EPIDEMIOLOGY OF PHYTOPHTHORA ON COCOA IN NIGERIA

Final Report of the International Cocoa Black Pod Research Project

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Front cover : Development of an infection sequence initiated by a black pod infected from the flower cushion

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Contents

Chapter 9

A GENERAL VIEW OF ANT BIOLOGY IN RELATION TO COCOA

Brian Taylor and S. F. Adedoyin

The majority of insects on cocoa are ants (87%, Entwistle, 1972). This fact, coupled with existing evidence for the involvement of insects, including ants, in the transmission of black pod (Okaisabor, 1974) indicated that an in-depth study of ant populations on cocoa in Nigeria would be a necessary part of the work of the International Black Pod Research Project.

This chapter presents the results of a number of investigations carried out at the Cocoa Research Institute of Nigeria (CRIN) and of a survey of 76 farms scattered throughout the cocoa growing region of western Nigeria.*

The Ant Mosaic

The occurrence of ants on cocoa had been shown by various authors (Strickland, 1951a, b; Leston, 1970, 1973; Room, 1971; Majer, 1972) to be influenced by a relatively few dominant species, which are distributed in a mosaic, or patchwork manner. A dominant ant was defined by Leston (1973) as 'one which is numerically superior where it occurs and excludes other dominants, i.e., ants which elsewhere are numerically superior'. All these authors worked in Ghana and very little was known about the ant mosaic in Nigeria.

Ant Taxonomy

The generic status of the ants collected was determined using Bolton's (1973) keys but the specific epithets were based primarily on the ant specimens in the reference collection maintained at CRIN. The use of code letters and numbers for some species was necessitated by the confused state of ant taxonomy and a lack of up-to-date revisions of many of the genera. An illustrated guide to 195 species of ant originating from the Nigerian forest zone, which are preserved in the CRIN reference collected was prepared by the senior author and has been published in the CRIN Research Bulletin series (Taylor, 1976, 1978, 1979, 1980a, b). A set of specimens has also been deposited in the British Museum (Natural History). An updated list of the ants observed on cocoa, together with brief notes on their known biology, are to be found as Appendix 2 (nomenclature advice given by Bolton, pers. commun.). The names *Acantholepis capensis, Crematogaster gabonensis, Camponotus foraminosus dorsalis* and *Pheidole minima* are used in this paper for convenience although probably they are not correct.

Two-Dimensional Mosaic

Twice-weekly recording of ant tents commenced in April 1975 as part of a detailed study of the epidemiology of black pod disease on the South 1/1 block of cocoa at CRIN. This is an isolated block of some 400 cocoa trees with no other cocoa planted nearer than 300 m; bounded on two sides by metalled roads and on the other two sides by cleared ground. On 7 July the whole block was surveyed and all ant species visible on the cocoa trees were noted. Figure 9.1 shows the distribution on a two-dimensional basis. Clear areas of dominants *(Oecophylla longinoda* (Latreille), *Crematogaster clariventris* Mayr at the canopy level and *A. capensis* at the off-ground level) can be seen together with a number of less abundant species (including *Odontomachus troglodytes* Santschi, *Pheidole megacephala* (F.), *(Crematogaster gambiensis* (E. André), *Crematogaster* sp. A[1] and *Camponotus acvapimensis* Mayr).

*This Chapter is based largely on the already published work by Taylor (1977) and Taylor & Adedoyin (1978). The authors gratefully acknowledge the kind permission of the respective publishers, Blackwell Scientific Publications and the Commonwealth Institute of Entomology, for the reproduction of certain of the tables and figures.

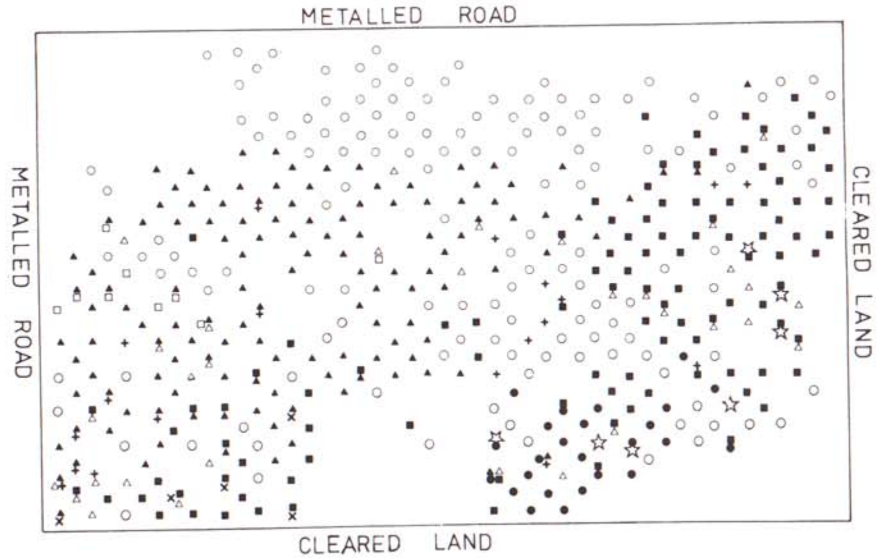

Fig. 9.1 Block S1/1. Key to species : ▲, *O. longinoda;* ■, *A. capensis;* ●, *Cr. clariventris;* △, *Ph. megacephala;* □, *Crematogaster* sp. A[1]; ☆, *C. acvapimensis;* +, *O. troglodytes;* ×, *Cr. gambiensis;* ○, no ants seen. Each symbol or cluster of symbols represents a single tree.

The Onipe 1/1 block of cocoa lies on the south-eastern edge of CRIN some distance from any other cocoa planting. It is bordered on three sides by primary/secondary forest and on the fourth side by a narrow teak plantation. The original planting in 1968 was an establishment trial of Trinidad introductions. The block at present is fragmented with shade trees and plantains. Many of the original cocoa trees have died or been damaged by falling trees. However, in early 1975 we defined 17 plots of 25 trees and commenced weekly recording of ant species, of other insect species apparently associated with ants, of healthy pods and of black pods. The ant records were based primarily on visual identification *in situ* but check laboratory identifications were made of all the species seen. Figures 9.2, 9.3 and 9.4 show the three-dimensional mosaic (drawn isometrically) on some of the plots. The illustrations are diagrammatic and no scale is meant to be implied. The canopy of each tree can be assumed to interlock with those of the neighbouring trees except where shown on the diagrams. There were, of course, seasonal changes in the canopy density. The vertical tapered lines represent the cocoa trees and the horizontal lines of symbols connect trees on which a particular dominant species was found. Capital letters indicate regular observations of a particular species and lower case letters indicate species seen on several occasions but not regularly. The approximate positions of shade trees are also shown but again no scale of size or canopy area is meant or implied. Certain species are dominant at the canopy level *(O. longinoda, Tetramorium aculeatum* (Mayr), *Crematogaster depressa* (Latr.) and *Cr. africana* (Mayr) and others at the ground of lower trunk level *(Acantholepis* sp. T[2] and *Ph. megacephala)*. The diagram of Plot N (Fig 9.4) illustrates the complexity of an undominated situation. The apparent close association of *Camponotus vividus* (F. Smith) with *Cr. africana*, and of various small *Crematogaster* species with *O. longinoda*, can also be seen from the diagrams. *O. troglodytes* is fairly commonly found ascending trees.

