

# Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis

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I evaluated the hypothesis that leaf-cutting ants are more common in early successional forests than in old-growth forests because pioneer species, which dominate in early successional habitats, appear more susceptible to leafcutters than shade-tolerant species, which dominate primary forests (palatable forage hypothesis). The relative importance of pioneer and shade-tolerant species as plant resources for leaf-cutting ant colonies was evaluated (1) by literature review of leaf-cutting ants' diet, and (2) experimentally, using field assays to determine leafcutter's selectivity. Pioneer species were harvested three times more frequently than shade-tolerant species and made up the largest component of the diet in all the studies reviewed. The amount harvested was not correlated with the plant species abundance. In addition, leaves from pioneer plants were selected eight times more than leaves from shade-tolerant species in the field assays. These results support the palatable forage hypothesis. Leafcutters probably select pioneer leaves because of their low level of chemical defenses and high nutrient content. The high availability of pioneer species in early successional forest probably decreases the cost to locate palatable resources. Therefore, early successional habitats support more ant colonies than old-growth forests. On the other hand, the effective defense mechanisms of mature plant species and the high dispersion of palatable plants could explain the low density of leaf-cutting ant colonies in old-growth forests. The palatable forage hypothesis is compared with other hypotheses that explain leaf-cutting ant density. The preference of foundress queens for forest clearings, the dependence of small colonies on herbs, and the importance of pioneer plant species for mature colonies (palatable forage hypothesis) can be considered complementary, because they focus on different stages of the colony's life history. Consequently, the availability of pioneer plants appears to be one of the most influential factors determining mature leaf-cutting ant nest densities in Neotropical forests.

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Within their geographical ranges, some species are relatively numerous in some habitats and regions, but scarce or absent in others. What factors determine the abundance of local populations? Such patterns of local abundance of organisms can result from many physical and biotic variables that influence survival and reproduction (Brown 1995). Abiotic (e.g. microclimate) and biotic factors (e.g. competition and pre-

dition) can constrain the occurrence of a species within its geographic range. The local abundance of species, however, may often be determined by the local abundance of food resources that they are able to exploit. For example, the abundance of palatable plants may have primacy in determining the local abundance and distribution of the herbivores (Quinn et al. 1997).

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Sessile organisms cannot move once established and their survival is entirely dependent on how local conditions affect their fitness. Consequently, the habitat's availability of palatable plant species represents a very strong selective pressure for sessile herbivores. Leaf-cutting ants (*Atta* and *Acromyrmex*) are considered both sessile and herbivorous organisms. Despite they eventually abandoned their nests (see Farji-Brener and Illes 2000); once established leaf-cutter ant colonies often remain at the same nest-site for many years (Weber 1982, Cherrett 1989). To support their large colonies, the leaf-cutting ants continually search out and harvest suitable plants which they carry back to their nests in order to culture fungi (Howard 1991). Leaf-cutter ants are the most important native herbivores throughout the Neotropics, where *Atta* alone cuts between 12 and 17% of leaf production in some forest ecosystems (Cherrett 1989).

However, leaf-cutting ants are not equally distributed within forests. Their colonies are generally much more common in early successional forests than in old-growth forests (Haines 1978, Fowler 1983, Jaffe and Vilela 1989, Vasconcelos and Cherrett 1995). For example, in early secondary forests of the Brazilian Amazon, *Atta* spp. can have 30 times higher densities than in primary forests (Vasconcelos and Cherrett 1995). In undisturbed old-growth rain forest in the Orinoco-Amazon basin, the density of *Atta* spp. is very low (Jaffe and Vilela 1989). In Costa Rica, *Atta cephalotes* vary from 7–16 nests/ha in 10-yr second-growth forest to 3 nests/ha in old-growth forests (Perfecto and Vandermeer 1993, Farji-Brener unpubl.).

It has been proposed that leaf-cutting ants are more common in early successional forests than in old-growth forests because pioneer species, which dominate in early successional habitats, are more susceptible to leaf-cutting ants than shade-tolerant species, which dominate in primary forests (Fowler 1983, Sheperd 1985, Jaffe and Vilela 1989, Nichols-Orians 1991a). Foliage may differ in quality for leafcutters for at least two reasons. Pioneer species allocate fewer resources to chemical defenses, and have higher nutritive status than shade-tolerant species (Coley 1983, Coley et al. 1985). Consequently, leaf-cutting ant populations may occur in low densities in old-growth, undisturbed forests because of effective defense mechanisms of shade-tolerant plants and high dispersion of palatable plants. Although several authors (Sheperd 1985, Jaffe and Vilela 1989, Nichols-Orians 1991a, Vasconcelos and Cherrett 1995) have proposed this hypothesis (hereafter referred as the palatable forage hypothesis), it has not yet been explicitly tested.

