# Bemisia tabaci (Hemiptera: Aleyrodidae) trap catches in a cassava field in Côte d'Ivoire in relation to environmental factors and the distribution of African cassava mosaic disease 

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#### Abstract

African cassava mosaic virus (ACMV), vectored by the whitefly, Bemisia tabaci (Gennadius), is considered the most damaging pathogen of any African crop. Information about vector movement is important for understanding the epidemiology of this disease and the experiments reported here were designed to examine $B$. tabaci flight activity both in and around a cassava crop in relation to time of day, crop growth stage, wind direction and speed, and to the resulting pattern of infected plants within the field at harvest. At wind speeds of $<0.4 \mathrm{~ms}^{-1}$, adult B. tabaci approached the yellow traps by flying upwind. At greater wind speeds, significantly fewer B. tabaci adults approached the traps from downwind, thus reversing the directionality of the catch. When the direction of the prevailing south-west wind reversed, so did the directionality of the catch. Bemisia tabaci adults were flight active throughout the day and the greatest percentage were caught above the canopy between $06.00-08.00 \mathrm{~h}$, when wind speeds were lowest. Trap height and position significantly affected catch with the greatest numbers caught on the lowest traps. More than three times as many $B$. tabaci adults were caught on traps situated downwind from the field compared to those upwind, suggesting that the field was acting as a source of whiteflies. In both years, African cassava mosaic disease (ACMD) incidence was highest and lowest, respectively, on the edges and in the middle of the trials, with the highest incidence occurring on the edges facing the prevailing wind direction. These results are discussed in relation to the epidemiology of ACMD and to potential cultural control methods such as the use of ACMD-resistant guard rows to protect a mainly susceptible crop.


Introduction
African cassava mosaic disease (ACMD) was first
reported in East Africa by Warburg (1894) and, since then,
has spread to all cassava, Manihot esculenta (Euphorbiaceae)
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growing areas in Africa where the incidence may approach $100 \%$ (Fauquet \& Fargette, 1990). In two recent economic assessments, ACMD was reported to be the most damaging vector-borne disease of any African crop, causing estimated annual losses of 49 million tonnes associated with devastating social consequences (Fargette et al., 1988; Geddes, 1990; Thresh et al., 1994; Otim-Nape et al., 1996).

African cassava mosaic geminivirus (ACMV), the causal agent of ACMD, is vectored by the whitefly, Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) (Storey \& Nichols, 1938; Dubern, 1979, 1994). The 'biotype' of B. tabaci found on cassava is restricted almost solely to this crop in Côte d'Ivoire (Burban et al., 1992) and Uganda (Legg, 1995) and therefore alternative ACMV-source plants are considered unimportant in the epidemiology of the disease (Fauquet \& Fargette, 1990).

In southern Côte d'Ivoire, where this research was conducted, cassava is the most important staple food crop and is grown traditionally in a patchwork of small plots of mainly ACMV-susceptible local varieties. Cassava is most susceptible to ACMV infection during its first six months of growth and plants are rarely harvested before they are a year old. These factors, combined with asynchronous planting, means that young cassava is always available for $B$. tabaci colonization and for ACMV infection (Fishpool et al., 1995).

ACMD is also disseminated in infected cassava cuttings used by farmers as planting material. After planting, however, ACMV spread both into and within the crop is a consequence only of the movement of viruliferous adult $B$. tabaci and so information on the movement of $B$. tabaci is important to obtain a better understanding of the epidemiology of the disease. The experiments reported here were conducted to examine the flight activity of $B$. tabaci in relation to time of day, crop growth stage, wind direction and speed, and to the resulting pattern of ACMD-infected plants within the field at harvest.

