Bulletin of Entomological Research (1995) **85**, 197–207

The phenology of *Bemisia tabaci* (Homoptera: Aleyrodidae) populations on cassava in southern Côte d'Ivoire

L.D.C. Fishpool
Natural Resources Institute, Chatham, Kent, UK

C. Fauquet, D. Fargette, J.-C. Thouvenel, C. Burban
Laboratoire de Phytovirologie, ORSTOM, Abidjan, Côte d'Ivoire

J. Colvin
Natural Resources Institute, Chatham, Kent, UK

Abstract

Population phenologies of the whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae), in young cassava crops in Côte d'Ivoire, West Africa, are described for three field seasons. Populations of all stages were consistently greatest 6–12 weeks after the crop was planted. The number of adults on plants as well as on attractive and non-attractive sticky traps displayed cycles of buildup and decline each year, the periodicity of these cycles corresponding to the generation time of *B. tabaci* under field conditions. Adult population declines were probably caused by emigration from the crop. Rainfall was negatively correlated with both nymph and adult populations, possibly due to reduced oviposition after rain. *B. tabaci* is the vector of African cassava mosaic geminiviruses (ACMV) and the observed *B. tabaci* population trends fit well with the pattern of ACMV buildup in the crop.

Introduction

The whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae), has become an increasingly important cosmopolitan pest, both directly and as a vector of plant viruses (Byrne *et al.*, 1990). One of these viruses, apparently specific to *B. tabaci*, is the African cassava mosaic geminivirus (ACMV) which is the most economically important insect-transmitted plant pathogen in sub-Saharan Africa (Geddes, 1990; Thresh *et al.*, 1994).

Cassava, *Manihot esculenta* (Euphorbiaceae), is the most important staple food of southern Côte d'Ivoire. It is traditionally grown in a patchwork of small plots, comprising a range of local cultivars many of which are susceptible to ACMV. Cassava from these plots is harvested only when needed and rarely before it is a year old. This, together with the lengthy rainy season and extended planting period, means that stands of cassava of differing age are always available to *B. tabaci* and virtually all show African cassava mosaic disease (ACMD) symptoms.

Ecological studies of *B. tabaci* on cassava have been undertaken in Nigeria (Mound, 1963; Leuschner, 1978), Kenya (Seif, 1981; Robertson, 1987), Togo (Dengel, 1981) and more recently in Côte d'Ivoire (Abisgold & Fishpool, 1990; Fishpool *et al.*, unpublished data). In addition, a recent taxonomic study identified a biotype of *B. tabaci* from Côte d'Ivoire which is largely restricted to cassava (Burban *et al.*, 1992).

Research on the ACMD pathosystem in southern Côte d'Ivoire began in 1981 (for a review see Fauquet & Fargette, 1990). This paper stems from that investigation and describes the phenology of *B. tabaci* populations in relation to cassava-crop growth, climatic factors and the spread of

Correspondence: Dr J. Colvin, Natural Resources Institute, Central Avenue, Chatham Maritime, Chatham, Kent ME4 4TB, UK.

ACMD. Other aspects of the ecology of *B. tabaci* on cassava such as spatial distribution and flight behaviour are considered elsewhere (Fishpool *et al.*, unpublished data).

Materials and methods

Experimental site and trial layout

The work described here was undertaken on the 50 ha ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération) experimental farm at Adiopodoumé (05° 19'N, 04° 13'W), ca. 20 km west of Abidjan in the lowland rain-forest zone of Côte d'Ivoire, West Africa. The farm consisted of 1 ha plots supporting a mixture of different crops including cassava. It was bounded on two adjacent sides by a rain-forest reserve and on the others by farmers' fields.

The site usually receives some 2000 mm of rain per annum, mainly between the periods of April to July and October to November. Mean monthly temperatures are broadly similar throughout the year and the hottest and coldest months respectively, e.g. February and July, have mean temperatures of ca. 28°C and ca. 25°C. The wettest and driest months, respectively, are also the coolest and hottest. Winds are predominantly south-west for more than 11 months of the year.

The cassava cultivar used in all experiments was Kasimbidgi Green, a tall, late branching selection of Kenyan origin and considered resistant to ACMD (Fauquet & Fargette, unpublished data). The cassava was propagated in the form of leafless cuttings, comprising sections of stem from apparently disease-free parents. Although the new crop was initially whitefly free, some cuttings rapidly developed ACMD symptoms implying that not all planting material was disease-free.

The experimental layout comprised 49 blocks (7 by 7) spaced 2 m apart, each containing 100 plants spaced 1 m×1 m apart (4900 plants in all). Separate trials, planted in November/December and run for a minimum of four months, were conducted in 1988, 1989 and 1990. Trials were planted at the beginning of the dry season, contrary to local agricultural practice in which it is customary to plant at the start of the rains (April–May). Previous research demonstrated, however, that *B. tabaci* populations are greatest at the beginning of the dry season and maximal on young plants (Fargette, 1987; Fishpool *et al.*, 1988). It was decided, therefore, that the benefits of working with large populations of *B. tabaci* outweighed the disadvantages of unseasonality. The same site was used for the 1988 and 1990 trials, with the trial-site being moved to an immediately adjacent area in 1989. Trials usually required irrigation two or three times in the first three weeks after planting to facilitate crop establishment. Each year, the 0.75 ha trial site was orientated such that the dominant south-west winds crossed the upwind field border at right-angles.

Data collection

Adult *B. tabaci* monitoring began two to three weeks after planting, when the new crop had developed sufficient foliage to support an adult population. Adults were monitored twice weekly, by making counts on ten plants per block. One weekly count followed set transects through the blocks, monitoring the same 490 plants on each occasion. For the other count, two randomly selected plants per block plus their four nearest neighbours were chosen. Data were obtained by counting the adults on the undersurfaces of the top five leaves of one growing apex per plant. Counts were made mid- to late-morning when the wind speed had increased, conditions under which *B. tabaci* is reluctant to fly. Earlier work demonstrated this technique to be suitable for monitoring adults since 50–80% of the adult *B. tabaci* population on a stem are confined to the top five leaves (Fargette *et al.*, 1985; Fishpool *et al.*, 1988).

