

BEMISIA TABACI: THE WHITEFLY VECTOR OF CASSAVA MOSAIC GEMINIVIRUSES IN AFRICA: AN ECOLOGICAL PERSPECTIVE

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ABSTRACT

The ecology of the *Bemisia tabaci*/cassava/African cassava mosaic virus (ACMV) pathosystem is reviewed briefly with special attention given to the parameters affecting the pattern of population development of *B. tabaci*. Significant gaps in our understanding of this system remain, particularly concerning the importance of interactions of *B. tabaci* with other arthropod pests of cassava and the influence of ecological factors such as soil nutrients indirectly through their effects upon cassava. An holistic ecological approach to future work on *B. tabaci* as vector of ACMV is proposed.

Key Words: Cassava, whitefly vector, *Bemisia tabaci*, ecology, African cassava mosaic virus disease

RÉSUMÉ

L'écologie du pathosystème *Bemisia tabaci*/manioc/virus de la mosaïque africaine du manioc (ACMV) est brièvement passée en revue avec une attention particulière apportée aux paramètres qui influencent les modalités de développement des populations de *B. tabaci*. D'importantes lacunes subsistent dans notre connaissance de ce système, tout particulièrement celles relatives à l'importance des interactions de *B. tabaci* avec les autres arthropodes ravageurs du manioc et à l'influence des facteurs écologiques tels les nutriments du sol qui agissent au travers de la plante. Une approche écologique holistique est proposée pour un travail futur sur *B. tabaci* vecteur de l'ACMV.

Mots Clés: Manioc, Aleyrodidae, vecteur, *Bemisia tabaci*, écologie, mosaïque Africaine du manioc

INTRODUCTION

Bemisia tabaci (Gennadius)(Homoptera: Aleyrodidae) is the vector of African cassava mosaic geminiviruses (ACMV) which have been recognised as being the most economically important vector-borne pathogens of crops in sub-Saharan Africa (Geddes, 1990). Understanding the ecology of *Bemisia tabaci* is the key to understanding its role in the epidemiology of the plant viruses it transmits. As a precursor to ecological studies, certain fundamental questions have had to be addressed

concerning the identity of the cassava whitefly (taxonomy), the relationship between the cassava whitefly and its host(s) (life history and bionomics), and the association between the cassava whitefly and ACMV (transmission).

TAXONOMY

The taxonomy of the family Aleyrodidae has traditionally been based on differences in the morphology of the final stage of the fourth instar nymph (or pupa). In early taxonomy of *Bemisia* in Africa, a number of species were described on

this basis from different crop hosts and localities. Many of these species were later synonymised under the name *Bemisia tabaci* (Russel, 1957), although Mound (1963) subsequently demonstrated that pupal characters were labile and determined by the host rather than the insect's genome. More recently, there has been an increasing awareness of the genetic heterogeneity of *B. tabaci*. Most notably, in the south-western states of the USA a new 'strain' of *B. tabaci* designated 'b' has replaced the original 'a' strain. Marked biological differences are evident between the two, with the 'b' strain having a more rapid development rate (Cohen *et al.*, 1992), wider host range (Perring *et al.*, 1991), greater insecticide resistance and greater capacity to transmit viruses (Bedford *et al.*, 1992) than the 'a' strain. Isozyme analyses (Perring *et al.*, 1992) and random amplified polymorphic DNA obtained via the polymerase chain reaction (PCR) have indicated important biochemical differences between the strains (Perring *et al.*, 1993). It has also been suggested that the new strain is a distinct species named *B. argentifolii* Bellows and Perring (Bellows *et al.*, 1994).

On cassava in Africa, Burban *et al.* (1992), working in Ivory Coast, demonstrated two host-restricted 'strains' of *B. tabaci*, one of which colonised cassava whilst the other colonised a wide range of crop and weed host species but not cassava. In Uganda, there is evidence of both geographical and host-associated strains of *B. tabaci* (Legg *et al.*, 1994). In both Ivory Coast and Uganda recent evidence suggests, therefore, that cultivated cassava is the only significant host of the cassava strain of *B. tabaci*. Whether a similar situation exists in other African countries remains to be seen. Current understanding of the taxonomy of *Bemisia* spp., therefore, remains poorly developed.