## Materials and methods <br> Trial layout and trap design

The research was conducted on the 50 ha Institut Français de Recherche Scientifique pour le Développement en Coopération experimental farm at Adiopodoumé $\left(05^{\circ} 19^{\prime} \mathrm{N}\right.$ $04^{\circ} 13^{\prime} \mathrm{W}$ ), situated in the lowland rain-forest zone of Côte d'Ivoire, West Africa. The trial layout is described in detail in Fishpool et al. (1995) and consisted of a $7 \times 7$ array of 49 cassava blocks (rows A-G and columns 1-7), spaced 2 m apart, each block containing 100 plants (var. Kasimbidgi Green) spaced $1 \times 1 \mathrm{~m}$ apart ( 4900 plants in all). Cassava-stem cuttings used for the trials were taken from ACMD symptom-free parent plants. Separate trials, planted in November/December and run for a minimum of four months, were conducted in 1988 and 1989. Trials were planted at the beginning of the dry season, as whitefly populations are greatest during this period and maximal on young plants (Fargette, 1987; Fishpool et al., 1988). Immediately adjacent 0.75 ha areas were used for the trial

Table 1. The percentage of the Bemisia tabaci yellow-trap catches, above the crop canopy, for six time periods during the day.

| Time (h) | \% of total catch <br> caught above <br> the canopy | Approx. s.e. <br> $(45 \mathrm{df})$ |
| :--- | :---: | :---: |
| $06.00-08.00$ | 24.6 | 1.24 |
| $08.00-10.00$ | 9.8 | 0.71 |
| $10.00-12.00$ | 3.8 | 0.51 |
| $12.00-14.00$ | 2.6 | 0.34 |
| $14.00-16.00$ | 3.9 | 0.44 |
| $16.00-18.00$ | 2.0 | 0.38 |

sites in the two years and in both cases the upwind field borders of the trials were orientated at right angles to the prevailing SW wind. In both years, cassava fields with mature plants and a high incidence of ACMD surrounded the trial sites.

The flight activity of adult $B$. tabaci in the two years was monitored using yellow sticky traps positioned on 3 m upright poles of 9 cm -diameter grey PVC tubing. Traps consisted of 10 cm -wide adhesive-backed strips of brilliant yellow plastic (Starcolors, no. 74100), ten per pole, wrapped around the poles at 25 cm intervals. These were divided into eight equal vertical sections using an indelible pen, corresponding to the eight principal points of the compass. Slightly wider, transparent, removable, cellophane strips were then placed over the traps, fixed with sticky tape and then covered in insect adhesive (TangleTrap ${ }^{\mathbb{Z}}$ ). In each year, twelve poles spaced at 24 m intervals were placed in two SW/NE oriented lines running along the middle of the second and sixth columns of blocks. Poles at the ends of each line were placed 4 m from the edge of the experimental area. The four remaining poles of each line were placed in the first (A), second (B), fourth (D) and sixth (F) row of blocks. Throughout the season, adults were counted twice weekly on the traps when the sticky cellophane strips were changed.

## Directional trends

To examine directional trends, mean whitefly numbers were calculated for each of eight directions. The data were then $\log$ transformed to equalize variances and also to facilitate graphical presentation. Using a logistic model (Genstat ${ }^{T M}$, 1993), a circular regression equation of the form:

$$
\log _{e}(B t)=b_{0}+b_{s} \times \sin (\theta)+b_{c} \times \cos (\theta)
$$

was fitted for each category separately, where $\mathrm{Bt}=$ mean numbers of $B$. tabaci, $\theta=$ angle ( North $=0^{\circ}$; East $=90^{\circ}$; etc.) and $b_{0}, b_{s}$ and $b_{c}$ are model co-efficients to be estimated.

Table 2. The percentage of total Bemisia tabaci adults caught on yellow traps situated above the crop canopy, on four days, for six time periods.

| Time (h) | \% of total catch caught above the canopy |  |  |  |
| :--- | :---: | :---: | :---: | :---: |
|  | Day 1 | Day 2 | Day 3 | Day 4 |
| $06.00-08.00$ | 36.1 | 7.2 | 36.3 | 9.4 |
| $08.00-10.00$ | 15.8 | 5.2 | 11.8 | 4.8 |
| $10.00-12.00$ | 10.2 | 2.2 | 3.3 | 0.3 |
| $12.00-14.00$ | 10.2 | 1.7 | 0.2 | 0.9 |
| $14.00-16.00$ | 14.1 | 2.2 | 1.7 | 0.0 |
| $16.00-18.00$ | 3.7 | 1.7 | 1.9 | 0.8 |



Fig. 1. The relationship between $\log ($ mean Bemisia tabaci catch $) \pm$ standard errors and yellow-trap height for poles positioned both inside and outside the cassava crop.