In 1988 and 1989, adults were also monitored using 12 yellow and six grey sticky traps which, respectively, are attractive and unattractive to *B. tabaci* (Mound, 1962; Vaishampayan *et al.*, 1975). Yellow traps comprised 3 m upright lengths of 9 cm diameter grey PVC tubing, with ten 10 cm wide adhesive-backed strips of brilliant yellow plastic (Starcolor®, no. 74100) wrapped around the tubes at 25 cm intervals. Slightly wider, transparent, removable, cellophane strips were then placed over the yellow bands, fixed with sticky tape and then covered in insect adhesive (Tangle-Trap®). Grey traps differed only in the absence of the yellow strips. Traps were placed in south-west/north-east oriented lines spaced 24 m apart, with yellow traps running along the middle of the second and sixth row of blocks and grey traps along the fourth row of blocks. Traps at the ends of each line were placed 4 m from the edge of the experimental area. The four remaining traps of each line were placed in the second, fourth and sixth column of blocks as well as the south-west facing edge of the experimental area. Adults were counted twice-weekly on the yellow traps and weekly on the grey traps when the cellophane strips were changed.

Bemisia tabaci nymph monitoring began ca. five weeks after planting and thereafter continued weekly using two different methods. In one method, field counts of third and fourth instars were made using a hand lens, the latter including the so called 'pupae'. Counts were conducted on one plant per block and were restricted to the central three folioles of leaves 11–20 from the growing tip. On actively growing plants, most of the viable fifth instar nymphs are restricted to these leaves, due both to the adult preference for ovipositing on leaves at the growing tip and to the sessile nature of the nymphs (Abisgold & Fishpool, 1990). In the other method, the thirteenth leaf down from the growing tip was removed from one randomly selected plant per block and the numbers of fourth instars were counted in the laboratory using a stereomicroscope.

In 1989 and 1990, whole plants were destructively sampled each week and the numbers and position (leaf number) of *B. tabaci* eggs were recorded. These plants, of the same variety and planting date as the main trial, were taken from a small stand of cassava located a few metres from it. Initially, five plants were sampled each week but towards the end of the trial, as the plants grew in size, the number was reduced to one.

Estimates of the developmental rates of immature stages were obtained in the field by examining individually identified eggs and nymphs daily. Eggs of known age were obtained by confining adult females in clip cages for 24 hours.

Mean root weight was obtained each week from a sample of five plants taken from the same stand used to sample destructively for nymphs. Other weekly plant growth parameters including the numbers of stems, apices

and new leaves produced were obtained by selecting one plant per block from the main trial.

The trial was also checked weekly for ACMD incidence. All newly infected plants were tagged and the date plus their location recorded.

Rainfall and temperature data were obtained from the ORSTOM field station's meteorological site, some 300 m distant.

Data analysis

The adult and nymph field counts as well as the trap data were examined by time-series analysis using Statgraphics software (STSC, 1991). The adult data, comprising twice weekly counts at alternating three and four day intervals, were divided into two subsets at weekly intervals since such analyses require that data points be separated by constant intervals. Periodograms were generated and the lengths of the most 'powerful' cycles in the data calculated. Cross-correlation coefficients were also calculated to test for relationships between the adult and nymph data.

The relationships between the adult, nymph and yellow-trap data sets and various meteorological and plant growth parameters were examined by stepwise regression. The variables, tested as weekly means, were rainfall, maximum and minimum temperature, root weight and leaf production. For this analysis the corresponding data for all three trials were treated as continuous series, although the adult data were divided in two as before. For analysis, the adult and nymph data were square-root transformed and the yellow-trap data were log transformed. After testing and removal of autocorrelation and trend, they were regressed with the meteorological and plant growth covariates. In each case, they were regressed with time lags of 0, 1, 2 and 3 weeks on the *B. tabaci* data sets.

Results

The phenologies of the adult populations for the three trials, expressed as mean numbers per apex, are given in figures 1A, 2A and 3A. All three data sets show a number of common features: an initial slow buildup of the population as immigrant adults colonize the crop; a more rapid increase 35–40 days after planting (DAP), representing the onset of local recruitment; a variable number of population peaks interspersed with rapid declines and a decrease in the population ca. 110–120 DAP to a 'residual' level that is maintained for the remainder of the life of the crop. The maximum number of adults per apex in 1989 was approximately half that of 1988 and 1990.

The years 1988 and 1989 show three distinct adult population peaks. The pattern is less well defined in 1990 where extreme oscillations occurred between 50 and 80 DAP. This coincided with the harvesting of 2 ha of mature cassava 44–55 DAP, at a minimum distance of ca. 220 m upwind of the trial. Immigration at this time, therefore, probably contributed to the fluctuations in the adult field count. A discrete peak, however, was still evident ca. 95 DAP.

In all three years, ca. 1% of the crop showed ACMD symptoms 20 DAP (figs 1A, 2A, 3A). Newly infected plants take a minimum of 3–4 weeks to exhibit symptoms (Fargette *et al.*, 1990) and so diseased plants showing symptoms so early in the trial probably derived from infected cuttings. After the initial high, the incidence of new ACMD infections declined in all three years, followed by second and third peaks at various intervals throughout the season. The highest incidence of ACMD occurred in 1989, although the adult *B. tabaci* population was only ca. 50% the size attained in the other two years.

For a given trial, the different methods of sampling for nymphs produced population curves similar in structure and size (figs 1B, 2B, 3B). There is also a similarity between trials in overall trend as well as with the phenology of the corresponding adult populations. Thus, the pattern recurs of build up to one or more peaks from initial low levels, followed by a crash 90–100 DAP. The nymph data, however, generally lack the abrupt fluctuations between counts seen in the adult data probably because of the sessile nature of nymphs. In agreement with the adult data, the 1989 nymph numbers are much lower than those of 1988 and 1990.

Egg population data for the 1989 trial are shown, together with rainfall, in figure 2C. There is an initial peak in egg numbers around 50 DAP, immediately following the first peak in adult numbers (fig. 2A). Thereafter, there is a rapid decline such that by 70 DAP the number of eggs is only about 10% that of three weeks earlier and it then remains at approximately this level. The phenology of the 1990 data (fig. 3C) differs in that egg numbers peak at 73 DAP and then fluctuate over the remainder of the trial around a level attained ca. 40 DAP.

Figure 4 shows the yellow- and grey-trap data for 1988 and 1989. Apart from the obvious quantitative differences between the numbers caught on the different coloured traps, the two data sets in each year show very similar trends in the coincidence of both the maxima and minima. For the 1989 trial in particular, there are also obvious similarities in the pattern of abundance of adults on the crop and trap-catches (figs 2A & 4B), with the three peaks and troughs of the trap-catch data occurring slightly later than those of the field counts. Thus, peak trap catches coincide with a decline in field populations. Similar trends are seen in the 1988 data (figs 1A & 4A).

