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

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sequences to be shorter in 1975 than in 1974, perhaps as a result of available pods being fewer in 1975 (25% down on 1974). There was also an indication that low level initiators (soil and litter) gave more short sequences, but examples were too few for the trend to be established firmly. Generally, the mean length of sequence from the different sources varied little, hence the close relationship between the incidence of initiators from a given source and the proportion of total black pods attributed to that source (Table 5.4). For example 36.6% of initiators had 'no obvious source', and together with their

sequences they accounted for 38.2% of all black pods.

'No obvious source' sequences resulted in consistently high losses, while other sources and associations differed in importance in the two years. The separate presentation of data for the main site trees and the sixteen guard row trees (Table 5.3) gives an indication of the variability in the site as a whole. Overall, sequences from the soil and litter gave losses of 10-20%, and inoculum from the tree itself (flower cushions and cankers) was responsible for 5-10% of total black pods. The remaining categories where infection of initiators was associated with living vector activity showed considerable differences in the two years. For example, 18.8% of such infections were associated with mirid lesions in 1974, compared with 0.7% in 1975. This reflects the incidence of mirid damaged pods in the two years, namely 47.0% in 1974 and 4.4% in 1975. Tent-building activity by ants (mainly Pheidole megacephala and Crematogaster sp. 1) was restricted to certain trees, but appeared responsible for appreciable loss in both

years, particularly in 1975. These estimates of relative importance can be refined by examining the incidence of the various categories of initiator through the season (Fig. 5.2, main site trees only). In both years infections from the soil and litter and their sequences began the epidemic in April or May, and continued through July into August, by which time most of the pods close to the ground had been infected. Ants building tents with soil added to the effects of soil contact and splash as from June in 1975. Six to twelve weeks after the first soil-associated infections, other categories of initiator began to appear. A proportion of these, i.e. infections associated with insect damage and some of the 'no obvious source' infections, may have depended on the soil sequences for inoculum. Once established, these sequences could themselves act as a source for further living vector dispersal. The few infections from the flower cushion occurred in the second half of July, with just one case in September. Infections with 'no obvious source' tended to dominate the epidemic from the middle of July, though ant tents built from debris, and infections associated with insect and rodent damage

also played a part, especially in the canopy.

To summarise, the soil was all important during the early part of the season, but later became subordinate to infections higher in the tree, which either were associated with living vectors or had no obvious source. Infections identified as

from the tree itself played a relatively minor part.

The study as a whole confirms the complexity of Phytophthora pod rot epidemic, even in a small group of trees, and has shown that a large variety of factors will influence disease outbreak and spread. Strictly, the estimates of relative importance obtained for the various sources and routes of infection apply only to the selected 25 trees, but it is likely that the basic conclusions are generally applicable for Amelonado cocoa in Western Nigeria. Moreover, with suitable simplification the detailed recording and sequence analysis approach could be applied to larger areas of cocoa of any type to give a generalised picture of the epidemic in that locality.

Chapter 6

SOURCE OF INFECTION

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Following its successful application to a small group of Amelonado trees, the approach using frequent observation and detailed recording (Chapter 5) was simplified and used to study the epidemic on more trees to obtain a more general picture of sources and routes of infection. Attention was turned to Amazon cocoa which is becoming common in Nigeria and may support a somewhat different epidemiology from that on Amelonado (difference in the importance of flower cushion and canker infections, for example see Okaisabor,

The mapping experiment showed that about 70% of all infections came as a result of splash from infected pods. Suppression of these splash infections by removal of the 'initiators' before they sporulate (an 'ultimate hygiene' treatment) has several potential effects on the incidence of the various categories of initiator. Firstly, more pods are available to become initiators because the pod population is not depleted as rapidly under an ultimate hygiene treatment as it is when splash sequences are allowed to develop. Secondly, no inoculum is produced on pods within the treated area for dispersal by living vectors. And thirdly, there is a long-term possibility for assessing the effects of breaking what appears to be an annual circulation of inoculum: from the soil to the pods at the beginning of the black pod season, and from the pods to the soil thereafter. The return of inoculum to the soil is prevented or at least reduced to an extremely small amount by an ultimate hygiene treatment, while the initial phase can be interfered with by creating a pod-free zone at the base of the tree (Okaisabor, 1965).

In large observation experiments carried out at Gambari Experimental Station between 1975 and 1978 we looked at the epidemic in various situations: under the 'ultimate hygiene' treatment with daily removal of black pods; in a 'normal' situation with removal of black pods every three weeks; and also with basal pod suppression in conjunction with three-weekly harvests of black pods. None of the experiments involved fungicide, but insecticide sprays were applied in one experiment, mainly to check their effect on 'no obvious source' infections.

Materials and Methods

Observation and recording procedures

Three sites of F₃ Amazon cocoa were examined daily for new black pod infections. Information for each black pod was recorded in a standardised manner suited to storage and subsequent retrieval by computer. The following were noted: day number, tree number, height of lesions (to nearest 0.1 m a.g.l.), pod length, position and number of lesions, probable sources or route of infection (Plates 4, 5 and 6) and associated ant species, if any. Once recorded, the diseased pod was either removed the same day (ultimate hygiene treatment) or marked with a wire pin and removed at the next three weekly harvest. All mummified fruits were removed before the experiment started, and thereafter wilting cherelles were removed daily. Ripe pods and damaged pods were harvested every three weeks and recorded together on a tree-by-tree basis.

Records of tents and tent-building ants were taken at least once per week (twice per week in 1975) and general ant surveys were also made periodically. Pod numbers (all fruits from newly set cherelles to ripe pods) were counted for each tree every week; from 1976 a separate count was made of available pods

within 0.7m of the ground.

Experimental sites and treatments

Site South 1/1 was subjected in 1975 to the ultimate hygiene treatment. Initially it contained 420 (400 by the end of the season) trees at 5.5 feet by 5.5 feet (1.68 m by 1.68 m) spacing in an area 60 m by 40 m. It was isolated (nearest cocoa 300 m away), exposed all sides, and unshaded.