The purpose of this study was to evaluate the palatable forage hypothesis. To test this idea several complementary approaches were used. (1) The relative importance of pioneer and shade-tolerant plants species in the diet of leaf-cutting ants was compared reviewing

data available from the literature. (2) In those studies that provide a list of plant species' abundance in the nest area, the influence of plant species abundance on leafcutters' diet composition was also analyzed. (3) To experimentally test the preference of leaf-cutting ants for pioneer species, single leaf disks of each category of plants were simultaneously offered to *Atta cephalotes* ants.

According to the palatable forage hypothesis, I expect three main results of my analysis. First, the relative importance of pioneer species should be greater than of shade-tolerant species in the leaf-cutting ants diet. Second, the leaf-cutting ants' preference for pioneer plant species should not be accounted for simply by the high abundance of pioneer species in the habitat where leafcutters occur. Third, leafcutters should show a strong preference for pioneer over mature species in field assays.

## Methods

### Quantification of pioneer and mature plant species harvested by leaf-cutting ants

A quantitative assessment of the influence of the life history of plant species on foraging preferences of leaf-cutting ants was obtained indirectly by examining studies of Cherrett (1968a), Rockwood (1976), Pintera (1983), Sheperd (1985), Therrien et al. (1986), Hubbell and Rockwood (1987), Howard (1988), and Wirth et al. (1997). As far as I know, these are the only studies to provide detailed lists of the species as well as the amount of each plant species harvested by leaf-cutting ants in Neotropical areas. Blanton and Ewel's (1985) study was not incorporated in this analysis because their study site was an experimental agroecosystem field without mature plant species, but was used to determine the influence of plant species abundance on leaf-cutting ant diet composition. All species harvested by leaf-cutting ants in these eight studies (167 plant species total) were examined and categorized as 'pioneer' or 'shade-tolerant'. Although tropical trees vary continuously in the conditions they require for establishment (Lieberman et al. 1995), two broad categories are generally recognized and widely used (Coley 1983, Brokaw 1985, Whitmore 1989, Coley and Aide 1991, Coley and Kursar 1996). Pioneer or gap species, also referred to as light-demanding or shade-intolerant species, generally need high-light environments to establish and grow, such as those found in treefall gaps or disturbances. In contrast, shade-tolerant species, also called persistent or mature forest species, survive and grow in deep shade, as well as in the high-light environment of gaps and clearings. I was able to assign 121 of a total of 167 species compiled (72.5%) to one of these two categories based on existing literature and on opinions of four

plant ecologists with extensive experience in tropical areas (Orlando Vargas, Diana Lieberman, Pia Paaby and Sandra Patiño, Appendix 1). The remaining 46 plant species did not fit readily into these categories: the opinions of experts were not in agreement and/or the plant in the original work was unidentified at the species level.

The importance of pioneer and mature plant species in the diets of leaf-cutting ants was estimated in two ways. First, relative importance (in percent) of pioneer or mature species in each study was calculated by adding the relative importance of each plant species for each of the two categories. Second, all the plant species in each study were ranked and the ranks of the three most important species in each plant category were averaged. Because palatability of fruits and flowers does not necessarily depend on the successional status of the plant species, those items were not included in the analysis.

To determine if leaf-cutting ants diet could be predicted simply by plant species abundance around nest areas, regressions analyses were performed using the information provided by Cherrett (1968a), Blanton and Ewel (1985), Sheperd (1985), and Hubbell and Rockwood (1987).