The rates of development of immature stages under field conditions are given in table 1. Developmental time from egg to adult took 20–21 days, which is comparable to that found elsewhere at similar temperatures (Gerling *et al.*, 1986; Powell & Bellows, 1992) both in overall duration and in the relative proportions spent in each stadium.

Of particular interest is the periodicity between both the peaks and the troughs in the adult and nymph data sets and time series analyses suggested that there are population peaks every 3–4 weeks (table 2). The length of cycle varies between years for both adults and nymphs and the cycles in the nymph data are generally rather longer than those for adults. Reasons for these differences are more likely to be attributable to the variability of the data rather than to any biological factor.

Table 3 shows the cross-correlations between the adult and nymph data. Overall there is little consistency, with only the 1989 nymph data giving a significant result. The lack of significant correlations, however, does not necessarily imply that conclusions cannot be drawn, since the pattern of the coefficients may be more informative than the significance level (Diggle, 1990). Consequently, it is suggestive that in five of six cases, a time lag of +1 gives one of the two highest correlations. This implies that an increase

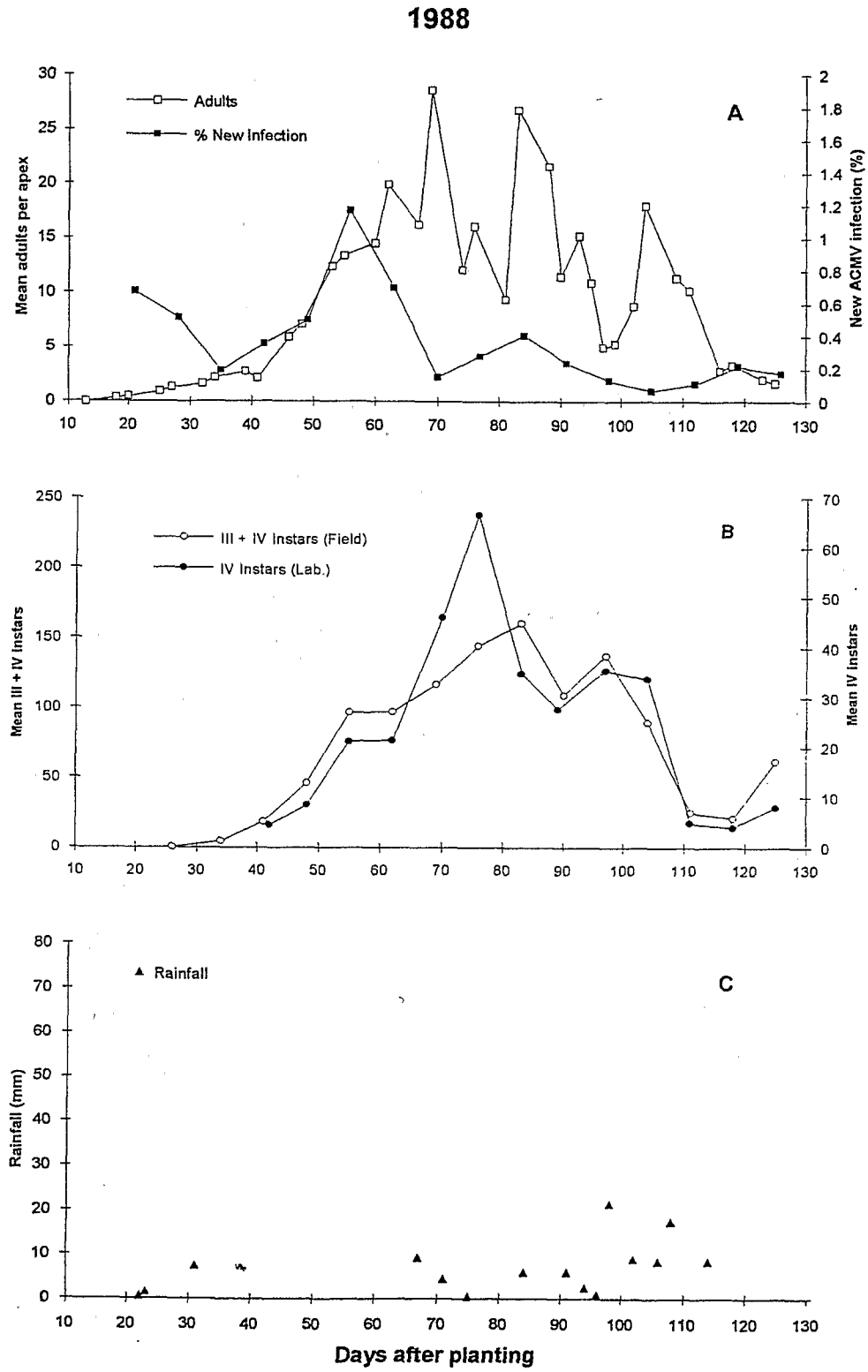

Fig. 1. 1988 data for: A) field counts of adult *Bemisia tabaci* expressed as mean numbers of adults per apex (ca. 2.1 apices per plant), as well as new ACMV infection expressed as a percentage of remaining healthy plants developing symptoms; B) mean numbers of nymphs derived from field counts of third and fourth instars as well as laboratory counts of fourth instars; (C) rainfall.

