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LEAF-CUTTING ANT HERBIVORY IN SUCCESSIONAL AND AGRICULTURAL TROPICAL ECOSYSTEMS[1]

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Abstract. Herbivory by *Atta cephalotes* was measured in four plant communities of different complexity in Costa Rica. The four communities were a monoculture of cassava (*Manihot esculenta*) and three diverse assemblages, each 1.5 yr old: (1) successional vegetation, unmodified by the investigators; (2) imitation of succession, a community of investigator-introduced species designed to mimic the unmodified succession; and (3) enriched succession, a successional vegetation that the investigators had augmented by propagule inputs. Each ant colony had access to all four community types simultaneously. The average herbivory rate (daily cutting of leaf per square metre of ground, all treatments combined) was ≈150 mg (or 38 cm^2).

In communities with greater leaf area index, structural complexity, and species richness, *A. cephalotes* cut lower portions of total leaf area. Before harvest of the cassava monoculture, the herbivory rate of *A. cephalotes* was 87.9 $cm^2 \cdot m^{-2} \cdot d^{-1}$ in the monoculture, 21.4 in the imitation, 14.7 in the succession, and 6.8 in the enriched succession community. These amounts represented 0.3% of total leaf area in the monoculture and a mean of 0.03% of total leaf area in the three complex ecosystems. Cassava, which occurred in three of the four communities, was attacked most heavily (per unit leaf area) in the imitation successional community, least heavily in the enriched succession, and at intermediate intensity in the monoculture. In response to loss of their preferred forage (cassava) through harvesting by humans, the ants cut more leaf tissue in the three species-rich communities, especially the imitation. As cassava resprouted in the monoculture, *A. cephalotes*' rate of attack on the three diverse treatments reurned to preharvest levels.

Atta cephalotes cut only 17 of 332 available plant species. They cut proportionally more woody than herbaceous species, more introduced species than natural colonizers, and species with below-average water contents. Plant relative abundance alone did not determine host plant selection, but most of the attacked species were cut in proportion to their total leaf area.

Key words: ants; Atta cephalotes; *Costa Rica; herbivory;* Manihot esculenta; *succession; tropical agriculture; tropical succession.*

INTRODUCTION

Developing nations, particularly those with limited fossil fuel resources, face difficult decisions in selecting appropriate agricultural ecosystems to keep pace with food and fiber needs of their rapidly expanding populations. Monocultures are notorious for pest outbreaks (Gibson and Jones 1977), whereas mixed cropping systems sometimes do and sometimes do not afford more protection to their component plants (Perrin and Phillips 1978, Risch 1981, Ewel et al. 1982). One promising line of research suggests that useful characteristics of natural ecosystems may be incorporated into agroecosystems (Hart 1980). We are part of a team of researchers that has been working in Costa Rica since 1978, testing this idea. An integral part of such research is to study how herbivores interact with host plants in simple and diverse ecosystems (van Emden and Way 1972, Root 1973, Feeny 1976, Rausher 1981).

From the time our study plots were cleared and planted in early 1979 (Ewel et al. 1981), it was obvious that the leaf-cutting ant *Atta cephalotes* L. was one of the most important herbivores on the site. This impression was reenforced by observations made by Brown (1982) while measuring overall herbivory rates. The ants had an opportunity to select forage from a broad range of ecosystems, all within easy access of their nests: old forest, young forest, pasture, plantations of exotic trees (*Gmelina* and *Pinus*), and four kinds of experimental ecosystems established as part of the research project. The latter ranged from monocultures to ecosystems even more diverse than successional vegetation.

Atta cephalotes, a member of the myrmicine fungus-growing tribe Attini, is a conspicuous, widespread herbivore whose populations increase under human stewardship of ecosystems (Gonçalves 1967, Haines 1975). This gap-loving forest-dweller frequently invades subsistence and plantation agriculture from Mexico to Brazil (Cherrett and Peregrine 1976, Cherrett 1981). Over this geographic range *A. cephalotes* is a generalist (sensu Feeny 1976); i.e., it attacks species of several chemically unrelated plant families, although local populations may have a very specialized diet (Rockwood 1976). When harvesting substrate for their fungal garden, leaf-cutters remove a very select portion of the total standing crop of leaves, flowers, and fruits (Lugo et al. 1973, Rockwood 1978). Herbivory by *A. cephalotes* can reduce plant reproductive potential (Rockwood 1972) and undoubtedly affects net primary productivity as well. Furthermore, the ants' refuse dumps concentrate nutrients and their nest-building disturbs

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soil profiles, creating point sources or sinks of nutrients (Haines 1975, 1978, 1983, Alvarado et al. 1981).