### Acceptability bioassays

Leaf preference tests were carried out at La Selva Biological Station (10° 26' N, 83° 59' W), a wet premontane forest located on the Atlantic lowlands of Costa Rica (Holdridge et al. 1971). I used *Atta cephalotes* colonies for leaf preference tests because this species is the most abundant leaf-cutter within La Selva and is widely distributed geographically (Perfecto and Vandermeer 1993, Cherrett 1989). Field bioassays were carried out in February 1994 and February 1998. I used 18 woody plant species (nine pioneer and nine shade-tolerant) in a standard 'pickup' assay to determine experimentally the influence of plant species category on leafcutters preference. Plant species were randomly selected along TR, CCL and CCC trails, areas where leaf-cutting ant nests are common. Pioneer, shade-intolerant species selected were *Hampea appendiculata*, *Rollinia pittieri*, *Castilla elastica*, *Cecropia obtusifolia*, *Laetia procera*, *Luehea seemanii*, *Casearia arborea*, *Goethalsia meiantha*, and *Psychotria elata*. Shade-tolerant, mature species selected were *Swartzia simplex*, *Anaxagorea crassipetala*, *Piper trigonum*, *Symphonia globifera*, *Rinorea deflexiflora*, *Pentaclethra macroloba*, *Minuartia guianensis*, *Ocotea atirrencis*, and *Escheweileira caliculata*. The 'pickup' assay is designed to determine preferences between leaf types based on chemical defenses or nutritional quality, and has been used commonly in other food preference studies involving leaf-cutting ants (Howard and Wiemer 1986,

Howard 1987, 1988, 1990, Nichols-Orians 1991a, b). In the pickup assay, two leaf discs, one from a pioneer and the other from a shade-tolerant plant species, were presented to ants simultaneously along with oat flakes. The pioneer and shade-tolerant plant species used in each trial were randomly reassigned in each test from the plant species pool. Oat flakes were used as statistical control for differences in ant trail activity from bioassay to bioassay because of their high acceptability to leaf-cutter ants (pers. obs.; also see Howard 1987, 1988, 1990). Leaves were collected from three marked branches on three different plants per species. Disks were cut from mature, shaded leaves from both pioneer and shade-tolerant species in each sample using a paper puncher. All palatability measurements were initiated within 1 h and completed within 3 h to time collection, before the appearance of observable changes in palatability (Howard 1987). A single oat flake and two leaf discs were placed in a single file beside a leaf-cutting ant trail and replaced as ants harvested them to maintain constant and equal availability. To eliminate possible position effects, leaf disk locations were randomized every 10 min. The chemical acceptability of the two leaf types was expressed as the number of leaf discs removed from each category (pioneer or shade-tolerant leaves) divided by the number of oat flakes removed in 30 min. This preference index takes values between 0 (rejection) to 1 (maximal preference). This test was conducted a total of two times on 10 colonies (five nests in 1994 and five nests in 1998). Each trial was replicated twice per colony and the replicates averaged. Because preference by leaf-cutting ants for leaf categories was consistent between years ( $F = 0.08$ ,  $P = 0.78$ ,  $DF = 1$ ), I compared the preference index for pioneer and mature with a  $t$ -test using each nest as a replicate (sample size = 10 nests).

## Results

### Quantification of pioneer and mature plant species harvested by leaf-cutting ants

A clear pattern emerged from the survey of plant species attacked by leaf-cutting ants. In all studies, the species categorized as pioneer were better represented in leaf-cutting ant diets than those categorized as shade-tolerant (Table 1). Considering each study as an independent statistical replicate, the mean percentage of pioneer species harvested was significantly greater than the mean percentage of shade-tolerant species ( $47.6 \pm 5$  versus  $15.9 \pm 2.7$  respectively, mean  $\pm 1$  SE,  $t = 5.54$ ,  $df = 18$ ,  $P < 0.001$ ). While the percentage of pioneer plant species harvested ranged from 25% to 69%, shade-tolerant plant species varied between 4 and 32%. Using ranks, the same pattern emerged. In all studies, the mean rank of the three first pioneer species was

lower (= more frequent in the ants' diet) than the mean rank of the three first shade-tolerant species. Considering all studies, pioneer species were characterized with a mean rank ( $\pm 1$  SE) of  $3.8 \pm 0.5$ , while the mean rank of shade-tolerant species was  $8.3 \pm 0.7$  ( $t = 5.07$ ,  $df = 18$ ,  $P < 0.001$ ).

The high representation of pioneer species in leaf-cutting ant diet cannot be explained simply by their high abundance around the nest area. While plant species abundance explain 19% ( $P < 0.01$ ) of leafcutters diet composition in Sheperd (1985, old forest colony), there was no correlation between the amount cut by leafcutters of each plant species and its abundance in the foraging area in Cherrett (1968a), Sheperd (1985, young forest colony), Blanton and Ewel (1985) and Hubbell and Rockwood (1987) studies ( $R^2 = 0.02, 0.07, 0.07$  and  $0.001$  respectively, all  $P > 0.10$ ).

