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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Chapter 8

THE ROLE AND RELATIVE IMPORTANCE OF DIFFERENT ANT SPECIES IN THE DISSEMINATION OF BLACK POD DISEASE OF COCOA

Brian Taylor & M. J. Griffin

Few papers have been published on the role of invertebrates as vectors of black pod of cocoa (Dade, 1927a, b; Gorenz, 1970; Okaisabor, 1971b; Evans, 1971, 1973). Evans gives quantitative results indicating the actual role of invertebrate vectors rather than their potential role. Moreover, Evans concentrated more on diseased pods than on healthy pods and thus, apart from his observations on tent-building ants, he did not actually evaluate the role of invertebrates as vectors.

Okaisabor (1974) summarised the evidence for the role of insects in the black pod disease cycle and concluded that by controlling the population of insect vectors the upward movement of the fungus from the ground or from pods near the ground could be slowed considerably thus delaying the development of the epidemic.

This Chapter gives the results of large scale observations of the disease incidence on cocoa at Gambari Experimental Station, in relation to the distribution pattern, or mosaic, of ant species (Hymenoptera: Formicidae). The general abundance and mosaic of ant species ar CRIN is dealt with in Chapter 9 and here the results and discussion will relate primarily to work carried out on three plots of cocoa; N4/1A, Onipe 1/1 and E5/1.

The taxonomy of the ant species involved is considered in Chapter 9, but the nomenclature of many of the species is somewhat confused. Thus certain of the specific epithets used are indicated as questionable, e.g. *Crematogaster gabonensis*, and others are referred to solely by code letters or numbers.

Site N4/1A

In 1974, the N4/1A block of 500 cocoa trees at CRIN was divided into three experimental plots of 110 trees with several guard rows between each plot. After preliminary work to remove all extant black pods and to clean the plots, a 30 cm band of dieldrin (0.5%) was sprayed around the base of each tree in two of the plots (B & C). Plot A was left untreated as a control. *Phytophthora*-infected pods were deposited on the ground at the base of each tree to provide a uniform source of infection. This source was renewed fortnightly. On 6 August a mist blower was used to treat Plot B with 0.1% pybuthrin and Plot C with HCH (gamma-BHC) at 300 g/ha. These treatments were repeated on 15 August but with the use of a knapsack sprayer and extension lance. Weekly records were kept of the invertebrates seen on the trees. Twice weekly the numbers of healthy pods and black pods were recorded and the black pods removed. The heights of the black pods were noted before removal. Harvesting of ripe pods took place at 3-weekly intervals. On 5 September it was decided that the HCH treatment had been ineffective in controlling, let alone eliminating, many of the invertebrates and 0.5% dieldrin was applied on a whole tree basis to Plot C. On 25 September the bases of trees in Plot B were resprayed with 0.5% dieldrin and on 27 September this plot was resprayed with 0.001% bioresmethrin.

The objective of the treatments was to investigate the effect on the incidence of black pod of: (1) eliminating crawling invertebrates (Plot B); and (2) eliminating crawling and flying invertebrates (Plot C). The graph (Fig. 8.1) illustrates the results in terms of percentage black pod on each plot. Clearly the whole tree spraying with dieldrin on Plot C reduced the amount of black pod infection. The elimination of crawling insects and prevention of reinvasion from the ground, Plot B, had apparently little effect on the incidence of black pod.

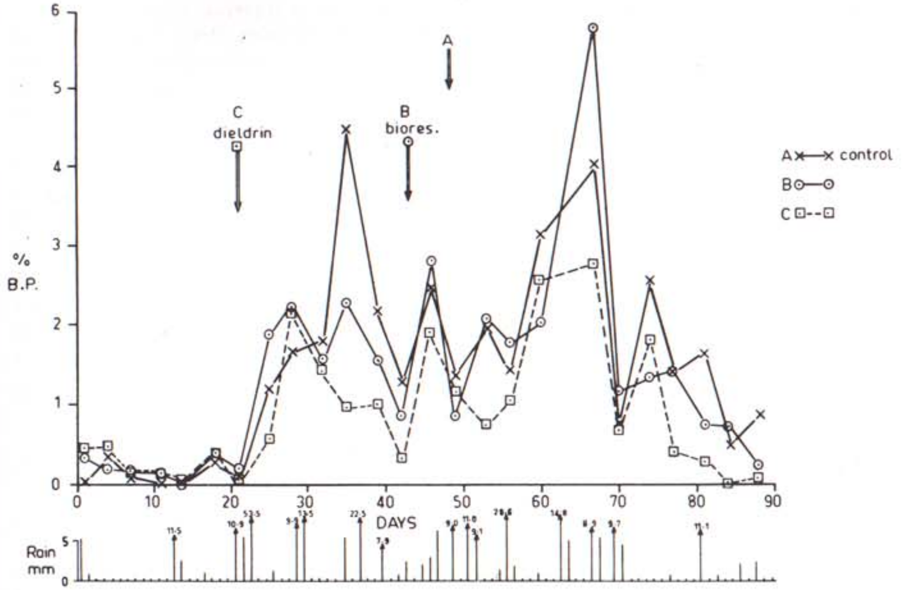

Fig. 8.1 Incidence of black pod disease following treatment with: B, 0.1% pybuthrin (day 0) and 0.001% bioresmethrin (day 43); C, 300 g/ha HCH (day 0) and 0.5% dieldrin (day 21); compared with A, untreated control. %BP is the percentage of pods infected on each plot.

However, the results of the weekly recording of invertebrates clearly showed the dangers of oversimplification. Plot A had a colony of *Oecophylla longinoda* (Latreille), the red tree ant, well known for its pugnacious foraging activities. Thus, its presence in Plot A could well have had the same effect on crawling invertebrates, especially on ground ants such as *Camponotus acvapimensis* Mayr, as the dieldrin banding had on Plot B.

There were many other complexities with respect to the ant colonisation patterns in N4/1A. Plots B and C were initially occupied by colonies of *Crematogaster* ants, principally *Cr. clariventris* Mayr and *Cr. sjostedti* Mayr. The dieldrin treatment on Plot C cleared out the resident ants but the record on day 54 showed some invasion by *Cr. sjostedti*. *Tetramorium aculeatum* (Mayr) which originally colonised a couple of trees on one edge of Plot A gradually extended its territory across B and even reached C. Plot B was invaded to a certain extent by *Acantholepis ?capensis* Mayr. Around the 50th day a small *Crematogaster* sp. was found to have invaded Plot A and cohabited the plot with *O. longinoda*. This *Crematogaster* species builds discrete tents over stictococcids at the junction of the pod stalk and the pod. *Cataulacus guineensis* F. Smith was seen foraging fairly extensively over Plot B but *O. longinoda* never reached more than the row nearest to Plot A.