Site North 4/1A was observed in 1976 with black pods removed every three weeks. There were 469 trees (planted 1965) at 8 feet by 8 feet (2.44 m by 2.44 m) spacing in an area 125 m by 30 m. The plot was moderately exposed on the two narrow ends, had cocoa adjacent across a track on one side, and on the other was bordered partly by cocoa and partly by kola. It was unshaded.

The site in East 5/1 was a band 51 m by 103 m across the middle of this 255 m by 103 m, 1963 planting: The Amazon spacing and thinning trial (Freeman, 1965, 1966). The open edges of the band were separated from other cocoa by tracks. It was unshaded and the canopy was not closed everywhere. The basic arrangement of a central ultimate hygiene zone (103 m by 25 m with 569 trees) sandwiched between two three-weekly black pod removal zones (each 103 m by 13 m with a total of 570 trees) was the same throughout the period 1975-1978. Several spacings occurred within the three zones: 5 feet by 5 feet (1.52 m by 1.52 m), 5 feet by 10 feet (1.52 m by 3.04 m), 7 feet by 7 feet (2.13 m x 2.13 m) and 10 feet by 10 feet (3.04 m by 3.04 m).

In 1975 the areas with black pods harvested every 21 days were subdivided into ten plots, five (261 trees) having pods, flowers and flower buds removed below 0.8 m a.g.1. (basal pod suppression), while the other five plots (309 trees)

remained untouched.

In 1976 there was no basal pod suppression but the insecticide dieldrin was applied by knapsack sprayer at 0.1% a.i. on 11 May, 29 June, 22 September and 10 November to the trunks and lower branches (including pods) of trees in selected plots (Fig. 6.1) of both the ultimate hygeine (174 trees) and the three-weekly pod harvest zones (249 trees). Extension lances gave coverage to about 3.5 m a.g.1.

		1976	
3W	3W	DAILY	3 W
10		1 H	
8		1 G	
		1 E	
		1 D	
4		1 B	
2		1 A	
	10	6	3W 3W DAILY 10 1H 1G 1F 1 E 1 D 1 C 1 B

Fig. 6.1 Layout of site East 5/1, showing areas with black pods removed every three weeks ('3W'), or daily (='ultimate hygiene treatment'). In 1975, hatched areas had basal pod suppression. In 1976, stippled areas received dieldrin spray.

In 1977 and 1978 there was neither basal pod suppression nor insecticide application, only the basic ultimate hygiene and three-weekly harvest treatments. Daily black pod recording was restricted to the ultimate hygiene strip in 1978.

Results

Relative Importance of Sources and Routes of Infection

Harvests of black pods every three weeks

End of season results. — In areas where the black pods were allowed to sporulate within the three-weekly harvest regime, rain-splash infections from already sporulating pods outnumbered those from any other source and, with the exception of East 5/1 in 1977, accounted for more than 50% of total black pods (Table 6.1). Infections from the soil and litter were numerous in both sites, as were infections with 'no obvious source'. Few pods became infected through the peduncle from the flower cushion, and even fewer from recognised sporulating bark cankers. Infections originating under or close to ant tents (Plate 5) were numerous in East 5/1 in 1975 but not in subsequent years, nor in site North 4/1A. Disease associated with insect or rodent damage (Plate 6) was not common generally, though Site North 4/1A did yield an appreciable number of lesions connected with caterpillar, borer and mirid damage.

Table 6.1 Incidence of black pods from various sources and routes of infection for different plots and years: black pods harvested every three weeks. Numbers of splash infections from other black pods; numbers of initiators (I); initiators plus their sequence pods as a percentage of total pods lost (I+S)

			Si	te and Y	l'ear	
Route, source or association for infection		East 5/1 (Blocks 2, 5. 6, 9, 10) 1975	(Blo	East 5/ ocks 5, 0		North 4/1A 1976
From another black pod by splash or contact (% of total)		566* (56·0)	357* (56·6)	234 (52·0)	47 (42·3)	1128 (57·6)
Soil and litter	I I+S	189 27·5	111 28·1	110 34·0	29 41·4	304 26·2
Flower cushion, canker	I I+S	21 5·7	16 7·4	5 3·3	1 1·8	20 2·9
Ant tents	I I+S	102 25·8	73 29·3	9 2·9	1 0·9	3 0·2
Rodent damage	I I+S	4 2-7	1 2·4	3 3·6	0.0	13 1·1
Insect damage	I I+S	11 2·1	5 1·7	7 3·1	1 0·9	80 10·5
No obvious source	I I+S	118 35·4	68 29·8	82 53·1	32 55·0	410 59·2
Total Black Pods		1011	631	450	111	1958
Total harvest		6373	3536	2400	1606	6308
Trees with black pod		170	99	97	33	289
Total trees		309	188	188	188	469

^{* 8} black pods through splash from initiators in adjacent blocks



Plate 4. A, Rain-splash spread of *P. megakarya*: multiple water soaking and necrosis following splash diagonally upwards (arrows) from a sporulating black pod. B, Infection from the flower cushion: two pods, heavily sprayed with fungicide, infected through their peduncles from an extensive canker occupying the flower cushion and part of the trunk. Surface layers removed to show extent of infection. C, Infection through contact with the soil/litter. D, Infection through rain-splash from the soil. Note soil particles on pods, and *Phytophthora* lesion on one pod. (Photos by A. C. Maddison)

The data from East 5/1 show a decrease in total black pod numbers from 1975 to 1977. (Results from Blocks 5, 6 and 9 in Table 6.1 give a direct comparison for the three years, other blocks in the three-weekly harvest zones had basal pod suppression in 1975 and/or dieldrin treatments in 1976). This downward trend occurred generally in cocoa at Gambari and presumably reflected the combination of decreasing yields and weather unsuitable for black pod. Reductions in the number of splash infections from existing black pods and in those associated with ant tents accounted for much of the decrease between 1975 and 1976. The incidence of infection from the soil in the two years was unchanged, while that for 'no obvious source' infections actually increased. The



Plate 5. A, Infection closely associated with an ant tent: soil tent built by *C. acvapimensis* over the peduncle, shoulder and pod/trunk contact point. B, Infection loosely associated with soil piled against tree base by the ant *O. troglodytes*. C, Close association with *C. acvapimensis* tent. Tended coccids or their scars are visible where tent has fallen away (arrows). D, Proximal infection loosely associated with a soil tent built on the peduncle by *Ph. megacephala*. (Photos by A. C. Maddison.)

reduction from 1976 to 1977 was again largely in the number of splash infections from diseased pods, though infections from the soil and litter and those with 'no obvious source' were reduced considerably too. This decline in black pod incidence was reversed in 1978, when 497 pods became diseased out of a total for plots 5, 6, and 9 of 1475 pods.

