

Methods of surveying the incidence and severity of cassava mosaic disease and whitefly vector populations on cassava in Africa: a review

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Abstract

Field surveys in many cassava growing areas of Africa have assessed the incidence and severity of cassava mosaic disease (CMD), populations of the whitefly vector (*Bemisia tabaci*), and the distribution of cassava mosaic begomoviruses (CMBs). The methods employed differ greatly between countries and attempts at standardization were made in recent CMD surveys in East and Central Africa, notably in the systemwide Whitefly IPM Project, which provides a paradigm for future work on CMBs and whiteflies on cassava in Africa and also elsewhere. However, there is a need for greater standardization so as to assess the continued expansion of the current CMD pandemic in eastern Africa. Standardized methods will facilitate the collection of reliable data, which can be used to predict future disease spread, develop appropriate management strategies and compare disease development between seasons and locations. In this review, the methods used and the problems encountered during such surveys are discussed and recommendations made on future procedure.

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1. Introduction

Cassava mosaic disease (CMD) is caused by viruses of the genus *Begomovirus*, family Geminiviridae. These are transmitted by the whitefly *Bemisia tabaci* and disseminated in the stem cuttings used routinely for new plantings. Eight cassava mosaic begomoviruses (CMBs) have been recognized, of which six occur in Africa, either alone or in combination (Fauquet and Stanley, 2003).

CMD has been known since 1894 and it has long been regarded as the most important disease of cassava in Africa. However, until the late 1980s there were no data to confirm or deny this supposition (Thresh et al., 1998b). The situation changed when detailed surveys were made of the incidence and severity of CMD and of the CMBs present in 17 of the 38 main cassava-growing countries of sub-Saharan Africa, which collectively account for ca. 90% of total production in the continent (Legg and Thresh, 2003). This paper considers the methods used in the surveys and the results obtained.

2. Factors to consider in cassava mosaic disease surveys

2.1. Selection of survey area

The area to be surveyed should be selected to meet the overall objectives of the study. In assessing CMD, the emphasis has been on areas where cassava is an important crop, or where the disease has caused serious problems. Administrative boundaries, agro-ecology and disease prevalence are used to define sampling domains. In countrywide surveys, the major cassava growing zones are selected for study. In Uganda, for example, the country was divided into regions for the surveys undertaken as part of an Integrated Pest Management project (Sseruwagi et al., 2004) and into districts, counties and sub-counties for previous surveys (Otim-Nape et al., 1998a, 2001).

2.2. Sample size

There are two features of sample size:

1. The number of plants selected per field.
2. The number of fields selected per sampling domain.

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In developing an overall sampling plan it is necessary to compromise, since sampling too many plants per field will mean fewer fields per domain and vice versa. Moreover, the number of cassava fields (n) sampled per locality will depend on the type, amount and precision of the information required and on the resources and time available. Too few samples (<5) will result in unreliable and unrepresentative data, whereas numerous samples (>100) provide better quality data, but require more time and resources. Therefore, the sample size should be sufficiently representative to give a valid assessment of the disease situation at the least cost possible. It should also suffice to detect statistically meaningful differences between sampled fields, yet should not be so large as to make the cost and duration of the survey excessive. For comparisons between fields, it is usual to sample at least 30–50 plants per field, while if the principal comparison is between domains at least ten fields should be sampled. It is, however, important that the sample size is uniform at each level (i.e. plants per field and fields per domain) to avoid problems during statistical analysis due to differences in sample size.

2.3. Sampling procedure

A convenient approach is to stop at regular predetermined intervals along motorable roads traversing each sample area, or to preselect sites at random from grid references (Wydra and Msikita, 1998). For the former, the intervals between stops will depend on the size of the sample area and the availability of suitable cassava fields. Those typically 3–6 months after planting (MAP) are sampled. At this stage of growth a distinction is possible between cutting-derived (C) and whitefly-derived (W) infections and populations of whiteflies are assessed when they are most numerous. ‘W’

infections cause disease symptoms on only the upper-most leaves, whereas ‘C’ infections also cause symptoms on the lowest first-formed leaves. Later than 6 MAP, the earliest leaves often become senescent and absciss, making it very difficult or impossible to distinguish between the two types. Moreover, large plants form such an interlocking canopy that it is difficult to traverse the crop and examine the shoot tips where adult *B. tabaci* occur.