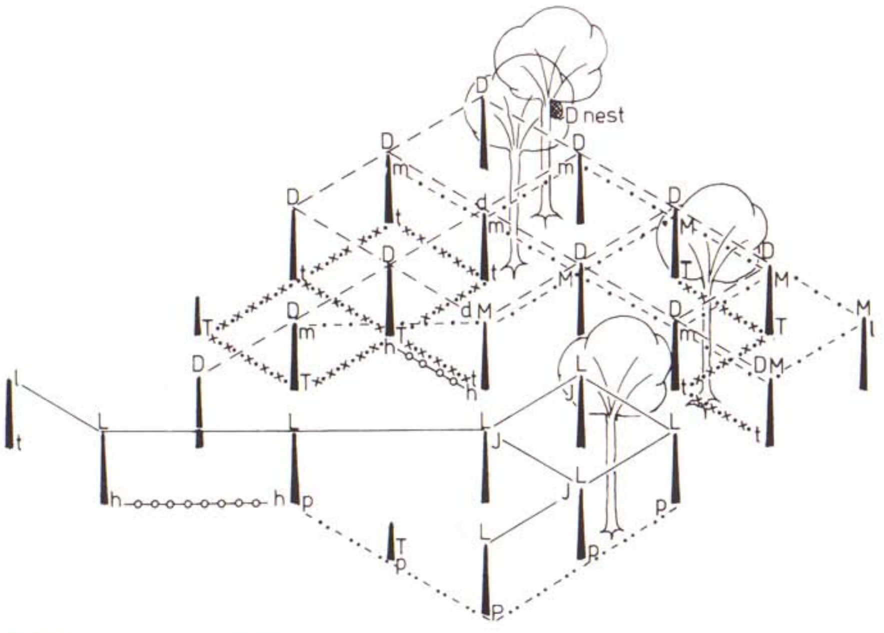

Fig. 9.2 Plot C at Onipe 1/1. Key to species : Dd, *Cr. depressa;* Hh, *O. troglodytes;* Jj, *Crematogaster* sp. A^1; Ll, *O. longinoda;* Mm, *T. aculeatum;* Pp, *Ph. megacephala;* Tt, *Acantholepis* sp. T^2. Capital letters indicate regularly observed, lower case letters indicate seen on several occasions.

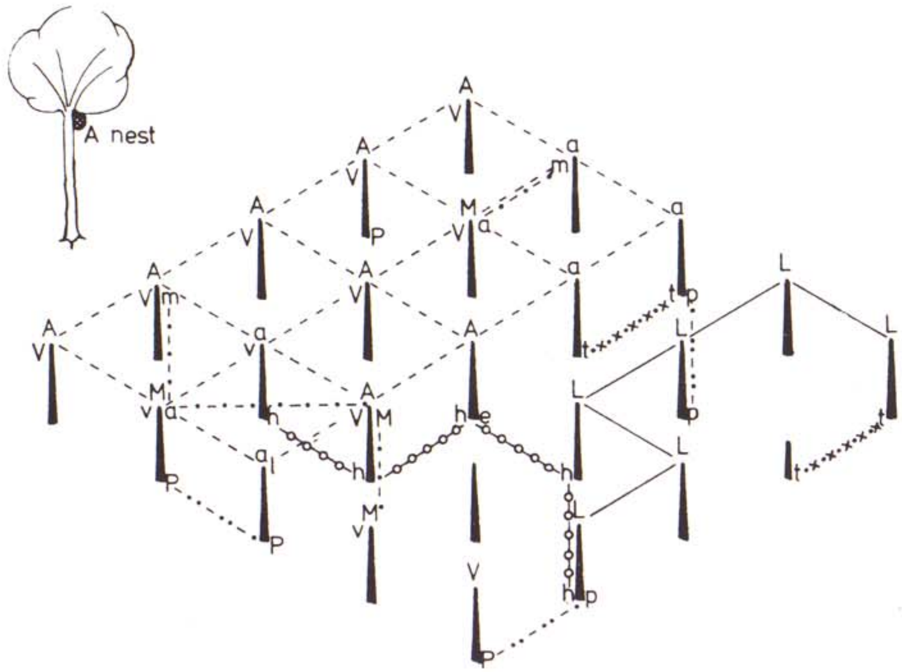

Fig. 9.3 Plot G at Onipe 1/1. Key to species as in Fig. 9.2, plus Aa, *Cr. africana;* Ee, *Ph. minima;* Vv, *C. vividus.*

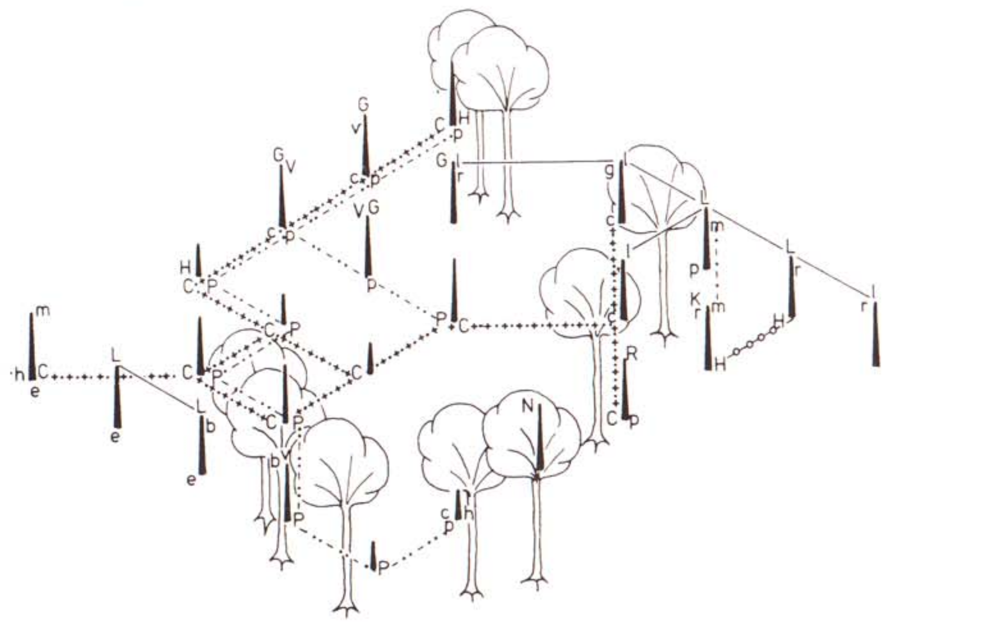

Fig. 9.4 Plot N at Onipe 1/1. Key to species as in Figs 9.2 and 9.3, plus Bb, *Cr. bequaerti;* Cc, *A. capensis;* Gg, *Cr. gambiensis;* Kk, *Crematogaster* sp. 1; Nn, *Crematogaster* sp. 2; Rr, *Cat. guineensis.*

Association Analyses

In August 1975 a number of special surveys were made on several cocoa blocks at CRIN (West 7/1, West 12/1, West 14/1, West 17/1, North 4/1, South 6/1). The surveys were biased to include four sets of 50 trees, dominated by *O. longinoda, T. aculeatum, Cr. africana* and *Cr. depressa* respectively, and 100 supposedly non-dominated trees. In fact the 'non-dominated' trees turned out to be dominated in the main by *A. capensis* and/or *Ph. megacephala.*

The results of the special surveys together with the results of detailed checks made of the Onipe 1/1 plots and the South 1/1 surveys gave enough data for association analyses to be performed. These were done using a nomogram for comparison of two populations from which samples of size *m* and *n* are taken having percentages *p* and *q* with the same attribute (Rosenbaum, 1959). The analysis is the equivalent of some forms of 2x2 tables but the nomogram eliminates the need for any calculations.