In addition to the incidence of initiators, Table 6.1 give a sequence analysis summary in which, for each source category, the sum of initiators plus splash

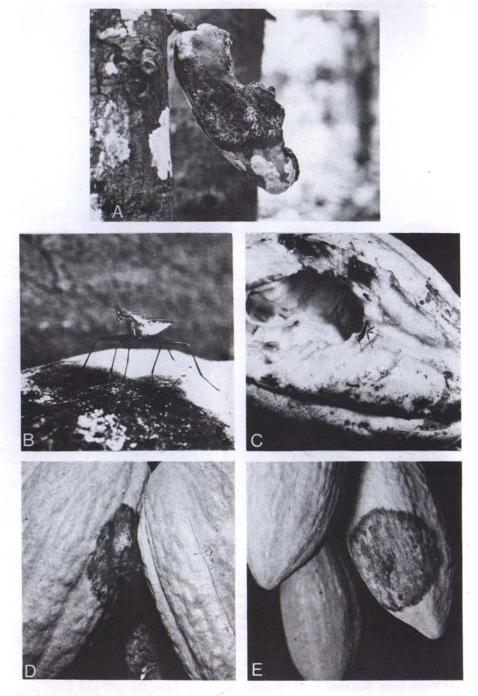


Plate 6. A, Infection closely associated with severe rodent damage. B, Chaetonerius latifemur, one of the many invertebrates which feed on sporulating lesions. C, Some lesion feeders also visit damaged pods: C. latifemur feeding on edge of hole made in a ripe pod by a squirrel. D, Lesion originating from the site of Characoma borer damage: wet frass from the borer is visible at the centre of the lesion. E, Infection originating from a wound caused by the cutlass used for harvesting ripe pods and black pods. (Photos by A. G. Maddison.)

and contact infections derived from them is expressed as a percentage of total pods lost. Sequences from the soil and litter and those from initiators with 'no obvious source' together accounted for nearly 90% of diseased pods, except in 1975 when ant tent-initiated sequences alone gave about 30% loss. Identified infections from the tree itself (flower cushions, cankers) caused relatively minor losses, likewise infections associated with damage by rodents and insects.

Timing of infections through the year. — Early season infections were generally close to the ground and appeared to result either through contact with or rain-splash from the soil and litter or, in certain parts of site East 5/1 in 1975, from the activities of ants carrying soil and debris from the ground to build tents over fruits and flowers (Fig. 6.2). Black pods with 'no obvious source' occurred early too, and at least initially paralleled the incidence of infections from the soil and litter. These early season infections generated few rain-splash sequences (e.g. Site East 5/1, April and May 1975). This situation soon changed

markedly.

In East 5/1 in 1975, rain-splash from diseased pods became the dominant cause of loss in June, and maintained this position until the end of the season. There was a dramatic fall in the incidence of such splash infections during the dry periods in August and early September, and the same occurred for infections from the soil and litter. Infections from other sources also fell during this period but generally to a lesser degree. With the resumption of more frequent rain, the second peaks for splash infections from other pods, and for 'no obvious source' infections, were nearly as high as the first. The recovery was not so marked for infections from the soil and litter or for those associated with ant tents. This may be in part because disease had depleted the number of trunk pods available for infection (while canopy pods were still plentiful). Also, the presence of a sporulating initiator above 0.7 m generally precluded the detection of subsequent 'splash from the soil' initiators on the same tree. Inoculum from both sources might be involved, but unless the infection pattern ruled it out, 'rain splash from a sporulating pod' was given as the more likely source. Infections from the flower cushion showed a peak in late July; other sources were too sparse to show any clear trend.

Effects of basal pod suppression. — Plots with pods and flowers removed below 0.8 m a.g.1. had only two-thirds as many black pods as the untreated plots. However, black pod numbers above 0.7 m were similar in the two treatments: 663 black pods with basal pods suppressed, 596 with basal pods present (Table 6.2). Hence, it appears that the reduction in disease associated with basal pod suppression was roughly what might have been expected simply as a result of

Table 6.2 Effect of basal pod suppression (BPS) on the numbers of black pods above and below 0.7 m from the various sources and routes of infection; black pods harvested every three weeks, site East 5/1 1975

7 / -	Abo	ve 0.7 m	0 to 0.7 m
	BPS	No BPS	No BPS
Soil and litter	*	*	189
Ant tent	70	77	25
Rodent damage	3	4	0
Insect damage	4	8	3
Canker or cushion	5	16	5
No obvious source	.150	118	*
Splash from another			
black pod and contact	431	373	193
Total black pods	663	596	415
			1011

^{*} In assessing sources, the category 'infection from the soil and litter' was not assigned to pods above 0.7 m, nor was 'no obvious source' given to pods at or below 0.7 m

preventing infection possibilities within the pod-free zone alone. There was no evidence that the maintenance of a black pod-free band at the tree base had a beneficial effect on the final amount of disease above. However, there was considerable variability from plot to plot in both black pod numbers and the incidence of the various sources and routes of infection (e.g. the mean values for black pods per plot of 133 and 202 in the two treatments were not significantly different even at p=0.1). So, one cannot expect to detect any but the coarsest quantitative effects of basal pod suppression.