During sampling, plants should be selected along representative transects of the field and a single diagonal or two diagonals in the form of an ‘X’ have been used. However, samples have also been selected from two sides and along a diagonal across the field in a ‘Z’ configuration (Otim-Nape, 1993; Otim-Nape et al., 1998a). Field size, any intercrops grown, the cassava cultivars present, the number and proximity of nearby cassava, sampling and planting dates, together with disease parameters and adult whitefly population, are recorded using a suitable record sheet (Table 1).

Several problems need to be considered when designing a sampling plan. Lack of sufficient resources and time often limit surveys to motorable roads. This may create a ‘road bias’, leading to the disease situation and whitefly populations being under or over estimated because less accessible more truly representative fields are omitted. Such problems may occur if remote areas differ from those near roads in field size, human population density or cropping system and intensity. Moreover, farmers tending roadside fields are likely to have better access to improved control methods, for example new CMD-resistant cultivars and better technical information, than those elsewhere. A random grid system of selecting areas to be sampled (Nweke, 1994a) overcomes this problem, but is likely to be time-consuming and inconvenient if some of the pre-selected areas are not readily accessible.

Table 1
Sample record sheet for field data collection during surveys of cassava mosaic disease in East and Central Africa

Field level data sheet							
District:		County:					
Sub-county:		Crop mixture:					
Researcher:		Cassava cultivars:					
Date & time:		Cultivar sampled:					
Field size:		Crop age (months):					
No. of nearby fields		GPS		Latitude	Longitude		
Plant no.	CMD infection			CMD severity (1–5 scale)	CMD systemicity	Wf. No.	Comments
	Cutting inf.	Whitefly inf.	Healthy				
1							
2							
3							
4							
Mean							

Wf. No. Whitefly adult population

CMD, Cassava mosaic virus disease; Inf., Infection (+/–); Sev., Severity score; Sys., Systemicity; GPS, Geographical positioning system.

In assessing CMD and adult whitefly populations, it is desirable to sample crops of similar age. However, farmers' fields are typically planted on different dates during different seasons and therefore there will be considerable variation in crop age. This can greatly influence whitefly populations, disease incidence and severity and also the ability to distinguish between C and W infections (Otim-Nape et al., 1996). However, if the main objective is to assess the overall incidence of CMD, crops of 1–12 MAP can be considered, although crops of 8–12 MAP are more appropriate. This is because sampling too early underestimates final disease incidence and the extent of spread occurring at the site.

Clear-cut differences between C and W infections are more easily seen in susceptible than in resistant genotypes. The phenomenon of symptom recovery (Fargette et al., 1994; Gibson et al., 1996) and sometimes the resurgence of symptoms after a period of remission may cause difficulties, leading to incorrect assignment of infection type. This necessitates great care in recording, especially when dealing with the most resistant cultivars that express limited and generally inconspicuous symptoms and may become symptomless during the late stage of crop growth. Moreover, inconsistent whitefly data are often a consequence of a failure to sample at a uniform crop age, as whiteflies are usually more abundant on young (3–6 MAP) than on older cassava (Otim-Nape, 1993; Fishpool and Burban, 1994; Legg, 1995; Fishpool et al., 1995). Crop age should, therefore, be well-defined and strictly adhered to, depending on the objectives of the study.