Many agricultural ecologists propose that structural and floristic complexity can reduce the probability of severe pest outbreaks in plant communities (see review by Altieri and Letourneau 1982). Because of our interest in the attributes, including losses to herbivores, of successional and agricultural communities of differing degrees of complexity, the following question was of key importance to our research: Do the ants preferentially forage in certain of the four experimental ecosystems? A related question was of agricultural significance: How do the ants respond to a dramatic reduction in availability of their preferred forage? The answer to this question was obtained by measuring herbivory before, during, and after harvest of the monoculture, which contained >85% (by leaf area) of the ants' preferred forage species, cassava. Finally, we asked a third question: What are the characteristics of those species and ecosystems that are especially attractive to the ants? This question was answered by comparing grazed and ungrazed plant species in terms of their importance in each plant community, their life forms, and the moisture content of their leaves.

METHODS

Study site

This study was carried out in the Florencia Norte Forest, near Turrialba, Cartago Province, Costa Rica. The site lies on lightly undulating terrain located at 9°53′ N, 83°40′ W, and at 650 m elevation. Mean annual rainfall approaching 2700 mm is concentrated between April and December. The area is in the Tropical Premontane Wet Forest life zone (Tosi 1969).

Four experimental ecosystems were established subsequent to slashing (in January 1979) and burning (in March 1979) 9–10 yr old second-growth (Ewel et al. 1981; species richness data from Brown 1982).

1) Succession: natural regrowth from seedlings and sprouts, unmanipulated by the investigators and containing 121 species.

2) Enriched succession: natural regrowth augmented by propagules (≥10 000 seeds of ≥20 species per replication per month) of additional taxa and containing 159 plant species. Introduced seeds were harvested opportunistically from off-site sources by researchers; they included cultivars and noncultivars, indigenous and exotic species. This self-design ecosystem was established to test hypotheses concerning susceptibility to invasion, facilitation, and functional attributes of species-saturated communities.

3) Imitation of succession: 82 nonindigenous species, both wild and cultivated, chosen to mimic the physiognomy of the natural successional vegetation. Natural colonizers were weeded out.

4) Monoculture: mature, weed-free cassava (*Manihot esculenta*), which is a shrub that produces an edible tuber. After the first 2 mo of this study it was harvested (September 1980), but the aboveground parts were returned to the plots after weighing and subsampling. The twigs continued to sprout for several months.

Six blocks were established, each containing the four treatments in randomized block design (Fig. 1). Each treatment occupied one quadrant of each block and thus had two sides contiguous with other treatments and two sides contiguous with the second-growth forest that surrounded each block. Because the 16 × 16 m quadrants were far smaller that the area foraged by a *A. cephalotes* colony, each colony had access to all four experimental ecosystems. The ants' preferred forage species, cassava, was available in all six replications of the monoculture, imitation, and enriched treatments.

Measurement of foraging

From late July through mid-November 1980 (rainy season months), experimental plots were searched several times weekly for leaf-cutting ants. Plots were visited in a predetermined random order to ensure that all received an equal number ($n = 33$) of surveys, about half during the day and half at night. Because daytime surveys normally began after dawn and ended in late afternoon, and nighttime surveys began after dusk and ended before daybreak, dawn and dusk were undersampled. Foraging on a given plot was measured only on trails leading from plants on that plot. To determine the area and mass of leaf tissue removed, laden ants passing an observation point on each active trail were counted for 5 min. The mean area and mass of each ant's burden were estimated by collecting ≥50 leaf fragments from each active trail during each observation. The combined area of these fragments was measured to within 1 mm^2 with an area meter; the composite sample was then dried at 70°C for 24 h and weighed to within 0.1 mg. Leaf fragments were identified to species using indumentum, color, texture, or other unique characteristics.

In addition to the weekly observations, total daily impacts of *A. cephalotes* foraging on seven representative trails were measured at approximately 1-h intervals over 24-h periods on three dates: 16 August, 8 September, and 12 October 1980. This was done to provide a second, independent estimate of *A. cephalotes* herbivory, one that included fluctuation in foraging activity in response to time of day, rain showers, and sun-fleck patterns. Observations and 5-min counts of laden foragers were as described above. Counts were converted to leaf area and plotted over time. The area beneath the curve thus represented total leaf area carried over 24 h.