Looking at the incidence of the various sources through the season, we see that the periodic removal of flowers did not prevent tent-building above 0.7 m; in fact infections associated with soil tents happened to occur earlier on trees with basal pod suppression than on those without (Fig. 6.2). But there seemed to be some effect later, because trees with their normal complement of flowers and pods showed a more rapid increase in tent-associated infections (even after deducting infections occurring below 0.8 m). There was hardly any difference in the incidence of 'no obvious source' infections until after the short dry season, when plots without basal pods inexplicably showed more than those with. Splash infections from sporulating black pods were similarly numerous above 0.7 m, as would be expected from the comparable numbers of initiators present in the two treatments.

In terms of healthy pod yields, the two treatments were very similar — 5388 pods with basal pod suppression, 5374 without. Perhaps the absence of yield below 0.8 m caused by basal pod suppression was more or less balanced by the considerable losses to *Phytophthora* which occurred below 0.8 m in untreated plots.

Ultimate Hygiene Treatments

The removal of 'initiators' before they sporulate prevents the development of infection sequences. If all new lesions had been seen prior to sporulation, no infection through splash from other black pods would have been recorded in this treatment except for those coming from adjacent three-weekly harvest plots. In practice, some sequences did develop from lesions that were hidden from view initially. The worst year in this respect was 1976 when a severe infestation by the surface borer *Marmara* made lesions difficult to distinguish even when sporulating. The number of 'missed' initiators that began sequences in East 5/1 in 1975, 1976, 1977 and 1978 respectively were 6, 23, 0 and 16 (0.5%, 7.4%, 0.0% and 2.2% of total initiators).

Site East 5/1, 1975. If we compare the incidence of initiators from various categories in the ultimate hygiene treatments with that in the three-weekly removal areas bearing their normal complement of basal pods (having excluded 'splash from other black pods' in the latter), we find close agreement in terms of proportional importance (Table 6.3). To compare numbers, we have to adjust for the fact that there were roughly twice as many trees in the ultimate hygiene area. While total production (black pods plus healthy pods) was almost exactly double that in the 'normal' (no basal suppression) three-weekly harvest areas, initiators were more than twice as numerous. Infections from the soil and litter were particularly common (Fig. 6.2). This albeit crude comparison suggests that in the three-weekly harvest areas in 1975 the numbers of initiators developing may have been restricted later in the season by a shortage of pods available for infection — especially near the ground. More trunk pods were likely to be available longer in the ultimate hygiene treatment because infection sequences were not allowed to develop.

The timing and incidence of 'no obvious source' infections were very similar whether or not black pods were left to sporulate.

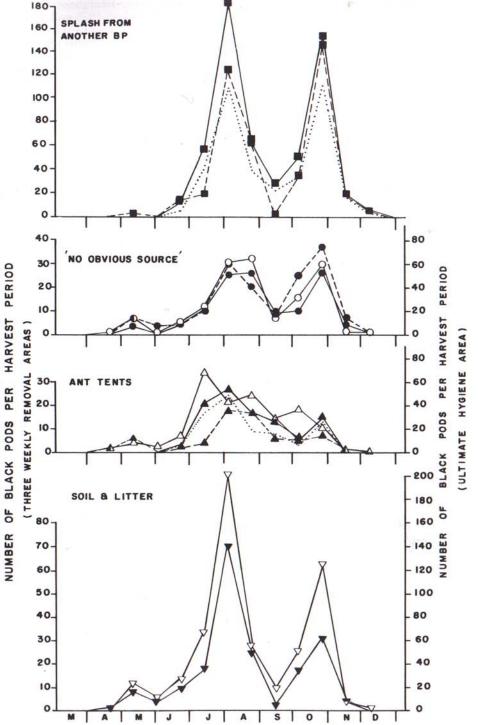


Fig. 6.2 Numbers of black pods from some sources and routes of infection through the season in East 5/1, 1975. Solid symbols, three-weekly harvest areas — continuous lines no basal pod suppression; dashed lines basal pods suppressed; dotted line no basal pod suppression, pods above 0.7 m only. Open symbols, ultimate hygiene area.

Site East 5/1 1976-1978.— The ultimate hygiene area, like those under three-weekly harvest, showed progressively fewer black pods in 1976 and 1977, but considerable numbers again in 1978 (Table 6.3).

The decrease in initiators between 1975 and 1976 was greater in the ultimate hygiene zone than in the three-weekly areas, and in 1976 no longer were initiators more abundant where infection sequences were being prevented. The three major categories of initiator: soil and litter, ant tents, and 'no obvious source' were all much reduced in size, in contrast to the situation in the three-weekly harvest areas where the decrease was confined mainly to ant tent-associated infections (and sequence pods). Nevertheless, the changes were such that the percentage incidence of the various initiators under the two harvesting regimes in 1976 were very similar (Table 6.3) — as they had been in 1975.

The small numbers of black pods generally in 1977 makes close comparisons of source importance questionable, but there was an indication that for the first time since 1975 'no obvious source infections' were reduced more than infections from the soil and litter in the ultimate hygiene treatment.

In 1978, detailed daily records were not made on the three-weekly harvest plots. Records for the ultimate hygiene area showed abundant infections from the soil and litter and a resurgence of ant tent-associated disease. These infections were not restricted to trees where the ultimate hygiene treatment had

Table 6.3 Comparison of the numbers (and %) of initiators in various source categories in the ultimate hygiene area (UH) and the three-weekly harvest areas (3W) of site East 5/1 (plots lacking basal pod suppression only in 1975 — 'No BPS'). Data for site South 1/1 also included

