The relative abundance of the mealybug vectors (Hemiptera: Coccidae and Pseudococcidae) of cocoa swollen shoot disease in Ghana

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Abstract
A census of the mealybug vectors of cocoa swollen shoot disease was made weekly on 238 Amazon cocoa trees at the Cocoa Research Institute, Tafo, Ghana, between 1971 and 1976. The six species encountered were ranked in descending order of abundance: Planococcoides njalenesis (Laing), Planococcus citri (Risso), Phenacoccus hargreavesi (Laing), Ferrisia virgata (Ckll), Pseudococcus concavocerarii James, P. calceolariae (Mask.). Planococcoides njalenesis occurred at a much higher density on infested trees than other species but was found on fewer trees than either Planococcus citri or Phenacoccus hargreavesi. Over 13-week periods the probability of finding a mealybug on a particular tree was 0.87 for Planococcus citri, 0.77 for Phenacoccus hargreavesi, 0.36 for F. virgata, 0.32 for Pseudococcus concavocerarii, 0.23 for Planococcoides njalenesis and 0.05 for Pseudococcus calceolariae. The results suggest that the first four species are more mobile than Planococcoides njalenesis and could be more important in the spread of disease than has previously been supposed.

Introduction
When it was first demonstrated that cocoa swollen shoot disease in West Africa was caused by viruses (Posnette, 1940), a number of sucking insects commonly occurring on cocoa were tested for their ability to transmit the disease. Between 1940 and 1942, Posnette (1941) and Cotterell (1943) tested 15 species of Homoptera in eight different families, a thrip and two species of Heteroptera. They obtained transmission with the mealybugs Planococcoides njalenensis (Laing) and Ferrisia virgata (Cockerell) and apparent transmission by a psyllid and an aphid. Attempts by Box (1945) to obtain transmission with aphids, psyllids, mealybugs, a ricaniid and thrips resulted only in transmission by the mealybugs. Posnette (1950) subsequently tested more species of mealybugs with a total of 17 virus strains, eight from Ghana, seven from Nigeria and two from the Ivory Coast, although the only species which was tested against all 17 strains was Planococcoides njalenensis. Eleven of the thirteen mealybug species tested proved capable of transmitting one or more of the virus strains.

Legg & Bonney (1966) used a number of vector species to transmit isolates from Adansonia digitata and Cola chlamydantha to other alternative host species. Planococcoides njalenensis, Planococcus citri (Risso), Planococcus kenyae (Le Pelley), Phenacoccus hargreavesi (Laing) and Planococcus sp. nr. P. cellis (Strickland) successfully transmitted all three Adansonia and all three Cola isolates, whilst Ferrisia virgata

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transmitted the *Cola* isolates but not the *Adansonia* ones. It is known from work with *Planococcoides njalensis* that cocoa viruses 1A, 1C and 1M can be transmitted to a number of wild alternative hosts, including *Adansonia*, and later transmitted back to cocoa (Posnette, Robertson & Todd, 1950), so it is probable that a number of mealybug species are potential vectors of viruses from wild hosts to cocoa.

Meanwhile, Strickland (1951a) had investigated the relative abundance of mealybug species on mature Amelonado cocoa at Tafo and found *Planococcoides njalensis* to be 100 times as numerous as *Planococcus citri*, which was itself 40 times as numerous as any other species. It was not unnaturally assumed that *Planococcoides njalensis* must be the most important vector of the disease, and much subsequent work has been concentrated on this insect to the exclusion of other species.

During the past 25 years, changes have taken place in cultural practices and in the ecology of cocoa farms. There has been a tendency to reduce overhead shade because higher yields can be obtained from unshaded cocoa, and the ravages of swollen shoot disease have led to a much more patchy distribution of farms, interspersed with food farms or scrubby fallow growth, than was previously the case. Furthermore, new plantings and replanting of areas destroyed by virus attack have been mostly with inter-Amazon crosses or Amazon hybrid cocoa, which is more vigorous and easier to establish than the traditional Amelonado. The more open conditions which have resulted could be expected to favour *Planococcus citri* over *Planococcoides njalensis*, a condition which prevails in Nigeria where *Planococcus citri* is the more common mealybug (Donald, 1955).

**Methods**

In order to assess the status of mealybugs on Amazon cocoa, a block of 238 cocoa trees at Tafo, Ghana, was investigated between 1971 and 1976. The block was part of an existing experiment designed to test the rate of spread of virus in a tolerant cocoa variety and contained two 50-tree plots of the inter-Amazon cross, T85/799 × T17/359 surrounded by guard rows of Series IIB Hybrid (an Amazon × local Trinitario hybrid). Two sides of the block were bordered by roads.