Two other whitefly species colonise cassava in parts of Africa. *Bemisia afer* Priesner and Hosny is widely distributed but generally occurs in relatively small numbers on lower leaves. Its relative abundance in low to mid-altitude areas of eastern and central Africa where cassava brown streak virus occurs (Thresh *et al.*, 1994) has led to the suggestion that it may be the vector of that virus (Storey, 1939; Robertson, 1985). The spiralling whitefly, *Aleurodicus dispersus* Russel

(Hom., Aleurodidae), of South American origin, was introduced to West Africa in 1992 and quickly became an economically important pest, causing direct feeding damage to cassava (Neuenschwander, 1994). It appears, however, that it came together with a parasitoid natural enemy, *Encarsia ?haitiensis* Dozier (Hym., Aphelinidae) which is already providing effective control in many areas. This introduction, although it seems unlikely to have a major impact on cassava cultivation in Africa, is nevertheless significant in highlighting the risk posed by the great diversity of cassava pests affecting the crop in the Neotropics. Amongst these are a number of whitefly species which cause direct feeding damage including *Aleurotrachelus socialis* Bondar, *Trialetrodes variabilis* (Quaintance) and *Bemisia tuberculata* Bondar (Bellotti *et al.*, 1994).

LIFE HISTORY AND BIONOMICS OF *B. TABACI*

Many publications describe characteristics of the life history and bionomics of *B. tabaci* on a range of host plants. This information has been summarised and reviewed by Gerling *et al.* (1986). Although there have been no detailed studies of the bionomics of *B. tabaci* on cassava, field observations indicate a concurrence between bionomics on cassava and on other hosts (Fishpool and Burban, 1994).

TRANSMISSION

Cassava mosaic disease was first shown to be transmitted by a *Bemisia* species by Kufferath and Ghesquière (1932) in the Congo and consequently they named it *Bemisia mosaicivectura* Ghesq. Subsequent studies (Storey and Nichols, 1938; Chant, 1958; Dubern, 1979) provided more detailed information on the characteristics of transmission as summarised by Dubern (1994). African cassava mosaic virus is transmitted by *B. tabaci* in a persistent manner. Optimal (and minimum) experimental times for acquisition, latent and inoculation periods were: 5 hours (3.5 hours), 6 hours (3.5 hours) and 30 minutes (5-10 minutes). The maximum retention time was 9 days, although the relatively low numbers of whitefly used to demonstrate this

means that it is likely to be an underestimate. Transtadial but not transovarial transmission of ACMV was demonstrated. Single insects were able to transmit but optimal transmission occurred with 10 insects per plant. From these data, it was estimated that 13% of the *B. tabaci* individuals reared on ACMV-infected plants were infective. This contrasts with results for *B. tabaci* adults collected from infected plants in the field in Ivory Coast, where the percentage of infective individuals ranged from 0.15 to 1.7% (Fargette, 1987). The epidemiological significance of these transmission characteristics is that many *B. tabaci* are likely to be required for the high rates of virus transmission associated with an epidemic and that the long retention time of the virus offers the potential for the virus to be transmitted over considerable distances.

ECOLOGY

To answer the question of how ACMV (where ACMV includes both African cassava mosaic and East African cassava mosaic geminiviruses) spreads at different rates in different agro-ecological environments requires an investigation of the ecology of *B. tabaci*. Fundamental ecological questions relate to the interrelationships between the principal elements of the ACMV pathosystem. The most basic ecological relationships, therefore, relate vector, virus and host. These, understandably, have received more attention than other less direct relationships.