	1975	19	975	19	76	19	77	1978
	UH S1/1	UH Whole	3W No BPS	UH Whole	3W Whole	UH Whole	3W Whole	UH Whole
Soil and litter	42 (66·7)	585 (48·3)	189 (42·5)	151 (48·6)	251 (45·1)	26 (66·7)	70 (51·9)	208 (28·9)
Ant tent	(1·6)	282 (23·3)	102 (22·9)	9 (2.9)	19 (3·4)	(5·1) ²	3 (2·2)	41 (5·7)
Rodent damage	9 (14·3)	4 (0·3)	4 (0·9)	(0.6)	7 (1·3)	1 (2·6)	(0·7)	2 (0·3)
Insect damage	(4.8)	16 (1·3)	11 (2·5)	23 (7·4)	29 (5·2)	(0.0)	4 (3·0)	47 (6·5)
Flower cushion and canker	5 (7·9)	37 (3·0)	21 (4·8)	3 (1·0)	(2·0)	(0.0)	2 (1·5)	(0.3)
No obvious source	3 (4·8)	288 (23·8)	118 (26·6)	123 (39·5)	239 (43·0)	10 (25·6)	55 (40·7)	420 (58·3)
Total initiators	63 (100·0)	1212 (100·0)	445 (100·0)	311 (100·0)	556 (100·0)	39 (100·0)	135 (100·0)	720 (100·0
Total black pods	65	1275	1011	418	1245	39	266	808
Total harvest	3324	12614	6383	7282	8109	4852	6184	7178
Trees with black pod	34	365	170	153	250	37	79	215
Total trees	400	569	309	563	570	563	570	563

failed through initiators being overlooked (in the current or in previous years) until after sporulation. The majority of the trees concerned had been free from sporulating black pods for the three previous years. Clearly, using the ultimate hygiene treatment over several years to prevent the return of inoculum from sporulating pods to the ground did not stop the soil and litter from acting as a recurrent source of inoculum.

'No obvious source' infections were more numerous in 1978 than in any previous year and exceeded those from the soil and litter for the first time since recording started. Infections associated with insect damage (mainly caterpillars and borers) also increased, which suggests that at least part of the rise in 'no obvious source' infections may have been connected with living vector activity. Numbers of infections from the flower cushion or cankers did not recover in the same way, and it appears that the ultimate hygiene treatment by preventing new infections of flower cushions had virtually eliminated this source of infection.

Site South 1/1 produced only 65 black pods (2.0% of total harvest) in 1975 compared with 1275 black pods (11.2%) from the ultimate hygiene area of Site-East 5/1 (Table 6.3). Many factors may be responsible for the small amount of disease, one of the principle contenders being an adverse microclimate as a result of the site being exposed on all sides and well drained. It was also far from other cocoa, and one might have expected this to reduce the amount (if any) of inoculum entering the site from outside. In fact, infections associated with insect damage and rodent damage (mainly Cricetomys gambianus) were relatively common (21.5%), but whether the inoculum came from within-plot or distant sources is not clear.

The proportion of 'no obvious source' infections was less than 5% in South 1/1, but more than 20% for East 5/1 where the ultimate hygiene area was surrounded by diseased cocoa. This could be explained in terms of reduced importation of inoculum, but other explanations are possible involving for example, the effect of the different microclimates on the sporulating ability and survival of cankers.

Effects of dieldrin applications (East 5/1 1976)

Effects of the invertebrate fauna.— Invertebrates crawling on the trunk and lower branches were rapidly reduced in number by the first and subsequent treatments with dieldrin. A few ant species began to return about five weeks after treatment, but soil tent-builders were not among them; the rare tents that did appear were of the debris or carton type, built high in the canopy by ants (e.g. Cr. gabonensis) which inhabited the upper parts of sprayed trees. Even in non-sprayed areas (and in sprayed areas before the first spray) there was much less tent building by soil-moving ants than in 1975. Flying insects were absent just after treatment, and there was an indication of some inhibitory effect continuing for several days. However, daytime observation and sticky traps showed that thereafter flying insects did enter the sprayed areas and some may have visited pods before the insecticide affected them.

The dieldrin apparently affected some non-treated areas too. Ant tent incidence in non-sprayed Plot C was reduced to zero, just as in the two treated plots B and D between which it was sandwiched. Conversely, untreated plots G and H, which were without tents initially, bore tents soon after the first application of dieldrin to neighbouring plots, probably as a result of surviving ants migrating from treated areas. The pod miner *Marmara* became very common in sprayed and non-sprayed areas alike, no doubt as a result of the inbalance created by the dieldrin in predator-prey populations.

Effects on black pod incidence. There were only minor differences in the incidence of black pods recorded in sprayed and non-sprayed areas. This was true both

for daily black pod removal (sprayed 6.2% black pod, unsprayed 5.6%) and for

three-weekly harvests (sprayed 13.0%, unsprayed 14.3%).

The presence of dieldrin apparently reduced the number and proportion of initiators from the soil and litter, and entirely prevented ant tents built from soil, and any associated infections (Table 6.4). Other categories of infections in which invertebrates might have been involved by causing wounds or carrying inoculum (insect damage, rodent damage and 'no obvious source' infections) generally were not suppressed by the sprays. Numbers in certain categories were too sparse to give a reliable indication; plot-to-plot variability meant that only large differences would be meaningful.

Total pod production was greater in sprayed than non-sprayed areas for the three-weekly harvest treatment, but the converse was true for ultimate hygiene plots. Heterogeneity in basic productivity was most likely obscuring any treatment effects. The greater abundance of pods in the sprayed three-weekly harvest areas was reflected in more splash infections from sporulating pods, relative to non-sprayed areas.