Summaries of the positive and negative associations between species are shown in Figures 9.5 and 9.6 respectively. The significance of the association between two species can be tested only if the species occur together and thus facilitate comparisons of percentage occurrence of one species with or without the other species. Thus no association was tested between *O. longinoda* and *Cr. africana* as they were never found together. For one species, *Paratrechina* sp. 3, no significant association could be detected with any dominant or even a non-dominated situation. A negative association between *A. capensis* and *O. troglodytes* has been omitted from Figure 9.6.

From the total 1426 possible occurrences, 56 species were seen. With the eight species regarded as dominants either at the canopy level or at the off-ground level there were only ten other species which occurred on more than 5% of the trees occupied by the dominants in one, two or all of the three sets of surveys. *O. troglodytes* can additionally be regarded as a dominant because it is quite common and has a positive association with the non-dominated situation.

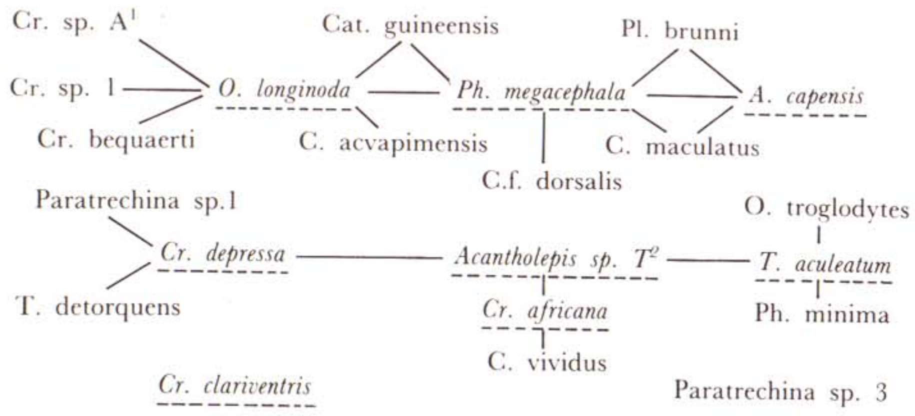

Fig. 9.5 Positive association between species (see text), dominant species underlined. *T. detorquens* = *Tapinoma* sp., *C. maculatus* = *Camponotus maculatus* (F.).

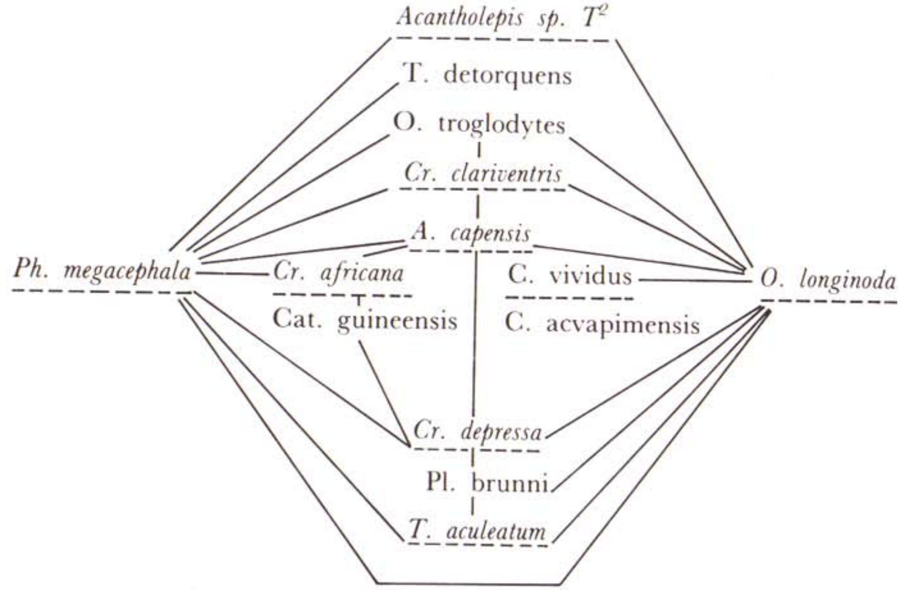

Fig. 9.6 Negative association between species (see text), dominant species underlined.

In the course of observations elsewhere on CRIN, *Cr. gabonensis* was also noted as a dominant. From our results we felt that Leston's (1973) definition of a dominant could rarely be applied in its strictest sense as co-dominance was quite a common occurrence and the influence of a dominant on the cocoa ecosystem was dependent not only on the behaviour of the dominant but also on the behaviour of co-dominants and associated species.

Abundance of Species

In addition to the surveys of Onipe 1/1 and South 1/1 we also surveyed 13 other cocoa blocks at CRIN in 1975. A total of 4898 trees were surveyed. Identifications were made in the field by naked eye and, thus, certain species could not be separated; *Cr. africana* and *Cr. depressa*, *Pheidole* species (as *Ph. megacephala*), *Acantholepis* species (as *A. capensis*) and *Cr. gabonensis/gambiensis* are the main examples. Table 9.1 summarises data for the ten most abundant species or species groups. Species which had an occurrence of over 1% on one or

Table 9.1 Species or species-groups with an arithmetic mean per cent occurrence of 1% or more on 4898 cocoa trees at CRIN G.E.S.

Species	Arithmetic % occurrence	Highest % occurrence	No. of blocks on which observed (of 15)
O. longinoda	18·31	53·92	13
'*Ph. megacephala*'	14·12	50·92	13
Cr. africana/depressa	9·96	35·29	14
'*A. capensis*'	9·08	27·36	11
C. acvapimensis	4·53	25·09	12
T. aculeatum	3·21	11·29	11
O. troglodytes	2·47	15·69	10
C. maculatus	2·47	12·50	11
Cat. guineensis	1·41	4·78	9
C. vividus	1·00	5·06	5

more of the cocoa blocks were principally those shown in Table 9.1 plus *Cr. gabonensis*, *Cr. gambiensis*, *Platythyrea conradti* Emery and *Polyrhachis militaris* (F.). Other species with a mean occurrence of between 0.1% and 1.0% were *Myrmicaria striata* Stitz, a *Monomorium* species and *Camponotus* sp. T[2]. A further 19 species were recorded in the surveys and in 1974-75 a further 39 species were collected on cocoa trees at CRIN.

Having established what seemed to be a valid picture of the distribution and abundance of ant species within the confines of CRIN, i.e. on a single farm, albeit a rather large and diverse farm; we decided to make a survey of a range of farms in the cocoa-growing area of western Nigeria. The survey was carried out between 19 January and 6 February 1976 by a team of experienced observers led by the junior author. Seventy-six farms were visited and their locations are shown in Figure 9.7. Fifty trees were examined at each farm, and all ant species visible from the ground were noted. Loose bark, dead twigs, dead pods etc. on the tree as far up as the hand could reach were examined for ant nests. As in the CRIN surveys, certain species were categorised together; e.g. *Cr. africana* and *Cr. depressa*; *Acantholepis* sp. T[2] and *A. capensis*; *Crematogaster* sp. A[1] and *Cr. bequaerti* (Forel).