Such complexities made us realise the vast scale on which an experiment would need to be carried out in order to determine the effects on the incidence and development of black pod disease of variation in ant populations.

Site Onipe 1/1

This study was aimed primarily at elucidating the patterns or mosaics, of the distribution of ant species on a cocoa farm. However, in addition to recording ant species, observations were made of the numbers of healthy pods and black pods on the study trees. These observations yielded some useful information on the incidence of black pod disease, particularly early in the season.

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 fallen trees. In early 1975, we defined 17 plots of 25 trees each, and weekly records were taken of ant species, or other insect species apparently associated with ants, of healthy pods and of black pods. Three strips of trees running the full width of the block were sprayed with 0.5% dieldrin (on 1 April, 30 May and 20 August). This treatment maintained an almost completely ant-free state on the trees. Ripe pods and black pods were harvested at three-weekly intervals.

A detailed analysis of the ant population studies is given in Chapter 9 but, in brief, because of the fragmented nature and large size of the block, the ant population distribution was quite diverse and felt to be fairly typical of cocoa farm conditions as opposed to plantation management conditions. The most important or dominant ant species found were *O. longinoda* (frequency 40.4%), *Pheidole megacephala* (F.) (15.2%), *Crematogaster africana* Mayr (12.8%), *T. aculeatum* (11.3%) and *Acantholepis* species T^2 (10.8%).

The first black pod infections were seen in late April and were associated with tents built of soil by *Ph. megacephala* (Plate 5). Because the black pod disease was allowed to follow its normal course, apart from removal of infected pods at harvest, and because recording was only once per week, it soon became difficult to differentiate specific sources of infection. Indeed, once pods in the canopy or on the upper trunk became infected, the numbers of diseased pods increased rapidly due to rain splash from sporulating pod lesions. Another cause of rapid spread of the disease in parts of the block where there were numerous large shade trees was the activity of rodents, probably squirrels. Many infections could be seen to originate from rodent bites, some of which were no more than slight scrapes on the pod surface.

A useful comparison was possible between the dieldrin treated, ant-free rows and the unsprayed study plots. Table 8.1 shows the accumulated totals of black pods recorded to the end of July. There were markedly fewer early season infections on the dieldrin treated trees. Losses from rodent activity are shown also. There was a marked variation in black pod incidence in the unsprayed study plots, but it was not possible always to judge the sources of infections. However, an examination of the ant data, on a plot-by-plot and a tree-by-tree basis, allowed an impression to be formed of the relative importance of different ant species in terms of numbers of black pods on trees inhabited or visited by the species. On only seven of the 17 plots were the majority of the trees dominated by a single ant species. Six of these plots were dominated by *O. longinoda*, but the percentage of pods infected by black pod was very variable, ranging from 3.2% in plot J (with *O. longinoda* on 22 trees) to 43.9% in plot L (with *O. longinoda* on 24 trees). The latter plot contained a number of large shade trees with a consequent generally higher humidity and a lot of rodent activity. Plot D was dominated by *Cr. africana* but the majority of black pods actually occurred on three trees, on two of which *Ph. megacephala* tents were sources of infection, and on the third *Odontomachus troglodytes* Santschi tents were sources. In general, it seemed that where *Cr. africana*, *Cr. depressa* or *O. longinoda* were found alone on trees consistently fewer black pods occurred. Where *Ph. megacephala* was active black pod numbers were often higher than on surrounding trees. Similarly, the presence of *O. troglodytes* often was characterised by higher black pod numbers. However, the value of this particular study lies more in the findings regarding ant populations. The implications of these findings in relation to black pod disease will be discussed later in the chapter.

Site E5/1

In contrast to the Onipe 1/1 study, the experiment carried out during the 1975 season at the E5/1 site was aimed primarily at elucidating the outbreak and spread of black pod disease. The observations of ants and their role in the spread of the disease, therefore, formed only a part of the overall study. The general findings of that study are presented in Chapter 6, as are detailed notes on the methods employed in the experiment.

The experimental area, which was only part of the E5/1 planting, consisted of 1139 trees. A central block, Block 1, was defined which ran the length of the area and comprised half the total number of trees. On each side five smaller blocks were defined, Blocks 2 to 11. In Blocks 3, 4, 7, 8 and 11, referred to hereafter as the basal pod suppression (BPS) blocks, all set pods below 80 cm were removed from the trunk during twice weekly inspections. No treatment was applied to trees in Blocks 2, 5, 6, 9 and 10, referred to as the no-basal pod suppression (no-BPS) blocks.

Table 8.1 Summary of the accumulated harvest data up to the end of July in the Onipe 1/1 study, 1975

		Trees	Trees with pods	Trees with black pods (%)	Healthy pods	Black pods (%)	Total pods
No Dieldrin*	Mean and S.D.	25·0 ± 0·0	22·5 ± 1·9	10·5 ± 5·6	268·7 ± 121·7	41·6 ± 45·9	311·0 ± 141·2
	Totals	425	383	161[a](42·0)	4568	707 (13·4)	5275
Dieldrin†	Totals	128	105	16[b](15·2)	1640	42(2·5)	1682

* 17 plots each of 25 trees
† Three areas of 28, 46 and 54 trees
[a] 19 trees in 7 plots had black pods associated with rodent damage
[b] 3 trees in one of the areas had black pods associated with rodent damage

Among the items of information recorded, the most significant in the present context were height of pod and the adjudged source of the infection. The total number of pods of all sizes seen on each tree was counted weekly.

Twice weekly all trees with ant tents were noted. The next day entomology staff examined these trees and recorded the following information: date, block number, tree number, maximum height of tents (see below), insect being tended (see below), and ant species. The data, as with all the data from the experiment, were transposed into code form for eventual computer sorting and analysis. Tent material was classified as soil, organic debris, or carton (triturated or chewed wood), or a combination of any two or all three. Ant tent recording was done on a total of 56 days in 1975.

The site of the tent was classified as on a pod, on a flower cushion, or on a combination of both. Tended insects were identified, as far as was possible without disturbing the tent, if any, covering the insect; three classes were defined—aphids/undetermined, pseudococcids, and stictococcids, plus combinations of any two or all three. The tended insects were all Homoptera. Five ant species were coded as regularly occurring in the blocks, tending Homoptera and constructing tents; these were *Camponotus acvapimensis*, *Pheidole megacephala* (see below), *Myrmicaria striata* Stitz, *Odontomachus troglodytes* and *Crematogaster ?gabonensis*. The coding allowed for up to four ant species to be noted on any one date, and this proved adequate as rarely were four species seen on one tree at one time. The *Ph. megacephala* category, because of field identification problems, contained a number of small species but, by periodic sampling and laboratory identifications, it proved possible to separate trees by actual ant species when the analysis of computer separations was made.

