THE EFFECTS OF SOME ANT SPECIES, ESPECIALLY ATTA CEPHALOTES (L.), ACROMYRMEX OCTOSPINOSUS (REICH) AND AZTECA SP. (HYM. FORM.) ON CITRUS GROWING IN TRINIDAD

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SUMMARY

Citrus was an important export crop in Trinidad until the rising price of oil made it uneconomic. Citrus farmers controlled two types of ant pests. The leaf-cutting ants *Atta cephalotes* and *Acromyrmex octospinosus* kill both young and old trees by repeatedly defoliating them, and the cultural practices used by the farmers determine which ant species is dominant. The biting ant *Azteca* sp. which builds large arboreal nests on the fruit trees, makes harvesting difficult, and by tending and encouraging homoptera probably reduces fruit yield, and lowers quality by contamination. As *Azteca* sp. and some other ant species deter the leaf-cutting ants from defoliating the mature trees they inhabit, their presence is a mixture of advantage and disadvantage to the farmer. As control using modern toxic baits is simple, farmers aim to control both types of ants.

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RESUMEN

Los efectos de algunas especies de hormigas, especialmente Atta cephalotes **(L.),** Acromyrmex octospinosus **(Reich)** y Azteca **sp. en Trinidad**

Los cítricos fueron un importante cultivo de exportación en Trinidad, hasta que el alza en el precio del petróleo los hiciera incosteable. Los cultivadores de cítricos controlaban dos tipos de plagas de hormigas : las hormigas defoliadoras *Atta cephalotes* y *Acromyrmex octospinosus* que matan tanto los árboles jóvenes como los adultos defoliándolos repetidamente. Las prácticas de cultivo usadas por los agricultores determinan cuál de las especies de hormiga es dominante. Las hormigas mordedoras *Azteca* sp., las cuales construyen grandes nidos arbóreos en los árboles frutales, hacen difícil la cosecha, y por el cuidado y fortalecimiento de Homóptera, probablemente reducen la cosecha de fruta, y disminuyen la calidad por contaminación. Mientras que *Azteca* sp. y algunas otras especies de hormigas impiden la defoleación de los árboles que habitan, su presencia para los agricultores es una mezcla de ventajas y desventajas. Como el control usando cebos tóxicos modernos es simple, el objectivo de los agricultores es controlar ambos tipos de hormigas.

INTRODUCTION

Citrus, (oranges, grapefruit and limes) have been grown commercially in Trinidad for many years, and in the early sixties some 5500 ha were planted, yielding 48,000 tons for export and earning TT$ 7.8 million, making it the third most important export crop in the island (Maliphant, 1966 ; Lewis and Norton, 1973). With the rise in the price of oil in the seventies however, the economy of Trinidad which is an oil-rich country, underwent profound changes, the cost of labour to work the plantations became increasingly uneconomic, and the citrus industry went into decline, so that by the late seventies, Trinidad was importing citrus juice concentrates for home consumption.

Studies in Trinidad on the impact of the leaf-cutting ants *Atta cephalotes* (L.) and *Acromyrmex octospinosus* (Reich) on citrus have been carried out since 1966 (Cherrett, 1968a ; Cherrett & Sims, 1968 ; Cherrett & Merrett, 1969 ; Lewis & Norton, 1973 ; Cherrett & Lewis, 1974 ; Lewis, 1975), and these changes in the fortunes of the citrus industry made it possible to compare ant faunas and their impact in managed orchards, and in abandoned ones. This has provided valuable insights into their effects.

Citrus growers in Trinidad recognise the need to control two types of ant pests, – leaf-cutting ants (Bachacs) and *Azteca* sp. (Biting ants). The effects of these will be examined in turn.

EFFECTS OF LEAF-CUTTING ANTS

Only two species of leaf-cutting, fungus-growing ants are found in Trinidad (Cherrett, 1968a) the forest bachac *A. cephalotes*, which builds large nests up to 250 m^2 in surface area, containing several million ants, and the garden bachac *A. octospinosus*, which builds much smaller nests only one or two square metres in surface area and containing fewer than 10,000 ants (Lewis, 1975). Assessing their economic importance in managed citrus estates, Cherrett and Sims (1968) estimated a mean annual loss, including the cost of control measures of TT$ 49 ha^{-1} and Lewis and Norton (1973) gave a figure of TT$ 29 ha^{-1}. In both cases the figures were based on farmers' estimates of losses to newly-planted citrus saplings of 30 % and 16 % respectively. Neither study took any account of the effects of defoliation on mature trees, which Cherrett and Lewis (1974) regarded as trivial on trees older than 5 years. As all their studies were conducted in orchards where vigorous leaf-cutting ant control was practiced, the significance and the economics of control could only be assessed in the context of the losses still experienced despite these control measures.