At the time of planting in 1968, the site had been cleared of old Amelonado cocoa and larger shade trees and the new cocoa planted as seed at stake at 3·0 × 3·0 m under temporary shade of *Gliricidia sepium* and tree cassava. The tree cassava was progressively removed during the course of the experiment, but the *Gliricidia* and some small remnant forest trees remained throughout.

Weekly counts were made of the number of adults and older nymphs of each mealybug species by a visual inspection of each tree. The insects were not removed.

**Results**

Six species of mealybug were commonly encountered during the course of the survey: *Planococcoides njalensis, Planococcus citri, Phenacoccus hargreavesi, Ferrisia virgata, Pseudococcus conoocerarii* James and *Pseudococcus calceolariae* (Maskell).

The mean number of mealybugs on the whole plot of 238 trees during each year running from April to March is shown in Table I. When compared with the situation found by Strickland (1951b) it is evident that although *Planococcoides njalensis* was still the most abundant species, other species had all increased in importance. Whereas *Planococcoides njalensis* made up 98·9% of Strickland's sample, in 1971–76 it accounted for less than 49% of the total, and *Planococcus citri*, which previously accounted for 0·99%, in 1971–76 accounted on average for 38% and indeed in three out of the five years was more abundant than *Planococcoides njalensis*. *Phenacoccus hargreavesi, Ferrisia virgata* and *Pseudococcus conoocerarii*, which in Strickland's survey made up 0·03, 0·03 and 0·02% of the total, respectively, in 1971–76 accounted for 9·01, 2·47 and 1·33%.

The total number of mealybugs on the plot does not, however, give a true impres-
TABLE I. The annual mean numbers of mealybugs present on the whole plot of 238 trees

<table>
<thead>
<tr>
<th></th>
<th>Mean no. of mealybugs present</th>
<th>Overall mean s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Planococcus njalensis</td>
<td>590.1 602.1 909.9 954.9 210.5</td>
<td>652.5 ± 57.44</td>
</tr>
<tr>
<td>Planococcus citri</td>
<td>619.3 923.5 420.4 320.5 256.2</td>
<td>508.3 ± 35.34</td>
</tr>
<tr>
<td>Phenacoccus hargreavesi</td>
<td>94.1 212.6 170.0 61.7 63.5</td>
<td>120.2 ± 10.93</td>
</tr>
<tr>
<td>Ferrisia virgata</td>
<td>22.9 36.0 51.6 35.4 19.1</td>
<td>33.0 ± 4.32</td>
</tr>
<tr>
<td>Pseudococcus concavocerarii</td>
<td>13.0 20.3 23.7 17.4 14.7</td>
<td>17.8 ± 2.18</td>
</tr>
<tr>
<td>Pseudococcus calceolariar</td>
<td>1.7 5.8 3.2 1.0 0.3</td>
<td>2.4 ± 1.17</td>
</tr>
<tr>
<td>Totals</td>
<td>1341.1 1800.3 1578.8 1390.9 564.3</td>
<td></td>
</tr>
</tbody>
</table>

*The years run from April to March.

The mean proportion of trees infested on each sampling occasion during the year is shown in Table II. On this basis, Planococcus citri was the most frequently found, occurring on an average of 37% of trees at any one time. Planococcus njalensis, although present in large numbers, was found on only 10% of trees. The reason for this disparity is that much larger colonies of Planococcus njalensis built up on individual trees, and when looked at in terms of numbers per infested tree it will be seen that infested trees bore an average of 26.96 individuals of Planococcus njalensis as against 5.76 of Planococcus citri. Phenacoccus hargreavesi was also much more widespread than would be expected from its relatively low density on the plot as a whole because the mean number per infested tree was even lower.

In assessing the relative merits of the various species as virus vectors, movement around the plot must be taken into account. From Fig. 1 it will be seen that on a weekly basis the probability of a tree being occupied by Planococcus njalensis at any one time is about 0.1, but on a quarterly basis (13 weeks) the probability rises to about 0.23. Similarly, the probability of finding a tree infested by Planococcus citri rises from 0.37 to 0.87 and of Phenacoccus hargreavesi from 0.17 to 0.77. More importantly, however, it will be seen that the probability of finding Ferrisia virgata or Pseudococcus concavocerarii rises from 0.05 to 0.36 and 0.32, respectively, and so the probability of finding either of these species is now greater than that of finding Planococcus njalensis.