Table 6.4 Effect of dieldrin spray on black pod incidence for daily removal and three-weekly removal of black pods East 5/1, 1976. Numbers of initiators (I) from various sources; and initiators plus their pods as a % of total pods lost (I+S)

	Daily	removal	Three wee	kly removal
	Dieldrin Blocks IC, IE, IG	No Dieldrin Blocks IB, ID, IF	Dieldrin Blocks 2, 3, 10, 11	No Dieldrin Blocks 4, 5, 8, 9
Soil and litter	I 41	45	I 90 I+S 26·9	117 35·0
Ant tents	I 0	2	I 5* I+S 1·5	9 2.5
Rodent damage	I 0	0	$\begin{array}{cc} I & 2 \\ I+S & 2\cdot 4 \end{array}$	1 1·0
Insect damage	I 3	5	I 11 I+S 16·6	11 5·0
Flower cushion and cankers	I 2	1	I 5 I+S 3·5	5 3·1
No obvious source	I 21	14	I 109 I+S 47·5	87 53·2
Total initiators	67	67	222	230
Splash from another black pod %	38†	11††	321 59·1	247 52·0
Total black pods	105	78	543	477
Total healthy pods	1594	1887	3653	2456
Trees with black pods	35	44	111	100
Total trees	174	178	249	239

^{*} Three infections prior to first dieldrin application and two post application in the canopy

The timing and height distribution of infections through the season were not consistently affected by the dieldrin sprays, though there were some differences (Fig 6.3). On both three-weekly harvest and ultimate hygiene areas non-sprayed trees tended to show black pods high in the canopy somewhat earlier than sprayed trees, but this difference was not apparent after the middle of August, when disease had reached 5-6 m a.g.l. in both treatments.

Infections with 'no obvious source'

Infections lacking an obvious source or association are an important group. They may have been caused by unrecognised cankers, symptomless living vector activity, rain-splash beyond the limits set from diseased pods or from the soil, or by other unidentified causes. Clues to their origin might be discernible from their distribution amongst trees and their timing through the season. For example, trees with bark cankers could show recurrent infections within the year and from year to year, as could trees which are on rodent 'highways', or which are particularly attractive to other living vectors. In addition to looking for individual trees with more than their share of 'no obvious source' infections, another possibility to be examined is whether or not such infections within the ultimate hygiene area were more numerous along the borders with the three-weekly harvest areas — as would be expected if wind-blown splash and/or short range living vector spread from sporulating pods were involved.

Frequency distributions.— This approach is complicated by the variability from tree to tree in productivity and cropping pattern, and also by general changes from year to year in disease incidence. A full analysis will not be given here. However, the indications are that 'no obvious source' infections are not distributed randomly. Certain trees did appear prone to these infections (Table 6.5) and these were not always trees which produced large numbers of pods during the black pod season. On most of the 'prone' trees, the majority of 'no obvious source' infections appeared in groups on just a few occasions, rather than in ones or twos intermittently through the season.

Looking at the distribution from year to year, in the daily removal area 354 trees remained free from 'no obvious source' infections throughout, 143 trees had them in one year, 62 had them in two years and 13 had them in three years. (No trees had such infections in all four years.) Trees having 'no obvious source'

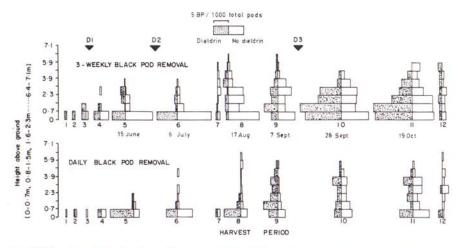


Fig. 6.3 Numbers of black pods per harvest period at different heights above ground — adjusted for productivity — from the three weekly harvest areas of site East 5/1 in 1976, with and without dieldrin spray.

[†] From four "missed" initiators

^{††} From three "missed" initiators

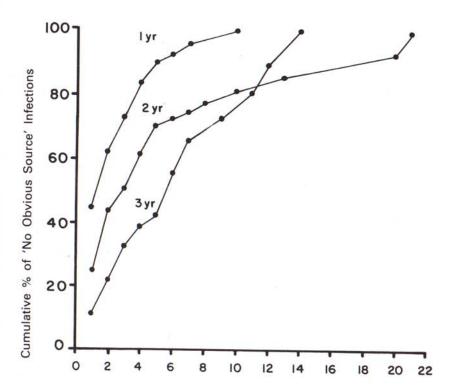
Table 6.5 Frequency distribution of numbers

461 59 28 1 6 2 3 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1																							
1975 461 59 28 1 1976 505 40 11 3 1977 554 8 1 1978 426 78 17 15	97	0	-	2	3	4	5	9	7	8	6	10	Ξ	12	13	14	15	91	17	18	19	20	21
1975 461 59 28 1 1976 505 40 11 3 1977 554 8 1 1978 426 78 17 15																							
1976 505 40 11 3 1977 554 8 1 1978 426 78 17 15 Teal 1946 195 66 99	1975	461	59	28	-	9	2	3	-	-						= 1							
1977 554 8 1 1978 426 78 17 15 Teal 1946 195 66 99	9261	505	40	Ξ	3	-	-		-														
Tetal 1046 105 56 00	1977	554	8		-																		
Total 1046 195 56 90	1978	456	78	17	15	6	9	3	2		-	5	-	-								-	
1340 103 30 70	Total	1946	185	56	20	91	6	9	4	-	-	2	-	-	-	-						-	

infections in several years had a disproportionately large number per tree per year compared with those having them in only one year. The distribution of 'no obvious source' infections per tree per year is highly skew (Table 6.5), and comparisons using means have their limitations. Nevertheless together with Fig. 6.4 they give an idea of the situation. Trees with 'no obvious source' infections in three years had a mean of 3.46 ± 3.35 (S.D.) such infections per tree per year, compared with means of 2.31 ± 2.98 and 1.60 ± 1.31 for trees with 'no obvious source' infections in two years and one year respectively.

In the three-weekly removal area where data are available only for three years, 356 trees never had a 'no obvious source' infection, 151 trees had in one year, 52 trees in two years and 12 trees in all three years. The mean numbers of 'no obvious source' infections per tree were 1.86 ± 2.26 , 1.68 ± 1.03 and 1.35 ± 0.73 for trees having such infections in three years, two years and one year respectively.

Spatial distribution. Looking now at the distribution of 'no obvious source' infections tree by tree on a plan of the site, there is little evidence of a consistent gradient when one moves from the three-weekly to the daily removal areas, whether one is considering total number of 'no obvious source' infection per tree (Fig. 6.5), or the number of years in which trees had 'no obvious infections' (Fig. 6.6). When infections are totalled for lines of trees parallel to the long axis of the three-weekly and daily removal areas (Fig. 6.7) again no clear overall



NUMBER OF NO OBVIOUS SOURCE INFECTIONS PER TREE PER YEAR

Fig. 6.4 Cumulative % of 'no obvious source' infections for increasing numbers of 'no obvious source' infections per tree per year: curve for trees having 'no obvious source' infections in 1 yr, 2 yr and 3 yr.