From such an equation, the direction of maximum or minimum numbers, $\theta_{m}$, can be estimated from the directional co-efficients as follows:

$$
\theta_{\mathrm{m}}=\tan ^{-1}\left(\mathrm{~b}_{\mathrm{s}} / \mathrm{b}_{\mathrm{c}}\right)
$$

The direction, $\theta_{\max }$, for maximum number of whiteflies is therefore either $\theta_{\mathrm{m}}$, or, $\theta_{\mathrm{m}}+180^{\circ}$.

Time of day effect on the percentage of B . tabaci adults caught above the canopy
On four days during the 1988 season ( $1 / \mathrm{Feb} / 88$, $8 / \mathrm{Feb} / 88,22 / \mathrm{Feb} / 88$ and $7 / \mathrm{Mar} / 88$ ), data were collected separately for six yellow-trap poles (four inside the crop area and two outside it), for six two-hourly periods. For the four poles inside the crop, the numbers of $B$. tabaci above and below the canopy were totalled for each of the 96 pole by date by time combinations. A logistic model was used to analyse how the percentage of $B$. tabaci adults caught above the canopy varied with time of day.

## Relationship between trap height and pole position (inside or outside the crop)

To examine the relationship between yellow-trap height and position (whether the pole was inside or outside the crop), mean counts at each height were calculated for each of the 24 pole by date combinations, averaged over the six times of day. The effect of height was analysed with a repeated measurement analysis of variance to allow for any correlation between values at adjacent heights. Because numbers of whiteflies in the higher traps were small and the data were means of only six values, a log transformation
was required to equalize the variances for the different values.

## Wind speeds and directions

Throughout the experimental periods, anemometers were situated above and below the crop canopy as well as outside the crop to measure both wind speed and direction.

## Spatial distribution of ACMD and B. tabaci

All plants were checked weekly for the presence of ACMD symptoms and newly infected plants were tagged and the date plus their location recorded.

## Results

Catch distribution in relation to time of day and pole position (inside or outside the crop)

The proportions of the total catch over the four days in the six, two-hour time periods within the crop, starting with $06.00-08.00 \mathrm{~h}$, were $0.13(n=1539), 0.19(n=2171), 0.16$ ( $n=1846$ ) , $0.18 \quad(n=2098), 0.18 \quad(n=2083), 0.16 \quad(n=1823)$. Outside the crop, the respective proportions were 0.21 $(n=344), 0.16(n=260), 0.16(n=265), 0.18(n=286), 0.17$ ( $n=269$ ), $0.12(n=197)$ indicating that the pattern of activity inside and outside the crop was very similar and that B. tabaci was flight active throughout the day.

Table 3. Results of the directional regression analysis for Bemisia tabaci catches on yellow traps, positioned above and below the crop canopy.

| Position | Co-efficients |  |  |  | Residual | $F$-test | $\mathrm{R}^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\mathrm{b}_{0}$ | $\mathrm{b}_{3}$ | $\mathrm{b}_{\mathrm{c}}$ | $\theta_{\text {max }}$ | sd ( 5 df ) | prob. |  |
| Below | 1.107 | 0.299 | 0.325 | $43^{\circ}$ | 0.075 | $P<0.001$ | 0.96 |
| Above | -1.809 | 0.220 | 0.057 | $75^{\circ}$ | 0.073 | $P=0.004$ | 0.89 |

Time of day effect on the percentage of B. tabaci adults caught above the crop canopy
The logistic model showed that the time of day significantly affected the percentage of $B$. tabaci caught above the canopy ( $P<0.001$; table 1 ) and that the effect varied from day to day (table 2). The greatest percentage of adults caught above the canopy occurred between $06.00-08.00 \mathrm{~h}$, although, even during this period, $c$. thuee times as many B. tabaci were caught beneath compared to above the canopy.

## Relationship between trap height and pole position (inside or outside the crop)

Trap height affected B. tabaci numbers significantly ( $P<0.001$ ) and there was also a significant interaction between trap height and pole position inside/outside the crop ( $P<0.001$ ), demonstrating that the effect of height depended on the pole's position (fig. 1). The difference between catches inside and outside the crop was larger $55-175 \mathrm{~cm}$ above ground than at either 25 cm or $\geq 205 \mathrm{~cm}$ (fig. 1). The maximum height of the crop canopy during the period when these data were collected was $c .175 \mathrm{~cm}$.