There are often great differences in the range of cassava cultivars encountered in farmers' fields, even within the same area (Nweke, 1994b; Nweke et al., 1994; Otim-Nape et al., 1998a, 2001; Hillocks et al., 2002). Some cultivars are partially resistant to CMD and have generally low incidences and severities, whereas many others are more susceptible and may be severely affected. Big differences are also encountered in cassava cropping systems. Some farmers grow cassava as a sole crop, often using a mixture of cultivars even in a single field, while others inter-plant cassava with one or more other crops (Nweke, 1994b; Hillocks et al., 2002). In most surveys, therefore, disease and whitefly assessments were made on cassava in diverse cropping systems, which may influence the data collected and complicate analysis. For instance, less spread of CMD was observed in cassava grown as an inter-crop (Fargette and Fauquet, 1988; Ahohuendo and Sarkar, 1995; Fondong et al., 2002) and also as a cultivar mixture (Sserubombwe, 1998; Sserubombwe et al., 2001) than in sole crops or single cultivars. Therefore, the cropping system should be clearly defined.

For cassava crops of more than one cultivar, each should be recorded, but a common approach is to assess the disease parameters and whitefly populations on the predominant cultivar. This was done in the Uganda surveys in the 1990s in which the first 30 plants of the predominant cultivar were recorded and any others were listed, but not assessed (Otim-Nape et al., 1998a, 2001). By comparison, in

Tanzania and Mozambique, records were taken on the first 30 plants encountered in each of the fields sampled, irrespective of cultivar (Hillocks et al., 1999, 2002; Thresh and Hillocks, 2003). The latter method can provide at least some information on the whole range of cultivars being grown, but a disadvantage is that the number of plants of any one cultivar may be too small to provide a statistically useful sample. As cultivar mixtures and intercropping are common, these issues are important and additional information is required on the relative merits of the two methods of assessment.

2.4. *The timing and frequency of sampling*

The timing and frequency of sampling depend on the objectives, the occurrence of events, the requirement for information at different stages in an epidemic and economic considerations. Some examples of typical requirements are:

- Annual or less frequent assessments to monitor the changing disease situation
- 'Before and after' assessments at intervals of 2–4 years to assess the impact of control measures or the adoption and performance of new cultivars
- More frequent assessments to examine seasonal effects, or for detailed monitoring of CMD epidemics.

Successive assessments may be conducted on the same or different fields and sites. Decisions on the timing and frequency of sampling are affected by seasonal variability of weather conditions (especially, rainfall and temperature) that influence crop growth and symptom expression (Massala, 1987; Gibson, 1994) and consequently the quality and consistency of the data collected. Rainfall and temperature also influence adult whitefly populations (Fargette et al., 1994; Fishpool et al., 1995; Legg, 1995). Temperatures are usually below 35 °C during the rainy season(s) in Africa and sufficient rainfall/moisture is available to support plant growth, whereas in the dry season temperatures may exceed 35 °C and low soil moisture usually restricts growth and may cause premature leaf senescence and abscission. According to Storey and Nichols (1938) and Massala (1987), cool temperatures enhance CMD symptoms, whereas temperatures exceeding 35 °C suppress symptoms (Chant, 1959; Kartha and Gamborg, 1975; IITA, 1979; Gibson, 1994). In contrast, whitefly populations are favoured by high temperatures and solar radiation and moderate rainfall and relative humidity (Golding, 1936; Fargette et al., 1992; Otim-Nape, 1993; Fishpool and Burban, 1994).

Time and resources are often limiting and so surveys may have no clearly specified and consistent duration or completion date. Hence, whitefly populations may be assessed at different seasons or stages of crop growth and so do not necessarily relate closely to the amount of CMD spread observed. In part, this is because of the delay of several weeks between whitefly inoculation and symptom expression (Fauquet and Fargette, 1990; Fargette et al., 1994). Consequently, the amount of spread of CMD recorded in a survey

is not directly related to the whitefly populations at the time, but rather to populations several weeks earlier (Fargette et al., 1994; Legg and Ogwal, 1998). Surveys should therefore be timed so as to minimise variability in the data due to weather conditions. Strict time limits should be observed during the survey and more focused whitefly studies incorporating more frequent sampling are required to relate whitefly populations to disease spread (e.g. Fargette et al., 1994).