At intervals during the season the work of the field staff was cross-checked and the blocks were surveyed for other ants occupying the ecosystem. The process of data coding from the field record sheets, although involving extra time and effort, allowed a running check to be kept on individual trees to detect any changes and inconsistencies in the field records. Ant population distribution is something that, in general, does not change overnight but tends to remain constant, once established, for a period measurable in weeks if not longer. At mid-season the shade levels in the blocks were surveyed to find the effect of canopy density on ant species distribution.

East 5/1 Results

Each fresh black pod infection was adjudged, on the first day it was observed, to have a probable, or 'first' source. A 'second' source was added to provide further information on the circumstances of the infection or as a less likely alternative source. In this chapter considerations will be limited to the two sources involving ants; a 'close association with ant tents' and a 'loose association with ant tents' (Plate 5). The close association was usually a first source, but the loose association could be a first or second source. Three other sources proved to be of major significance and will be referred to. These are: 'soil splash' which was restricted to less than 80 cm above ground level; 'splash from other (earlier infected) pods'; and 'not obvious'. In Block 1 'splash from other pods' was prevented by the removal of infected pods as soon as lesions were seen. In the basal pod suppression blocks 'soil splash' was precluded by the removal of all pods within the 80 cm zone. In the remaining blocks, i.e. those with no basal suppression, all sources were possible.

The importance of the second sources is debatable but they were of some value in providing information on the presence of ant tents which were not considered to be sources of infection.

A detailed breakdown of the importance of all the sources is given in Chapter 6, but a simplified breakdown is given in Table 8.2. The total number of black pods was 1275 in Block 1, 665 in the basal pod suppression blocks and 1011 in the remaining blocks. It can be seen from Table 8.2 that in the ultimate hygiene

Table 8.2 Simplified breakdown of black pod sources in East 5/1, 1975

Source	Percentage frequency of various sources					
	Black pods removed daily		Black pods removed every three weeks			
	(Block 1 'ultimate hygiene')		Basal pod suppression		No basal pod suppression	
Soil splash	48·1		prevented		18·5	
Splash from other pods	prevented*		64·4		54·6	
Close association with ant tents	8·9	23·4	3·5	10·6	3·6	10·1
Loose association with ant tents	14·5		7·1		6·5	
No obvious source	23·8		22·6		11·9	
Remaining sources	4·7		2·4		4·9	

* Some splash infections from 'missed' initiators did occur — see Chapter 6, 'Ultimate Hygiene Treatments'

area (Block 1) where diseased pods were removed daily before they sporulated, 23% of black pods were adjudged to have ant-transported material as the primary origin of infection. In the other two treatments where diseased pods were removed every three weeks when ripe pods were harvested, in accordance with recommended farmer practice, only 10% of black pods had ant tents as the primary origin of infection.

When expressed simply as numbers of black pods, or as percentages of those numbers, the results, in fact, conceal rather more than they reveal. This is particularly true of the ant tent associated infections. Trees on which black pods were recorded during the season could be divided into three categories: Category A, trees with black pods but no ant tents at any time; Category B, trees on which black pods and ant tents were seen but with no ant tent associated infections; and Category C, trees on which black pods were seen, some of which were associated with ant tents (Table 8.3).

The results from Block 1, where the infections were nearly all initiators (see Chapter 5), show that the ant tents which were first sources gave rise to a similar number of infections to the totals in the Category A and B trees, and to nearly 43% of the total in Category C. The number of non-ant tent associated infections in Category C was similar to the totals in Categories A and B. Thus it seems obvious that where ants are present and building tents with material containing black pod inoculum there is a considerable rise in the number of black pods on the trees.

However, in order to obtain a more meaningful analysis it was necessary to examine the productivity of all the trees. For this exercise, the trees were grouped into six categories. Three of these categories have been outlined in the preceding paragraphs and the others are: non-productive trees; trees with no black pod and no ant tents; and trees with no black pod but with ant tents.

Table 8.4 shows the number of trees in each category for each of the tree treatments. From the weekly counts of the number of pods of all sizes that were present on each tree it was possible to derive what we have called the 'productivity factor'. This was done by totalling the highest number of pods observed on each tree in each category and dividing by the number of trees in

Table 8.3 Black pod incidence in relation to treatment and tree category* in E5/1, 1975

Treatment	Tree category	No. of trees	No. of black pods	Black pods per tree	% of black pods in treatment
Ultimate Hygiene (Block 1)	A	118	352	3·0	27·6
	B	102	265	2·6	20·8
	C	113	658	5·8	51·6(22·1)
Basal pod suppression	A	33	145	4·4	21·8
	B	28	78	2·8	11·7
	C	49	442	9·0	66·5(10·5)
No basal pod suppression	A	61	282	4·6	27·9
	B	56	191	3·4	18·9
	C	53	538	10·2	53·2(10·1)

Figures in parenthesis show the percentage of black pods in the entire treatment with an ant tent as first source

*

Category A: Trees with black pods but no ant tents at any time
Category B: Trees with black pods and ant tents but no ant tent associated infection
Category C: Trees with black pods, some of which were associated with ant tents

Table 8.4 Numbers of trees in each category in E5/1, 1975

Tree categories	UH Block 1	BPS blocks	No—BPS blocks	Total
Non-productive trees	36	32	43	111
Trees no BP, no tents	113	67	56	236
Trees no BP, with tents	87	52	40	179
Trees with BP, no tents (A)	118	33	61	212
Trees with BP, with tents no tent/BP association (B)	102	28	56	186
Trees with BP, with tents,* some tent/BP association (C)	113	49	53	215
Total	569	261	309	1139
Dead Trees	1	1	1	3

* Category C trees include some where the ant tent/black pod association was at only the second source level

the category. Table 8.5 summarises the productivity factors according to categories and tree treatments.

For the purpose of the study, hand pollination was carried out to enhance fruit set. However, this in no way distorted the picture of productivity factors, but simply reflected the number of flowers present on the tree at the time of the pollination.

As a result of the layout of the original spacing and thinning trial (Freeman, 1965, 1966) and of establishment problems, spacing between trees was extremely variable (Fig. 8.2). A major effect of uneven distribution is a variation in the density of the canopy, which in turn affects the amount of light getting through to the lower tree parts and to the ground. Figure 8.2 shows the layout of the plot as demarcated for our study. The position of each tree is indicated by one of six symbols; the symbols denote the tree categories listed above.