Vegetation characteristics

To estimate the plant resource available to *A. cephalotes,* Leaf Area Index value (LAI, the area of leaf tissue [one side of leaf] per unit ground area) was measured using a plumb-bob method (detailed analyses in

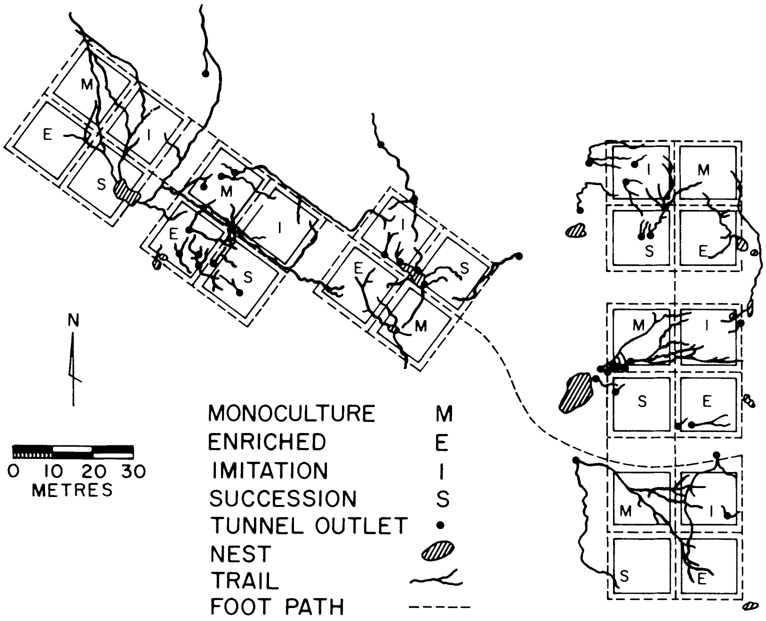

FIG. 1. Map of the study site, showing experimental communities and *A. cephalotes* nests and trails.

Brown 1982, Ewel et al. 1982). At 30 points in each plot, leaves touching a thin cord extended vertically through the vegetation were identified to species and recorded by 25-cm height classes. The mean number of leaf-line intersections per point estimates overall plot LAI. The percentage of all intersections attributed to a given plant species indicates its relative abundance in the ecosystem. Cassava monocultures were measured on 5 September 1980, prior to harvest. LAIs of other treatments were measured 1 October 1980.

We also measured foliar moisture content of species that *A. cephalotes* cut for substrate and/or species that comprised ≥80% of the LAI of each experimental treatment. Approximately 300 g of fresh leaves of each species were weighed to 0.1 g, dried for 24 h at 70°, and reweighed.

RESULTS

Averaged over all vegetation types, the mean (±SD) rate of leaf-cutting per square metre of ground surface area per day was 37.6 ± 36.1 $cm^2 \cdot m^{-2} \cdot d^{-1}$ or 0.149 ± 0.132 $g \cdot m^{-2} \cdot d^{-1}$. These rates are based on weekly observations during the 5-mo study period. Leaf areas cut by *A. cephalotes* varied greatly from one set of surveys to the next. In 506 out of 792 plot surveys, the ants cut no vegetation, which indicates that leaf-cutting was spotty through time (see Fig. 2). In the remaining 286 surveys, there were, on average, 1.5 active trails per plot. This activity pattern skewed the frequency distribution of herbivory rates to the right. A Kolmogorov-Smirnov test ($D = 0.35$, $P < .01$) confirmed that the data were not normally distributed. Analyses were therefore performed on $\log(Y + 1)$-transformed values, which met the condition of normality for analysis of variance (ANOVA) (Kolmogorov-Smirnov test: $D = 0.037$, $P > .15$).

The model for ANOVA was split-split plot in space and time, with replications as blocks subdivided by treatments, time of day (i.e., day or night), and state of the cassava monoculture. The four states of cassava were 1) mature; 2) leaves still fresh (after having been returned to the plot following harvest); 3) no leaves (because of postharvest decay and herbivory); and 4) resprouting. Ninety percent of the variation in transformed mean herbivory rates was accounted for by the model. There were significant F tests for interactions among treatments, states of the cassava monoculture, and time of day, but not for any of these variables individually. Therefore, analyses of differences among levels of each interacting variable were performed at fixed levels of the others.

Atta cephalotes herbivory rates based on three 24-h sampling periods varied little: 21.4, 20.9, and 21.9 m^2/24 h. Over all treatments, most leaf area was cut at night, although daytime foraging predominated in the more heavily vegetated enriched and succession vegetations. This estimate of herbivory rate is lower than the rate derived from weekly foraging measurements. Weekly measurements may overestimate the true mean because sampling seldom occurred at dawn or dusk, which were times of low foraging activity.

Foraging differences among ecosystems

The ants consumed an average of 3.5 times more leaf tissue per unit ground area per day in the cassava monoculture and cultivar-dominated imitation