The vector-virus relationship. A first step in studying the ecology of *B. tabaci* in the ACMV pathosystem was to relate insect numbers to ACMV incidence. Leuschner (1978) studied the phenology of *B. tabaci* at Ibadan, Nigeria, monitoring population size using counts of pupae on leaves and adults attracted to sticky yellow traps. Both he, and subsequently Dengel (1981) in Togo, associated large numbers of *B. tabaci* with rapid ACMV spread. Robertson (1985, 1987) found no such association in coastal Kenya, although this may be because yellow attractive sticky traps were set 1.5 m above ground to measure adult numbers, rather than a direct count of adults on upper leaves where they can transmit. Fargette *et al.* (1985, 1990) in Ivory Coast

demonstrated the correspondence in fields between the spatial patterns of spread of ACMV and of infestation by *B. tabaci*. In Uganda, both the spatial correspondence (Otim-Nape, 1993) and that between numbers and virus incidence (Legg, J.P. and Fishpool, L.D.C., unpublished data) have been verified.

No evidence is available on possible differences in virus transmission efficiencies within or between populations of *B. tabaci* on cassava, or between different isolates of ACMV. Given the existence of two distinct African cassava mosaic geminiviruses (Hong *et al.*, 1993), circumstantial evidence of mild and severe strains of ACMV (Storey, 1936) and the occurrence of geographical strains of *B. tabaci*, differences in transmission efficiency are likely. Currently, however, these appear to be less important epidemiologically than differences in numbers since numbers of *B. tabaci* alone have provided a good indication of the potential for spread in most situations studied to date.

The host-vector relationship. A number of host-associated parameters influence *B. tabaci* populations including chemistry, architecture, age and pattern of growth.

Host chemistry. Golding (1936) first indicated that cassava varieties with greater resistance to ACMV supported lower numbers of *B. tabaci*. The important proviso, however, was that 'varieties which did not develop Mosaic owed their apparent immunity to an inherent resistance to the virus rather than to a repellent effect upon the Aleurodid vector'. Dengel (1981) noted major differences in *B. tabaci* numbers on sweet, intermediate and bitter varieties of cassava (with high, intermediate and low populations, respectively) and hypothesised that this reflected a preference of *B. tabaci* for leaves with a lower concentration of cyanogenic glucosides (which were associated with the bitter taste).

In trials with a wide range of varieties in Ivory Coast, the relationship between field resistance (proportion of infected plants) and vector resistance was weak (Fauquet and Fargette, 1990). Resistance of the cassava plant to *B. tabaci per se* was considered, therefore, to offer limited potential for exploitation by breeders, although the

advantage of combining vector resistance with virus resistance was recognised. It is known that ACMV infection has significant effects upon the chemistry of cassava leaves (Almazan and Theberge, 1989). No information is available on how these changes affect nymph or adult stages of *B. tabaci*.

Host architecture. Field observations indicate that cassava varieties with relatively wide leaflets support greater numbers of *B. tabaci* than those with narrow leaflets, possibly offering a more sheltered micro-environment. Similarly, shorter plants are favoured over taller ones of the same variety and age (personal observations). Leaf posture also seems to be important, as varieties with leaflets partially reflexed upwards about the midrib support lower numbers of whiteflies than those with leaflets partially reflexed downwards (including ACMV-infected leaves).

Leaf hairiness is sometimes associated with resistance to cassava green mites (*Mononychellus* spp.) (IITA, 1981) and may also affect the suitability of cassava as a host for whiteflies, although this has yet to be documented. Leaf shape and whole plant architecture, however, are often associated with desirable agronomic characteristics (e.g. wide leaflets with high yield potential). This restricts the potential for manipulation through breeding to render cassava plants less favourable to *B. tabaci*.

Host age. *B. tabaci* populations have consistently been reported to peak three to six months after planting, before declining more or less rapidly to a relatively low level for the remainder of the crop life (Leuschner, 1978; Dengel, 1981; Fishpool *et al.*, 1995; Legg, J.P. and Fishpool, L.D.C. unpublished data). Squire (1961) provided the first suggestion that the physiological age of cassava plants was an important determinant of the pattern of *B. tabaci* population development, by demonstrating a reduction in population size as plants matured. This was emphasised by Dengel (1981) and more recently by Fishpool *et al.* (1995) who cited a publication (IITA, 1990) recording tuberisation in cassava roots as commencing 30-60 days after planting. They suggest that the diversion of photosynthates associated with this

change is likely to render the aerial parts of the plant less suitable as feeding sites for *B. tabaci*.