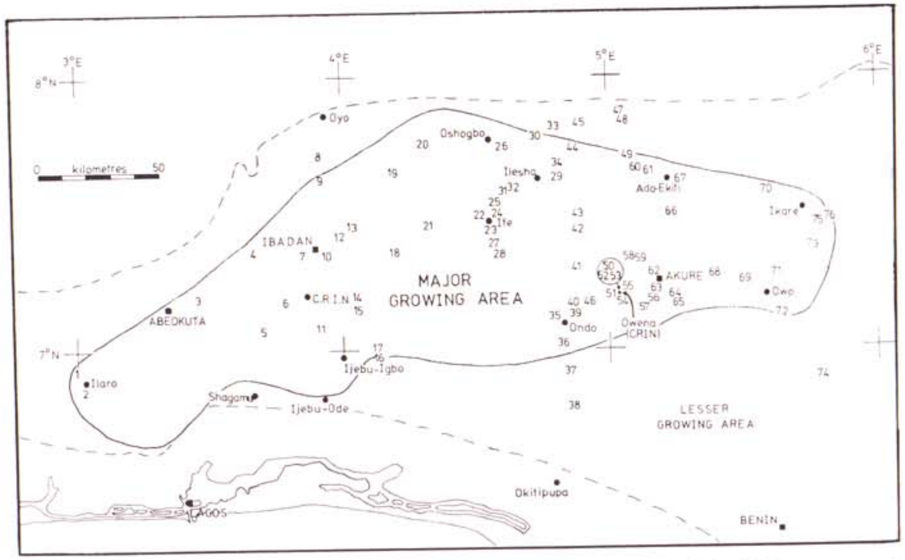

Fig. 9.7 The cocoa growing area of western Nigeria showing the locations of the 76 farms surveyed.

Results

A summary of the results from the 76 farm survey is given in Table 9.2, together with the results from the survey of 4898 trees at CRIN. From Table 9.2 it can be seen that the order of priority of the 16 most common species or species-groups varies when determined by different criteria. For instance, *O. longinoda*, although the most abundant species in terms of frequency of occurrence on the 3800 trees studied, was only fourth in terms of the number of farms at which it was observed. A more extreme example is that of *Cr. clariventris*, which was the sixth most abundant species but was thirteeenth in priority of number of farms and third in priority by number of trees occupied per farm.

Geographical distribution

The distribution of the ten most common species was plotted on the map of the farms. *O. longinoda* was widely distributed throughout the area with no obvious localisation. Although *T. aculeatum* was found on a greater number of farms, the highest levels were in the somewhat wetter southern and eastern localities. *Ph. megacephala* showed little obvious localisation. *Cr. africana/depressa* was found on only half the farms and, apart from a group of high density records around Akure, there was no localisation. *Acantholepis* sp. T[2] and *A. capensis* were widely distributed, although there was a very high incidence at only a few farms. *Cr. clariventris* was present on only 26 farms and noticeably absent from eastern and western localities. *Plagiolepis brunni* Mayr showed no obvious localisation and this applied also to *Crematogaster species* A[1]/*bequaerti*. *C. acvapimensis*, which has been described as being of savannah origin, had its highest levels in the wetter southern localities, except for one instance west of Ibadan. *Cataulacus guineensis* F. Smith showed no obvious localisation.

Inter-specific relations

The inter-specific relations of the ten most common species or species-groups were examined by the multivariate analysis technique known as principal components analysis. In this analysis, a set of variates, denoted by $x_1 \ldots\ldots x_n$, is transformed linearly and orthogonally into an equal number of new variates, $y_1 \ldots\ldots y_n$, that have the property of being uncorrelated. These are chosen such that y_1, has maximum variance, y_2 has maximum variance subject to being uncorrelated with y_1, and so on. The latent roots and vectors of the covariance of the correlation matrix can then be obtained, and when the first few components, or axes, account for a large proportion of the total variance of the *x*- variates, they may be used to summarise the original data (Lawley & Maxwell, 1971). More simply, Kendall & Stuart (1976) described principal components analysis as a statistical tool that is, perhaps, best regarded as an exploratory instrument to enable one to find the effective number of dimensions or how dominant certain linear combinations of the variables are. The interpretation of the most relevant of the variables is based on field observations made by us in the course of 1974-76. The survey data were analysed, using a number of different criteria, by Dr. J. B. Hall of the Department of Forest Resources, at the Computer Centre, University of Ibadan.

Table 9.2 Summary of the occurrence of ants on 76 cocoa farms in western Nigeria

	No. of trees with ants	Occurrence of ants on trees (%)	No. of farms with ants	Average no. of trees with ants per farm	Occurrence at CRIN* (%)
Oe. longinoda	1257	33·08 (1)	60 (4)	20·95 (1)	18·31
T. aculeatum	546	14·37 (2)	71 (2)	7·69 (5)	3·21
Ph.. megacephala	477	12·55 (3)	72 (1)	6·62 (6)	14·12
Cr. africana/Cr. depressa	452	11·89 (4)	36 (9)	12·56 (2)	9·96
A. capensis/sp. T[2]	442	11·63 (5)	53 (6)	8·34 (4)	9·08
Cr. clariventris	311	8·18 (6)	26(13)	11·96 (3)	0·7
P. brunni	281	7·39 (7)	65 (3)	4·32(10)	0·8
Cr. bequaerti/sp. A[1]	180	4·74 (8)	41 (7)	4·39 (9)	1·1
C. acvapimensis	162	4·26 (9)	33(10)	4·91 (8)	4·53
Cat. guineensis	136	3·58(10)	57 (5)	2·39(12)	1·41
Cr. gabonensis	91	2·39(11)	14(16)	6·50 (7)	0·5
C. vividus	83	2·18(12)	24(14)	3·49(11)	1·00
C.f. dorsalis	57	1·50(13)	27(12)	2·11(13)	0·5
Tetraponera anthracina	57	1·50(14)	41 (7)	1·39(16)	—
O. troglodytes	49	1·29(15)	30(11)	1·63(15)	2·47
Ph. minima	41	1·08(16)	20(15)	2·05(14)	—
Total surveyed	3800	—	76	50	—

* From the survey of 4898 trees

The analyses of species by samples (trees) or by sites (farms) as exemplified in Figure 9.8 confirm the separation of dominant species and the grouping of co-dominant and sub-dominant species that was so characteristic of the work at CRIN. Because of its very similar habitat requirements, the survey data for *Ph. minima* were grouped with those for *Ph. megacephala*.