### Acceptability bioassays

The pickup assay used to assess differences in chemical acceptability, showed that all *Atta cephalotes* colonies found leaves from pioneer species more acceptable than leaves from mature plant species. Pioneer species were preferred eight times more than shade-tolerant species by leaf-cutting ants ( $0.57 \pm 0.04$  versus  $0.07 \pm 0.08$ , mean preference index  $\pm 1$  SE,  $t = 12.3$ ,  $P < 0.0001$ ,  $df = 18$ ). Additionally, while leaf discs of all the nine pioneer species were harvested at least once by the ants, leaf discs from four of nine shade-tolerant plant species were never harvested (Fisher's exact test,  $P = 0.04$ ).

### Discussion

The present study shows that pioneer species are more frequently harvested by leaf-cutting ants than shade-tolerant plant species, and the high representation of pioneers in the ants' diet ( $\sim 50\%$ ) is not due to their high abundance in the habitat where leafcutters occur. The present study also shows that leafcutters actively prefer mature leaves from pioneer plants to leaves from shade-tolerant species. These results suggest that the dominance of pioneer plant species in early successional, disturbed forests may explain why mature leaf-cutter ants' nests are usually located in these habitats, supporting the palatable forage hypothesis. An important assumption to support this argument is that the leaf-cutting database utilized in this work is broad and unbiased in terms of the objective of this study, and plant species are correctly classified into the two life history groups. I believe these assumptions are valid. First, this survey includes data on four leaf-cutting ant species, five different countries, several habitats, work periods between 1–12 months, and 41 nests sampled. Second, plant species were classified into pioneer or mature in an extremely rigorous manner (at least three of the four expert opinions should agree) and therefore both are probably equally underestimated. In spite of this potential bias, pioneer species represented up to 70% of the diets of leaf-cutting ants and were harvested three times more than mature species.

One alternative explanation to the relatively high representation of pioneer species in the diet of leaf-cutting ants is that leafcutters harvest more pioneer than mature plant species simply because pioneers are more abundant in areas surrounding ant nests. At least three lines of evidence suggest that the larger representation

Table 1. Quantitative assessment of pioneer and mature plant species in diets of leaf-cutting ants inhabiting tropical forests. Diet composition is reported as the percent of all species in each study that could be unequivocally classified as pioneer or mature species (note that percentages do not add to 100%). The numbers in parentheses are the mean ranks of the first three pioneer and shade-tolerant plant species (lower value represents higher preference).

Species	Habitat	Diet composition		Study period	Method	Source
		Pioneer	Mature			
<i>A. cephalotes</i>	Moist-dry forest, CR	58.5 (3)	6.7 (14)	20 months	A	1
<i>A. cephalotes</i>	Dry forest, CR	65.6 (2.7)	21.4 (6.3)	11 months	A	2
<i>A. cephalotes</i>	Dry forest, CR	69.0 (4.3)	3.9 (8)	3 months	A	3*
<i>A. cephalotes</i>	Moist forest, GUY	25.6 (5.6)	20.4 (8.3)	2 months	A	4
<i>A. colombica</i>	Dry forest, CR	60.7 (2)	18.0 (8.3)	12 months	A	2
<i>A. colombica</i>	Moist forest, PAN	40.1 (5.7)	32.5 (7.3)	11 months	B	5
<i>A. colombica</i>	Moist forest, COL	47.8 (4.6)	20.3 (9.2)	11 months	C	6
<i>A. colombica</i>	Moist forest, COL	25.0 (5.6)	15.3 (9)	10.5 months	C	6
<i>A. insularis</i>	Moist forest, CU	35.6 (4.3)	14.4 (7.8)	12 months	A	7
<i>Ac. octospinosus</i>	no data, GUA	48.0 (3)	6.1 (5)	12 months	A	8*

(\*) Only around 75% of the species harvested were listed in the original work. Source: (1) Hubbell and Rockwood 1987, (2) Rockwood 1976, (3) Howard 1988, (4) Cherrett 1968a, (5) Wirth et al. 1997, (6) Sheperd 1985, (7) Pintera 1983, (8) Therrien et al. 1986. Methods: (a) total number of fragments cut or taken from laden ants, (b) dry weight leaf, and (c) mean number of leaf fragments. Countries represented: CR = Costa Rica, COL = Colombia, CU = Cuba, GUA = Guadeloupe Island, GUY = Guyana, PAN = Panama. Leaf-cutting ant genus: *A* = *Atta*, *Ac* = *Acromyrmex*. Blanton and Ewel's (1985) study was not incorporated in the analysis because their study site was an experimental agro-ecosystem field without shade-tolerant plant species.