Host growth. Squire (1961) was also the first to document the association between the rate of cassava leaf production and *B. tabaci* population change, with increases in numbers of *B. tabaci* occurring during periods of rapid cassava growth. This relationship was subsequently quantified (Dengel, 1981; Robertson, 1985). Figures 1 and 2 illustrate the relationship between rates of cassava leaf production and numbers of adult *B. tabaci* recorded from two sites in Uganda. Clearly apparent are the declines in whitefly numbers during periods of slow cassava growth.

THE *B. TABACI*/CASSAVA/ACMV PATHOSYSTEM

In addition to the direct relationships between vector, host and virus, other major parameters influencing vector populations are climate, natural enemies and other cassava pest species, some of which compete directly with *B. tabaci* for the cassava food source. The system is illustrated diagrammatically in Figure 3.

Meteorological parameters. Climatic factors have both a direct bearing on *B. tabaci* and an indirect one through effects on cassava growth. The influence of a range of parameters has been investigated, although most attention has been directed towards temperature and rainfall.

Temperature. The direct effects of temperature on the bionomics of *B. tabaci* on cassava have not been studied in detail, although it is suggested that information obtained using other crop hosts can be applied to *B. tabaci* on cassava (Fishpool and Burban, 1994). Thus it is indicated that the 'higher the temperature the quicker the development up to about 30-33°C', but a rapid decrease in development rate is recorded above this. Storey (1936) in Tanzania first noted the greater whitefly vector 'activity' at Kiwanda, c. 170m above sea level (a.s.l.), than at Amani, a relatively cool site c. 900 m a.s.l. In Nigeria, Leuschner (1978) confirmed the important effects of temperature and solar radiation on flight activity and the

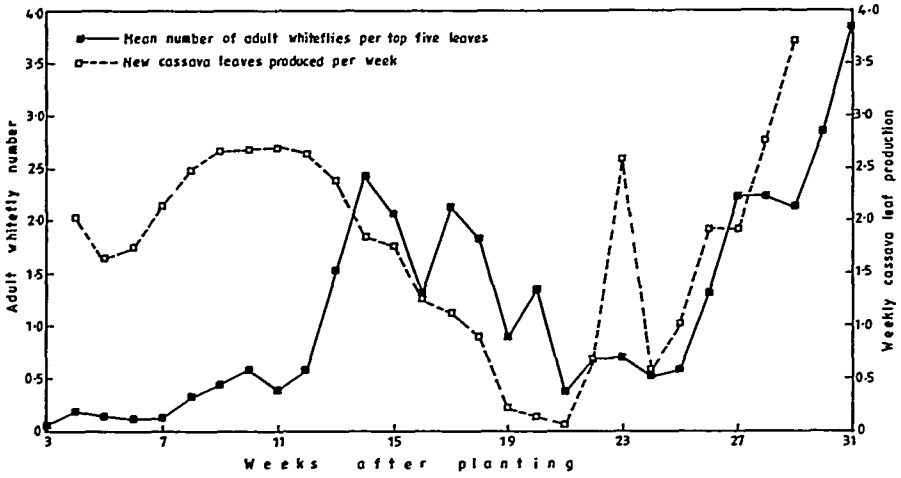


Figure 1. Numbers of whitefly adults and new cassava leaf production- Nakasongola-trial planted 14 October 1992