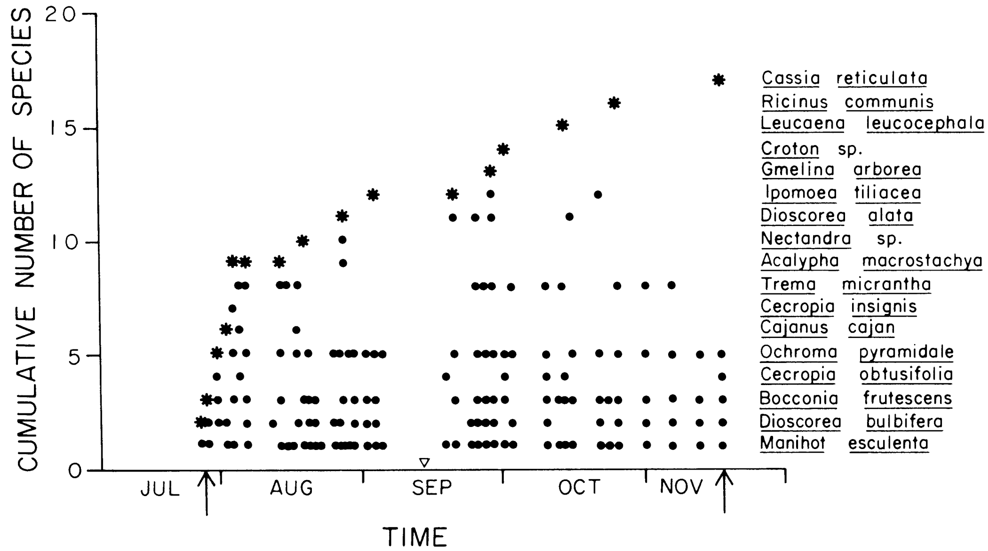

FIG. 2. Plant species cut by *A. cephalotes* through time on experimental treatments. Arrows indicate duration of study. ▽ above horizontal axis indicates date of cassava harvest. Dots indicate each date on which a plant species was observed being cut and asterisks indicate both a cutting observation and the cumulative number of species cut since the beginning of the study.

of succession ecosystems (combined mean: 59 $cm^2 \cdot m^{-2} \cdot d^{-1}$) than they did in the succession and enriched vegetation ecosystems (combined mean: 17 $cm^2 \cdot m^{-2} \cdot d^{-1}$) (Table 1).

With mature cassava available in the monoculture, treatment differences in herbivory rates were not significant because of large within-treatment variances. These resulted in part from the ants' diel foraging preferences: *A. cephalotes* consistently foraged more at night than during the daytime in the monoculture. Though maximum leaf removal by *A. cephalotes* occurred in the monoculture, the ants were found foraging during a slightly (but not significantly) greater proportion of the observations in the imitation ecosystem (55.6% compared to 51.4% in the monoculture) and slightly less in the succession (43.1%) and enriched (29.2%) systems.

During the 1-wk cassava harvest, mean *A. cephalotes* leaf consumption on experimental treatments more than doubled. Over 80% of their foraging effort was concentrated on the large mounds of leaves in the monoculture. As this leaf supply dwindled due to decomposition and *A. cephalotes* attack, the ants' daily leaf consumption per unit ground surface area continued to increase dramatically in the other three vegetation systems, reaching a maximum of 160 $cm^2 \cdot m^{-2} \cdot d^{-1}$ in the imitation ecosystem. Furthermore, the total rate of ant foraging over all treatments combined temporarily increased significantly after the cassava supply was exhausted. Apparently, *A. cephalotes* activity was stimulated by the cassava harvest; no other obvious environmental changes occurred during this period to account for the increased rate of leaf removal.

As cassava resprouted in monocultures in mid-October, *A. cephalotes* herbivory in the other treatments returned to rates not statistically different from preharvest levels.

The plant resource

During the study period, 332 plant species were growing on the experimental plots. Of these, *A. cephalotes* cut measurable amounts of only 17 (5.1%) (Table

TABLE 1. Herbivory rates by *A. cephalotes* in the four experimental ecosystems.

State of cassava monoculture	Leaf tissue cut per unit ground area per day (amount·$m^{-2} \cdot d^{-1}$)					
	Leaf area (cm^2)*					Mean biomass (mg)
	Succession	Enriched	Imitation	Monoculture	Mean	
Mature	14.65^{a}	6.78^{a}	(n) 21.44^{a}	(n) 87.86^{a}	32.68	117.6
Harvested	6.64^{c}	(d) 16.65^{b}	(d) 42.30^{b}	(n) 277.48^{a}	85.77	281.3
No leaves	35.93^{c}	40.15^{b}	160.66^{a}	0.0^{d}	59.19	280.2
Resprouting	8.42^{b}	17.02^{ab}	29.06^{a}	(n) 24.43^{ab}	19.73	82.0
Mean	15.53	17.47	51.42	66.06	37.62	149.1

* Means in the same row accompanied by the same superscript are not significantly different ($P < .05$). Significantly greater (Duncan's Multiple Range Test, $P < .05$) day or night herbivory rates within a mean are denoted by (d) and (n), respectively.

TABLE 2. Attributes of plants together comprising ≥ 80% of leaf area in each treatment. Asterisks indicate taxa cut by *A. cephalotes*.