of pioneer plants in ants' diet is a consequence of selective harvesting. First, in spite of the fact that some authors do not publish lists of plant species abundance, they affirm that species abundance in the ant foraging area does not determine host plant selection in leaf-cutting ants (Rockwood 1976, Therrien et al. 1986). It is well known that ant colonies sample many plants but are highly selective, cutting large quantities of leaves from only a few – and often uncommon – species, while avoiding other more abundant species (Cherrett 1968a, 1989, Rockwood 1976). Second, the amount harvested by the leafcutters of each plant species was not correlated with its abundance in the studies of Cherrett (1968a), Blanton and Ewel (1985), Sheperd (1985), and Hubbell and Rockwood (1987). The absence of a correlation does not mean that the relative harvest of the most palatable plant species is not influenced by their relative abundance, but it suggests that plant abundance is not the primary factor determining which plant species are harvested. Third, leaf-cutting ants selected pioneer over shade-tolerant leaves in the equal-food availability field assays performed in this study, showing experimentally that the ants' preference for pioneer plants depend on their high palatability. Thus, the large quantity of pioneer species harvested by leaf-cutter ants appears to be a consequence of an active search for palatable resources, rather than simply a 'response' to plant abundance. Then why is there a positive correlation between high density of pioneer plants and leaf-cutting ant colonies? Costs influence leaf-cutting ants foraging patterns, and searching, accessing (e.g. trail construction) and harvesting palatable plant species contribute to overall costs of obtaining resources (Sheperd 1985, Farji-Brener and Sierra 1998). A high availability of pioneer plants within the foraging area decreases foraging costs due to decreasing the time cost of harvesting, thus increasing the net rate of energy gain for the colony (Howard 1991).

Leaf-cutting ant preference for pioneers with respect to shade-tolerant plants is based on the assumptions that leaves from pioneers have fewer secondary compounds and better nutritive status than leaves from mature species, and that these factors strongly influence leaf-cutting preferences. Although I did not specifically test these assumptions, others studies have demonstrated that leaves from pioneer species generally have lower levels of quantitative defenses and higher nutritive status than leaves from shade-tolerant species (Coley 1983, Coley et al. 1985). Both, chemical defenses and nutritive value of leaves are implicated as prominent factors in selection by leafcutters (Waller 1982, Bowers and Porter 1981, Hubbell and Wiemer 1983, Berish 1986, Nichols-Orians and Schultz 1989). Patterns of secondary chemistry are considered the best predictor of preferences by leaf cutting ants (Hubbell et al. 1983, 1984), and may interact with nutritional quality to determine palatability (Howard 1987, 1988, 1990,

Nichols-Orians 1991a, b). Therefore, leaf-cutting ants harvest a large quantity of pioneer species probably because their leaves have lower defense levels, and higher nutrient quality than leaves from shade-tolerant species. Additionally, inherently fast-growing plants in non-tropical habitats also have lower amounts of defensive chemistry than slow-growing species (Cates and Orians 1975, Reader and Southwood 1981, Coley et al. 1985, Coley 1987), and support greater population densities of herbivores (Edwards-Jones and Brown 1993). This is consistent with the observation that leaf-cutting ant colonies are also abundant in disturbed habitats within subtropical and temperate areas, where fast-growing plants are dominant (Jonkman 1979, Bucher 1982, Farji-Brener 2000).

At least two different hypotheses, aside from the palatable forage hypothesis, have been proposed to explain why leaf-cutting ant colonies are more common in early successional habitats than in old-growth forests. The first alternative hypothesis proposes that availability of nesting sites is limiting. The nest founding stage begins with the nuptial flight, in which the virgin queen departs from the nest in which she was reared, and is then inseminated by one or more males. After the nuptial flight, the foundress queen must locate a suitable nest site in the soil (Hölldobler and Wilson 1990). Some studies have shown that foundress queens prefer forest clearings for establishing a new nest (Cherrett 1968b, Vasconcelos 1990), apparently because incipient colonies require a certain degree of insolation on their nest-heaps (Jaffe and Vilela 1989). Ant queens thus depend on forest clearings and/or disturbances with naturally less vegetation. The second hypothesis focuses on the dependence of recent-founded colonies on small herbaceous plants near the ant nest (Wetterer 1994). It has been proposed that the first workers produced by a new queen (smaller than the smallest workers produced by a mature colony) forage more efficiently on leaves from herbaceous plants (Wetterer 1994). Leaf-cutting ant colonies may be able to establish only in areas with sufficient herbaceous undergrowth, as observed in recently disturbed areas and early successional stages of the forest. However, these hypotheses are nor mutually exclusive, and could be even considered complementary because they focus on different stages of the colony's life history. The high abundance of leaf-cutting ant colonies in early successional, disturbed forests, can be understood as a consequence of several connected processes, summarized as follows: Foundress queens prefer to initiate their nests in forest clearings or disturbed, open areas. These areas are generally characterized by small herbaceous plants, which are the principal resource for small, incipient colonies. As young colonies (and the new workers produced) grow in size, the ants change from selectively foraging on herbs to foraging mainly on palatable woody species (e.g., pioneer species), which are also