The analyses of sites by species, of which Figure 9.9 is an example, shows clear grouping of sites. To gain an understanding of this grouping of sites, the occurrence, on a maximum of 50 trees, of the different species of ant, at each site position in Figure 9.9 was plotted. The influence of the dominant species of ant is clearly illustrated in the summary diagram, Figure 9.10. The separation of sites strongly resembles the single farm mosaics found at CRIN. On those farms

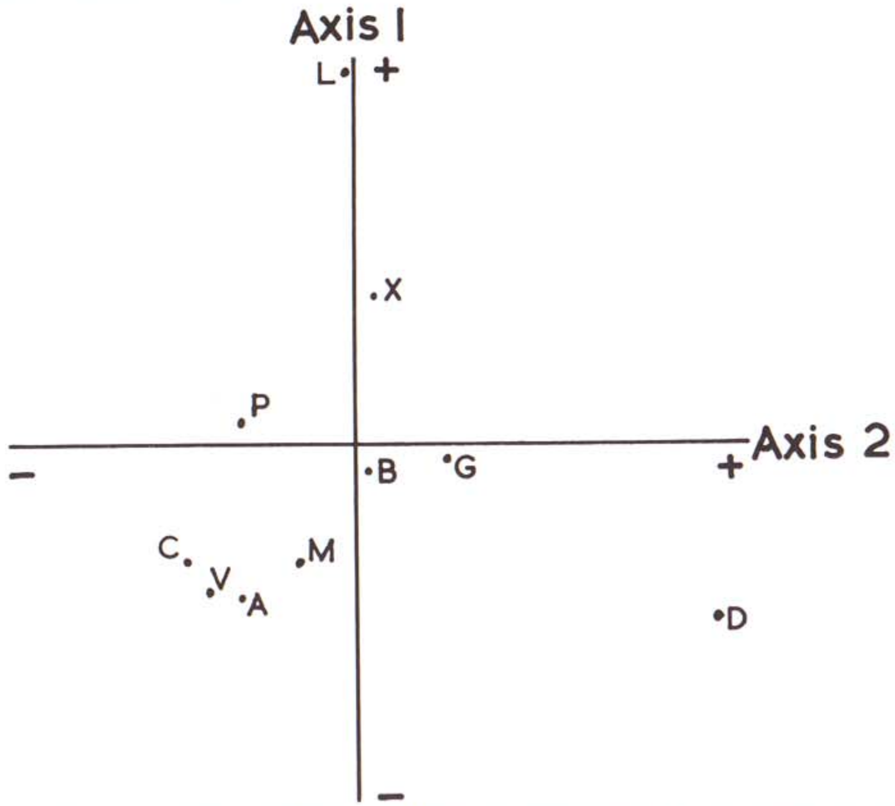

Fig. 9.8 Species ordination, 10 species × 3800 trees. (L = *Oe. longinoda*, M = *T. aculeatum*, P = *Ph. megacephala*, D = *Cr. africana/Cr. depressa*, A = *Acantholepis* sp. T[2]/*A. capensis*, V = *Cr. clariventris*, B = *P. brunni*, X = *Crematogaster* species A[1]/*Cr. bequaerti*, C = *C. acvapimensis*, G = *Cat. guineensis*.)

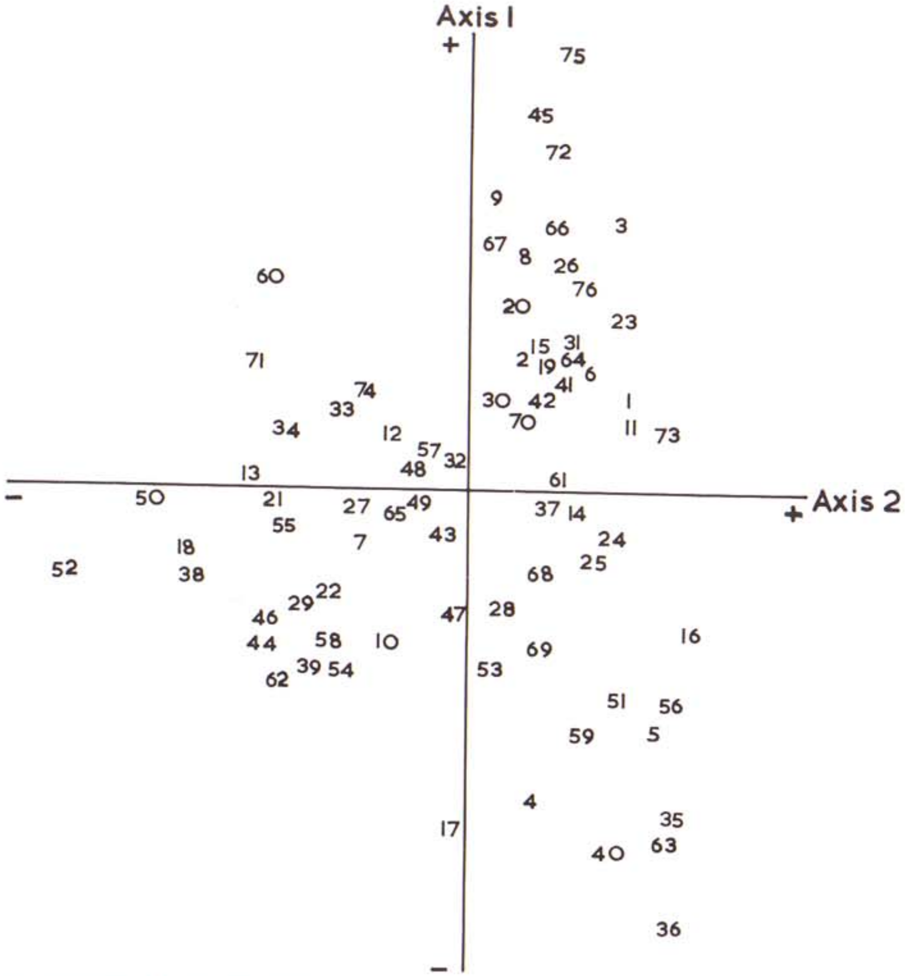

Fig. 9.9 Site ordination, standardised by species, quantitative (frequency per site). Sites shown by reference numbers.

that were not dominated by the six main species or species-groups plus *C. acvapimensis*, *Cr. gabonensis*, which was a rare dominant at CRIN, was the most common species. The occurrence of *Acantholepis* sp. T^2/*A. capensis* with *Cr. africana/depressa* in Figure 9.10 almost certainly denotes a separation of the two species of *Acantholepis*, as species T^2 was found to be positively associated with *Cr. africana* and *Cr. depressa* at CRIN, whereas the reverse was true for *A. capensis*.

Habitat

Majer (1976a) suggested that the inter-specific ant mosaic is maintained by a combination of habitat requirements, inter-specific resource competition and inter-specific aggressive competition. A simplified and rather arbitrary summary of the habitat requirements of the dominant ants on cocoa, based on our observations at CRIN and during the present survey, is shown in Figure 9.11. No time-scale is given as, apart from the first few years of initial growth, the development of the canopy will be affected by agronomic factors such as soil type, inter-tree spacing, weed management, and presence or absence of shade trees. The degrading and breaking of the canopy may be a result of ageing of the trees, adverse weather, pests, diseases and so on. On any one farm, the canopy