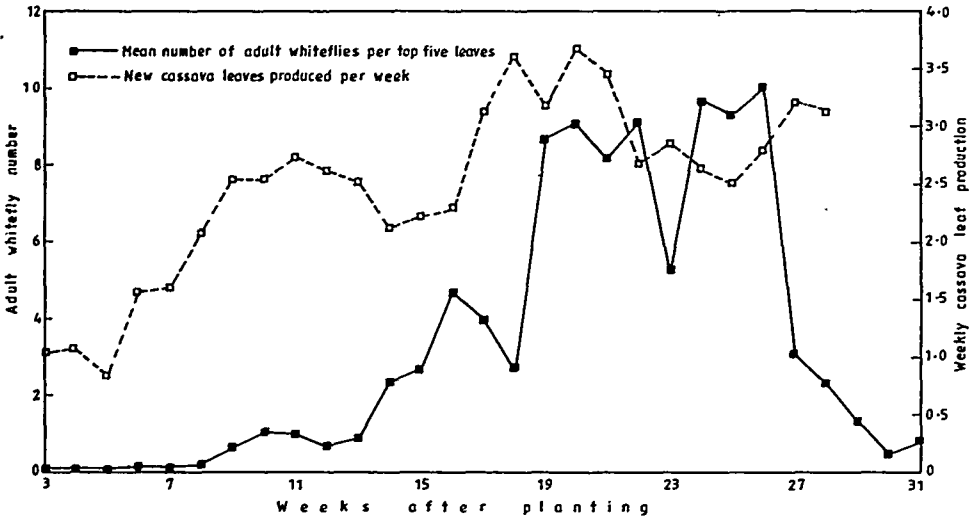


Figure 2. Numbers of whitefly adults and new cassava leaf production-Isimba-trial planted 14 October 1992

association of high populations of *B. tabaci* with high temperatures at the beginning of the main rainy season (April-June). These observations were confirmed by Dengel (1981) in Togo, who also reported that cassava planted and sustained by irrigation during the dry, hottest months of the year (January-March) supported even higher populations of *B. tabaci*.

In the humid lowland rainforest region of Ivory Coast, temperature appeared to be the key variable driving population development of *B. tabaci* (Fauquet *et al.*, 1985; Fargette *et al.*,

1993b), although the qualification has subsequently been advanced that this was established in an area where availability of soil moisture does not seasonally limit cassava growth (Fargette *et al.*, 1993a).

In Uganda evidence for the effect of temperature is somewhat contradictory. Multi-location trials indicated that numbers of *B. tabaci* and virus spread are greatest in locations with highest temperatures and that, as in West Africa, high whitefly populations occur during the main rainy season (April-June) following a period of hot dry

weather (January-March) (Legg, J.P. and Fishpool, L.D.C. unpublished data). The paradox is that high populations of *B. tabaci* have also been observed in a cooler, higher altitude location at Mubende, c. 150 km west of Kampala and c. 1500 m a.s.l. The contradiction is further emphasised by the southward extension of the zone of high ACMV incidence into relatively cooler areas, of similar elevation, previously characterised by low populations of *B. tabaci* and little ACMV spread by vectors. Large populations of *B. tabaci* are associated with the border, or 'front', between this high incidence area and the zone of low incidence to the south. The possibility that heterogeneity between populations of *B. tabaci* from different locations (and implied by isozyme analysis evidence discussed previously) explains this apparent anomaly remains to be thoroughly tested. Current work is investigating the possibilities that the changes are the result of the advance southwards of either a new *B. tabaci* biotype or a novel strain of ACMV or both.

of adults after heavy rain showers and inferred from this that the mechanical action of heavy rain destroys adults. In contrast, Leuschner (1978), also in Nigeria, and Dengel (1981), in Togo, recorded highest populations of *B. tabaci* adults during high rainfall months and related this to the occurrence of flushes of new leaves. In Ivory Coast, Fishpool *et al.* (1995) showed rainfall to be negatively correlated with population size, possibly due to a reduction in oviposition. On the coastal strip in Kenya, high *B. tabaci* populations were generally found in areas of higher mean annual rainfall (Robertson, 1985), although it was not clear if this was a result of the rain itself or a greater density of cassava plantings associated with higher rainfall areas. In Uganda, no direct relationship between rainfall and population size is apparent, although there is a strong indirect relationship between the two through the dependence of rate of cassava growth upon soil moisture.