Analysis of the available data shows that productivity is lowest where the trees are most evenly and closely planted. Block by block examination of the productivity factors confirms that the lowest tree productivity is in Block 11, with an average maximum of 5.87 pods per productive tree, then Blocks 9, 8, 5, 10, 6, 2, 4 and 7, in ascending order, to Block 3, with an average maximum of 26.70 pods per productive tree.

A relation between productivity factors and ant tent activity is suggested by the results in Table 8.5, in that the greater the number of pods the more likely that ants will be found building tents on the tree, and the trees with black pod associated with ant tents have the highest numbers of pods. Table 8.5, however, as with Fig. 8.2, separates trees by ant tents being observed on a particular tree but this may have been on no more than one occasion. A more detailed analysis of the ant tent records for Block 1 is given in Table 8.6. This shows quite clearly that the regularity of ant tent observations during the season is considerably higher on those trees where tents were associated with black pod infections. Ant tent building activity is a consequence of the presence on the tree of Homoptera which, because of their sugar-containing exudate, attract the ants (Plate 5). The ants construct the tents to protect the Homoptera from adversities, such as rainfall and predators. The Homoptera are habitually found feeding on young plant tissue; the most abundant young tissue, at least on the lower parts of the tree, is produced by the flower cushions. This includes flowers, from bud to maturity, and, after flower set, pods throughout their growth. As pods mature, however, they cease to be a food source for aphids and, therefore, the attraction of ants is limited to coccids. Tent building activity tends to decline somewhat as flower numbers decline.

From the productivity factors, it was possible to estimate black pod incidence in relation to productivity. Table 8.7 shows proportional black pod incidence recorded during the season for the three categories of trees with black pod infections. In preparing the analyses for Table 8.7 (and Tables 8.8-8.10) we decided that for the present purpose it was not appropriate to include results for the small numbers of trees which were included in Category C but on which ant tents were only second source infections.

Table 8.5 Comparisons of productivity factors in E5/1, 1975

Tree categories	Productivity factor (mean max. pods/tree)		
	UH Block 1	BPS blocks	no–BPS blocks
Trees no BP, no tents	6·27	6·60	5·45
Trees no BP, with tents	11·03	13·19	13·30
Trees with BP, no tents (A)	17·15	18·94	15·92
Trees with BP, with tents, no tent/BP association (B)	20·23	23·46	20·14
Trees with BP, with tents,* some tent/BP association (C)	23·59	33·31	23·45

(Based on maximum number of pods recorded during the season)

* See Footnote Table 8·4

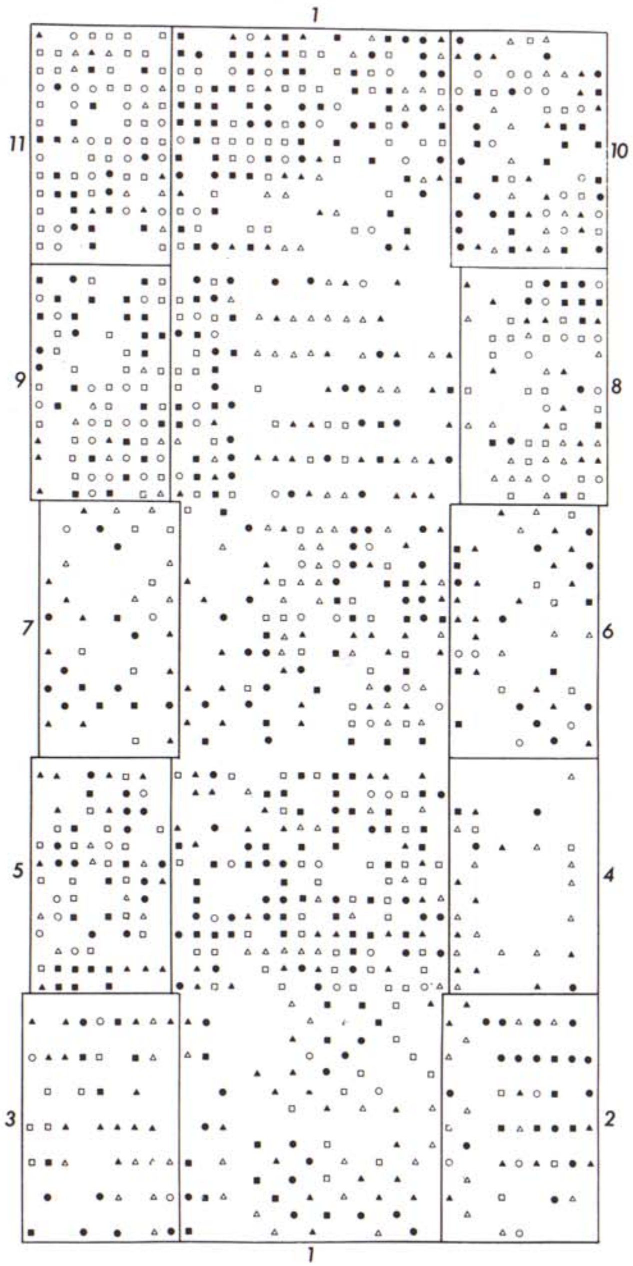

Fig. 8.2 Layout of the E5/1 site in 1975; showing tree positions and the occurrence of black pods and ant tents. Key:
Non-productive trees .... ○
Trees with no black pod and no ant tents .... □
Trees with no black pod but with ant tents .... △
Trees with black pod but no ant tents .... ■
Trees with black pod and ant tents, but no infections attributed to ant tents .... ●
Trees with black pod and ant tents, some infections attributed directly or indirectly to ant tents .... ▲

Table 8.6 Analysis of productivity factors and ant tent observations in the ultimate hygiene area, Block 1 E5/1, 1975

Category	No. of days on which tents seen	Number of trees (and %)	Productivity factors (nos. of pods) 1–5	6–10	⩾11
Trees without black pod, but with ant tents (A)	1– 5	48 (55·2)	18	14	16
	6–15	28 (32·2)	11	11	6
	16–56	11 (12·6)	0	2	9
	Total	87	29	27	31
Trees with black pod and ant tents, no tent/BP association (B)	1– 5	66 (64·7)	8	14	44
	6–15	30 (29·4)	5	7	18
	16–56	6 (5·9)	0	0	6
	Total	102	13	21	68
Trees with black pod and ant tents, some tent/BP association (C)	1– 5	27 (23·9)	1	2	24
	6–15	27 (23·9)	3	5	19
	16–56	59 (52·2)	2	11	46
	Total	113	6	18	89
Trees without black pod or tents		113	73	20	20
Trees with black pod without tents		118	17	33	68