Trap catches outside the crop were highly biased towards the lower traps with more than $50 \%$ of the catch on the lowest trap ( 25 cm ). Moreover, $3.6(n=1272$ ) times as many B. tabaci were caught on the traps situated downwind of the field compared to those upwind ( $n=349$ ).

Directional trends above/below the crop canopy in relation to wind direction

During the period when the 'time of day' data were collected, moderate winds blew from the SW-WSW. The data show again that significantly more $B$. tabaci were caught on traps beneath the canopy than above it and that a similar significant trend in the direction of catch occurred both above and below the canopy with a peak in the NE or E (table 3 and fig. 2).

For the short pexiods during the trials when the 'Harmattan' winds occurred, the wind direction reversed and blew from the NNE. In 1988 and 1989, respectively, Harmattan winds blew during the periods $28 / \mathrm{Dec} / 87-7 /$ $\mathrm{Jan} / 88,10-12 / \mathrm{Jan} / 88$ and $16-27 / \mathrm{Dec} / 88,1-10 / \mathrm{Jan} / 89$. In these periods, the direction of the total catch also reversed with the most (c. $22 \%$ ) and least (c. $7 \%$ ) numbers of B. tabaci, respectively, caught on the southern and northern facing sections of the traps.

## Directional trends in relation to time of day

Examination of the two directional co-efficients ( $\mathrm{b}_{\mathrm{s}}$ and $\mathrm{b}_{\mathrm{c}}$ ) in table 4 shows that the catch was less strongly directional before 08.00 h , compared to the other time periods, with a peak in the south-easterly direction (and a negative $b_{c}$ ). Other differences are less pronounced, but the two periods between $08.00-12.00 \mathrm{~h}$ were very similar to each other with a peak at


Fig. 2. The relationship between log(mean Bemisia tabaci catch) and direction, above and below the canopy, for yellow traps positioned within the cassava field on days when moderate winds blew from the SW-WSW.

Table 4. Results of the directional regression analysis for Bemisia tabaci catches on yellow traps, at different times of day.

| Time (h) <br> Time (h) | Co-efficients <br> $\mathrm{b}_{\mathbf{s}}$ |  |  | $\mathrm{b}_{\mathrm{c}}$ | $\theta_{\text {max }}$ | Residual <br> $\mathrm{SD}(5 \mathrm{df})$ | $F$-test <br> prob. |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| $06.00-08.00$ | -0.255 | 0.304 | -0.181 | $121^{\circ}$ | 0.081 | $P=0.001$ | $\mathrm{R}^{2}$ |
| $08.00-10.00$ | 0.022 | 0.564 | 0.271 | $64^{\circ}$ | 0.103 | $P<0.001$ | 0.97 |
| $10.00-12.00$ | -0.139 | 0.580 | 0.240 | $68^{\circ}$ | 0.081 | $P<0.001$ | 0.98 |
| $12.00-14.00$ | 0.060 | 0.131 | 0.289 | $24^{\circ}$ | 0.122 | $P=0.010$ | 0.84 |
| $14.00-16.00$ | 0.031 | 0.037 | 0.439 | $5^{\circ}$ | 0.114 | $P=0.002$ | 0.92 |
| $16.00-18.00$ | -0.111 | 0.196 | 0.449 | $24^{\circ}$ | 0.100 | $P=0.001$ | 0.95 |

c. $70^{\circ}$. The two periods after 14.00 h were also similar to each other with a peak close to the north (fig. 3).

## Directional trends in the catch with trap height

The results for different trap heights are given in table 5 and fig. 4. It can be seen from the regression intercept $\left(b_{0}\right)$ that the numbers of B. tabaci caught. decreased as trap height increased. Also, up to 145 cm there were clear directional patterns, with the peak B. tabaci numbers in the north-easterly direction. With higher traps, the directional trend was not always statistically significant and where there was a detectable trend, the peak B. tabaci numbers tended to be in a southerly or south-easterly direction.