Rainfall. The earliest reference to the effect of rainfall upon *B. tabaci* comes from Golding (1936) in Nigeria, who observed reductions in the numbers

Wind. Wind speed and direction have not been cited as influencing numbers of *B. tabaci* and Dengel (1981) stressed that these factors were unimportant. The importance of wind has been

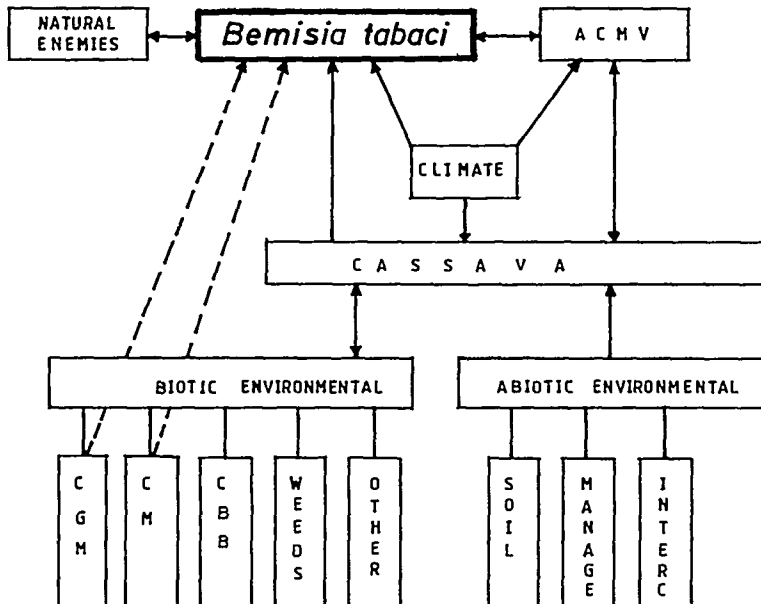


Figure 3. Ecological interrelations in the *B. tabaci*-cassava-ACMV system
 CGM = Cassava green mite, CM = Cassava mealybug, CBB = Cassava bacterial blight,
 Manage = Management, Inter = Intercropping

emphasised, however, in facilitating dispersion. The small size of *B. tabaci* means that it is a weak flier. It has been estimated that its speed of flight is *c.* 0.2 m/s (Yao *et al.*, 1987). Based on this, the layer above ground level within which it can control its flight in an open situation is usually only a few centimetres. This pattern changes beneath the canopy of a cassava crop, however, where *B. tabaci* adults appear able to control their flight and tend to move upwind (Fishpool *et al.*, 1987).

The distance that *B. tabaci* adults can move successfully in wind currents is obviously an important element in their capacity to colonise new cassava plantings and introduce ACMV. There are frequent references to their ability to move over distances of a few kilometres (Fargette *et al.*, 1985; Fauquet *et al.*, 1988). Evidence for long distance flight was reviewed by Thresh (1983). Whitefly catches from aircraft have been reported from up to 1800 m above the irrigated cotton-growing areas of the Sudan Gezira scheme. In Israel, evidence for long distance movements has been obtained in mark and recapture studies using fluorescent dyes, in which marked *B. tabaci* individuals were trapped on sticky yellow traps up to 7 km from the point of release (Cohen *et al.*, 1988). Blackmer and Byrne (1993) have also provided evidence suggesting that *B. tabaci* is capable of active long duration flight (up to two and a half hours) using the artificial environment

of a flight chamber. The significance of long distance vector movements for the spread of ACMV has yet to be demonstrated for field populations.

Other meteorological parameters. In Kenya, Seif (1981) using a limited data set indicated that the strongest association with numbers was provided by the interaction between relative humidity and temperature. Solar radiation has been associated positively with population increase of *B. tabaci* (Leuschner, 1978; Dengel, 1981). This relationship is generally considered, however, to be rather less clear as a determinant of *B. tabaci* numbers than temperature (Fauquet *et al.*, 1985). Fargette *et al.* (1993a) highlighted the close association of temperature with global radiation, and reported a positive influence of radiation on ACMV spread through its effect on cassava growth rate.