dominant in these areas. The preference of foundress queens for clearings represents the immediate necessities of the queen (e.g. soil temperature), as well as the short-term necessities of a small colony (e.g. herbs) and the long-term necessities of a mature colony (e.g. palatable woody species). In other words, by selecting a forest clearing or disturbed area, a foundress queen likely will secure an adequate availability of palatable resources to the colony for its entire life (10–20 yr, Weber 1982). If the presence of mature colonies is in part determined by the capability of the foundress queen to detect forest clearings, the foundress queen should bear strong selective pressures to select disturbed areas. However, selective forces acting on mature colonies are likely to be different from those affecting ant queen ants and/or incipient colonies.

This work provides the first evidence that the availability of pioneer plants is an important factor to determine mature leaf-cutting ant nest densities in Neotropical forests. This dependence may not only have a strong influence on leafcutters distribution in early successional forests, but on the manner in which they colonize old-growth forests. Leaf-cutting ants should expand their local geographic range into old-growth forests mainly by colonizing and foraging on tree fall gaps and/or forest clearings created by man.

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**Appendix 1.** Characteristics of 121 plant species harvested by leaf-cutting ants in the reviewed studies, presented in alphabetical order. Plant species that were not classified into pioneer or shade-tolerant are excluded from this list. Successional status: P = pioneer, shade-intolerant, M = mature, shade-tolerant. Life form: LT = large trees, ST = small trees and shrubs, L = lianas and vines, H = herbs, HE = hemi-epiphytes.

Source	Plant species	Family	Life form	Successional status	References
2	<i>Acacia farnesiana</i>	Leguminosae	LT	P	7
2, 8	<i>Acacia</i> sp.	Leguminosa	LT	P	7
6	<i>Acalypha macrostachya</i>	Euphorbiaceae	ST	P	7
7	<i>Alchornea latyfolia</i>	Euphorbiaceae	LT	P	7
5	<i>Alchornea costarricensis</i>	Euphorbiaceae	LT	P	2, 6, 8
5	<i>Alchornea polyantha</i>	Euphorbiaceae	LT	P	7
2	<i>Alibertia eludis</i>	Rubiaceae	ST	M	6
5	<i>Allophylus psilospermus</i>	Sapindaceae	LT	M	6
2, 5	<i>Anacardium excelsum</i>	Anacardiaceae	LT	P	6, 7
4	<i>Anaxagorea petiolata</i>	Annonaceae	LT	M	7
2	<i>Annona holoserica</i>	Annonaceae	LT	P	7
1	<i>Annona reticulata</i>	Annonaceae	LT	P	7
5, 6	<i>Apeiba membranacea</i>	Tiliaceae	LT	P	2, 6, 7, 8
2	<i>Apeiba tibourbou</i>	Tiliaceae	LT	P	2, 6, 8
2	<i>Ardisia revoluta</i>	Myrcinaceae	ST	P	7
8	<i>Artocarpus altilis</i>	Moraceae	LT	M	7
7	<i>Bauhinia cumanensis</i>	Caesalpinaceae	L	M	7
1	<i>Bauhinia unguolata</i>	Caesalpinaceae	L	M	7
6	<i>Bellucia axinantha</i>	Melastomataceae	ST	P	7
8	<i>Bidens pilosa</i>	Compositae	H	P	7
2	<i>Bocconia frutensis</i>	Papaveraceae	ST	P	7

Appendix 1. (Continued)