Taxon	Family	Origin†	Life form‡	Moisture content (percent by mass)	Leaf area index§ (m^2/m^2)				Percent of total LAI‖
					Succession	Enriched	Imitation	Monoculture	
Panicum maximum Jacq.	Gramineae	nat.	herb	82.6	1.07	1.37			15.4
**Bocconia frutescens* L.	Papaveraceae	nat.	shrub	91.0	0.68	0.54			7.7
Clibadium surinamense L.	Compositae	nat.	shrub	83.7	0.34	0.36			4.4
Other Gramineae¶		nat.	herb	86.9	0.26	0.64			5.7
**Trema micrantha* (L.) Blume	Ulmaceae	nat.	tree	76.0	0.23	0.01			1.5
Frantzia pittieri (Cogniaux) Pittier	Cucurbitaceae	nat.	vine	91.5	0.14				0.9
**Acalypha macrostachya* Jacquin	Euphorbiaceae	nat.	shrub	83.4	0.13	0.04			0.3
Lasiacis procerrima (Hack) Hitchc.	Gramineae	nat.	herb	83.2	0.12	0.10			1.4
Panicum trichoides Sw.	Gramineae	nat.	herb	85.7	0.12				0.8
Scleria spp.#	Cyperaceae	nat.	herb	79.9	0.12	0.10			1.4
Vernonia patens HBK	Compositae	nat.	tree	85.6	0.11	0.37			3.0
Mikania micrantha HBK	Compositae	nat.	vine	88.8	0.10	0.07			1.1
Cordia inermis (Mill.) I. M. Johnston	Boraginaceae	nat.	shrub	82.5	0.08				0.5
**Ochroma pyramidale* (Cav.) Urb.	Bombacaceae	nat.	tree	74.8	0.02				0.1
**Nectandra* sp.	Lauraceae	nat.	tree	74.5	<0.01				0.1
**Ipomoea tiliacea* (Willd.) Choisy	Convolvulaceae	nat.	vine	91.6	0.03	0.10			0.8
**Cecropia insignis* Liebm.	Moraceae	nat.	tree	77.8	<0.03	<0.01			0.3
**Cecropia obtusifolia* Bertol.	Moraceae	nat.	tree	84.4	<0.03	<0.01			0.3
**Croton* sp.	Euphorbiaceae	nat.	shrub	81.8	0.02	0.01			0.2
**Cassia reticulata* Willd.	Leguminosae	intro.	tree	78.2		0.01			0.1
Cordia alliodora (Ruiz & Pavon) Oken	Boraginaceae	nat.	tree	73.8		0.09			0.6
Goethalsia meiantha (Donn. Smith) Burret	Tiliaceae	nat.	tree	75.3		0.07			0.5
Ipomoea neei (Spreng.) O'Donell	Convolvulaceae	nat.	vine	85.7		0.15			0.9
Musa paradisiaca L.	Musaceae	intro.	herb	84.2		0.11	0.13		1.5
**Dioscorea bulbifera* L.	Dioscoreaceae	intro.	vine	80.7		0.04	0.01		0.3
**Dioscorea alata* L.	Dioscoreaceae	intro.	vine	83.5			0.01		0.1
**Cajanus cajan* (L.) Millsp.	Leguminosae	intro.	shrub	75.1			0.04		0.3
**Leucaena leucocephala* (Lam.) de Wit	Leguminosae	intro.	tree	75.4			<0.01		0.1
**Ricinus communis* L.	Euphorbiaceae	intro.	tree	83.3			0.07		0.5
**Gmelina arborea* L.	Verbenaceae	intro.	tree	77.9			<0.01		0.1
Cymbopogon citratus (D.C.) Stapf.	Gramineae	intro.	herb	80.6			1.14		7.2
Natural colonizers (weeds)		nat.	···	83.5			0.59		3.7
Crotalaria micans Link	Leguminosae	intro.	shrub	84.1			0.56		3.5
**Manihot esculenta* Crantz.	Euphorbiaceae	intro.	shrub	81.6		0.01	0.49	2.91	21.5
Others		···	···	···	0.70	0.82	0.56	···	13.2
Totals					4.34	5.03	3.62	2.91	100.0

† nat. = natural colonization; intro. = introduced by investigators.

‡ vine = herbaceous climber (vs. liana = woody climber).

§ Leaf area per unit ground surface area.

‖ All treatments combined.

¶ Complex of species that are nearly indistinguishable when sterile.

\# Includes *Scleria pterota* and *S. secans*, and possibly some other sedges.

2). The ants cut 14 of 156 woody species on the plots (9.0%), but only 3 of 176 herbaceous species (1.7%). Mean leaf water content of plant species cut by *A. cephalotes* (80.7%) was significantly lower than background levels (83.6%) calculated from all species together comprising ≥80% of leaf area (*t* test, $P < .05$). Proportionally more introduced species (8 of 85, or 9.4%) than natural colonizers (9 of 247, or 3.6%) were cut. Total leaf area available on all experimental treatments included 61% natural colonizers, 21% cassava, and 18% other investigator-introduced species.