Jutsum el al. (1981) however, studied a citrus orchard abandoned in 1972, and in 1976 they noted that 20 of the 108 trees examined (19 %) were dead. Because broad trails of *A. cephalotes* were common throughout the area, and because 27 of the 88 living tress were at least 50 % defoliated, they concluded that the dead trees had been killed through repeated defoliation by ants. During a visit in 1979, the original surveyed area was difficult to distinguish, as the dead trees had disappeared. However in an area considerably larger, only 40 living citrus trees could be found. This illustrates why farmers practice leaf-cutting ant control even in mature orchards because in many areas citrus culture would be impossible without it. This was confirmed by farmers around Bartica in Guyana who were questioned in 1963 about the shortage of citrus fruit. They claimed that citrus was not worth growing there because of leaf-cutting ants.

The species causing most damage in Trinidad depends upon whether or not control measures are carried out (Cherrett, 1968a ; 1981). With control, *A. octospinosus* which reproduces more rapidly and has inconspicuous nests is favoured (Table I). It reaches worker ant densities of 28 m^{-2} and nest densities of 36 nests ha^{-1} (Lewis, 1975). The large nests of *A. cephalotes* however are readily detected and killed. In the abandoned orchard without control, only three *A. octospinosus* nests were seen, and *A. cephalotes* appeared to be regaining the dominance it possesses in tropical rain forests where, with 0.6 nests ha^{-1} (Cherrett, 1968a), the worker ant density may be about 180 m^{-2}. This species difference between forest and cultivated land is in part

Table I – A comparison of the leaf-cutting ant faunas of tropical rain forest and nearby cultivated or cleared land (modified from Cherrett 1968a).

Tabla I – Comparación de las faunas de hormigas defoliadoras entre la selva tropical y las cercanas de las áreas abiertas o cultivadas.

	Cultivated or cleared land		Forest		
	Atta cephalotes	*Acromyrmex octospinosus*	*Atta cephalotes*	*Acromyrmex octospinosus*	Significance (P) of the difference *
Number of nests in 8 ha	3	21	5	0	<0.001
Number of founding queens caught in 20 pitfall traps during 15 months	2	30	9	0	<0.001

* Using a Fisher exact test on a 2 x 2 contingency table

due to the settling preferences of the flying queens when seeking a nest site (Table I), but it is not known if the species shift between cultivated and abandoned citrus estates is assisted by hostile interactions. In the field, both species show intraspecific aggression (Jutsum et al., 1979), although interspecific aggression could only be demonstrated if workers of one species were placed very close to the nest entrance of the other (Jutsum, 1979).

EFFECTS OF *AZTECA* SP.

The most obvious arboreal-nesting ant found in Trinidad citrus orchards is a species of *Azteca* building large dark-brown carton nests shaped like an inverted cone, which hang from the trunk and larger branches. As the genus is in need of revision, specific identification was not considered possible (B. Bolton, W.L. Brown Jr., personal communications). The species is polydomous, one colony making a series of carton nests in nearby trees (Jutsum et al. 1981). The number of nests in infested citrus trees in 1976 is shown in Table II.

Table II – The number of large nests of *Azteca* sp. found in eighty-eight citrus trees surveyed in 1976.

Tabla II – Número de nidos grandes de *Azteca* sp. encontrados en ochenta y ocho cítricos monitoreados en 1976.

Number of nests per tree	0	1	2	3	4	5	6	7	8	>8
Number of trees	51	10	4	3	2	3	2	1	2	10

In a well-maintained citrus estate, only one tree in a hundred contained an *Azteca* sp. nest, whilst in the abandoned orchard, part in a steep-sided enclosed valley, had only one tree in thirty-four (3 %) with a nest. In the main study area however, on a more open sunny site, thirty-seven out of eighty-eight living trees (42 %) possessed nests in 1976 with an increase to forty-six out of seventy-nine (58 %) in 1977.