3. Parameters to measure during a survey

3.1. CMD incidence, prevalence, intensity and systemicity

Several parameters have been used to quantify CMD, including *incidence*, *prevalence*, *intensity* and *systemicity*. Disease incidence refers to the number of visibly diseased plants, usually in relation to the total number assessed and so expressed as the proportion or percentage of plants in a stand with symptoms on a scale of 0–1 (*P*) or 0–100 (%) (Fargette, 1985). Disease *prevalence* is the proportion or percentage of production units (usually fields) in which the disease is found (Butt and Royle, 1980). *Intensity*, by contrast, is used to describe the severity of symptom expression and not incidence or the area or volume of diseased plant tissue. *Systemicity* can also be used to quantify CMD (Rossel et al., 1992) and is the proportion of shoots per plant expressing disease symptoms.

Assessments of CMD incidence, prevalence, intensity and systemicity are all based on the accurate and reliable visual assessment of symptoms. Reliability can be impaired if those responsible lack a thorough understanding of the biotic and abiotic factors that affect cassava growth and symptom expression (Malathi et al., 1987; Thresh, 1987) and may thereby lead to erroneous records of either the presence or absence of CMD. Leaf damage by cassava green mite (CGM) (*Mononychellus tanajoa*), cassava mealybug (*Phenacoccus manihoti*), cassava bacterial blight (*Xanthomonas campestris* pv. *manihotis*), drought and mineral deficiencies can all be confused with CMD. The most common confusion is with damage due to CGM or mineral deficiencies, especially of zinc (Fulton and Asher, 1997). A key distinction, however, is that both mineral deficiency symptoms and mite damage are usually similar on each half of the

lamina on either side of the mid-rib, whereas the symptoms of CMD are usually asymmetrical and the two sides differ.

3.2. CMD severity

Disease severity usually refers to the degree of symptom expression as assessed visually using an arbitrary scale. Scales of 0–5 (Cours, 1951; Fauquet and Fargette, 1990) and 1–5 (Hahn et al., 1980) have been used for CMD, where 0 or 1 represent no disease symptoms and 4 or 5 the most severe symptoms, including leaf distortion and stunting of plants, respectively. The scale of 1–5 (Table 2) has been used most commonly for individual plants. A similar scale can also be used for individual leaves or shoots, or for whole plots or fields. If the objective is to relate severity to the marketable yield of tuberous roots, an assessment of overall severity is required of each plant. In contrast, if the objective is to relate severity to the virus(es) present, only the diseased portions of a plant are considered.

Two contrasting methods have been used to calculate mean severity and this causes considerable confusion, misunderstanding and controversy. One approach is to consider records for *all* the plants in the stand being assessed, including those free of disease, whereas the other only considers data for *diseased* plants. For example, four plants having CMD severity scores of 3, 4, 4 and 1 on the 1–5 scale have a mean of 3.0 using the first method and 3.7 using the second. The second method has been used in recent surveys and field experiments in Uganda and elsewhere, and is recommended for use more widely as it provides a true evaluation of disease severity in the stand assessed. The first method underestimates disease severity to an extent dependent on the proportion of disease-free plants present and so disease incidence and severity are confounded. Nevertheless, the method is widely used by plant breeders and many others, even though it can be very misleading. For this reason Mahungu et al. (1994) record *maximum* symptom score for a cultivar or breeding line as well as the *overall* score calculated for all plants.

3.3. Type of infection

The distinction between ‘C’ and ‘W’ infection is important because the occurrence of W indicates spread at

Table 2
The cassava mosaic disease symptom scale of 1–5^a

Symptom description	Scale
1 Unaffected shoots, no symptoms	1
2 Mild chlorosis, mild distortions at bases of most leaves, while the remaining parts of the leaves and leaflets appear green and healthy	2
3 Pronounced mosaic pattern on most leaves, narrowing and distortion of the lower one-third of the leaflets	3
4 Severe mosaic distortion of two thirds of most leaves and general reduction of leaf size and stunting of shoots	4
5 Very severe mosaic symptoms on all leaves, distortion, twisting, mis-shapen and severe leaf reductions of most leaves accompanied by severe stunting of plants	5

^a From Hahn et al. (1980).

the locality, whereas cuttings that grow into infected plants could have been introduced from elsewhere. Moreover, farmers and even researchers in Africa make extensive use of infected planting material, in part due to the limited availability of virus-free stocks of the cultivars being grown.