The mean amount of leaf tissue available to the ants was highest in the enriched (LAI = 5.03) and slightly (but not significantly) lower in the succession and imitation treatments (LAIs = 4.37 and 3.62, respectively). LAI in the monoculture was initially 2.91, but was

TABLE 3. Amount and frequency of *A. cephalotes* attack on various species of plant. The number of observations (932) is greater than the number of plot surveys (792) because some surveys included measurements on more than one active trail.

	Leaf tissue cut				Observations		
Taxon	Area ($m^2 \cdot ha^{-1} \cdot d^{-1}$)	Percent of leaf area cut	Percent of available leaf area	Mass ($g \cdot ha^{-1} \cdot d^{-1}$)	No.	Percent of total ($n = 932$)	Percent of all active observations ($n = 426$)
Manihot esculenta	28.6843	76.25	0.336	1032.52	213	22.85	50.00
Bocconia frutescens	4.2585	11.32	0.140	198.83	75	8.04	17.61
Ochroma pyramidale	1.6028	4.26	4.007	119.57	36	3.86	8.45
Dioscorea bulbifera	1.4125	3.76	1.284	45.42	46	4.94	10.80
Cecropia obtusifolia	0.5679	1.51	0.631	40.12	8	0.86	1.87
Trema micrantha	0.4186	1.11	0.071	23.40	22	2.36	5.16
Dioscorea alata	0.2649	0.71	1.325	8.58	6	0.64	1.41
Ipomoea tiliacea	0.1047	0.28	0.033	5.39	4	0.43	0.95
Cassia reticulata	0.0856	0.23	0.856	3.57	1	0.11	0.23
Acalypha macrostachya	0.0695	0.18	0.016	3.93	4	0.43	0.95
Cajanus cajan	0.0456	0.12	0.041	2.64	4	0.43	0.95
Croton sp.	0.0450	0.11	0.075	3.67	1	0.11	0.23
Ricinus communis	0.0214	0.06	0.013	1.00	1	0.11	0.23
Nectandra sp.	0.1926	0.05	0.196	0.98	2	0.21	0.47
Gmelina arborea	0.0065	0.02	0.065	0.33	1	0.11	0.23
Leucaena leucocephala	0.0063	0.02	0.063	0.32	1	0.11	0.23
Cecropia insignis	0.0039	0.01	0.039	0.36	1	0.11	0.23
None					506	54.29	
Total	37.6176	100.00		1490.63	932	100.00	100.00

reduced to 0 after harvest, then increased slightly as cassava twigs resprouted in mid-October.

Cassava was removed most frequently (213 of 426 measurements) and extensively, accounting for >76% of total leaf area cut (Table 3). Other species that accounted for >1% of total leaf area cut were the natural colonizers *Bocconia frutescens, Ochroma pyramidale, Cecropia obtusifolia,* and *Trema micrantha,* plus the investigator-introduced *Dioscorea bulbifera.* All of these were cut during the first month of observations (Fig. 2) and consistently thereafter throughout the study. All other species that the ants added to their cumulative repertoire contributed a combined total of <2% of the leaf area cut.

Some species heavily cut by *A. cephalotes* were dominant components of treatment and overall LAI; together the cut species made up 34% of the total leaf area available (sum of values of percent of total LAI for species marked with * in Table 2). Cassava accounted for the greatest proportion of overall LAI due to its abundance in the monoculture. *B. frutescens* made up 7.7% of the total LAI; *T. micrantha* accounted for 1.5% of the total LAI (Table 2), or, expressed as leaf area per square metre of ground, nearly ¼ m^2/m^2 in the succession treatment. Not all common species were consumed, however. The exotic grass *Panicum maximum* was the most abundant species (15.4% of total LAI) but was shunned by the ants.

There was a highly significant correlation ($r = 0.97$ with cassava, 0.89 without; $P < .01$ in both cases) between leaf area cut (Table 3) and contribution of the cut species to total LAI (Table 2). The correlation was not significant when abundant plant species that *A. cephalotes* did not cut were included. Thus, selection of a species could not be predicted by its LAI. However, once attacked by *A. cephalotes,* the extent of attack was related to available leaf area.

DISCUSSION

Ecosystem losses

The mean amount of leaf removed by *A. cephalotes* per square metre of ground per day in the young experimental ecosystems, 0.149 g (or 37.6 cm^2), surpasses previous estimates of 0.081 g (Lugo et al. 1973) and 0.027 g (Haines 1978) for *Atta colombica* in mature lowland tropical forests. Other estimates in the literature are nest-specific and cannot be converted to leaf consumption per unit area of ecosystem.