Directional trends in relation to trap height on a day with strong wind
On days when the wind was strong (consistently $>1 \mathrm{~ms}^{-1}$ above the canopy), the direction of the catch above and below the canopy differed. When the wind blew strongly from the south on the $27 / \mathrm{Feb} / 89$, for example, the results for circular regression revealed significant directional trends for up to 85 cm (beneath the canopy), with the peak numbers
caught in a northerly direction (table 6). At 115 cm , the approximate height of the canopy, the directional trend was very weak and at 145 cm (above the canopy) the peak was in a southerly direction, opposite to that for the lower traps. For the traps at 205 and 295 cm there was evidence that the circular regression did not fit the data (fig. 5). At these heights, two separate peaks were evident, the main peak in a southerly direction and a minor peak in the opposite, northerly direction. The following modified equation improved the fit of the line:

$$
\begin{gathered}
\log \left(\mathrm{Bt}_{25} s\right)=1.527+0.040 \times \sin (\theta)-1.787 \\
\times \cos (\theta)-2.507 \times \sin \left(\frac{(3}{2} \theta\right)-0.020 \times \cos \left(\frac{1}{2} \theta\right) .
\end{gathered}
$$

For traps at 295 cm , the $R^{2}$ value improved from 0.81 to 0.97 and the residual standard deviation (RSD) decreased from 0.296 to to 0.149 , implying a better fit and indicating that the more complex model is preferable. For traps at 205 cm , the $R^{2}$ value improved from 0.48 to 0.98 and the RSD decreased from 0.598 to 0.146 .

## Wind speed and direction

As reported by Yao et al. (1986), the lowest wind speeds $\left(0-0.4 \mathrm{~ms}^{-1}\right)$ in the study area occurred during the early


Fig. 3. The $\log$ (mean Bemisia tabaci catch) on yellow traps in relation to their orientation during the different times of day. The amplitude of the curve indicates the level of directionality in the catch.

Table 5. Results of the directional regression analysis for Bemisia tabaci catches on yellow traps positioned at different heights.

| Height (cm) | $\mathrm{b}_{0}$ |  | icients $b_{c}$ | $\theta_{\text {max }}$ | Residual <br> SD ( 5 df ) | F-test prob. | $\mathrm{R}^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 25 | 1.269 | 0.256 | 0.209 | $51^{\circ}$ | 0.059 | $P<0.001$ | 0.96 |
| 55 | 0.885 | 0.255 | 0.342 | $37^{\circ}$ | 0.081 | $P<0.001$ | 0.96 |
| 85 | 0.648 | 0.354 | 0.374 | $43^{\circ}$ | 0.142 | $P=0.002$ | 0.91 |
| 115 | -0.034 | 0.492 | 0.357 | $54^{\circ}$ | 0.115 | $P<0.001$ | 0.96 |
| 145 | -1.113 | 0.245 | 0.219 | $48^{\circ}$ | 0.113 | $P=0.006$ | 0.87 |
| 175 | -1.970 | 0.176 | -0.112 | $122^{\circ}$ | 0.175 | $P=0.15$ | 0.53 |
| 205 | -2.544 | 0.139 | -0.400 | $161^{\circ}$ | 0.230 | $P=0.04$ | 0.73 |
| 235 | -2.649 | 0.034 | -0.028 | $129^{\circ}$ | 0.305 | $p=0.96$ | 0.02 |
| 265 | -2.890 | 0.191 | -0.166 | $131^{\circ}$ | 0.456 | $P=0.58$ | 0.2 |
| 295 | -3.412 | 0.463 | -0.573 | $141^{\circ}$ | 0.294 | $P=0.011$ | 0.83 |

morning between approximately $06.00-09.00 \mathrm{~h}$ for all trap heights, both within and outside the crop. After 09.00 h and above the canopy, wind speeds could exceed $0.4 \mathrm{~ms}^{-1}$ with maximum speeds of more than $1.0 \mathrm{~ms}^{-1}$ recorded at the highest trap height. Beneath the canopy, wind speeds usually remained below $0.4 \mathrm{~ms}^{-1}$ until mid-day and were lowest closest to the ground. In the four days when trap catch was monitored in relation to time of day, the wind blew from the west in the early moming and backed towards the south west during the rest of the day.

## Spatial distribution of ACMD and B. tabaci

At the end of the season, there were approximately three times more diseased plants in 1989 than in 1988. In both yeais, however, ACMD incidence was highest and lowest, respectively, on the edges and in the middle of the trials (fig. 6). In 1988 and 1989, the highest incidence of ACMD occurred, respectively, on the western and eastern corners of the trial (fig. 6). The numbers of B. tabaci adults caught on
traps in the same field row over the first 130 days after planting (DAP) is shown in fig. 7. Within the field, the largest numbers of $B$. tabaci were caught on traps situated in the middle and at the downwind end of the field (rows $B$, D and F).