Azteca sp. is predatory (it will feed readily on liver baits) ; saccharophilic (it tends scale insects and builds carton shelters over some species) , possesses several static nests, and is arboreal. Leston (1973) has listed all of these as characteristic of dominant ants in a mosaic. As a consequence, *Azteca* sp. has a profound influence on the fauna of the trees it inhabits. Jutsum et al. (1981) found that citrus trees with *Azteca* sp. were much more likely to be infested with the soft green scale *Coccus viridis* (Green), and a stem-living coccid *Toumeyella* sp. n. normally found under protective shelters built by the *Azteca* sp. workers. They also has substantial quantities of sooty moulds (Erysiphales) on their leaves, giving the whole tree a black appearance (Table III). There was evidence that the arboreal-nesting termite *Nasutitermes costalis* Holmgren was not found on trees occupied by *Azteca* sp., and an indication (not statistically significant as very small numbers were involved) that a polybiine wasp (possibly *Polybia rejecta* (Fab.)) was positively associated with the ant.

Table III – The influence of *Azteca* sp. on the fauna and flora of citrus trees (modified from Jutsum et al., 1981).

Tabla III – Influencia de *Azteca* sp. sobre la fauna y la flora de cítricos (modificado de : Jutsum et al., 1981).

	Percentage of all the trees examined (n) with the organisms present		Significance (P) of the difference *
	Trees with *Azteca* sp.	Trees without *Azteca* sp.	
Nests of wasp (*Polybia* sp.)	11(37)	2(51)	>0.05
Nests of termite (*Nasutitermes costalis*)	0(37)	18(51)	<0.01
Soft green scale (*Coccus viridis*)	80(20)	20(10)	<0.01
Stem coccid (*Toumeyella* sp.n)	65(20)	0(10)	0.001
Sooty moulds (*Erysiphales*)	95(20)	10(10)	<0.001

* Using a Fisher exact test on a 2 x 2 contingency table

Farmers regard *Azteca* sp. as a pest, primarily because the workers are aggressive and bite if the tree is disturbed. This impedes harvesting the fruit. *Polybia* nests are especially feared by farm workers and if the association with *Azteca*, suggested by Kirkpatrick (1957) is confirmed, it would be regarded as a further disadvantage of *Azteca* sp. The effects of the enhanced numbers of scale insects have not been quantified, but yield is almost certainly reduced. Rai (1977) showed that *Azteca* sp. on coconuts in Guyana increased the incidence of the coconut scale *Aspidiotus destructor* Sign., and the mealybug *Nipaecoccus nipae* (Mask) and reduced the yield of nuts by 62 %. Contamination of citrus fruit by scales and sooty mould growth lowers its market value. As a result, farmers usually control *Azteca* sp. numbers by a combination of cutting down and spraying their nests.

However, the effects of *Azteca* sp. are not all deleterious. Vello (1971) recorded increased pollination in cocoa trees inhabited by *Azteca chartifex spitini* Forel, although the mechanism by which pollinating insects are attracted is not clear, and Eberhard and Kafury (1974) showed that the arboreal-nesting *Azteca trigona* was a possible defence against leaf-cutting ant attack.

INTERACTIONS BETWEEN ANT SPECIES

Leston (1973) working in Africa pointed out that the dominant ant species occupy different individual trees, and so form a mosaic in tree crops and forests. As the dominants are mutually exclusive, the other insect species associated with them may also form a mosaic. Leston (1978) extending his studies to the Neotropics, showed that in natural forest, *Dolichoderus attelaboides* (Fabricius) chemically repulsed individuals of *A. cephalotes* or physically removed them from the trunk.

Jutsum et al. (1981) noted that the incidence of defoliation by *A. cephalotes* in the abandoned citrus orchard was very patchy. Trees without *Azteca* sp. or either of the other two dominants, *Crematogaster brevispinosa* Mayr and *Dolichoderus bidens* L. had an average 54 % foliage loss in 1977 whilst those with *Azteca* sp. suffered only à 5 % loss. They observed *Azteca* sp. and *C. brevispinosa* attacking isolated *A. cephalotes* workers (presumably scouts seeking new sources of leaves) which had wandered on to the trunks of the trees they inhabited. On trees otherwise completely defoliated by *A. cephalotes*, they also noted that branches in the immediate vicinity of the small felt and leaf nests of *D. bidens* were fully foliated and bore flowers and fruit, and they surmised that this must be due to aggression towards the leaf-cutters. A survey of ten trees without *Azteca* sp. revealed one with *C. brevispinosa* and two with *D. bidens.*