Source	Plant species	Family	Life form	Successional status	References
1, 2, 3	<i>Bombacopsis quinatum</i>	Bombacaceae	LT	P	6, 7, 8
8	<i>Borreria laevis</i>	Rubiaceae	H	P	7
5	<i>Brosimum alicastrum</i>	Moraceae	LT	M	6, 8
1, 2, 3	<i>Bursera simaruba</i>	Burseraceae	LT	P	7
1, 2, 3	<i>Calycophyllum candidissimum</i>	Rubiaceae	LT	P	7
2	<i>Casearia aculeata</i>	Flacourtaceae	LT	P	7
6	<i>Cassia bacillaris</i>	Leguminosae	ST	P	7
2	<i>Cassia biflora</i>	Leguminosae	ST	P	7
8	<i>Cassia obtusifolia</i>	Leguminosae	ST	P	7
4	<i>Cassia pteridophylla</i>	Leguminosae	ST	P	7
2	<i>Cassia reticulata</i>	Leguminosae	ST	P	7
2, 5	<i>Cecropia insignis</i>	Moraceae	LT	P	2, 3, 7, 8
2	<i>Cecropia obtusifolia</i>	Moraceae	LT	P	1, 2, 3, 5, 7, 8
6	<i>Cecropia tesmannii</i>	Moraceae	LT	P	7
1	<i>Cedrela odorata</i>	Meliaceae	LT	P	6
6	<i>Cespedezia spathulata</i>	Ochnaceae	LT	P	7
7	<i>Chamissoa altissima</i>	Amarantaceae	L	P	7
7	<i>Cissampelos pareira</i>	Menisioermeaceae	L	P	6, 7
7	<i>Cissus caustica</i>	Vitaceae	L	P	7
4	<i>Clussia fockeana</i>	Clusiaceae	HE		P
2	<i>Coccoloba caracasana</i>	Polygonaceae	LT	M	7
1, 4	<i>Cochlospermum vitifolium</i>	Cochlospermaceae	LT	P	6
1, 4	<i>Cordia alliodora</i>	Boraginaceae	LT	P	2, 6
6	<i>Croton killipians</i>	Euphorbiaceae	LT	P	7
2	<i>Croton sp.</i>	Euphorbiaceae	LT	P	7
4	<i>Cybianthus brownii</i>	Myrsinaceae	ST	M	7
6	<i>Dendropanax caucanum</i>	Araliaceae	LT	P	7
6	<i>Didymopanax morototoni</i>	Araliaceae	LT	P	6, 8
2	<i>Dioclea megacarpa</i>	Papilionaceae	L	P	7
2	<i>Dioscorea alata</i>	Dioscoreaceae	L	P	7
2	<i>Dioscorea bulbifera</i>	Dioscoreaceae	L	P	7
5	<i>Dipterix panamensis</i>	Papilionaceae	LT	M	3, 8
6	<i>Dolioscarpus dentatus</i>	Dilleniaceae	L	M	6
6	<i>Entada gigas</i>	Papilionaceae	L	P	7
1, 2	<i>Enterolobium cyclocarpum</i>	Mimosaceae	LT	P	7
4	<i>Eschweilera corrugata</i>	Lecythidaceae	LT	M	7
8	<i>Euphorbia hirta</i>	Euphorbiaceae	H	P	7
8	<i>Euphorbia hypericifolia</i>	Euphorbiaceae	H	P	7
3	<i>Genipa americana</i>	Rubiaceae	LT	P	7
2	<i>Genipa caruto</i>	Rubiaceae	LT	P	7
7	<i>Gonzalagunia sagreana</i>	Rubiaceae	ST	M	7
6	<i>Grafenrieda galleottii</i>	Melastomataceae	ST	M	7
2	<i>Guazuma ulmifolia</i>	Sterculiaceae	LT	P	6, 7
5	<i>Heisteria concinna</i>	Olcaceae	LT	M	6
7	<i>Hibiscus elatus</i>	Malvaceae	ST	P	7
2, 5	<i>Hippocratea volubilis</i>	Hippocrateaceae	L	M	6, 7
5	<i>Hura crepitans</i>	Euphorbiaceae	LT	P	6, 7, 8
1, 2	<i>Hymenaea courbaril</i>	Caesalpinaceae	LT	M	7
5	<i>Inga pezizifera</i>	Mimosaceae	LT	P	5
4	<i>Ischnosiphon gracilis</i>	Marantaceae	H	P	7
6	<i>Jacaranda copaia</i>	Bignoniaceae	LT	P	2, 6, 7, 8
1, 2	<i>Licania arborea</i>	Chrysobalanaceae	LT	M	7
2	<i>Lonchocarpus acuminatus</i>	Fabaceae	LT	P	7
2	<i>Lonchocarpus minimiflorus</i>	Fabaceae	LT	P	7
5	<i>Macrocnemum glabrescens</i>	Rubiaceae	LT	M	2, 6
2, 4	<i>Mangifera indica</i>	Anacardiaceae	LT	P	7
2	<i>Mastichodendron tempisque</i>	Sapotaceae	LT	M	7
4	<i>Matayba opaca</i>	Sapindaceae	LT	M	7
6	<i>Miconia sp.</i>	Melastomataceae	LT	P	7
2	<i>Mimosa pudica</i>	Mimosaceae	H	P	7
1, 7	<i>Muntingia calabura</i>	Elaeocarpaceae	LT	P	7
7	<i>Nectandra antillana</i>	Laureaceae	LT	M	7
4	<i>Neea constricta</i>	Nyctaginaceae	ST	M	7
1	<i>Ocotea veraguensis</i>	Lauraceae	LT	M	7
2	<i>Pavonia sp.</i>	Malvaceae	H	P	7
8	<i>Phyllanthus debilis</i>	Euphorbiaceae	H	P	7
1	<i>Picramnia latifolia</i>	Simaroubaceae	ST	M	6, 7
7	<i>Piper aduncum</i>	Piperaceae	ST	P	4, 7
4	<i>Pithecellobium eperuetorum</i>	Leguminosae	LT	M	7