Table 8.7 Comparison of black pod incidence in relation to productivity in E5/1, 1975

Tree Category	Treatment	Black Pod Sources: ant tents	soil splash	sporulating pods	other	totals	No. of trees
A	UH (Block 1)	na	0·11	—	0·07	0·17	118
	BPS blocks	na	—	0·16	0·08	0·23	33
	No BPS blocks	na	0·09	0·15	0·05	0·29	61
B	UH (Block 1)	na	0·09	—	0·04	0·13	102
	BPS blocks	na	—	0·06	0·06	0·12	28
	No BPS blocks	na	0·05	0·08	0·04	0·17	56
C	UH (Block 1)	0·13	0·06	—	0·06	0·25	89*
	BPS blocks	0·06	—	0·18	0·04	0·28	35*
	No BPS blocks	0·10	0·04	0·27	0·05	0·47	42*

Category A — trees without black pod but with ant tents
Category B — trees with black pod and tents, but no tent associated infections
Category C — trees with black pod and tents, some infection associated with tents

na, Not applicable; —, Prevented

Black pod incidence in relation to productivity is calculated by dividing the number of black pods per tree by the mean maximum numbers of pods per tree

* Trees with first source ant infections, see Tables 8.8–8.10

Trees with some black pods associated with tents, in addition to having the most black pods, also had the highest proportional incidence of disease and, not surprisingly, loss through splash from sporulating pods was greatest in this, the most productive category. Below 80 cm, tent-associated infections (and their sequences) occurred on pods which might otherwise have been infected through soil splash, hence the incidence of soil splash infections in Category C trees was relatively low. Nevertheless, the combined effect of soil through tents and splash below 80 cm was greater than that for splash alone in the other two categories. Additionally, the activity of ants extended the importance of soil as a source of inoculum because ant tents constructed of soil were found at heights of up to 400 cm. The incidence of infections due to initiators other than soil splash or ant tents (i.e. the balance of infections) was of the same order in all of the treatments and categories.

The number of trees (102) with black pod and with ant tents but with no tent/black pod associations (i.e. Category B) was nearly as high as Category C trees (113). On the surface this suggests that ant tents might not be such an important source of *P. megakarya*. However, the explanation for this is shown in Table 8.6. Only 5.9% of Category B trees had tents on 16 or more recording days compared with a figure of 52.2% for Category C trees; also, 64.7% of B trees had tents on less than 6 days during the season. Trees with ant tents on less than 6 occasions generally had fewer tents than those in the other categories. Moreover, some of the Category B trees in the 6-56 categories (Table 8.6) were those with *Cr. gabonensis* tents which were rarely a source of *P. megakarya* inoculum.

Distribution of tent-building species of ant

By now it should be quite clear that what seemed, when the study area was first delineated, to be a fairly uniform area of cocoa, in fact was far from uniform. Tree productivity varied significantly according to the inter-tree spacing. This in turn affected the likelihood of infestation of the trees by Homoptera and, consequently the amount of ant tent building activity. If the records are examined on the basis of individual ant species then a new element of complication comes into sight. This complication, moreover, is one that cuts across the experimental treatments.

The most important ant species, at least in terms of numerical abundance, was *C. acvapimensis*. It was observed at some point in the season building tents on 258 of the 569 trees in Block 1, on 92 of the 261 trees in the basal pod suppression blocks, and on 112 of the 309 trees in the no basal pod suppression blocks. Figure 8.3 shows the distribution of *C. acvapimensis*, with the occurrence differentiated according to the frequency of observation, with a maximum of 56 'tent days' in the season, and according to the incidence/absence and/or association between black pod tents. Quite clearly the distribution of the ant is far from even; in Block 11, for example, it occurred on a few trees on few occasions and was never associated with black pod infections. At first sight, the distribution may seem random but, as can be seen in Figure 8.3 there appears to have been in the order of 15 colonies, each centering on a nest in an insolated or unshaded area of ground. Where tree density was highest the likelihood of *C. acvapimensis* was least. (The postulated colony boundaries in Figure 8.3 were drawn by plotting the frequency of observation and also considering the level of light intensity at ground level, as measured using a conventional photography light meter at mid-day at the equinox.)

The distribution of five other tent building species is shown in Figure 8.4. The occurrence of the different species is differentiated in each case only according to the incidence/absence and/or association between black pods and tents. *M. striata* appeared to occur only in perhaps six colonies with tent building centering around nests in insolated ground; five of these colonies were in the west central area of Block 1. *O. troglodytes* occurred as 20 to 25 nests from each of

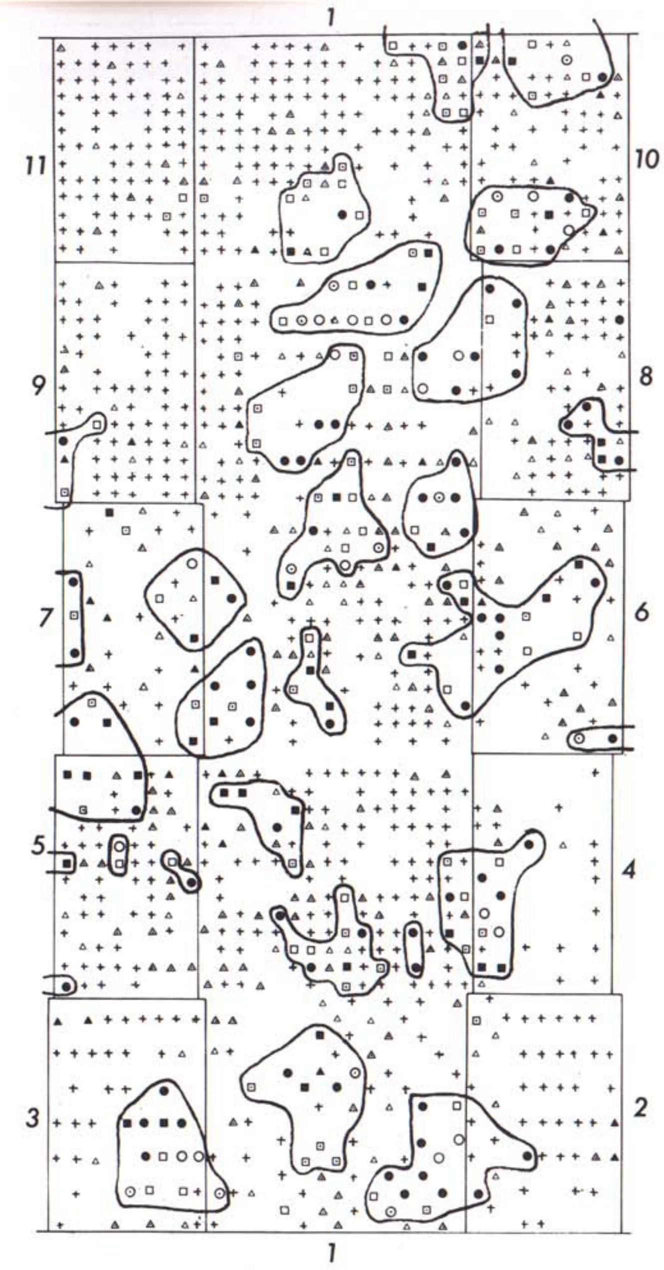

Fig. 8.3 Occurrence, tent building activity and black pod association of *C. acvapimensis;* E5/1 in 1975