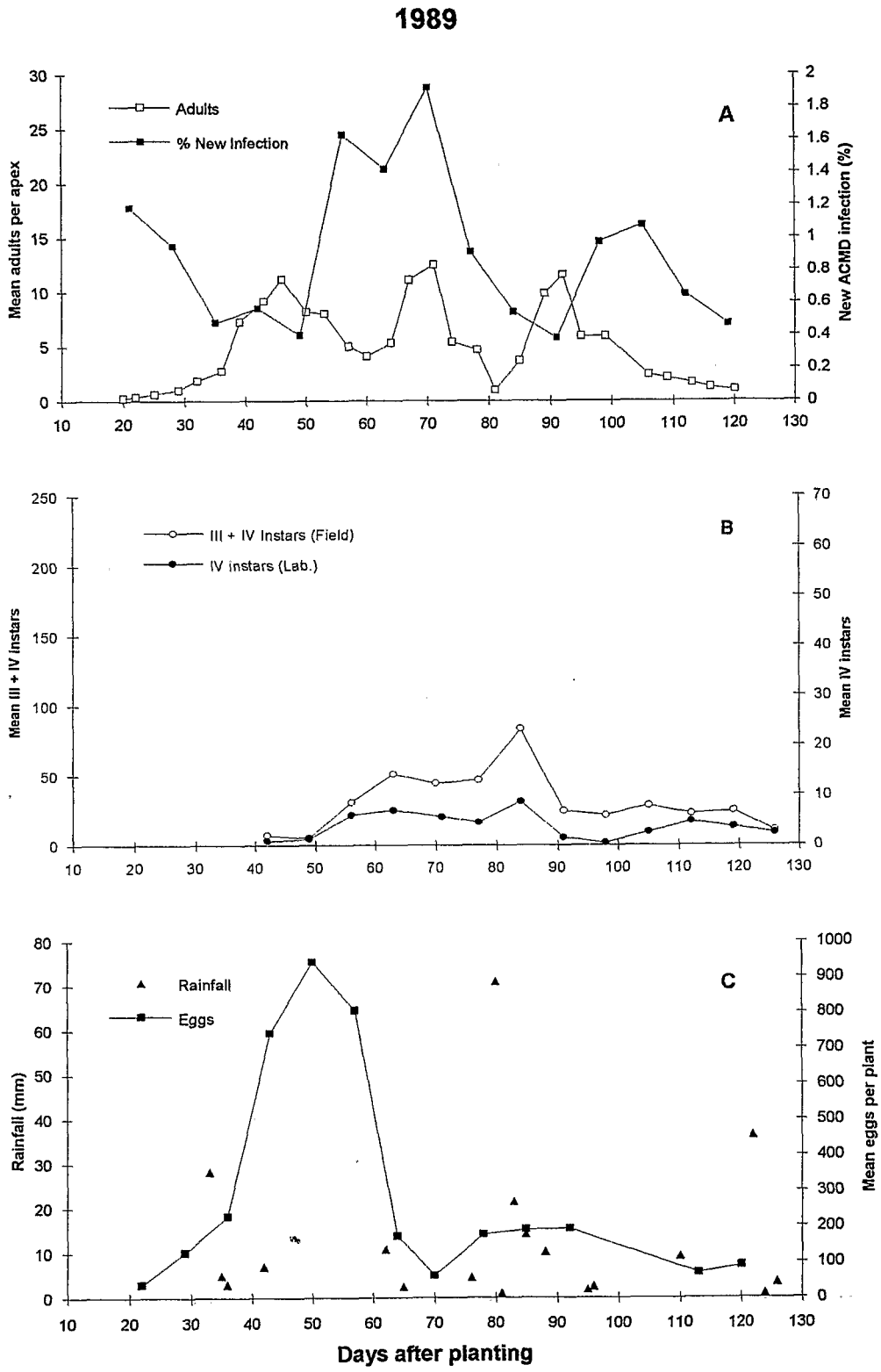

Fig. 2. 1989 data for: A) as for figure 1A except that there were ca. 1.77 apices per plant; B) as for figure 1B; C) rainfall plus mean numbers of eggs per cassava plant.

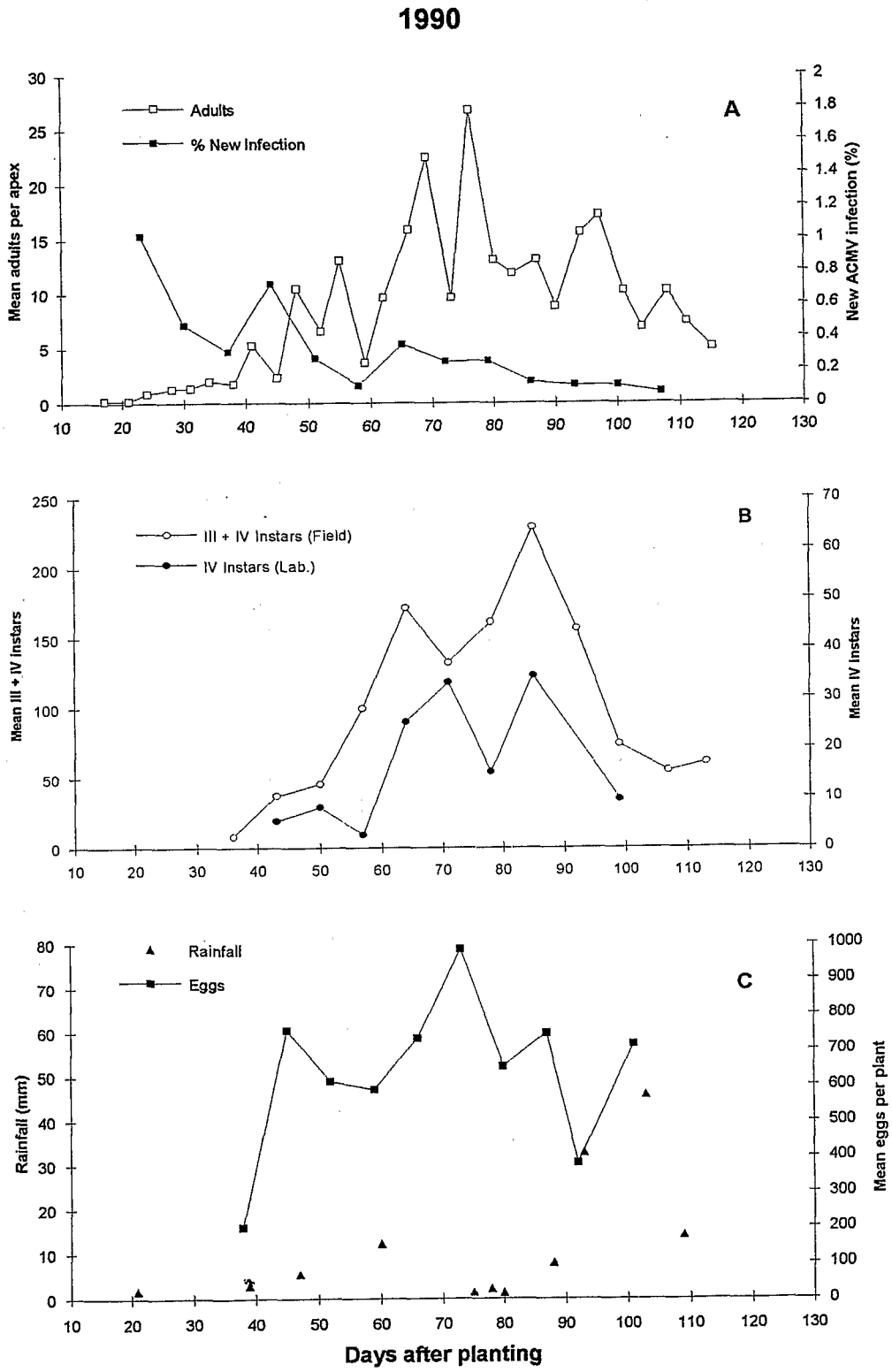

Fig. 3. 1990 data for: A) as for figure 1A except that there were ca. 1.75 apices per plant; B) as for figure 1B; C) as for figure 1C.