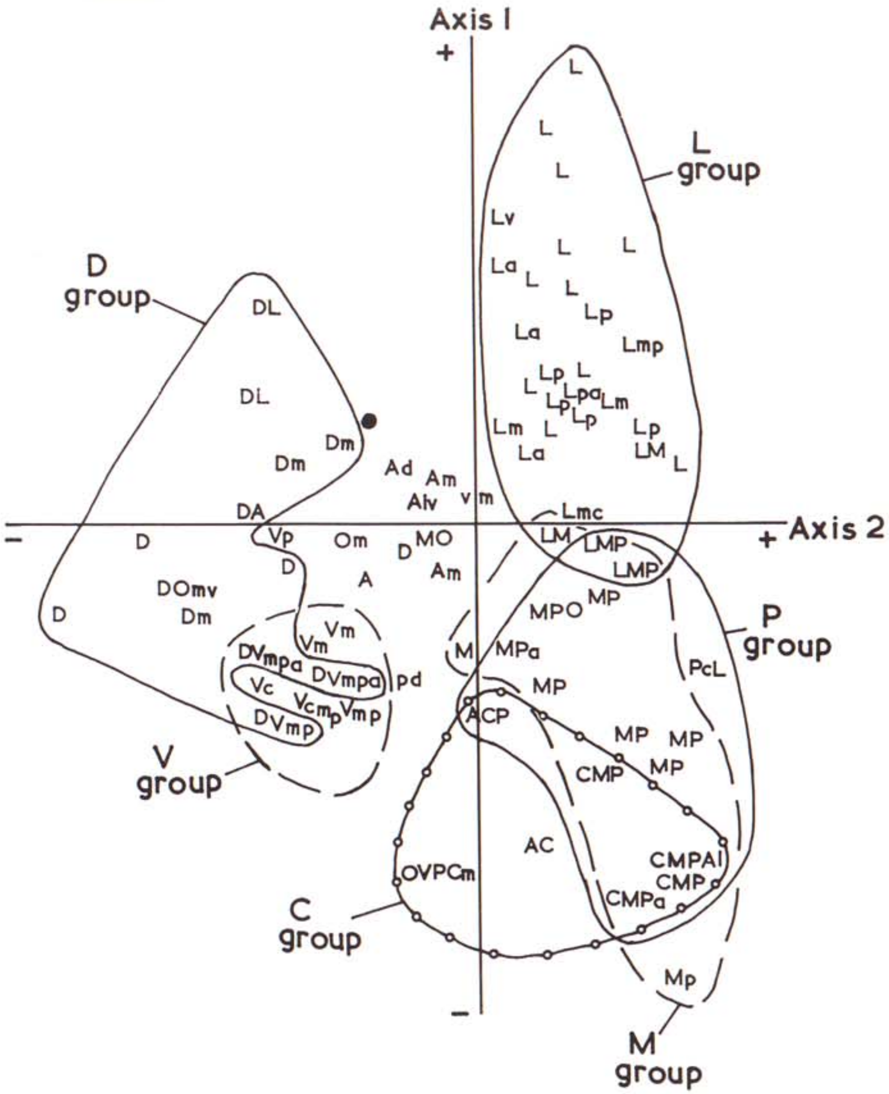

Fig. 9.10 Site ordination from Fig. 9.9 showing the dominant species at each site. (Key as in Fig. 9.8, plus ○ = *Cr. gabonensis* and ● = no dominant (*C. vividus* most common species). Upper case letter, e.g., L, = main dominant; lower case letter, e.g., l, = lesser dominant.)

state is unlikely to be wholly uniform and there will usually be open spaces at least where there are paths and at the edges of the farm.

Bionomics

When the habitat requirements overlap, the elements of competition are involved, and these are influenced by several factors including colony size, foraging habits and nesting sites. Clearly, these factors cannot be separated wholly from habitat requirements, and the following notes, based primarily on our own observations, summarise the factors for the different species. The habitats of some of the species have been observed in Ghana but not all the findings agree with ours.

O. longinoda, which constructs its nests by weaving leaves together with larval silk, is found in multi-nest colonies occupying as many as 100 cocoa trees. The

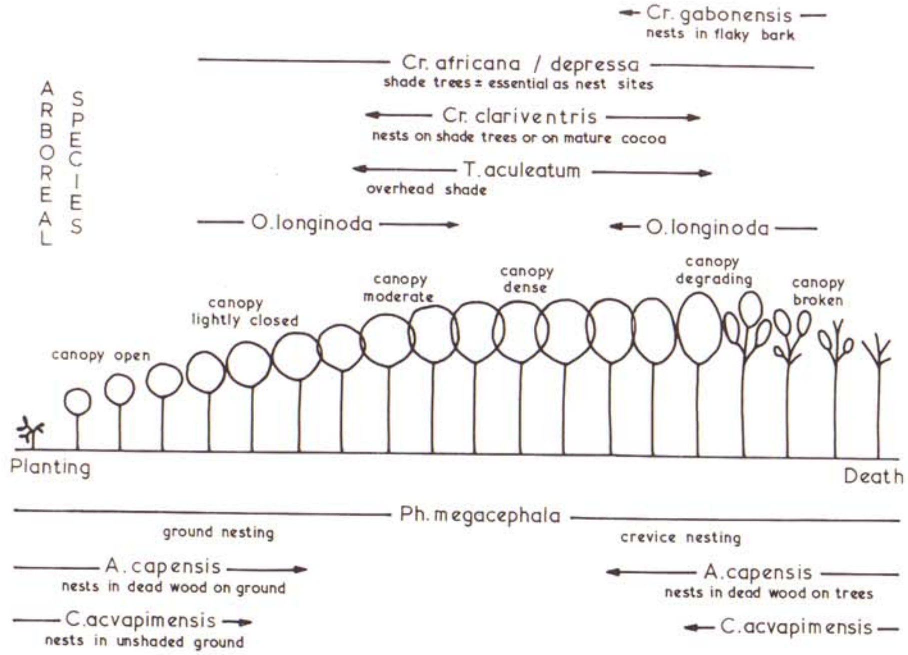

Fig. 9.11 Summary of habitat factors influencing the presence of dominant species of ant on cocoa in western Nigeria.

main restrictions to its colony size are the need for an interlocking of the tree canopies and interactions with other dominant ant species.

Cr. africana and *Cr. depressa* construct large nests of carton, chewed wood, which are usually sited on certain of the large indigenous trees. From the main nest, foragers spread out in columns across the cocoa canopy or, if necessary, across the ground. The foraging area can be quite extensive, covering 60 to 100 cocoa trees in a neatly planted farm. The restrictions to the foraging area are probably distance, abundance of food and interactions with other species of dominant.

Cr. clariventris also constructs carton nests, but the colony, which may occupy a large number of cocoa trees if the canopy is interlocking, is made up of a number of moderately sized nests sited on medium-sized trees, including cocoa trees.

T. aculeatum constructs nests of fibrous plant material (felt) between leaves or on the underside of leaves where there is a good dense canopy. A particular colony appears to be made up of a few nests only, and the foraging area is thus restricted to a small group of trees.

The above species can all be regarded as dominants that primarily nest and forage within the cocoa canopy. *O. longinoda* sometimes forages on the ground round tree bases, but this seems to occur because of a shortage of food on the tree itself. *Cr. africana* and *Cr. depressa* are most often seen on the ground, but usually this is because columns of foragers descend to the ground to pass between trees when unable to follow a cross-canopy route.

The next group of dominants differs in that the ground is their primary habitat. The ants ascend trees in search of food but do not move from tree to tree at the canopy level. *Ph. megacephala* nests either in the ground or in soil or debris collections in crevices, such as the jorquette, on trees. Colonies are usually relatively small, and foraging covers no more than six to ten fairly closely planted trees.

Acantholepis sp. T[2] and *A. capensis* appear to prefer to nest in dead wood either on the ground or on the tree. Either the colony size is large or, more probably, a number of individual colonies can occur adjacent to each other, thus occupying the ground area round a large number of cocoa trees. *C. acvapimensis* is a wholly ground-nesting species, which appears to form large colonies and forages over a wide area. However, it nests only in ground exposed to the sun, and on a cocoa farm it is usually found foraging round the edges of the farm or in areas of poor canopy.