No. of days on which tents seen	Trees with *C. acvapimensis* recorded: No black pod	Black pod but none ant tent assoc.	Black pod some ant tent assoc.
1 to 5	△	◬	▲
6 to 15	□	▣	■
16 to 56	○	⊙	●

Other trees +

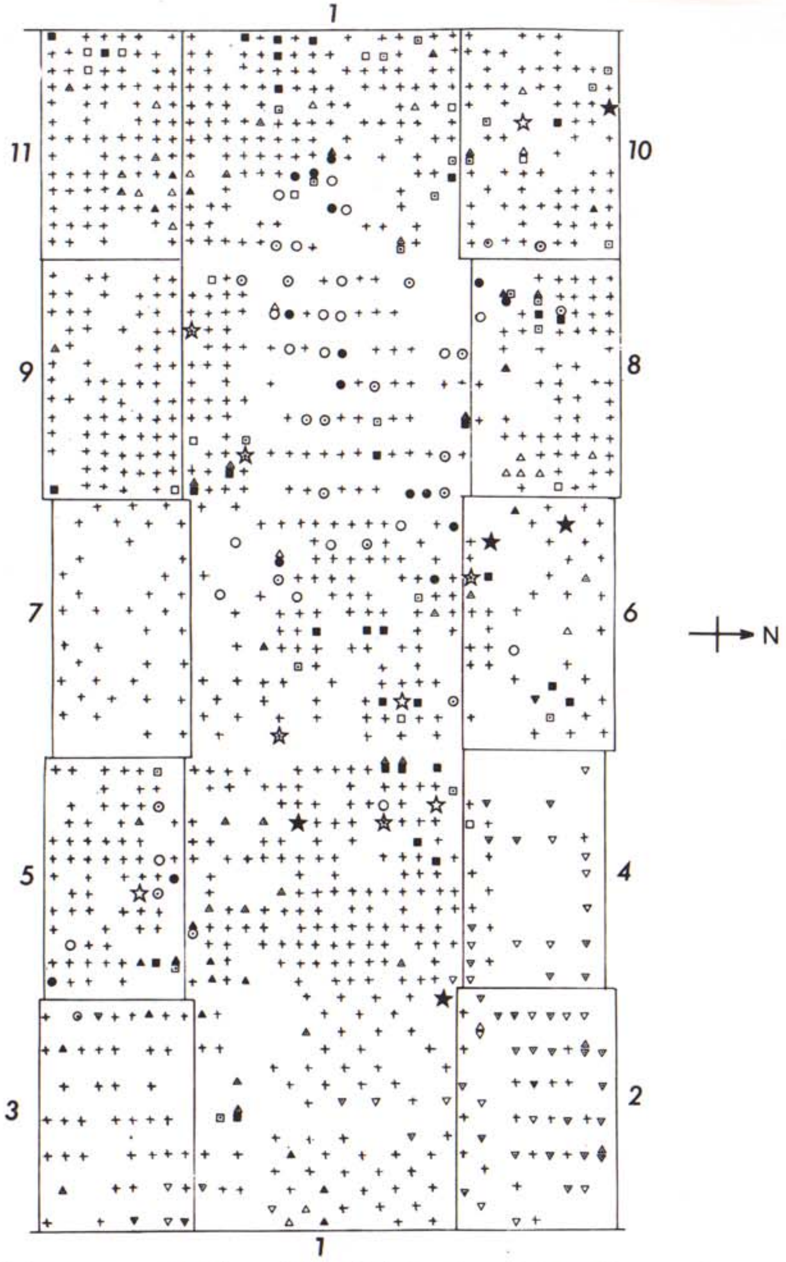

Fig. 8.4 Ocurrence, tent building activity and black pod association of *M. striata*, *O. troglodytes*, *Ph. megacephala*, *Cr. gabonensis* and *Paratrechina* sp. 3 in E5/1 in 1975

	Trees with ant tents recorded		
Ant species	No black pod	Black pod but none ant tent assoc.	Black pod some ant tent assoc.
M. striata	○	⊙	●
O. troglodytes	□	⊡	■
Ph. megacephala	△	△	▲
Cr. gabonensis	▽	▽	▼
Paratrechina sp. 3	☆	★	★

Other trees +

which foragers visited two to five trees; most of the nests were in moderately insolated areas. *Cr. gabonensis* occurred in one large colony occupying most of the trees in Blocks 2 and 4; a small colony was present in one corner of Block 3. *Ph. megacephala sensu stricto* was present as three distinct colonies; each occupying 4 to 10 trees, one at the eastern end of Block 1, one at the junction of Blocks 1, 3 and 5, and one in Blocks 1 and 11; and a few 1 to 2 tree colonies. Of the other species recorded in the field as *'Ph. megacephala'* only one, *Paratrechina* species 3, is shown in Figure 8.4. This species appeared to be restricted to single nest colonies, rarely foraging over more than one or two trees. Three unnamed species of *Pheidole*, sp. B, sp. E and sp. T3, were recorded occasionally building tents but none was ever associated with black pod infections.

A further complication is added by the fact that trees with Homoptera infesting them were often visited by two or more of the tent building ant species. In these cases, usually one of the ant species was recorded more often than the other(s). Where *C. acvapimensis* and *M. striata* were recorded this was not the case, both occurring on a similar number of occasions. On those trees where *C. acvapimensis* and *Cr. gabonensis* were both recorded the species tended to be spatially separated on the trees; *Cr. gabonensis*, which is wholly arboreal in its nesting and foraging habits, being present on the upper portions of the tree and *C. acvapimensis* being restricted to the lower parts.

Individual species of ant and black pod infections

Tables 8.8, 8.9 and 8.10 give analyses of the sources of black pod infections on those trees where some of the infections were associated with ant tents. As can be seen, the numbers of trees involved, except in the case of *C. acvapimensis*, are small and, therefore, it would be unwise to draw firm conclusions about the effects of different species on black pod incidence.

