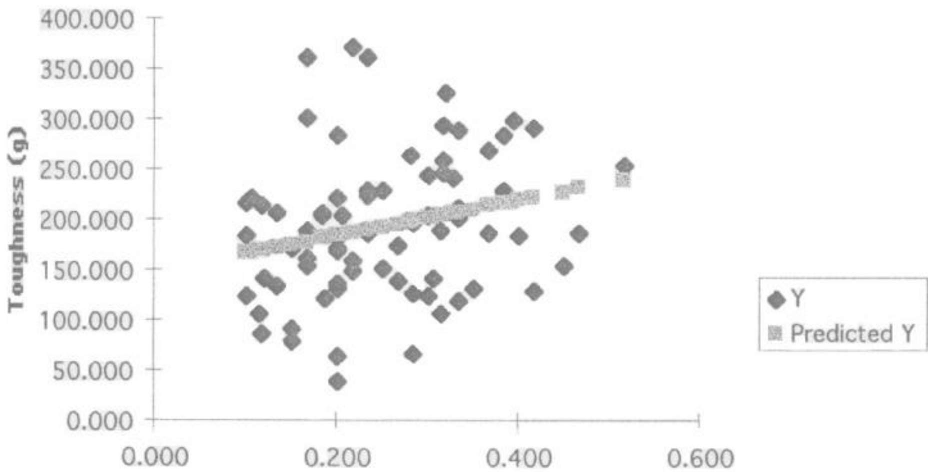

Figure 1. Toughness vs Thickness Regression. Toughness is significantly correlated to thickness ($p = 0.039$, $R^2 = 0.058$)