Appendix 1. (Continued)

Source	Plant species	Family	Life form	Successional status	References
2	<i>Pithecolobium longifolium</i>	Leguminosae	LT	P	7
2	<i>Pithecolobium saman</i>	Leguminosae	LT	P	7
2	<i>Polygonatum punctatum</i>	Polygonaceae	H	P	7
5	<i>Poulsenia armata</i>	Moraceae	LT	M	2, 6
4	<i>Pouteria engleri</i>	Sapotaceae	LT	M	7
5	<i>Quararibea asterolepis</i>	Bombacaceae	LT	M	2, 6, 8
2	<i>Quercus oleoides</i>	Fagaceae	LT	M	7
4	<i>Rheedia kappleri</i>	Clusiaceae	LT	M	7
1, 3	<i>Sapium thelocarpum</i>	Euphorbiaceae	LT	P	7
2, 6	<i>Schizolobium parahybum</i>	Leguminosae	LT	P	7
8	<i>Senecoides cinera</i>	Malvaceae	H	P	7
8	<i>Sida rhombifolia</i>	Malvaceae	H	P	7
2	<i>Sloanea ternifolia</i>	Elaeocarpaceae	LT	M	6, 8
6	<i>Solanum stromaniifolium</i>	Solanaceae	H	P	7
2, 3	<i>Spondias mombin</i>	Anacardiaceae	LT	P	6, 8
1, 3	<i>Spondias purpurea</i>	Anacardiaceae	LT	P	7
4	<i>Swartzia benthamiana</i>	Leguminosae	ST	M	7
1	<i>Tabebuia rosea</i>	Bignonaceae	LT	P	2, 6, 8
4	<i>Talisia squarrosa</i>	Sapindaceae	ST	P	7
4	<i>Terminalia amazonica</i>	Combretaceae	LT	P	6, 8
6	<i>Tetrathylacium macrophyllum</i>	Flacourtiaceae	LT	P	7
4	<i>Tovomita cephalostigma</i>	Clusiaceae	LT	M	7
5	<i>Trattinickia aspera</i>	Burseraceae	LT	P	2, 6
7	<i>Trema micrantha</i>	Ulmaceae	LT	P	1, 2, 6, 7, 8
1	<i>Trichilia colimana</i>	Meliaceae	LT	M	7
1, 3	<i>Trichilia hirta</i>	Meliaceae	LT	M	7
3	<i>Trichilia martiana</i>	Meliaceae	LT	M	7
6	<i>Unonopsis pittieri</i>	Annonaceae	LT	M	7
7	<i>Vigna luteola</i>	Leguminosae	L	P	7
4	<i>Vismia guianensis</i>	Clusiaceae	ST	P	7
3	<i>Zanthoxylum setulosum</i>	Rutaceae	LT	P	6, 8

Sources for leaf-cutting ant diet: (1) Hubbell and Rockwood 1987, (2) Rockwood 1976, (3) Howard 1988, (4) Cherrett 1968a, (5) Wirth et al. 1997, (6) Sheperd 1985, (7) Pintera 1983, (8) Therrien et al. 1986.

References for successional status: (1) Ackerly and Bazzaz 1995, (2) Coley 1983, (3) Clark and Clark 1992, (4) Greig 1993, (5) Lieberman et al. (1995), (6) Schupp and Feener (1991), (7) Orlando Vargas, Pia Paaby, Diana Lieberman and Sandra Patiño, pers. comm., and (8) Foster and Brokaw (1985).