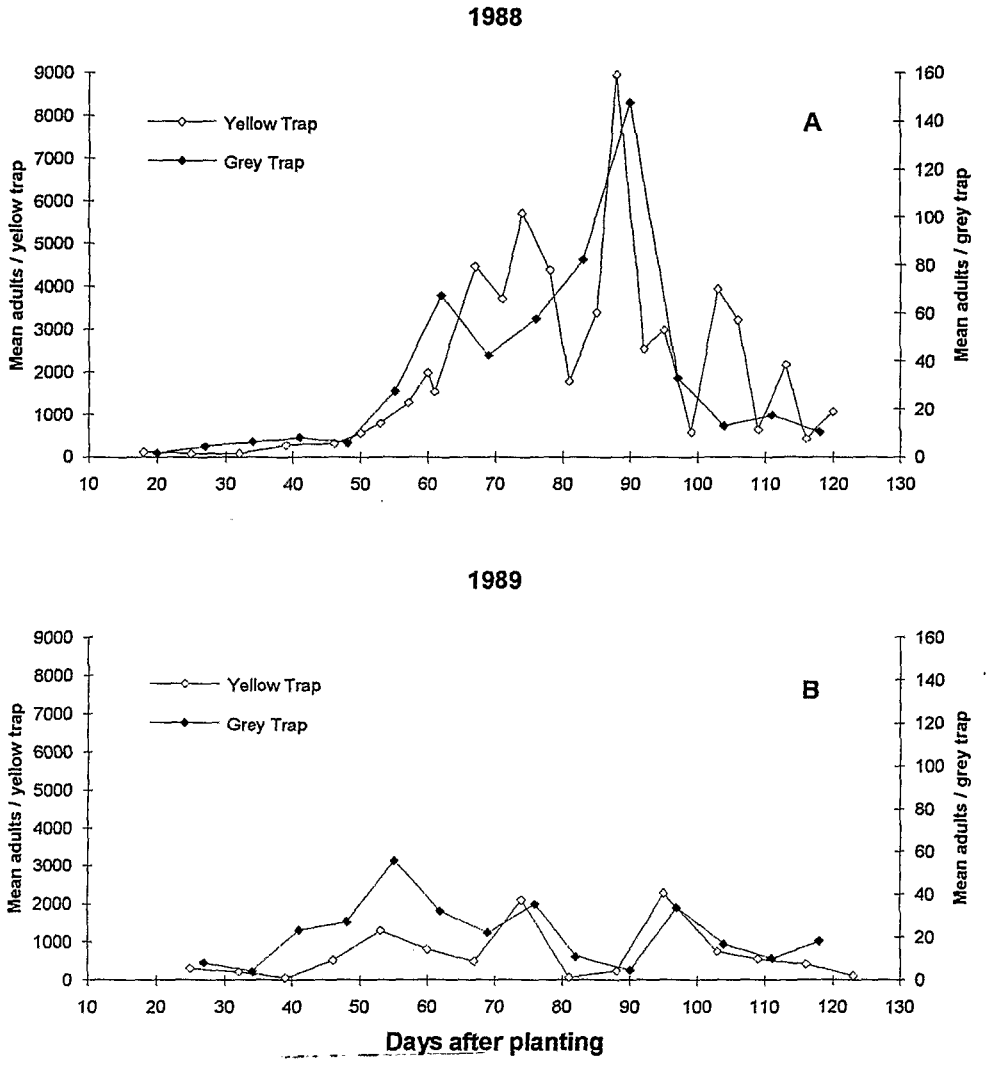

Fig. 4. Attractive (yellow) and unattractive (grey) trap catches of adult *Bemisia tabaci* for: A) 1988; B) 1989.

in fourth instar numbers in a given week would lead to a corresponding rise in adult numbers 8–13 days later. This is evident in 1989 (fig. 2), where two of the three adult maxima are preceded by peaks in nymph numbers ten days earlier. Such a time lag approximates well to the developmental period of the final instar (table 1). Similarly, a lag of −2 is positively correlated in three of the six cases, i.e. an adult peak is succeeded 14–21 days later by a peak in fourth instars. This is also consistent with the developmental period of egg to fourth instar (table 1). Of the other correlations little can be inferred.

For the stepwise regression analysis, only those parameters with time lags giving significant correlations are shown (table 4). These results suggest that rainfall, and in fewer instances, minimum temperature, influence the size of the *B. tabaci* populations. In all cases these correlations were negative, i.e. increasing rainfall and higher minimum temperatures were associated with lower population size. The time intervals over which these effects operate vary with the different data sets. Thus, adult field counts decline as a result of rainfall 22–28 days previously, while nymphs are affected by rain 8–14 days earlier. Yellow-trap catches were

Table 1. Developmental periods under field conditions of immature stages of *Bemisia tabaci* on cassava. Fourth instar includes the so-called pupal stage. Average maximum temperature for observation period was 31.5°C; average minimum was 23.6°C.

	Egg	Instars				Total
		I	II	III	IV	
Mean duration ± SEM (days)	6.1 ± 0.05	3.5 ± 0.12	2.3 ± 0.07	2.7 ± 0.09	6.2 ± 0.15	20.8
N	46	46	47	47	24	

Table 2. Cycle length (C.L.) in days, obtained from time-series analysis of adult and nymph data. Twice-weekly adult counts were divided into two series at weekly intervals for analysis. Fourth instars include 'pupae'.

	1988 C.L. (days)	1989 C.L. (days)	1990 C.L. (days)
Adults (series 1)	17–19	20–22	none
(series 2)	17–19	22–24	21–28
Nymphs (III+IV) (field counts)	25	26, 20	23
Nymphs (IV) (lab. counts)	28	28	21

suppressed following rainfall both in the week immediately preceding the catch and, to a lesser degree, by rain 22–28 days before. The effects of minimum temperature are less consistent, having a significant effect only in three of the six data sets and with different time lags for the two adult field count series.

Table 4. Significant correlations found by stepwise regression between meteorological variables and *Bemisia tabaci* data sets. All correlations negative. Time lags: t-3=3–4 weeks (22–28 days), t-1=1–2 weeks (8–14 days), t=1–7 days. Data sets for all three years have been treated as continuous series.