Natural enemies. There are few reports of the natural enemies of *B. tabaci* on cassava in Africa. Although work on natural enemies of *B. tabaci* is well advanced elsewhere, there are few references to such studies on cassava in Africa and these largely relate to incidental observations and identification rather than experimental studies. Natural enemies recorded in published studies are listed in Table 1. Golding (1936) provided the first observation, describing a 'small spider' as the principal natural enemy in Nigeria, but noting

TABLE 1. Recorded natural enemies of *Bemisia tabaci* on cassava in Africa

Author	Country	Natural enemy
Squire (1961)	Nigeria	<i>Serangium cinctum</i> (Wse.), Coccinellidae <i>Encarsia</i> sp., Aphelinidae
Leuschner (1978)	Nigeria	Typhlodromid mite, Phytoseiidae
Robertson (1985)	Kenya	<i>Encarsia transvena</i> (Timberlake), Aphelinidae <i>Eretmocerus mundus</i> (Mercet), Aphelinidae Predatory mites (Phytoseiidae) Thrips (<i>Scolothrips</i> sp. ?) Coniopterygid larvae Cecidomyiid larvae (<i>Theradiplosis</i> ?)
Fishpool and Burban (1994)	Ivory Coast	<i>Euseius</i> sp. (mite) <i>Stethorus jejunos</i> Casey, Coccinellidae <i>Holoborus pallidicornis</i> (Cameron), Staphylinidae <i>Scolothrips latipennis</i> Priesner
Nyirenda <i>et al.</i> (1993)	Malawi	<i>E. transvena</i> <i>Eretmocerus</i> sp. <i>Scymnus</i> sp., Coccinellidae <i>Semidalis</i> sp., Coniopterygidae

the absence of insect parasites or predators. One of the most recent identifications is the coniopterygid, *Conwentzia africana* Meinander (Fishpool, L.D.C. unpublished observations), recorded from cassava in Kenya and Uganda.

The only intervention reported in Africa to date has been the introduction to Malawi of the parasitoid *Encarsia deserti* Gerling and Rivnay, from California, USA in 1986 (Nyirenda *et al.*, 1993), although its establishment has yet to be confirmed.

In Uganda, a significant reduction in the proportion of parasitised *B. tabaci* nymphs has been observed during the extended dry period in savanna ecosystems characteristic of the northern and eastern parts of the country. This could be an important contributing factor in the rapid increase in numbers of *B. tabaci* encountered within these ecosystems at the start of the main rains following this dry period.

Interactions of *B. tabaci* with other pest species.

Two of the most important pests of cassava in Africa, the cassava green mite [*Mononychellus tanajoa* (Bondar)] and the cassava mealybug (*Phenacoccus manihoti* Mat.-Ferr.), compete directly with *B. tabaci* for space and plant nutrients. Important interactions may exist, therefore, where any two or all three arthropods are present on the same cassava plant, especially if nutrients or plant growth are limiting. Such interactions remain largely undocumented.

There are general references to a relationship between mites and *B. tabaci*. Robertson (1985) in coastal Kenya recorded both cassava green mite and red spider mite (*Tetranychus* sp.) and suggested that their damage rendered the leaves less attractive for *B. tabaci*. Fishpool and Burban (1994) observed that the presence of green mites on the undersides of cassava leaves discourages oviposition of *B. tabaci*.

In Uganda, green mite damage score and numbers of adult *B. tabaci* on the upper five expanded leaves were recorded for 2500 plants of cassava variety Bao at five months after planting. Mean numbers of adult *B. tabaci* for each damage score are presented in Figure 4. There was a strong negative association between mite damage and *B. tabaci* numbers is clear from these data.

Indirect ecological interactions. These interactions operate primarily through effects upon cassava growth. African cassava mosaic virus is known to cause nutritional changes in cassava leaves: ACMV-infected leaves have lower total (free and bound) cyanide and protein contents (Almazan and Theberge, 1989), although there is no information relating these possible nutritional effects to

B. tabaci. Indirect effects of climate act by influencing the pattern of cassava growth as discussed previously. Two key characters of soil which influence *B. tabaci* through their effect on cassava are the capacity to retain moisture and