The role of *Azteca* sp. in preventing *A. cephalotes* defoliation was demonstrated experimentally (Jutsum et al., 1981). Nineteen trees with *Azteca* sp. nests were treated with a toxic bait made from ground liver using Mirex (dodecachlorooctahydro-1,3,4-metheno-2H-cyclobuta (cd) pentalene) as the toxicant, and ten untreated trees with *Azteca* sp. were left as controls. Within twenty-five days, *Azteca* sp. activity had ceased on all nineteen trees, there being no living ants in the nests. On only one of the ten untreated trees was the *Azteca* sp. killed, and this was due to their foraging on a nearby baited tree. One tree was defoliated by *A. cephalotes* only 72 h after baiting, the leaf-cutter workers standing in apparently aggressive attitudes beside the carton shelters still housing the dying *Azteca* sp. workers. By the end of the observation periods (a maximum of 33 days), fifteen trees (79 %) had been attacked by *A. cephalotes*, compared with only one (10 %) of the untreated control trees patrolled by living *Azteca* sp.

Following the death of the *Azteca* sp. on the baited trees, the majority of the *Coccus viridis* and *Toumeyella* sp. n. scales died within a month. This was associated with an increase in the numbers of larvae of a coccinellid predator *Azya*, a probable increase in fungus disease on *C. viridis*, and the disintegration of the carton shelters built over the dead *Toumeyella* sp. n. by *Azteca* sp.

CONCLUSIONS

It is clearly established that *Azteca* sp. can inhibit the defoliating activities of *A. cephalotes* on the citrus trees it occupies. However, some leaf-cutting does occur even on *Azteca* sp. inhabited trees. This may be due to *A. cephalotes* workers gaining access to the tree where it touches another, or via a liane, so allowing cutting to occur well away from the *Azteca* sp. nest without the leaf-cutters having to climb up the normally well-defended trunk. The observation that *A. cephalotes* invaded trees before all the *Azteca* sp. had died, suggests that when numerically superior, they may be able to inhibit *Azteca* sp. attack. The continuing tree death in the abandoned orchard from 1972 to 1979, probably from leaf-cutting ant defoliation suggests a progressive breakdown in *Azteca* sp. defence. As *Azteca* sp. is polydomous, it may only require a temporary withdrawal of workers from one tree, or a failure of one satellite nest, to permit that tree to be defoliated. As defoliation removes all the *C. viridis*, the tree will become less attractive to the *Azteca* sp. so lessening the vigour of its defence and permitting further defoliations. This may cause *Azteca* sp. to abandon the tree before it is killed by repeated defoliation.

As *Azteca* sp. nests are not normally encountered on small citrus trees, they do not provide any protection to newly-planted, saplings, the most vulnerable stage in citrus culture. Because they bite, and encourage such high populations of homoptera, *Azteca* sp. is not likely to be acceptable to farmers as a competitive displacement agent for the biological control of leafcutting ant damage. *D. bidens* is effective over such a short distance from its nest that acceptable sized populations would not provide control, but *C. brevispinosa* might repay closer study to see how effective it is, and what are its disadvantageous side effects.

For the present, citrus growers in Trinidad like to keep their trees free of both *Azteca* sp. and leaf-cutting ant damage. By using toxic baits this can be done simply, cheaply and with minimum toxic hazard to the environment (Lewis, 1973 ; Lewis & Phillips, 1973 ; Jutsum et al., 1981).The use of arboreal-nesting dominant ants to control leafcutting ant damage in forestry may be more promising as the disadvantages of biting ants disrupting harvesting operations, or of enhanced homoptera populations reducing yield and contaminating the crop may be less important. However the effectiveness of defensive ants in limiting leaf-cutting ant damage in tropical forests is far from clear. Leston (1978) found lacunae in the defence of a forest stand in Brazil, and if a large proportion of trees are normally undefended, then Cherrett's (1968b) explanation of why the ants travel so far from the nest to cut trees, namely that they are adopting a conservational grazing system to even out the rate of exploitation over their territory, may still be valid. Some of the large grass-cutting ants such as *Atta vollenweideri* For. and *Atta capiguara* Gonçalves seem to adopt a similar foraging pattern, although a mosaic is unlikely to be operating. If many trees in natural forest are undefended, the reasons for this may make it difficult for man to increase (as a biological control) the proportion defended in his plantations. This is an area where more research is needed.

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