	Parameter	Time lag	F Value	d.f.
Nymphs				
Field	Rainfall	t-1	10.79**	29
Lab. (IV)	Rainfall	t-1	7.36*	20
Lab. (all)	Rainfall	t-1	7.43*	22
	Min. Temp.	t-1	5.82*	22
Adults				
Data set 1	Min. temp.	t-3	7.73**	36
	Rainfall	t-3	4.85*	36
Data set 2	Min. Temp.	t-2	4.95*	36
	Rainfall	t-3	4.11*	36
Yellow Trap	Rainfall	t	22.21**	35
	Rainfall	t-3	4.12*	35

*$P < 0.05$; **$P < 0.01$.

Discussion

Whitefly identification currently relies almost entirely on nymph morphology and thus adult determination is inferred by association. Consequently, all adults counted in the field and on traps in this study were assumed to be *B. tabaci*. Studies of nymphs, however, revealed the presence of a second species of whitefly at Adiopodoumé, *Bemisia afer* (Priesner & Hosny) (=*B. hancocki* Corbett), a species not yet tested as a vector of ACMD. *Bemisia afer* comprised up to ca. 5% of the total nymph population (Fishpool, unpublished data), so its frequency in the adult population is unlikely to have been greater than this. The occurrence of two biotypes of *B. tabaci*, one largely confined to cassava, the other polyphagous but avoiding cassava (Burban *et al.*, 1992), is a further complication, particularly in the interpretation of the trap-catch data and emphasises the importance of monitoring nymphs. The overall congruence of the cassava and trap data, however, suggests that the non-cassava biotype was probably not a significant component of the trap catches.

The shape of the population curves recorded here (figs 1, 2 & 3) show similarities with those frequently found for *B. tabaci* on cotton, where four phases can be identified: initial moderate growth rates, exponential growth, stability (not always present) and decline (Horowitz, 1986). However, elsewhere in West Africa, similar shaped curves were obtained for an adult population in coastal Togo on a crop planted in April (Dengel, 1981) and in Nigeria, for a crop of unspecified planting date, using yellow sticky traps (Leuschner, 1978).

Table 3. Cross correlations between adult and numph data. Only the three lags with the highest correlation coefficients are given. Time lags (T.L.): 0=1–7 days; +1 or −1=plus or minus 8–13 days respectively; ±2=±14–21 days; ±3=22–28 days; ±4=29–35 days. Corr.=positive or negative correlation and higher correlations are presented above lower ones.

	1988		1989		1990	
	T.L.	Corr.	T.L.	Corr.	T.L.	Corr.
Nymphs (III+IV)	−2	+ve	+1	+ve*	0	+ve
(field counts)	+1	+ve	−2	+ve*	+1	+ve
	−1	−ve	0	−ve*	−3	+ve
Nymphs (IV)	+3	−ve	−2	+ve	−2	−ve
(lab. counts)	+1	+ve	+1	+ve	−3	+ve
	+4	+ve	0	−ve	+1	−ve

*$P < 0.05$.

The three major fluctuations in adult population counts between 40–100 DAP (figs 1A, 2A & 3A) are suggestive of discrete generation peaks. Evidence of partial separation of generations is provided both by direct counts of adults and nymphs (table 2) as well as by trap catches (fig. 4). A slow but steady influx of immigrant adults into the crop over the first six weeks after planting (figs 1A, 2A & 3A), however, suggests that generations must also be overlapping to some extent.

Compared with reports for other hosts, *B. tabaci* populations on cassava are generally relatively small and do not, for example, reach the densities reported on cotton in the Sudan (von Arx *et al.*, 1984). This may be partly because the 'system' is a new one–*B. tabaci* is possibly of Indian origin (Mound, 1965), while cassava was originally introduced into Africa from South America in the 16th century (Fauquet & Fargette, 1990). Only the virus is of Afrotropical origin, although its original host(s) remain unknown (Fargette, 1987). Furthermore, although *B. tabaci* occurs as an introduced species in South America, it does not infest cassava there and can only be induced to do so with extreme difficulty and under laboratory conditions (Costa & Russell, 1975). The adaptation by *B. tabaci* to cassava in Africa (and Asia), therefore, is of recent origin and, at least in Côte d'Ivoire, has given rise to an identifiable, host-adapted biotype (Burban *et al.*, 1992).

The causes of the abrupt declines in the adult populations which occur 0–110 DAP (figs 1A, 2A & 3A) are uncertain, although the absence of corresponding rapid decreases in third and fourth instar populations prior to these 'crashes' (figs 1B, 2B & 3B) indicates that they are not caused by large fluctuations in recruitment rate from the final instar. There is also no evidence to suggest that they are due to rapid changes in adult mortality, although almost nothing is known about this factor and, therefore, it cannot be discounted completely. The most probable explanation of this phenomenon is emigration from the crop by a proportion of the adult population. The close correlation between peaks in mean daily trap catch with periods of rapid

decline in the adult field populations (figs 1A, 2A & 4) is consistent with this hypothesis.

Dispersal of *B. tabaci* populations has also been observed from cotton, where it is linked to decreasing food quality caused by host-plant ageing (Gerling & Horowitz, 1984; Berlinger, 1986; Cock, 1986; van Lenteren & Noldus, 1990). In cassava, tuberization begins 30–60 DAP (IITA, 1990) and the resultant changes in resource partitioning within the plant may adversely affect the nutritional quality of the aerial parts. Root weight, however, was not selected by stepwise regression as a determinant of adult or nymph population size (data not shown).

Bemisia tabaci populations are also influenced by climatic factors (Horowitz, 1986), although there is little consensus as to what these factors are or how they operate. Rainfall for instance, has been reported as reducing populations both on cassava (Golding, 1936; Mound, 1960; Dengel, 1981; Robertson, 1988) and cotton (Khalifa & El-Khider, 1964; Gameel, 1970). Both Leuschner (1978) and Lal (1981), however, reported no effect of rainfall, while Seif (1981) thought its effects were indirect but positive.

The time intervals over which rainfall was associated with reductions in the size of *B. tabaci* populations can be interpreted in terms of the length of the insect's life cycle (table 1). With a developmental time from egg to adult of 3 weeks, the reduction in adult field counts following rainfall 22–28 days earlier (table 4) suggests that rain may act to suppress oviposition and/or increase the mortality of first instar larvae which are mobile. The reduction in the nymph populations 8–14 days after rain is also consistent with this. No significant correlation was found between rain and adult counts 1–7 days later, suggesting that rainfall has no direct effects on adult numbers, such as increased mortality or emigration.