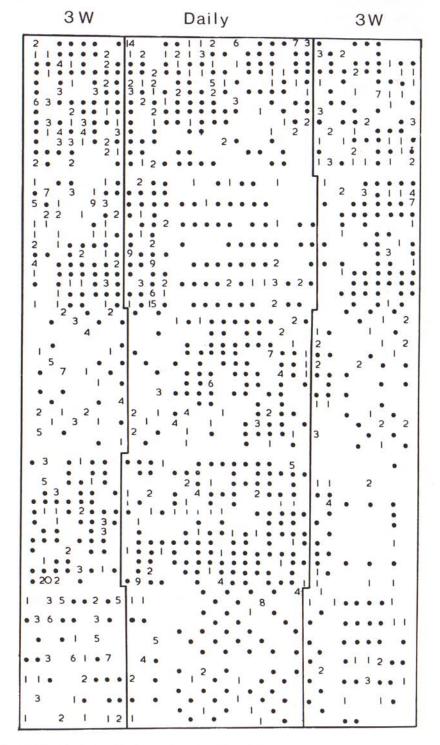


Fig. 6.5 Plan distribution showing total number of 'no obvious source' infections per tree in site East 5/1 during the years 1975, 1976 and 1977 (\bullet = 0).

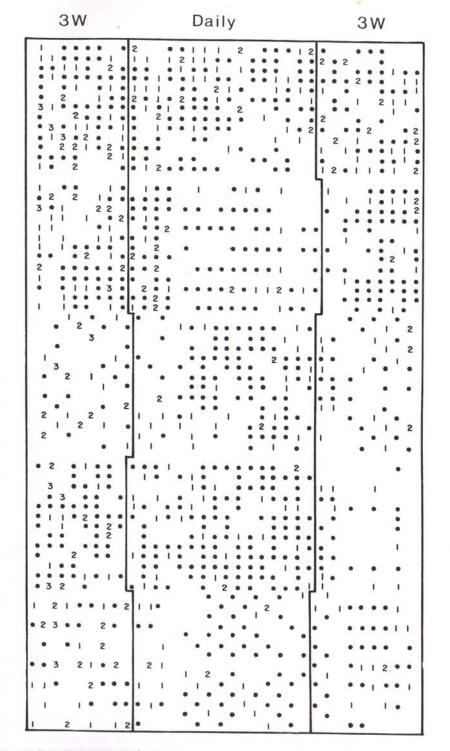


Fig. 6.6 Plan distribution of trees having 'no obvious source' infections in 1, 2 or 3 years during the period 1975 to 1977 in site East 5/1 (• = 0).

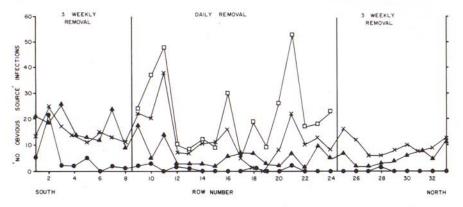


Fig. 6.7 Number of 'no obvious source' infections per row of trees (parallel to borders of the daily removal treatment) in site East 5/1 in 1975 (×), 1976 (▲), 1977 (●) and 1978 (□).

gradients are apparent, though the patterns were similar from year to year. The peaks three rows inside the southern boundary (row 1) and four rows inside the northern boundary (row 21) have no clear explanation in terms of inoculum movement from the three-weekly areas. Productivity varied considerably row by row as did black pod incidence e.g. in 1976 (Fig. 6.8).

Discussion

The results described above show that at least for Gambari Experimental Station the basic development of the epidemic in F₃ Amazon cocoa is essentially similar to that recorded for Amelonado cocoa in the mapping study. Splash from already sporulating pods was again the major means of spread, and even with removal of all black pods every three weeks, splash sequences generally accounted for more than 50% of pods lost. This compares with about 70% for the mapping site, where black pods were not harvested. As with Amelonado, early initiators were close to the ground and apparently associated with movement of inoculum from the soil and litter either by rain-splash or by the activities of tent-building ants. Contrary to expectations, infections from flower cushions and recognised cankers were no more important than in Amelonado, and again initiated relatively little pod loss. Infections lacking an obvious source were a major feature in the epidemics in both types of cocoa.

The data from the East 5/1 Site show great variation in pod loss from year to year, which was accompanied by some changes in the relative importance of the various sources of infection. Nevertheless, initiators from the soil, and those with 'no obvious source' dominated in every year. The great importance of ant tent-associated infections in Site East 5/1 in 1975 appears exceptional. Their incidence was much less in 1976 than in 1975, even in plots not treated with dieldrin. This may be due in part to effects of dieldrin beyond the treated zones, but environmental differences cannot be ignored, especially in view of the heavy pruning of the site done at the end of 1975. Various insecticides including dieldrin were applied to Site N4/1A in 1975, and this may have been partially responsible for the lack of tent building ants in 1976. Similar year-to year effects for dieldrin seem to have occurred in Site East 5/1 and in the Lafiaji Experiment (see Chapter 11).