3.4. Detection and characterization of cassava mosaic begomoviruses (CMBs)

Initially, CMD in Africa and the Indian sub-continent was attributed to one cassava mosaic geminivirus (Bock and Harrison, 1985). Subsequently, three separate geminiviruses were distinguished, of which two occur in Africa: African cassava mosaic virus (ACMV) and East African cassava mosaic virus (EACMV) (Swanson and Harrison, 1994). Five additional cassava mosaic geminiviruses of the genus *Begomovirus* have now been described, of which four occur in Africa (Fauquet and Stanley, 2003) and a recombinant virus referred to as EACMV-UG has been associated with the current pandemic in East Africa (Harrison et al., 1997). The increasing number of CMBs identified emphasises the importance of determining their geographic distribution.

3.4.1. Symptoms and virus detection

Many of the cassava landraces that predominate in farmers' fields in many parts of Africa are susceptible to CMD and express obvious symptoms when infected by one or more CMBs. The symptoms are variable, however, as mildly affected plants exhibit patchy leaf chlorosis and little or no mottling or impaired growth, whereas severely affected plants have smaller leaves, severe chlorosis and stunting. Symptom expression is influenced by several factors including: virus species/strain (Gibson, 1994; Harrison et al., 1997; Owor, 2003), host response (Otim-Nape, 1993; Byabakama et al., 1997; Otim-Nape et al., 1998b; Sserubombwe et al., 2001), plant age at infection (Otim-Nape, 1987; Fargette et al., 1988), temperature (Storey and Nichols, 1938; Chant, 1959; Kartha and Gamborg, 1975; Massala, 1987; Gibson, 1994) and soil fertility (Mollard, 1987; Spittel and Van Huis, 2000; Sseruwagi et al., 2003).

Nevertheless, visual assessments of symptoms provide a reliable indication of the incidence of virus infection in most situations. For example, mild and severe strains of CMBs have been detected in plants expressing mild and severe symptoms, respectively (Zhou et al., 1997; Harrison et al., 1997; Pita et al., 2001). Moreover, the severe symptoms that were prevalent at the CMD epidemic front in Uganda in the 1990s were due to dual infections of ACMV and EACMV-UG (Harrison et al., 1997; Pita et al., 2001). In partially resistant cultivars, symptoms may be localized and, sometimes absent on the young shoots. This complicates the assessment of CMBs, as plants that have recovered are usually excluded when selecting leaf samples for virus diagnosis. The frequent observation that leaf samples from mildly-diseased or symptomless portions of symptom-bearing plants give

negative results with both enzyme-linked immunosorbent assay (ELISA) and PCR-based diagnostic methods, confirms that visual assessments will continue to play an important role in surveying for CMD and the occurrence of CMBs.

3.4.2. Virus diagnostics

3.4.2.1. Enzyme-linked immunosorbent assay (ELISA).

The introduction of murine monoclonal antibodies (Mabs) in either double-antibody-sandwich (DAS) or triple antibody-sandwich (TAS) ELISA first made it possible to distinguish readily between ACMV and EACMV (Thomas et al., 1986; Fargette et al., 1987; Swanson and Harrison, 1994). ELISA is available in many African countries and has the advantage that it is quick, robust and permits a large throughput of samples. TAS-ELISA is somewhat more sensitive than DAS-ELISA, but both techniques have limitations in that they seldom detect CMBs in symptomless leaves. Moreover, ELISA does not detect EACMV in mixed infections with ACMV, or distinguish between ACMV and EACMV-UG, which have similar coat protein epitopes.