## Discussion

Our results indicate that $B$. tabaci adults in cassava fields in the Côte d'Ivoire are flight active throughout the day and that during the early morning, when wind speeds are lowest, a significant proportion of the population flies above the crop canopy. This agrees with wind-tunnel studies (Blackmer \& Byrne, 1993) in which B. tabaci adults took off at all hours of the photoperiod, but females in particular were more likely to exhibit phototactic flights from $06.00-10.00 \mathrm{~h}$.

Both inside and outside the crop, trap catches were highest nearest the ground. Benisia tabaci is a relatively weak flier and has an estimated flight speed of c. $0.2 \mathrm{~ms}^{-1}$ (Yao et al., 1986) and a maximum climb rate of c. $0.037 \mathrm{~ms}^{-1}$


Fig. 4. The relationship between $\log$ (mean Bemisia tabaci catch) on yellow traps versus direction for the different trap heights.

Table 6. Results of the directional regression analysis for Bemisia tabaci catches on yellow traps, on a day with strong wind.

| Height <br> $(\mathrm{cm})$ | Co-efficients <br> $b_{0}$ |  | $\mathrm{~b}_{\mathbf{s}}$ | $\mathrm{b}_{\boldsymbol{c}}$ | $\theta_{\text {Residual }}$ | F-test <br> SD $(5 \mathrm{df})$ | prob. |
| :--- | ---: | ---: | ---: | ---: | :---: | ---: | :--- |

$\dagger$ There was evidence that a simple directional curve did not fit the data adequately.
(Blackmer \& Byrne, 1993). The observed differences in catch size with height, therefore, probably reflects a preference to fly near the ground or beneath the cassava-crop canopy where wind speeds are lowest, thus allowing the insects increased control over their flight direction.

Under the low wind-speeds of early morning, the majority of $B$. tabaci were caught on the side of the trap opposite to the prevailing wind direction, suggesting that, in common with other insect genera (Vale, 1983), B. tabaci adults mainly approach and land on visually attractive objects by flying into the wind. For a relatively weak flier such as B. tabaci, this phenomenon might be explained aerodynamically, as movement upwind would allow the greatest control of approach speed, i.e. if an adult approached an object while flying downwind, it would have to generate backward thrust in order to avoid being blown onto it, a feat of which B. tabaci has yet to be shown to be capable.

When the wind speed exceeded $0.4 \mathrm{~ms}^{-1}$, only a few insects were able to approach the trap from downwind
because, even if they were orientated to fly facing into the wind, their overall ground-speed would take them away from the trap. Under strong wind conditions ( $>0.4 \mathrm{~ms}^{-1}$ ), therefore, most B. tabaci were caught on the sectors of the traps facing upwind, having probably been blown onto them.

The inability of $B$. tabaci to approach traps from a downwind direction when the wind speed exceeded $0.4 \mathrm{~ms}^{-1}$ implies that trap efficacy was reduced at wind speeds above this threshold. The relative numbers of B. tabaci caught on traps operating at above this thresKold, therefore, probably significantly underestimated the numbers of airborne $B$. tabaci at these levels.

Fauquet et al. (1988) found that ACMD incidence was consistently higher in cassava fields located downwind from infected cassava fields than upwind and they hypothesized that this was due to the emigration of viruliferous $B$. tabaci from the infected cassava fields situated upwind. Traps positioned outside and downwind from the trials caught $c$.


Fig. 5. The relationship between $\log$ (mean Bemisia tabaci catch) on yellow traps versus direction for the different trap heights on a day with strong wind.


Fig. 6. The distribution of ACMD-infected cassava plants at the end of the data collection period in 1988 and 1989.
3.6 times as many $B$. tabaci as those upwind, consistent with the view that the field was indeed acting as a source of whiteflies. In common with the results of Gerling \& Horowitz (1984), who used traps situated in fallow fields, most insects were caught during the early morning when wind speeds were low. It is unlikely, therefore, that these individuals would have been displaced far, although Glick \& Noble (1961) suggest that morning convection currents could carry B. tabaci up to 1600 m above ground, resulting in considerable displacements. It is not known, however, whether similar air currents occur in Côte d'Ivoire.