Atta cephalotes accounted for a surprisingly large proportion of the total herbivory (measured by Brown 1982) in the succession, enriched, and imitation treatments: 25% of all leaf consumption per square metre of ground (and 16% of all herbivory per square metre of leaf) prior to the harvest of the cassava monoculture, and nearly 50% of all leaf consumption per square metre of ground (31% of all herbivory per square metre of leaf) that occurred in these three treatments throughout the study period. Even though these high values may, in part, reflect differences between the methods used by Brown (1982) to measure overall herbivory and those used by us, *A. cephalotes* was clearly the most important herbivore on the study site.

The leaf-cutting ants consumed more leaf tissue in the monoculture than in the three species-rich communities. *A. cephalotes*' preference for the cassava monoculture was predictable in light of the ants' pest status in neotropical monocultures generally (e.g., Cherrett and Peregrine 1976, Fowler and Robinson

TABLE 4. Herbivory by *A. cephalotes* as a fraction of leaf area available, based in part on estimates of LAI of each ecosystem by Brown (1982).

State of cassava	Treatments				Mean ± SD
	Succession	Enriched	Imitation	Monoculture	
			Leaf area consumed ($cm^2 \cdot m^{-2} \cdot d^{-1}$)		
Mature	3.38	1.35	5.92	30.19	10.21 ± 13.45
Harvested	1.53	3.31	11.69	95.35	27.97 ± 45.14
No leaves	8.28	7.98	44.38	0	15.16 ± 19.85
Resprouting	1.94	3.38	8.03	74.03*	21.85 ± 34.89
Mean ± SD	3.78 ± 3.10	4.00 ± 2.81	17.50 ± 18.07	49.89 ± 42.92	

* Conservative estimate based on LAI = 0.33.

1979) and in cassava specifically (Weber 1972, Bellotti and van Schoonhoven 1978). The crop was a concentrated, spatially predictable source of palatable substrate. Before harvest the monoculture received two-thirds of all *A. cephalotes* attacks; daily losses (area of leaf lost per square metre of ground) were 88 cm^2/m^2 or 0.3% of its leaf area. This was an order of magnitude greater than the mean percentage cut by the ants in the more complex ecosystems (0.03%). The cassava was not devastated by these rates of herbivory, however, and maintained high LAI by continuous production of new leaves.

The difference between *A. cephalotes* attack on simple and on complex ecosystems is further reinforced when leaf-cutting is expressed as a fraction of leaf area available (Table 4). Leaf tissue in the succession and enriched treatments, for example, was consumed at a rate of ≈0.02%/d during the interval when the ants consumed ≈0.3%/d of the available leaf tissue in the mature cassava monoculture.

Of the three species-rich communities, the imitation treatment was attacked most heavily. What was there about the imitation treatment that resulted in more herbivory than in either the succession or enriched vegetations? It was not that attacked species accounted for a greater proportion of total LAI in the imitation than in the other treatments. For example, >80% of LAI in both the enriched and imitation treatments consisted of species that were not cut for substrate by *A. cephalotes,* yet the imitation treatment was much more heavily attacked. Differences in herbivory rates among these three communities must therefore have been due to characteristics other than the relative abundance of palatable species. One such factor might have been the homogeneity of the resource (number of palatable species involved and their spatial arrangement). In the imitation treatment only eight species, most of which were regularly spaced, were attacked, whereas in the enriched succession the ants attacked 15 species, most of which were irregularly spaced and not abundant.

Response to loss of forage

Leaf-cutting ants thrive following disturbances of native or agronomic ecosystems (Haines 1978, Jonkman 1979). The sudden increase in *A. cephalotes* foraging effort and leaf-cutting during and just after the cassava harvest was such a response, comparable to Rockwood's (1976) observation that foraging increased after he mechanically excluded ants from their preferred host.

Atta cephalotes' postharvest attack (leaf area cut per unit ground surface area per day) on plants in the imitation treatment reached 161 $cm^2 \cdot m^{-2} \cdot d^{-1}$; each day the ants removed nearly 3% of the standing leaf area of palatable host plants. The regular arrangement of cassava plants and the vining habit of another preferred host plant, *D. bulbifera,* appeared to facilitate the ants' switch to increased exploitation of that ecosystem. Once foragers had found an individual of one of these palatable species, the plants' interlocking crowns (cassava) or large leaf area (often > 1 m^2 of leaves per individual of *D. bulbifera*), regularly spaced along a trail-like vine, provided maximal substrate for minimal search effort.

Species abundances and characteristics

Six plant species constituted >97% of *A. cephalotes*' total substrate. Individuals of many other species had one telltale semicircle clipped from a leaf, suggesting that these plants had been sampled by *A. cephalotes* and subsequently rejected. The same was true for individual leaves of palatable species. This selectivity has been described elsewhere in relation to feeding strategies and relative numbers of host plants (Cherrett 1968, Rockwood 1973, 1978, Fowler and Stiles 1980), physical and chemical deterrents or arrestants (Cherrett 1972*a, b,* Gamboa 1975, Littledyke and Cherrett 1978), the welfare of the fungus (Martin 1970, Mudd and Bateman 1979), and ready availability of plant species to foragers early in the life of the colony (Fowler 1982).