In its first year, an ultimate hygiene treatment would not be expected to reduce the incidence of initiators from such sources as the soil, ant tents and flower cushions. On the contrary, by preventing pod loss in rain-splash sequences and thereby keeping pods available for infection longer, it may actually increase the incidence of initiators, as appears to have been the case for

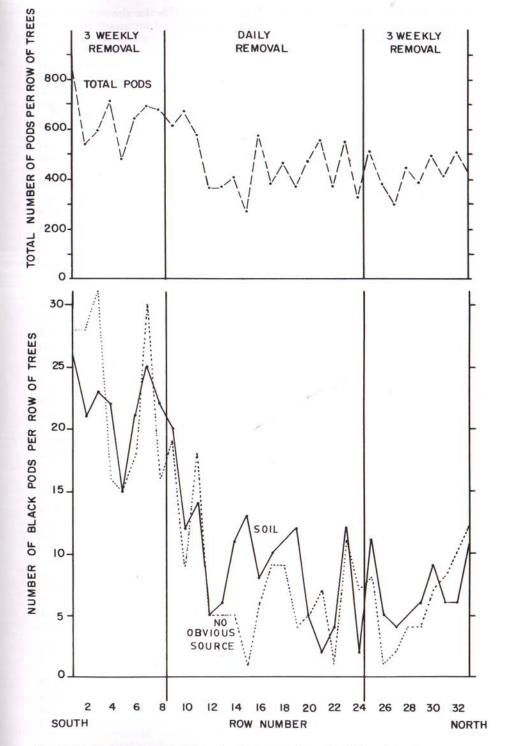


Fig. 6.8 Numbers of black pods and total pods per rwo of trees (parallel to the border of the daily removal treatment) in site East 5/1 in 1976.

soil and ant tent infections in Site East 5/1 in 1975. In the second and subsequent years there would again be the possibility of increased incidence through more pods being available longer. But there might also be an opposing trend towards fewer initiators, if the ultimate hygiene treatment of the previous year(s) had resulted in a substantial reduction in the amounts of inoculum in the soil or in the number of flower cushions infected. In 1976 and 1977 there was an overall beneficial effect for daily removal relative to three-weekly removal, through reductions in the number of infection from the soil, from flower cushions, and of those with 'no obvious source'. No comparative data are available for the three-weekly harvest areas in 1978, but in the ultimate hygiene treatment flower cushion infections remained few while infections from the soil and ant tents were more numerous than in 1976, but not as numerous as in 1975. So even after three complete years in which no inoculum had returned from sporulating pods to the soil, soil populations of P. megakarya were still sufficiently large and widespread to cause considerable numbers of infections. This is supported by the results of quantitative soil sampling (Chapter 4) which showed no drastic reduction in population levels as a result of the 'removal before sporulation' treatment.

Within the ultimate hygiene area there was no inoculum produced on pods for movement by living vectors (or by any other means). If 'no obvious source' infections were mainly dependent on dispersal of sporangia over short distances by crawling invertebrates, up the tree or from one to the next, then one would have expected a marked reduction in these infections (relative to the three-weekly areas) in Site East 5/1 for each of the years 1975-78. There was such evidence in 1976 and 1977, but not in 1975. One would also have expected 'no obvious source' infections to be fewer in the three-weekly areas treated with dieldrin than in those without, but this was not the case. It is possible that flying insects or rodents were moving inoculum over greater distances than crawling invertebrates i.e. from the three-weekly to the daily removal areas, or from non-sprayed to sprayed, and this may explain some of the apparent anomalies in the occurrence of 'no obvious source' infections. The dieldrin treatment was probably more effective against crawling invertebrates than against flying insects (and rodents), but in any case was unlikely to have prevented vectors from occasionally reaching and depositing inoculum on pods once any initial

repellent effect had disappeared.

The pipe-trap experiments (Chapter 3) showed that infective propagules are present in rain water flowing down the trunks of a small proportion of trees, and it was presumed that these came from unrecognised cankers on the trunk or branches. Such sources could account for a further proportion of the 'no obvious source' infections, which at least in the first year, 1975, would not be directly affected by the ultimate hygiene treatment. Nothing is known about the origins or lifespan of any supposed cankers. On some F₃ Amazon trees they may survive as sources of inoculum over several years, thus providing one explanation for certain trees appearing prone to 'no obvious source' infections year after year. On other, less susceptible, trees their life-span might be shorter and the ultimate hygiene treatment, by preventing new infections of the trunk and branches, might progressively reduce the number of infections from cankers. The three-weekly removal regime could also have some effect because infection of the trunk through the peduncle by *P. megakarya* requires several weeks from the first signs of infection on a pod.

Another likely cause of 'no obvious source' infections is the movement of inoculum in wind-blown splash droplets, over distances considerably greater than those set as the limits for 'splash from sporulating pods'. These working limits essentially cover the movement of trajectory droplets in calm air conditions, and were appropriate much of the time. However, we have experimental evidence (Chapter 3) that wind-blown splash from sporulating pods happens occasionally when winds of the necessary force occur at critical

times in relation to rain, and some of the 'no obvious source' initiators must, in fact, have been part of established sequences. For Site East 5/1, clearly one would expect more of the 'no obvious source' infections to be accounted for in this way in the three-weekly removal areas than in the ultimate hygiene area. Thus we have yet another factor complicating interpretation of differences in the occurence of 'no obvious source' infections between the two treatments.

The limit for rain-splash from the soil and litter was set at 0.7 m. The experimental evidence (Chapter 3) suggests that this was a reasonable limit, though a small amount of inoculum probably attained greater heights and could account for some of the 'no obvious source' infections. (Conversely, some of the infections occurring below 0.8 m which were classified as from the soil and litter, may in fact have been 'no obvious source' infections). One further point in regard to rain-splash concerns the possibility of propagules, either from sporulating pods or from the soil and litter, becoming truly airborne following the evaporation of the splash droplets which first lifted them into the air. This mechanism, if it occurs, would also contribute to the 'no obvious source' group, with a greater probability of long distance dispersal compared with wind-blown splash droplets.

From the foregoing it is apparent that we have a complex situation underlying the incidence of 'no obvious source' infections. The evidence does not rule out any of the possible causes mentioned, and neither does it indicate that one in particular dominates. What it does show is that the total absence of sporulating pods from a relatively restricted area of F₃ Amazon fails to bring about a rapid and sizeable reduction in the incidence of 'no obvious source' infections. It is not surprising, therefore, that the absence of sporulating pods below 0.8 m in the basal pod suppression treatment failed to have a marked

effect on 'no obvious source' infections above.