Beneath the cropeanopy, the preferred flight height of adults was probably $\leq 25 \mathrm{~cm}$ above ground level. Between 25 cm and the crop canopy, however, the remainder of the airborne B. tabaci population was relatively evenly distributed. This differs from the distribution of stationary $B$.
tabaci, where $50-80 \%$ of the adult population were found on the top five leaves of cassava-plant shoots (Fargette et al., 1985; Fishpool et al., 1988).

Two main flight-activity categories have been suggested for $B$. tabaci; short distance, trivial flights within and slightly above the crop canopy that are associated with 'vegetative' behaviours (sensu Kennedy, 1986) such as searching for mates, feeding and oviposition sites, and the longer distance, migratory flights which occur when the adults leave the crop and are carried downwind (Berlinger, 1986; Blackmer \& Byme, 1993). It is possible that particularly those B. tabaci caught on the traps above the crop canopy which had been blown onto the sections facing the prevailing wind, may have been involved in migratory behaviour. Most adults fitting these criteria were caught between $14.00-18.00 \mathrm{~h}$ suggesting that most long-distance down-wind displacement occurs during this period.


Fig. 7. The numbers of Bemisia tabaci caught on yellow-trap poles in 1988 and 1989. DAP = days after planting. Poles $1 \& 7$ and $6 \&$ 12 were situated outside the crop area. In 1988, data were not collected between 60 and 71 DAP.

In a study on the spread of ACMD into and within cassava fields in Côte d'Ivoire, Fargette et al. (1990) found that the monthly increase in disease incidence was directly related to the numbers of adult $B$. tabaci counted on plants six weeks earlier. Moreover, they found that most ACMD spread originated from outside sources and occurred along the south and west margins of initially healthy fields (Fargette et al., 1985; Lecoustre et al., 1989). ACMD also spread from large sources within the field and occurred similarly in all directions except 6.0 and 6.5 months after planting when there were significantly more diseased plants upwind of the source (Fargette et al., 1990). It was suggested, therefore, that there may be more upwind than downwind movement of adults within cassava fields and preliminary field experiments supported this (van Helden \& van Halder, unpublished data). On first inspection, the directionality of our trap-catch data appear to provide additional evidence of this phenomenon. However, if it were true, one might expect this behaviour to translate into a bias in the whitefly population towards the upwind edge of the field which was not observed. Indeed, towards the end of both seasons, the largest numbers of $B$. tabacici were caught in the middle and at the downwind end of the trials.

Our results also showed a very strong edge effect for the distribution of ACMD, supporting those of Fargette et al. (1990). This effect, caused by the arrival of viruliferous immigrant B. tabaci on the periphery of the trial, has previously also been recorded in the lowland forest area of Côte d'Ivoire (Fauquet et al., 1988). In our two trials, significantly more ACMD spread occurred in 1988 than in 1989, which was probably due to the higher numbers of $B$. tabaci which immigrated into the crop at the start of the season when plants are most susceptible to infection (Fargette \& Vié, 1994; Fargette et al., 1994).

Results of studies such as this can be used to assess the feasibility of proposed ACMD control measures. Two hundred kilometres north of Adiopodoumé at Toumodi, for instance, much less cassava is grown and there is little spread by whiteflies. In this situation, cultural practices such as roguing of diseased plants and siting new cassava fields away from older, diseased plantings, enable healthy material to be maintained (Fauquet et al., 1988). In areas of rapid spread such as Adiopodoumé, however, a strategy based on the release of healthy cultivars is unlikely to be successful unless the released varieties also have considerable resistance to ACMD. In addition, as most ACMD spread into healthy cassava fields occurs at the edges, our results suggest that the use of ACMD-resistant guard rows could potentially provide protection to a mainly susceptible crop.

## Acknowledgements

The authors are grateful to Drs M. Thresh, R. Cooter and A. Cook for perceptive comments on the manuscript. This research was funded by EEC grant number TS2A-0137$C(C D)$ and by the UK Department For International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID (ZA0152, Crop Protection Programme).

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# BULLETIN of ENTOMOLOGICAL Research 

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[^0]:    (Accepted 4 March 1998)
    (C) CAB INTERNATIONAL, 1998

[^1]:    PM $2: 6$
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