The actual distribution of trees bearing these species is shown in Fig. 2–7, which illustrate the highly aggregated distribution of Planococcus njalensis compared to the other species. Over the full five years, Planococcus citri and Phenacoccus.
Fig. 1.—The proportions of trees infested by various mealybug species each quarter (a) at least once in 13 weeks and (b) weekly as an average of 13 weeks.
Fig. 2.—Distribution of trees on the plot bearing Planococcoides njalenis each quarter from January 1971 to December 1975. The mean per tree averaged over 13 weeks lies between the limits shown in the key.
Fig. 3.—Distribution of trees bearing *Planococcus citri*.
Fig. 4.—Distribution of trees bearing Phenacoccus hargreavesi.
Fig. 5.—Distribution of trees bearing *Ferrisia virgata*.
Fig. 6.—Distribution of trees bearing *Pseudococcus concavocerarii*. 

*Key: 0 - 1 - 10 - 100 - 1000*
hargreavesi appeared at one time or another on all the trees of the plot (there were three trees missing), Pseudococcus concavocerasii on all but four trees and Ferrisia virgata on all but five trees, but Planococcoides njalensis was never found on 28 of the trees and Pseudococcus calceolariae on 49 (Fig. 8).
Fig. 8.—Mean numbers of (a) Planococcoides njalensis, (b) Planococcus citri, (c) Phenacoccus hargreavesi, (d) Ferrisia virgata, (e) Pseudococcus concavocerarii and (f) Pseudococcus calceolariae recorded per tree per week over five years. The means lie within the limits shown in the key.
Discussion

Three important conclusions arise from this work. The first is that the species composition on this plot is very different from that studied by Strickland (1951b) 25 years previously. Plot 4 of Strickland's ecological survey must have corresponded closely to the position of the present experiment and yet he recorded a total of 1697 individuals of Planococcioides njalensis, 26 of Planococcus citri and 9 of all other species collected over a year, a ratio heavily in favour of Planococcioides njalensis (Strickland, 1951b). Since then, the area has been clear-felled, the old Amelonado cocoa removed and Amazon cocoa planted under temporary shade. It seems reasonable to suppose that the more open conditions favour the build-up of species less dependent on ant attendance than Planococcioides njalensis, a conclusion borne out by the dominance of Planococcus citri in Nigeria, where cocoa is grown under drier and more exposed conditions, and on other plots at Tafo where similar conditions prevail. This is probably partly due to the lower humidity and partly to the disruption of colonies of ants which tend certain mealybug species for their honeydew. Young cocoa trees cannot carry sufficient coccids to satisfy the honeydew requirements of large numbers of ants, and so during the establishment of a cocoa plot the ants probably depend upon coccids within the canopy of shade trees for their main supply of food and supplement this with what they can glean from the few coccids on the cocoa trees. Assuming that the coccids benefit from ant attention, and there is reason to believe that they do, they will increase in number as the cocoa trees grow. Under these conditions, species like Planococcioides njalensis which are more frequently tended will increase at the expense of those species which are not tended. If, on the other hand, the shade trees are removed at planting time the coccid-tending ants lose not only their food supply but in many cases their nesting sites as well and will consequently die out. This will tend to favour the build-up of unattended mealybug species over attended ones. Planococcioides njalensis is particularly dependent on ant attendance in order to thrive, and its decline towards the end of the experiment can be attributed to displacement of the attendant ant Crematogaster castanea F. Smith by a non-tending species, Crematogaster clariventris Mayr.

The present trend in cocoa management is to replace Amelonado with Amazon and Amazon hybrid cocoa planted under temporary shade, so it would seem likely that the species composition of mealybugs will change more in favour of Planococcus citri and the minor species in the future.