3.4.2.2. DNA-based methods.

The limitations of ELISA explain the increasing use of DNA-based polymerase chain reaction (PCR) and restriction length polymorphisms (RFLPs) to detect and distinguish between the different CMBs and to assess their distribution. The techniques are not available in many laboratories in Africa and they are less suitable than ELISA for processing numerous samples. Nevertheless, DNA-based techniques have been used at a few laboratories in Africa and by collaborators in Europe and USA to provide important information on the range of CMBs present (Fondong et al., 2000; Pita et al., 2001; Fauquet and Stanley, 2003; Ogbe et al., 2003). This emphasises need for field studies that utilize the DNA-based diagnostic techniques now available to determine the biological and epidemiological significance of the biochemical diversity.

3.5. Adult whitefly populations

Fishpool and Burban (1994) describe two main approaches to assessing populations of *B. tabaci*: use of attractive or non-attractive traps for the flying adults and counts of adults and/or nymphs in situ. The method most commonly used to assess *B. tabaci* populations on individual cassava plants involves direct counts of adults on representative shoots. At sampling time, the five youngest apical leaves of the uppermost shoot are examined (Fargette, 1985). This is because the adults feed preferentially and oviposit on the youngest immature leaves (Khalifa and El-Khider, 1965; Avidov and Harpaz, 1969; Gameel, 1977; Ohnesorge et al., 1980; Fargette, 1985). Each leaf is held by the petiole and gently inverted so that the adults present on the lower surface can be counted (Seif, 1981; Fargette,

1985; Fargette et al., 1985; Fishpool et al., 1995). Adults of *B. tabaci* and *Bemisia afer*, which also occurs on cassava, are similar morphologically but can be distinguished using a hand lens. *B. tabaci* adults have a ‘rod-shaped’ appearance, as the wings are held upright and parallel to the body, commonly exposing the abdomen. *B. afer* adults appear slightly larger than those of *B. tabaci* and have a ‘wedge-shaped’ appearance, as the wings spread to the posterior and are held flatter, typically covering the abdomen (Legg, 1995).

B. tabaci is the vector of CMGs (Dubern, 1994), but the role of *B. afer* has not been determined (Fishpool and Burban, 1994), although it has been suggested as the putative vector of *Cassava brown streak virus* (Bock, 1994). The two whitefly species should be assessed separately in future studies, but this will require a change of procedure because they have contrasting distributions on cassava (Legg, 1995). *B. afer* tends to be more evenly distributed on leaves of different age than *B. tabaci*. However, in all areas of cassava cultivation, except southern Africa, *B. tabaci* is much more numerous than *B. afer* (Legg and James, 2004), and so even general counts of all whitefly on cassava will only slightly overestimate the prevalence of *B. tabaci*.

Assessments of whitefly populations on representative shoots of different cassava cultivars may give misleading estimates of numbers per plant due to differences in the branching habit of different cultivars and there is a need to standardize procedures. If the shoot basis is adopted, then a shoot should be clearly defined in a way that is appropriate for both branching and non-branching cultivars. Alternatively, if the whole plant is to be considered, the number of shoots per plant should be recorded so that the whitefly population per shoot can be adjusted to provide a valid estimate. However, in Uganda shoot number has seldom been counted in surveys, as in most situations there is considerable uniformity in plant architecture so counts of numbers on representative shoots are adequate.

An alternative method of assessing whitefly populations is to count the sessile nymphs rather than the active adults. This provides population estimates that are less prone to variation due to the dispersal of active winged adults, or to environmental disturbances such as strong winds, heavy rain or hail. The adults have a restless behaviour and the numbers seen on leaves depend on the time of day and weather conditions (Fishpool and Burban, 1994), although Legg (1995) recorded similar numbers of adult whiteflies in morning and afternoon assessments of the same plantings. Nymphs are relatively unaffected by rain or hail, but they are not randomly distributed on cassava leaves and the eggs and early instars are mainly confined to the apical leaves, where the adult females feed and oviposit (Fargette, 1985). The older instar nymphs and pupae occur on the older leaves and so a stratified sample of at least ten successive leaves of different ages should be counted per plant (Abisgold and Fishpool, 1990). This is laborious and rarely used in diagnostic field surveys of CMD because of time and resource constraints.