The significant effect of rain in reducing trap catches (table 4) can be explained because rain is usually associated with strong winds which inhibit flight. In addition, heavy rain also reduced the stickiness of the glue on the traps.

Evidence that oviposition declines with increasing rainfall is provided by the 1989 and 1990 regression analysis, which detected an inverse but not quite significant relationship between these two variables. That the relationship is not clearer is probably due to the quality of the egg population data which were obtained from whole plant destructive samples, a method not specifically designed to sample for eggs which are inconspicuous and usually aggregated on the youngest leaves of a shoot. The negative relationship between oviposition and rainfall is also evident from figures 2C and 3C and thus, while there was a marked decrease in oviposition from ca. 60 DAP in 1989 (fig. 2C), this did not occur in 1990 which was a much drier year (fig. 3C).

Egg mortality assessment was not specifically attempted in this study, although in agreement with data reported elsewhere (Horowitz *et al.*, 1984), observations made while monitoring individual *B. tabaci* development rates (table 1) suggest that egg mortality was very low.

Without further field work, the significant negative relationship between minimum temperature and adult population size (table 4) is difficult to interpret, especially given the different time lags over which its effects operate on the two data sets. One possibility, however, is that lower temperatures may reduce flight activity and hence emigration from the crop.

In an associated study of the causes of variation in rates of ACMD spread at Adiopodoumé, it was found that disease increment in the second month after planting was highly significantly ($P < 0.001$) and dependent both upon average maximum temperature as well as mean adult *B. tabaci* population size in the preceding month (Fargette *et al.*, 1994). Rainfall during the same period, although significant at the 5% level, was much less important. It is surprising, therefore, that maximum temperature was not found to be a significant determinant of *B. tabaci* population size in this study. Meteorological data used here, however, were weekly means, whereas Fargette *et al.* (1994) used monthly averages to allow time for disease symptom expression. In addition, their study continued over several years while this analysis is confined to the same four months of each year. It is also possible that the relative importance of the different meteorological parameters varies seasonally.

Yellow traps have been used extensively to monitor *B. tabaci* populations in cotton (Gerling & Horowitz, 1984; Butler *et al.*, 1985; Byrne *et al.*, 1986) and, to a lesser extent, in cassava (Leuschner, 1978; Fargette *et al.*, 1985; Fishpool *et al.*, 1988; Robertson, 1987, 1988). Although others have considered them unsuccessful, e.g. Seif (1981), they proved effective in this study. The overall correspondence in the trends of the yellow- and grey-trap catches (fig. 4A, B) indicates that, although the attractiveness of the yellow trap may modify the behaviour of the adult whitefly, the effects on this analysis of any such changes seem to be solely quantitative.

The fluctuations in the numbers of plants newly showing symptoms of ACMD infection (figs 1A, 2A & 3A) fit well with what is known of the epidemiology of the disease in Côte d'Ivoire (Fauquet *et al.*, 1988). Plants that develop disease symptoms immediately upon sprouting derive from infected cuttings. From 40–50 DAP onwards there is an increase in the number of newly infected plants and these represent the first to become infected as a result of virus transmission by immigrant *B. tabaci*. The expression of disease symptoms following infection takes a minimum of 3–4 weeks (Fargette *et al.*, 1990) which is consistent with the arrival of the earliest colonist in the crop. The number of new infections reaches a maximum ca. 60–70 DAP, declines thereafter and is succeeded by a second smaller peak 85–100 DAP. This reflects both the phenology of the *B. tabaci* populations and the decreasing susceptibility with age of cassava to infection with ACMD (Fauquet & Fargette, 1990).

Acknowledgements

The authors are very grateful to Cliff Gay, Bob Cheke and Andrew Madden for help with the statistical analyses and to Drs M. Thresh, G. Fabres and A. Cook for perceptive comments on the manuscript. This work was supported in part by EEC grant number TS2A-0137-C(CD).

References

Abisgold, J.D. & Fishpool, L.D.C. (1990) A method for estimating population sizes of whitefly nymphs (*Bemisia tabaci*) on cassava. *Tropical Pest Management* **36**, 287–292.

Berlinger, M.J. (1986) Host plant resistance to *Bemisia tabaci*. *Agriculture, Ecosystems and Environment* **17**, 69–82.

Burban, C., Fishpool, L.D.C., Fauquet, C., Fargette, D. & Thouvenel, J.-C. (1992) Host-associated biotypes within West African populations of the whitefly *Bemisia tabaci* (Genn.) (Hom.: Aleyrodidae). *Journal of Applied Entomology* **113**, 416–423.

Butler, G.D. Jr, Henneberry, T.J. & Natwick, E.T. (1985) *Bemisia tabaci*: 1982 and 1983 populations in Arizona and California cotton fields. *Southwestern Entomologist* **10**, 20–25.

Byrne, D.N., Bellows, T.S. Jr & Parrella, M.P. (1990) Whiteflies in agricultural systems. pp. 227–261 *in* Gerling, D. (*Ed.*) *Whiteflies: their bionomics, pest status and management.* Andover, UK, Intercept.

Byrne, D.N., Von Bretzel, P.K. & Hoffman, C.J. (1986) Impact of trap design and placement when monitoring for banded-winged whitefly and sweet potato whitefly (Homoptera: Aleyrodidae). *Environmental Entomology* **15**, 300–304.

Cock, M.J.W. (1986) Population ecology. pp. 37–41 *in* Cock, M.J.W. (*Ed.*) *Bemisia tabaci – a literature survey on the cotton whitefly with an annotated bibliography.* 121 pp. Ascot, CAB International Institute of Biological Control.

Costa, A.S. & Russell, M. (1975) Failure of *Bemisia tabaci* to breed on cassava plants in Brazil (Homoptera, Aleyrodidae). *Ciencia e Cultura* **27**, 388–390.

Dengel, H.J. (1981) Untersuchungen über das Auftreten der Imagines von *Bemisia tabaci* (Genn.) auf verschiedenen Manioksorten. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* **88**, 355–366.

Diggle, P.J. (1990) *Time series: a biostatistical introduction.* Oxford, Clarendon Press.

Fargette, D. (1987) *Epidémiologie de la mosaique africaine du manioc en Côte d'Ivoire.* PhD thesis, ORSTOM, Paris.