The second conclusion is that the importance of the minor species has been underestimated as potential virus vectors. Even allowing for the fact that they are now more numerous than they were, it is clear that low density, of itself, is not a sufficient criterion for dismissing a potential virus vector. Although it is not possible from the data to obtain accurate estimates of the amount of movement taking place within the plot, it would appear that Planococcioides njalensis is a relatively sedentary insect and that colonisation of new trees is slow and depends to a large extent on the presence of attendant ant species. On the other hand, the much larger differences in rate of infestation between weekly and quarterly samples of Phenococcus hargreavesi, Pseudococcus concavocerarii implies that they must be moving around the plot freely in order to colonise new trees. The large seasonal fluctuations shown by the last two species point to the same conclusion. It is less easy to make inferences about Planococcus citri because a greater proportion of trees are occupied at any one time and so movement taking place between trees already occupied is not detected. It has generally been assumed that Planococcioides njalensis is less mobile than other species, including Planococcus citri, although this has not been tested experimentally. In common with other species which rely heavily upon ant attendance, it has much shorter legs, which suggests an adaptation towards a more sedentary existence. Individual colonies of Planococcioides njalensis are larger than those of Planococcus citri, even though the average fecundity of a female of Planococcus citri is greater, suggest-
ing a greater tendency for the offspring to aggregate about their parent. It is possible also that Planococcus citri and Ferrisia virgata nymphs may be carried more readily by wind currents and so contribute to jump spread of virus, i.e. those outbreaks which appear at sites remote from the nearest source tree and which are thought to be initiated by wind-borne vectors. Of 45 mealybugs caught by Cornell (1960) on seedling trap plants floating on barrels on the Tafo reservoir and which could have only arrived there by aerial transport, 35 were reared to the adult stage for identification and of these 18 were Planococcus citri, 11 were Ferrisia virgata and only 1 was Planococcoides njalensis. This ratio may be no more than a reflection of the ability of different species to settle under inhospitable conditions, but it suggests that Planococcoides njalensis may be less well-adapted to aerial spread than are the other species.

The feeding sites of different species within the tree are of importance because virus is more readily acquired from some tissues than from others. Posnette & Strickland (1948) showed with Planococcoides njalensis that virus is more readily available from leaf tissue than from green shoots or from the hardened bark of the stem, and later work (Posnette & Robertson, 1950) demonstrated that immature leaves with red-veining symptoms provide the best virus source. On the other hand, when Planococcoides njalensis and Ferrisia virgata were confined on the stems or leaves of infected Amelonado seedlings in Nigeria (Igwebe, 1966), Planococcoides njalensis was the superior vector regardless of site but efficiency varied with phase of infection. In the acute–severe phase of infection, Planococcoides njalensis was more efficient on leaves than on stems, but in the chronic phase it was more efficient on stems than on leaves. Ferrisia virgata was more efficient on leaves in both cases. There is clearly a need for a critical appraisal of the relative efficiency of vector species in relation to their favoured feeding site. Campbell (1975) analysed the feeding sites of Planococcoides njalensis, Planococcus citri and Phenacoccus hargreavesi within the tree framework. The largest proportions of colonies of Planococcoides njalensis and Planococcus citri were found on the bark of canopy branches, whereas the greatest proportion of Phenacoccus hargreavesi were on green shoots. A similar analysis for Ferrisia virgata, which was not analysed by Campbell, showed the largest proportion of colonies (43%) to be on leaves. The situation is further complicated, however, because the proportions of colonies at different sites vary through the year (Bigger, 1973). This implies movement within the tree canopy and will be discussed at length elsewhere, but it seems likely that an insect such as Ferrisia virgata is adapted to exploit young flush growth and therefore will be feeding on plant material which is both physiologically in the best condition for the acquisition of virus and also at the periphery of the canopy where contact between adjacent trees is greatest. Ferrisia virgata and Phenacoccus hargreavesi have been less thoroughly tested than Planococcoides njalensis for ability to transmit viruses, but the former was shown by Posnette (1950) to transmit 11 out of 15 strains tested and the latter 11 out of 12. Both species transmitted the virulent New Juaben strain.

The very small size of first-instar mealybug nymphs (about 0.2 mm) renders their detection on a tree extremely difficult, and for all practical purposes it is only the adults and late second- or third-instar nymphs which will be detected by visual inspection. Clearly, the probability of recording an individual will be greater if it is part of an aggregation or if it is being tended by an ant, in which case the presence of the much larger ant calls attention to the mealybug. There will, therefore, be a tendency to underestimate those species which are both solitary and not attended by ants. It has recently been found that vegetative buds harbour large numbers of first- and second-instar nymphs, which are rarely associated with an adult. Unfortunately it has not proved possible to distinguish between species, but it is clear that a much larger population of first-instar nymphs exists than was previously detected, and because these nymphs are less than a week old and are not associated with an adult they must have migrated into the buds from elsewhere and hence movement must have
taken place through the canopy. Furthermore, the buds on the periphery of the canopy may well be in close contact with the foliage of a neighbouring tree, allowing for easy passage of the nymph from one tree to another.

It is likely that the role of species other than *Planococcioides njalensis* as virus vectors has always been underestimated, but the apparent change which has taken place in the relative abundance of different species makes it more than ever necessary to elucidate the relative importance of different species as vectors, balancing their efficiency in acquiring virus against their mobility at various stages of their life-cycle and the pattern of their dispersal within the tree against the numbers present. It would be dangerous to exclude any species as a potential vector merely because it is numerically inferior.

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**References**


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