Table 8.8 Ultimate hygiene treatment, Block 1 E5/1, 1975; numbers of black pods from various sources on trees where some infections had ant tents as the first source

No. of trees	Ant species building infective tents	Ant tent close	Ant tent loose	Soil splash	Others	Not obvious	BP Total
50	*C. acvapimensis*	42	71	66	27	24	230
6	*M. striata*	4	6	1	0	0	11
7	*C. acv.* + *M. str.*	18+6*	16+10*	12	0	0	62
17	*O. troglodytes*	24	59	33	6	37	159
6	*Ph. megacephala*	13	5	8	0	12	38
1	*Paratrechina* sp. 3	1	0	2	0	4	7
2	Misc./undetermined	1	1	8	0	9	19
89	Total	109	168	130	33	86	526

* "18 + 6" means 18 black pods associated with *C. acvapimensis* tents and 6 black pods with tents of *M. striata*

Table 8.9 Basal pod suppression blocks, E5/1, 1975; numbers of black pods from various sources on trees where some infections had ant tents as the first source

No. of trees	Ant species building infective tents	Ant tent close	Ant tent loose	Sporul. pods	Others	Not obvious	BP Total
22	*C. acvapimensis*	14	26	141	3	25	209
2	*C. acv.* + *M. str.*	1+1*	5+3*	9	0	3	22
3	*O. troglodytes*	1	8	8	0	1	18
2	*P. megacephala*	2	3	26	1	5	37
6	Misc./undetermined	4	2	26	0	8	40
35	Total	23	47	210	4	42	326

* see footnote to Table 8.8

Table 8.11 gives an analysis of the heights of ant tents, as recorded during the season.

C. acvapimensis, by virtue of its sheer abundance and wide distribution in the E5/1 plot, was the most important ant as far as numbers of black pods attributed to its tents were concerned. It climbs very readily, building tents to some 200 cm above ground with a not unusual maximum record of 380 cm. A total of 222 first source infections was recorded on 97 trees where *C. acvapimensis* was found alone. Sequence analysis showed that on several trees infections associated with *C. acvapimensis* were initiators for major infections sequences. On eleven trees where *C. acvapimensis* and *M. striata* tents were implicated there were a further 42 first source *C. acvapimensis* infections. At some time in the season, *C. acvapimensis* was noted at tents on a total of 462 trees; thus attribution of black pod to its tent activity was on about 23% of those trees. As can be seen from Fig. 8.3, there were 28 trees where *C. acvapimensis* was noted at tents on more than 16 recording days and on which the maximum number of pods was more than eleven, but on which there was either no black pods or no black pods associated with ant tents. The actual black pod incidence on those trees on which some infections were ant tent associated and on which *C. acvapimensis* occurred alone was closely similar to the incidence shown in Table 8.7 (C).

M. striata also carried soil containing black pod inoculum, although trees on which this species was found frequently had records of *C. acvapimensis* which sometimes utilised the same tents. Nevertheless, on 17 trees in the entire study area, *M. striata* tents were adjudged to be the first source of infection for a total of 35 black pods.

Cr. gabonensis, as the results in Table 8.11 show, rarely descends below about 100 cm or about the level of the first jorquette. Tents of *Cr. gabonensis* were attributed as the first source of only one close association infection and one loose association infection. This was despite the species being recorded building tents on some 60 trees. There were ten trees on which this species was recorded alone, plus four other trees on which it was recorded with other tent building species,

Table 8.10 Blocks with no basal pod suppression, E5/1 1975; numbers of black pods from various sources on trees where some infections had ant tents as the first source

No. of trees	Ant species building infective tents	Ant tent close	Ant tent loose	Soil splash	Sporul. pods	Others	Not obvious	BP Total
25	*C. acvapimensis*	26	43	18	201	16	22	326
2	*C. acv. + M. str.*	1+1*	1+4*	4	11	0	0	22
6	*O. troglodytes*	5	12	7	34	3	8	69
4	*Ph. megacephala*	1	3	3	4	0	1	12
3	*Paratrechina* sp. 3	1	2	3	2	0	0	8
2	*Cr. gabonensis*	1	1	3	14	2	2	23
42	Total	36	66	38	266	21	33	460

* see footnote on Table 8.8

Table 8.11 Height distribution of ant tents, E5/1 in 1975 (whole study area)

Ant species	Mean minimum height	S.D. minimum height	Mean maximum height	S.D. maximum height	Maximum recorded height
C. acvapimensis	96·7	±57·2	138·3	±66·5	380
M. striata	83·7	±52·2	156·9	±63·5	330
O. troglodytes	46·3	±41·1	82·6	±59·6	310
Cr. gabonensis	136·0	±41·8	186·4	±42·4	400
Ph. megacephala (s.l.)	93·4	±47·5	119·2	±53·2	320

but on which despite the tents being recorded on more than 16 tent recording days and there being a maximum of over 11 pods there were either no black pods or else no infections associated with ant tents. It seems reasonably sound, therefore, to suggest that *Cr. gabonensis* was not genuinely involved in the spread of black pod. Rather to the contrary, because it is a dominant species of ant, it may positively reduce ant tent mediated infections by keeping other ant species off the tree it is occupying (see Chapter 9).

Ph. megacephala tents were recorded from some 50 cm above ground level to around 170 cm, with quite frequent occurrences at up to 320 cm. Tents of this species were attributed as first sources for 27 infected pods on 12 trees. In all cases the tents in question were constructed using soil particles and, with one exception (where an infection at 280 cm was attributed to a soil tent) were below 100 cm. In general, tents higher up were constructed of plant or arthropod debris.

Where *O. troglodytes* was active, and especially when the nests were in the soil at the base of a cocoa tree, a relatively large number of infections were attributed to the crudely constructed soil tents. A total of 109 infections were attributed to ant tents as first sources on only 26 trees. The tent-associated infections also acted as initiators of considerable numbers of sequence infections on the lower trunk of many of these trees.

The high incidence of black pod associated with soil tents of *O. troglodytes* is considered to be a reflection of two separate factors. Firstly, *O. troglodytes* carried up much larger quantities of soil and crudely deposited it over a much greater area than other ant species. Secondly, the origin of the soil particles was from the base of the tree where inoculum of *P. megakarya* was likely to be most concentrated. *O. troglodytes* is a poor climber and usually tents were found below some 120 cm; with only a single record of a height of 310 cm. There was only one tree where *O. troglodytes* occurred alone on more than 16 recording days and on which there was a maximum of over 11 pods but no black pods.