The species most voraciously attacked by *A. cephalotes* during this study was cassava. It is not surprising that, before harvest of the cassava monocultures, the absolute amount of cassava cut by the ants in the monoculture, imitation, and enriched treatments was strongly correlated with its contribution to LAI of those systems ($r = 0.99$, $P < .05$). However, when the amount of cassava cut was expressed as a fraction of total cassava leaf area available in each treatment, herbivory on cassava was greatest in the imitation (2.3%), followed by the monoculture (1.8%) and enriched (0.9%)

treatments. Brown (1982) found the same trend in overall cassava herbivory (leaf area lost per unit available leaf area): the proportion of leaves losing >15 $cm^2 \cdot m^{-2} \cdot d^{-1}$ was 46% in the imitation, 13% in the monoculture, and 0 in the enriched treatment. This suggests that a cassava leaf located in the imitation treatment was more likely to be clipped by *A. cephalotes* or other herbivores than a cassava leaf located in the monoculture or enriched treatments. Cassava in the enriched successional vegetation, on the other hand, was less vulnerable to herbivore attack.

Some species were very heavily cut in relation to their total available leaf area (e.g., *O. pyramidale, Dioscorea* spp., and *Nectandra* sp.; Table 2). Brown (1982) also found that some uncommon species on this site were heavily attacked, although for most species in her study the leaf area damaged per unit available leaf area was <5 $cm^2 \cdot m^{-2} \cdot d^{-1}$. The ants attacked plants of many families, origins, and life-forms: a "susceptible-to-*Atta*" syndrome would be almost impossible to characterize. However, some generalizations seem to hold. *Atta cephalotes*' observed predilection for woody and investigator-introduced species agrees with previous reports (Weber 1972, Garling 1978, Mintzer 1979). Woody species typically offer a more concentrated, less ephemeral supply of leaves than do herbs. Many of the introduced species were cultivars and therefore might have been genetically selected for features other than herbivore defense.

Plant water content, perhaps linked to phytochemistry (Mattson 1980), may also influence *Atta*'s selection of substrate in different environments and during different seasons (Mudd and Bateman 1979, Bowers and Porter 1981). The prime example of *A. cephalotes*' response to water depletion or physiological stress during our study occurred when leaves of cassava wilted, abscised, or were cut. The ants then attacked these stressed leaves in preference to healthy leaves. In damaged cassava tissue the membrane-bound enzyme linamarase contacts and hydrolyzes the glucoside linamarin, liberating free hydrocyanic acid that can volatilize (Gondwe 1974). Perhaps the resulting decrease in hydrocyanic acid content of damaged cassava leaves made them more attractive to ants than healthy cassava leaves.

Succession and agriculture

When humans slash and burn forests, *Atta* colonies are likely to survive because their nests are deep in the soil. In this study several *A. cephalotes* colonies survived the burn and thereafter dominated herbivory on the site. Cultivators plant their seeds at the same time that *A. cephalotes* disperse: the onset of the rainy season. *Atta* queens that escape predation are likely to nest successfully in the moist soil. The claustral stage of colony formation allows surrounding vegetation a head start and, while colonies are small, their substrate requirements are low. Colony expansion parallels vegetation growth. After such expansion, humans and ants usually conflict.

If the ants' major source of substrate is removed by crop harvest, they must find new sources of substrate, perhaps neighboring fields or forests. If a palatable crop sprouts, the young plants will probably be heavily attacked.

If, however, succession proceeds, the ants will forage on a subset of suitable plants. Our study indicates that this is a small portion of available species, perhaps a smaller portion than in old forests (cf. Cherrett 1968). Succession brings nearly 100% of the canopy (where *Atta* prefers to forage) to the ants' preferred foraging range (<3 m above ground level; Cherrett 1968), so search and retrieval time for suitable substrate is minimized. Net primary productivity of the vegetation is high, providing a constant supply of the young leaves *Atta* prefers (Cherrett 1972*a*).

This study yields three conclusions useful in designing agroecosystems for areas prone to *A. cephalotes* outbreaks:

1) It is more advantageous to plant many species than few species. In the absence of information on specific plant defenses, choose species that are herbaceous and native.

2) *Atta cephalotes* is a "switch-forager" and responds to a decrease in favored resources by expanding its exploitation to alternate resources. Removal of one crop is likely to lead to increased herbivory elsewhere, rather than to a diminution in overall consumption.

3) Ecosystems containing large amounts of leaf area suffer lower losses, both relative and absolute, than equally accessible communities having less leaf tissue.

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