In addition to the dominants, there were three common species or species-groups: *P. brunni*, *Crematogaster* sp. A[1]/*bequaerti* and *Cat. guineensis*. *P. brunni* occurred on 65 farms and there was no obvious grouping of sites where it occurred. Its abundance is probably due to its discreet habits, which enable it to avoid contact with most of the dominant species. It was found to be positively associated with *Ph. megacephala* and *A. capensis* at CRIN. It nests in dead twigs still on the tree and thus its habitat requirements are probably older to degrading cocoa in Figure 9.11.

Crematogaster sp. A[1] and *Cr. bequaerti* were shown to be associated with *O. longinoda* at CRIN and this was confirmed by the site ordination. These species are sub-dominants rather than co-dominants. They have similar habits, both nesting in dead wood on the tree and foraging out over about six trees. In general, they and other similar small species of *Crematogaster* seem to be most abundant in the dry season.

Cat. guineensis appeared to be little affected by the dominants although the highest occurrences tended to confirm the associations with *O. longinoda* and *Ph. megacephala* seen at CRIN. It is a fairly large heavily armoured ant which nests in dead wood on trees. Colonies are made up of a single nest but foraging takes place over a wide area as long as there is an interlocking canopy.

Of the six remaining species listed in Table 9.2, only *Cr. gabonensis* is normally a dominant although *O. troglodytes* and *Ph. minima* can play a dominant role in the absence of more usual dominants. *Cr. gabonensis* is more selective in its habitats than the other large *Crematogaster* species, apparently preferring cocoa trees with flaky cankerous bark, a condition often related to earlier heavy mirid attack. *O. troglodytes* is a ground nesting species that prefers rotting wood as a nest site. It is one of the few ponerine species to ascend trees and the only one to construct tents, albeit rather crude ones of large particles of soil and debris. *Ph. minima* behaves in a similar manner to *Ph. megacephala* but its colonies are smaller and foraging is restricted to the tree on which the nest is sited.

Camponotus vividus (F. Smith) nests in dead wood of certain types of forest tree. 'Often the tree is the site of a *Cr. africana* nest. Foraging takes place over trees interlocking with the nest tree. *C. foraminosus dorsalis* is another arboreal species, nesting usually in dead wood but quite commonly found in old dried-up cocoa pods still on the tree. The colony consists of a single nest with a relatively small number of individuals, and the foraging area is no more than four to six adjoining trees. The final species found on more than 1% of the surveyed trees is *Tetraponera anthracina* (Santschi). Usually, only a few individuals were seen at any one time. It is arboreal and probably nests in dead wood, but its foraging area and habits are unknown. Members of the genus have large well developed eyes and are quick-moving in response to potential danger; thus they are difficult ants to observe.

Conclusions

The work during 1974-76 at CRIN and the 76 farm survey showed nine species of ant to be dominant on cocoa. Among these, *O. longinoda*, *T. aculeatum*, *Cr. africana*, *Cr. depressa*, *Cr. clariventris* and *Cr. gabonensis* are arboreal; *Ph.*

megacephala and *A. capensis* are subarboreal; and *C. acvapimensis* is terrestrial but readily ascends trees while foraging. Ten other species occurred on more than 1% of cocoa trees; all but two, *Acantholepis* sp. T^2 and *O. troglodytes*, are arboreal.

The geographical distribution of the ten most common species or species-groups within the survey area showed that, in general, the wetter south-eastern areas (Akure-Ondo) are preferred by all except *O. longinoda* and *A. capensis*. The nests of *O. longinoda* are particularly vulnerable to rain and storm damage, and *A. capensis* has a preference for relatively dry rotting wood for its nests.

The recording of ant abundance in Nigeria has all been on the basis of presence or absence of ant species on trees and there have been no measurements of absolute numbers, or biomass, of ant species. However, the dominant species all forage in moderate to large numbers on any one tree. *O. longinoda* forages over the whole tree, whereas *T. aculeatum* and species of *Crematogaster* tend to remain in the canopy rather than descend the trunk, and *Ph. megacephala*, *A. capensis* and *C. acvapimensis* mainly forage on the trunk and lower canopy.

The importance of the ant mosaic on cocoa lies not only in the specific behaviour of the dominants but also in that of co-dominants and associated species. The overlapping of the species grouping in the site-ordination graph (Figure 9.10) shows that it is rare for any one species to dominate completely any one farm although, as summarised in Figure 9.11, the habitat requirements of the dominants make it unlikely that any farm would be acceptable to more than one or two dominants at one time. Leston (1970, 1973), Room (1971, 1973) and Majer (1976b) have suggested that the structure of the ant mosaic could be altered to favour certain dominants, namely *O. longinoda* or *T. aculeatum*, which they regard as beneficial species in Ghana but, apart from Room (1971), they do not seem to have considered the problem of co-dominants or associated species.

Manipulation of the cocoa habitat in Nigeria, if it were possible, in favour of *O. longinoda* or *T. aculeatum* would almost certainly lead to an increase in *Ph. megacephala*, which in addition to being a tender of the mealy-bug vectors of swollen shoot virus, can have a significant effect on the level of black pod disease. An increase in *T. aculeatum* might also lead to an increase in *C. acvapimensis*, which tends mealy-bugs and is an important carrier of soil infected with black pod. At CRIN we found that *O. longinoda* has no effect on the amount of damage to cocoa pods by mirids because *Sahlbergella singularis* Haglund is more common in Nigeria than *Distantiella theobroma* (Distant), a reverse of the situation in Ghana. *T. aculeatum* reduces the level of mirid damage but *Cr. africana* is associated with a high level of damage.

Finally, not only did the need remain for much more information on the relations between ants and other insects in the cocoa farm ecosystem but also almost nothing seems to be known of the role of ants in the natural forest ecosystem from which the cocoa farms are derived.

APPENDIX 2

Ant Species Recorded on Cocoa Trees in Western Nigeria

B. Taylor

In alphabetical order, nomenclature according to B. Bolton (pers, comm.). Bracketed names are those used in Taylor's ant guides (1976, 1978, 1979, 1980a, 1980b) and/or in Taylor (1977) and Taylor & Adedoyin (1978).

Acantholepis sp. (*capensis*) — dominant on 9-10% of cocoa trees, tends Homoptera, builds soil tents.

Acantholepis sp. ((*spinosior*) — uncommon, tends Homoptera.

Acantholepis sp. T^1, — occasionally seen, tends Homoptera, builds vegetable tents.

Acantholepis sp. T^2 & T^3 — fairly common sub-dominant with *Crematogaster africana*, on 5-10% of cocoa trees, tends Homoptera, constructs debris tents.

Aenictus sp. (rotundatus) — rarely climbs cocoa trees while foraging.

Anochetus africanus (Mayr) — sometimes found nesting in debris in jorquette.

Anochetus pellucidus Emery — as *africanus*.

Anochetus sp. 1 — as *africanus*.

Anoplolepis tenella (Santschi (*Plagiolepis* sp. T^2) — found once on cocoa at Owena.

Atopomyrmex mocquerysi E. André — uncommon, nests in dead wood on trees.

Camponotus acvapimensis Mayr — dominant on about 4.5% of cocoa, nests in soil, tends Homoptera, builds soil tents, black pod associated with tents.

Camponotus brutus (Forel) — occasional forager on cocoa, nests in dead wood on trees.

Camponotus chrysurus Gerst. (*micispa*) - rare.

Camponotus flavomarginatus (Mayr) — fairly common, nests in soil, tends Homoptera, suspected of tent building.

Camponotus maculatus Fabricius — fairly common, at CRIN on 2.5% of cocoa trees, tends Homoptera.