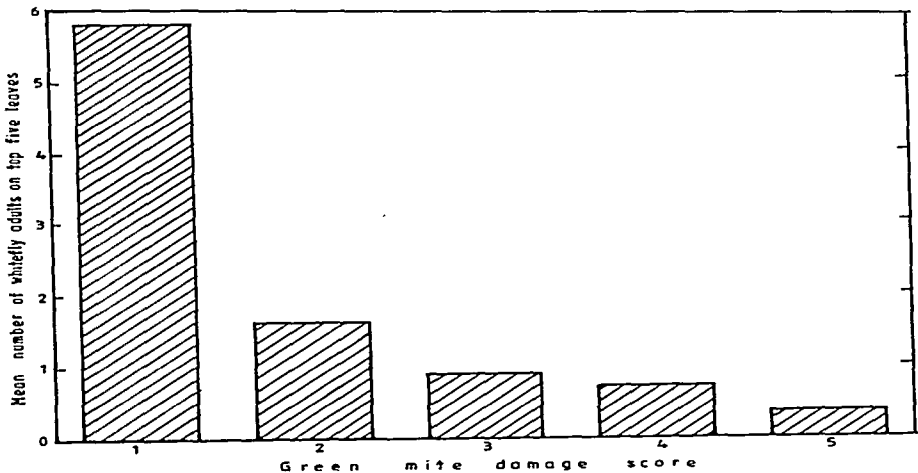


Figure 4. Association between cassava whitefly adult numbers and cassava green mite damage on five month old cassava-Nakasongola trial planted 14 October 1992.

nutrient status. Again there is no information relating these to populations of *B. tabaci*.

Management practices may have important effects upon *B. tabaci* populations. Fargette *et al.* (1985) demonstrated lower incidence of ACMV in fields planted at high than at lower density and attributed this to an effect on *B. tabaci* behaviour. Planting date has been shown to have important implications for temporal patterns of ACMV spread (Storey, 1938) and population development of *B. tabaci*. Fargette *et al.* (1993a), reporting on a series of monthly plantings between 1981 and 1986 in Ivory Coast, described a strong seasonal influence on disease progress with generally large increases between November and June and small increases from July to October. Much of this variation could be explained in terms of numbers of *B. tabaci*, which were in turn related to temperature and plant growth (see also Fargette and Thresh, 1994).

Possible effects of intercropping have received scant attention, which is a particularly serious shortcoming given the almost universal practice of inter-planting cassava with other crops. Fargette and Fauquet (1988) carried out a preliminary study to investigate the effect on the epidemiology of ACMV of intercropping maize with cassava but their results were inconclusive. Gold (1994) in Colombia identified an important beneficial effect of intercropping cowpea (*Vigna unguiculata* L. Walp.) with cassava in reducing numbers of whiteflies and thereby increasing yield. It was suggested that this effect was a consequence of the poor leaf production and aerial growth of cassava interplanted with cowpea. An important contrast between this scenario and that of *B. tabaci* on cassava in Africa is that both whitefly species studied in Colombia (*Aleurotrachelus socialis* and *Trialeurodes variabilis*) occurred in very large numbers and caused direct feeding damage. The potential for the exploitation of intercrops either as barriers, or to provide camouflage so impairing the early colonisation of cassava crops by *B. tabaci*, or as competitors, reducing the suitability of cassava for *B. tabaci*, remains unknown. Given the importance of intercrops in cassava cultivation in sub-Saharan Africa, this gap in our understanding of the ACMV pathosystem needs to be addressed.

CONCLUSIONS

Historically, research into the ecology of *B. tabaci* on cassava has focused on readily studied variables having a direct effect on the insect. Relatively limited attention has been given to less easily studied variables, such as natural enemies, variables having an indirect effect upon the insect and interactions within the system. Some of the resultant shortcomings in our understanding of the *B. tabaci*/ACMV/cassava pathosystem have been highlighted here.

Perhaps in part as a result of this lack of knowledge, there is currently no immediate prospect of controlling ACMV in Africa through control of the vector, and breeding for host plant resistance to the virus will undoubtedly remain the principal component of ACMV control strategies for the foreseeable future.

There is certainly a potential, however, to develop other complementary control measures, particularly in multi-pest situations, through an enhanced understanding of the ecology of the cassava cropping system. An holistic ecological approach should be encouraged in future studies, to provide an increased understanding of ecological interrelationships that will be crucial to underpin efforts to develop balanced control solutions for the cassava pest/disease complex.

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