The final species, *Paratrechina* sp. 3, was somewhat enigmatic in that it was recorded only occasionally. It was recorded building tents on 14 trees but on no more than one or two recording days on each tree. Nevertheless four first source infections were attributed to tents of *Paratrechina* sp. 3 on four trees.

From Table 8.7 (C), it appears that one of the effects of basal pod suppression was to reduce the incidence of ant tent associated infection. Initially it seemed possible that this occurred because in the cases of *C. acvapimensis*, *M. striata* and *O. troglodytes,* foraging trails are established from the ground upwards. The basal pod suppression treatment effectively removed or reduced the numbers of Homoptera on flower cushions below 80 cm, thus, perhaps lowering the likelihood of these ground nesting ants establishing foraging trails. Comparison of the data in Table 8.6 with the corresponding data from the other two treatments showed that this was not the case. The complete absence of pods below 80 cm could alone account for the reduced numbers of tent infections in the BPS treatment. Block by block examination of the black pod incidence and of the ant tent records for the BPS and no-BPS treatments suggests that the overall ecology of the blocks could also have had some effect in addition to any treatment effect.

Discussion and Conclusions

From the results obtained in E5/1 and Onipe 1/1 during 1975, there can be no doubt that certain species of ant can influence the pattern of outbreak and, probably, spread of black pod disease of cocoa in Nigeria. Taken in isolation, the E5/1 study would suggest strongly that *C. acvapimensis* can be of major importance as an abundant and active species of soil tent-building ant. *O. troglodytes,* however, appeared to give rise to higher numbers of infections on those trees where it built tents; although its general restriction to heights below

120 cm reduced its significance as an initiator of sequences of pod loss by splash from sporulating pods. *Ph. megacephala*, because it was often active at heights over 300 cm, was potentially a greater initiator of infection sequences, but it tended to use soil in tent construction only below 100 cm. Higher tents were made of plant or arthropod debris which might not be so important as a source of infection. However, in the course of other epidemiological studies at CRIN (the W9/1 3-D mapping site) and Lafiaji (see Chapters 5 and 11) debris tents built by *Ph. megacephala* between 200 and 500 cm above the ground did have infections associated. Direct observations, by A. C. Maddison, were that *Ph. megacephala* workers will carry surface material, including sporangia, from black pod lesions up the tree. Also at the 3-D mapping site, *Crematogaster* sp. 1, a small species not often observed, was present in 1975 constructing debris tents, which were associated with infections on 25 pods on seven different trees at heights ranging from 320 to 600 cm.

M. striata tents were also an important source of black pod inoculum although this ant was much less frequently found than *C. acvapimensis*. The significance of *Paratrechina* sp. 3 tents as sources of infection could not be determined.

The Onipe 1/1 study was characterised by an almost total absence of *C. acvapimensis*. The reason for this was not wholly clear as there was no shortage of insolated ground suitable for its nest sites. The most likely reason was the very different pattern, or mosaic, of the ant population at Onipe 1/1 compared with E5/1. Whereas surveys of the overall ant populations at E5/1 showed an almost total dominance of the tree at the higher trunk and canopy level, by *T. aculeatum*, this species was found on only 11.3% of trees at Onipe 1/1.

The ant mosaic and species association results obtained at CRIN and in a 76 farm survey in western Nigeria (see Chapter 9) showed that *C. acvapimensis, Ph. megacephala* and *T. aculeatum* tended to occupy farms with a similar environment. Their respective occurrences on trees were 4.3%, 12.6% and 14.4%; but of the 76 farms only 33 had *C. acvapimensis* compared with 72 for *Ph. megacephala* and 71 for *T. aculeatum*. *O. troglodytes* was found on only 1.3% of trees and on 30 of the 76 farms.

Species of large *Crematogaster* ants, notably *Cr. africana, Cr. depressa* and *Cr. clariventris,* exclude *Ph. megacephala, C. acvapimensis* and *O. troglodytes,* so could well reduce the incidence of ant tent mediated black pod infections. These *Crematogaster* spp., plus *Cr. ?gabonensis,* were found on a total of 22.5% of cocoa trees, averaging around 12 out of 50 trees on each of the farms where they were present.

O. longinoda, the most abundant of all the ants observed on cocoa trees, on over 33% of trees, on 60 out of the 76 farms and on an average of nearly 21 trees of 50 on each of those farms, exludes *C. acvapimensis* and *O. troglodytes* but does tend to have a positive association with *Ph. megacephala.*

Of the other species of ant found to be associated with black pod infections in the various studies, *Paratrechina* sp. 3 occurred often enough in the CRIN surveys, on about 0.1% of trees, for it to be shown that it was not associated with any of the dominant species; *M. striata* was found to have an occurrence of between 0.1 and 1.0% on cocoa trees at CRIN but in the 76 farm survey it was seen on only two farms; the small *Crematogaster* species, including sp. 1, are not common but are nearly always associated with *O. longinoda*-dominated cocoa.

An interesting and relatively abundant (11.6% of cocoa trees) group of species was *Acantholepis* species T^2/*Acantholepis ?capensis* Mayr. The recording system used in the 76 farm survey did not differentiate between the two species, which proved unfortunate as *A. ?capensis* regularly builds soil tents. The results of a study on the S1/1 Plot, similar to the E5/1 Block 1 experiment, gave no evidence of *A. ?capensis* tents as sources of black pod, and this was supported by a number of other observations of trees with *A. ?capensis* building tents on pods elsewhere on CRIN in 1975.

Considering Nigeria as a whole, the evidence supports *Ph. megacephala* as being likely to be the most important of the tent-building ant species found to be associated with black pod infections. It is present on *all* farms and on an average of over 12% of the trees on each farm. The earliest tent associated infections, if not the earliest of all infections, were attributed to *Ph. megacephala* soil tents.

An observation that may prove to be of some significance was that, among the species of Homoptera which attracted ants to construct tents, aphids, *Toxoptera aurantii* (Boy.), were the most abundant, especially in the early season. Usually, aphids are not regarded as being of any serious import as pests of cocoa. However, the findings of the E5/1 study suggest that aphids are worthy of elevation to true pest status and certainly a study in depth of their overall role on cocoa would seem justifiable.

The E5/1 study was extremely valuable in that it clearly demonstrated the importance of those ants which build soil tents in the development of the black pod epidemic. Clearly, however, the ant population in E5/1 was somewhat atypical as shown by the results of the CRIN survey and the 76 farm survey. Considered on a national basis, the E5/1 study exaggerated the importance of *C. acvapimensis, M. striata* and *O. troglodytes* and most definitely underestimated the importance of *Ph. megacephala.*