Camponotus vividus (F. Smith) — on 1.2% of cocoa trees, sub-dominant with *Cr. africana*, nests in dead wood on large trees (not cocoa).

Camponotus sp. (*foraminosus dorsalis*) — fairly common, up to 1.5% of cocoa trees, tends Homoptera, nests in dead wood including mummified pods on trees.

Camponotus sp. T^2 — occasionally on cocoa, tends Homoptera.

Cataulacus brevisetosus Forel — occasionally seen, tends Homoptera.

Cataulacus egenus Santschi — uncommon, nests in dead wood on trees.

Cataulacus guineensis F. Smith — on up to 3.5% of cocoa trees, often associated with *Oecophylla longinoda*, nests in dead wood on trees, tends Homoptera.

Cataulacus mocquerysi E. André — found once on cocoa at Olukunle.

Cataulacus vorticus Bolton — rare, will nest under bark of cocoa trees.

Cerapachys foreli (Santschi) (*Phyracaces langi)* — rare.

Crematogaster — many species.

Cr. africana Mayr and *Cr. depressa* (Latreille) are dominants with one or other on 10-12% of cocoa trees, construct large carton nests on shade trees.

Cr. clariventris Mayr — dominant on 8% of cocoa trees, builds carton nests on cocoa, tends Homoptera.

Cr. ?gabonensis — dominant on about 2% of cocoa trees, nest of carton under and around cankerous bark, tends Homoptera, constructs carton tents.

Several small species are sometimes found in association with *O. longinoda* — most abundant, on up to 1% of cocoa trees are *Cr. bequaerti* (Forel), *Cr.* sp.1 and *Cr.* sp.A^1, all tend Homoptera, latter two build tents, sp.1 of debris (may be black pod associated) and sp.A^1 of carton.

Other species occasionally found tending Homoptera are *Cr. buchneri* Forel, *Cr. gambiensis* (E. André) which builds debris tents, *Cr. kneri* Mayr also builds debris tents, *Cr. striatula* Emery and *Cr.* sp.2.

Also seen but rarely are *Cr. sjostedti* Mayr, *Cr. wellmani* Forel (*boxi*), *Cr.* sp.3, *Cr.* sp.A, *Cr.* sp.C/F409, *Cr.* sp.T^1, *Cr.* sp.T^2, and *Cr.* sp.T^3.

(Diplomorium ?lujae) Monomorium sp. — moderately common, on 0.1-0.2% of cocoa trees, tends Homoptera, may build or utilise tents.

Hypoponera camerunensis (Santschi) and *H. lea* (Santschi) — both sometimes found nesting in soil/debris in crevices of cocoa trunks.

Leptothorax angulatus Mayr (sp.T^1) — rare, will nest in crevices of cocoa trunks.

Meranoplus inermis (*nanus*, sp.T^1) — occasionally found tending Homoptera.

Miccostruma mandibularis (Szabo) (sp.T^1) — seen once only on cocoa flowers.

Monomorium bicolor Emery *M.* sp.A and M. sp. G — first and last of these have been found tending Homoptera, sp.G not too difficult to find.

Myrmicaria striata Stitz — moderately common at CRIN (0.1-1.0% of cocoa trees) but less common elsewhere in cocoa region, nests in open ground, tends Homoptera, builds soil tents, black pod associated.

Odontomachus troglodytes Santschi (*haematodus*) — can be dominant on 1.0-2.5% of cocoa trees but only on lower trunk, nests in soil or dead wood on ground, tends Homoptera, builds soil tents, black pod associated.

Oecophylla longinoda (Latreille) — dominant, commonest species, on up to 33% of cocoa trees, tends Stictococcids, builds nests by weaving leaves with larval silk.

Paratrechina — five species observed on cocoa, sp.1, sp.2, sp.3, sp.T^1 and sp.T^2; all tend Homoptera and all thought to build tents of soil or debris; sp.1 and sp.3 on 0.1-1.0% of cocoa trees.

Pheidole megacephala (Fabricius) — common dominant species, on 12-14% of cocoa nests in soil or in jorquette, avid tender of Homoptera, builds tents of soil or debris, black pod associated.

Other *Pheidole* species on cocoa are *Ph. crassinoda* (sp. T^1), sp. B. (*minima*), *speculifera* Emery sp.A, sp.E, sp.F. and sp.T^3; all of which tend Homoptera, spp.B., E, F and T^3 build tents of soil or debris. The only moderately common one of these species is sp.B (on 0.1% of cocoa trees).

Plagiolepis brunni Mayr — an abundant species (on over 7% of cocoa trees) but of no apparent influence in determining mosaic structure, nests in dead twig ends, tends Homoptera, utilises (may build) tents.

Plagiolepis sp.T^1 — uncommon, tends Homoptera.

Platythyrea conradti Emery — moderately common, on 1% or more of cocoa trees, but always in small numbers.

Platythyrea modesta Emery — uncommon.

Polyrhachis militaris (Fabricius) — on about 1% of cocoa trees, arboreal, role within mosaic unknown, a large species but colonies small.

Other *Polyrhachis* species occasionally seen on cocoa are *decemdentata* E. André, *laboriosa* F. Smith and *weissi* Santschi.

Serrastruma simoni (Emery (*lotti*) — rare, has been found nesting in dead wood on a cocoa tree.

Strumigenys — three species, *cacaoensis* Bolton, *pallestes* Bolton and *rufobrunea* Santschi, have been found nesting in soil in crevices on cocoa trees but all are rare.

Tapinoma sp. (*Technomyrmex detorquens*) — can be found on up to 5% of cocoa trees but usually not so common, can be associated with *Cr. depressa*, tends Homoptera, ground nesting.

Other *Tapinoma* species, sp.T^1 and sp.T^2, rarely found nesting under bark on cocoa trees.

Technomyrmex species — four species are found occasionally on cocoa trees; sp.IK, sp.T[2] and sp.T[3] nest in dead wood on the tree; sp.T[1] nests in soil; spp.T[1] and T[3] tend Homoptera, sp.T[1] will construct soil tents but association with black pod not established.

*Teratane*r sp. T[1] — found twice on cocoa, once seen in a debris tent on a cocoa flower.

Tetramorium aculeatum (Mayr) (*Macromischoides aculeatus*) — abundant, dominant on up to 15% of cocoa trees, characterisitc 'felt' nest on underside of, or between, leaves, tends Homoptera.

Tetramorium africanum (Mayr) (*Macromischoides* sp.T[2]) — rarely seen on cocoa.

Tetramorium species — several other species but all of soil or dead wood nesting habits sometimes can be found on cocoa trees; these are *T. ataxium* Bolton (sp.T[1]), *delagoense* Forel (sp.M), *lucayanum* Wheeler and *simillimum* (F. Smith) (sp.F), all of which tend Homoptera. Others seen on cocoa are *T. quadridentatum* (Stitz), (sp.K and sp.nr.K) which has nest specific colour variants and which is not infrequently found nesting in dead pods and debris filled crevices, and, found once only. *T. wadje* Bolton (sp.T[2]).

Tetraponera anthracina (Santschi) — may be found on up to 1.5% of cocoa trees but little is known of its biology, nests in dead wood on trees but colonies small and ants forage singly.

Other *Tetraponera* species recorded but rarely on cocoa are *T. opthalmica* (Emery) and *T.* sp. T[1].

Triglyphothrix minima Bolton (sp.T[1]) — rare.

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