Fargette, D., Fauquet, C. & Thouvenel, J.-C. (1985) Field studies on the spread of African cassava mosaic. *Annals of Applied Biology* **106**, 285–294.

Fargette, D., Fauquet, C., Grenier, E. & Thresh, J.M. (1990) The spread of African cassava mosaic virus into and within cassava fields. *Journal of Phytopathology* **130**, 289–302.

Fargette, D., Jeger, M., Fauquet, C. & Fishpool, L.D.C. (1994) Analysis of temporal disease progress of African cassava mosaic virus. *Phytopathology* **34**, 91–98.

Fauquet, C. & Fargette, D. (1990) African cassava mosaic virus: etiology, epidemiology and control. *Plant Disease* **74**, 404–411.

Fauquet, C., Fargette, D. & Thouvenel, J.-C. (1988) Some aspects of the epidemiology of African cassava mosaic virus in Ivory Coast. *Tropical Pest Management* **34**, 92–96.

Fishpool, L.D.C., van Helden, M., van Halder, I., Fauquet, C. & Fargette, D. (1988) Monitoring *Bemisia tabaci* populations in cassava: field counts and trap catches. *In Proceedings of the International Seminar on African Cassava Mosaic Disease, 4–8 May 1987, Yamoussoukro, Côte d'Ivoire.* pp. 64–76. Wageningen, CTA.

Gameel, O.I. (1970) The effects of whitefly on cotton. pp. 265–280 *in* Sidding, M.A. & Hughes, L.C. (*Eds*) *Cotton growth in the Gezira environment.* Wad Medani, Sudan, Agriculture Research Corporation.

Geddes, A.M.W. (1990) The relative importance of crop pests in sub-Saharan Africa. *NRI Bulletin* no. 36, 69 pp.

Gerling, D. & Horowitz, A.R. (1984) Yellow traps for evaluating the population levels and dispersal patterns of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). *Annals of the Entomological Society of America* **77**, 753–759.

Gerling, D., Horowitz, A.R. & Baumgärtner, J. (1986) Autecology of *Bemisia tabaci*. *Agriculture, Ecosystems and Environment* **17**, 5–19.

Golding, F.D. (1936) *Bemisia nigeriensis*, Corb., a vector of cassava mosaic in southern Nigeria. *Tropical Agriculture* **13**, 182–186.

Horowitz, A.R. (1986) Population dynamics of *Bemisia tabaci* (Gennadius): with special emphasis on cotton fields. *Agriculture, Ecosystems and Environment* **17**, 37–48.

Horowitz, A.R., Podoler, H. & Gerling, D. (1984) Life table analysis of the tobacco whitefly *Bemisia tabaci* (Gennadius) in cotton fields in Israel. *Acta Oecologica, Oecologia Applicata* **5**, 221–233.

IITA (1990) *Cassava in tropical Africa. A Reference Manual.* 176 pp. Nigeria, International Institute of Tropical Agriculture.

Khalifa, A. & El-Khider, E. (1964) Biological study on *Trialeurodes lubia* and *Bemisia tabaci* (Aleyrodidae). *Bulletin de la Société Entomologique d'Egypte* **48**, 115–129.

Lal, S.S. (1981) An ecological study of the whitefly *Bemisia tabaci* (Genn.) population on cassava. *Pestology* **5**, 11–17.

Leuschner, K. (1978) Whiteflies: biology and transmission of African mosaic disease. pp. 51–58 *in* Brekelbaum, T., Bellotti, A. & Lozano, T. C. (*Eds*) *Proceedings of the cassava protection workshop, CIAT, Cali, Colombia, 7–12 November* 1977. CIAT, Colombia.

Mound, L.A. (1960) Biology of *Bemisia* sp. pp. 30–33 *in Half yearly progress report No. 7, January–June* 1960. Ibadan, Nigeria, Federal Department of Agricultural Research.

Mound, L.A. (1962) Studies on the olfaction and colour sensitivity of *Bemisia tabaci* (Genn.) (Homoptera: Aleyrodidae). *Entomologica Experimentalis et Applicata* **5**, 99–104.

Mound, L.A. (1963) Host-correlated variation in *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). *Proceedings of the Royal Entomological Society of London* (A) **38**, 171–180.

Mound, L.A. (1965) An introduction to the Aleyrodidae of western Africa (Homoptera). *Bulletin of the British Museum (Natural History)* **17**, 115–159.

Powell, D.A. & Bellows, T.S. Jr (1992) Preimaginal development and survival of *Bemisia tabaci* on cotton and cucumber. *Environmental Entomology* **21**, 359–363.

Robertson, I.A.D. (1987) The whitefly, *Bemisia tabaci* (Gennadius) as a vector of African cassava mosaic virus at the Kenya coast and ways in which yield losses in cassava, *Manihot esculenta* Crantz caused by the virus can be reduced. *Insect Science and its Application* **8**, 797–801.

Robertson, I.A.D. (1988) The role of *Bemisia tabaci* (Gennadius) in the epidemiology of ACMV in East Africa. Biology, population dynamics and interaction with cassava varieties. pp. 57–63 *in Proceedings of the International Seminar on African Cassava Mosaic Disease, 4–8 May* 1987, *Yamoussoukro, Côte d'Ivoire.* Wageningen, CTA.

Seif, A.A. (1981) Seasonal fluctuation of adult population of the whitefly, *Bemisia tabaci*, on cassava. *Insect Science and its Application* **1**, 363–364.

STSC (1991) Statgraphics Graphics System by Statistical Graphics Corporation, Maryland, USA.

Thresh, J.M., Fishpool, L.D.C., Otim-Nape, G.W. & Fargette, D. (1994) African cassava mosaic virus disease: an underestimated and unsolved problem. *Tropical Science* **34**, 3–14.

Vaishampayan, S.M., Kogan, M., Waldbauer, G.P. & Woolley, J.T. (1975) Spectral specific responses in the visual behavior of the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). *Entomologica Experimentalis et Applicata* **18**, 344–356.

van Lenteren, J.C. & Noldus, L.P.J.J. (1990) Whitefly–plant relationships: behavioural and ecological aspects. pp. 47–89 *in* Gerling, D. (*Ed.*) *Whiteflies: their bionomics, pest status and management*. 348 pp. Andover, Intercept.

von Arx, R., Baumgärtner, J. & Delucchi, V. (1984) Sampling of *Bemisia tabaci* (Genn.) (Sternorrhyncha: Aleyrodidae) in Sudanese cotton fields. *Journal of Economic Entomology* **77**, 1130–1136.

(Accepted 9 January 1995)