3.6. Assessment of farm yields and losses due to CMD

There is an extensive literature on the losses due to CMD, as determined in field experiments in different countries and with diverse landraces and improved specially bred cultivars. The losses reported range from negligible to almost total and depend on several factors including the virulence of the virus(es) present, the sensitivity of the host, the stage of growth when infection occurs, soil fertility and growing conditions (Fargette et al., 1988; Fauquet and Fargette, 1990; Thresh et al., 1994b; Sserubombwe et al., 1999; Calvert and Thresh, 2002). However, an important limitation of the results available is that with few exceptions they have been obtained in trials at experiment stations with cassava grown at regular spacings and without intercrops.

There is little information on the effects of CMD in typical farmers’ plantings that are often at wide, irregular spacing and usually with one or more intercrops (Nweke, 1994b). Exceptions are a study on farms in Ivory Coast (Mollard, 1987) and one on local landraces in Uganda in which there was a negative correlation between yield and symptom score on the 1–5 scale of increasing severity (Otim-Nape et al., 1994). Farm sites were also used to study the interaction between soil fertility and yield loss due to CMD in Zanzibar (Spittel and Van Huis, 2000). Moreover, farmers’ fields have been sampled recently in Uganda to compare the performance of the improved CMD-resistant cultivars that were released recently with traditional local landraces, which were almost totally infected. The differences in growth and yield, as determined from representative 5 m × 5 m quadrats of the stands assessed, were very variable but on average improved cultivars produced 2.3 times the yield of landraces (A. Bua, unpublished). There is a need for much more information of this type from Uganda and elsewhere in sub-Saharan Africa to assess the yields of farmers’ plantings and the losses caused by CMD in different agro-ecologies and cultivars. Meanwhile, it has been assumed that diseased plants sustain losses of 30–40% in recent estimates of the impact of CMD in Africa (see Section 4.5).

4. Surveys on cassava mosaic disease in Africa

The main features of the most important surveys conducted regionally or nationally are presented in Table 3 and discussed in the following sections. The 18 countries for which results are available account for more than 90% of total production in Africa. They include Nigeria and Democratic Republic of Congo, which are the two leading cassava producers in Africa. The most detailed records are for Uganda, Tanzania and Kenya where the onset and progress of the current pandemic has been monitored in successive surveys since the early 1990s. Another feature of the results is that the overall incidence of CMD exceeds 50% in 11 of the 18 countries and was greatest in Congo (79%), Ghana (72%), western Kenya (up to 84%), Nigeria (up to 82%),

Table 3

Summary of surveys on cassava mosaic disease incidence and severity and whitefly populations in eighteen African countries

Country	Regions	Year	References	Institutions/ project	No. sites (no. of plants)	Cassava mosaic disease					CMBs identified
						Inc. (%)	W. Inf. (%)	C. Inf. (%)	Sev. 1–5	Wf. (Ave)*	
Benin	Countrywide	1994	Yaninek et al. (1994); Wydra and Msikita (1998)	ESCaPP	31	53	–	–	–	–	–
Benin	Transition forest, wet and dry savannah	1997/1998	Gbaguidi et al. (2004)	SP-IPM	60	39	–	–	2.1	2.8	P
Cameroon	Countrywide	1994	Yaninek et al. (1994); Wydra and Msikita (1998)	ESCaPP	61	67	–	–	–	–	–
Cameroon	South-west, north-west and centre-south	1997/1998	Ntonifor et al. (2004)	SP-IPM	70	61	–	–	2.3	3.2	P
Chad		1992	Johnson (1992)	US: AID	48	40	–	–	–	–	–
Congo	Four regions	2002	N. Ntawuruhunza (unpublished)	DGRST/IITA	105	79	74	6	2.8	2.8	P
DR Congo	Nine regions	2002/2003	P. Ntawuaruhunga (unpublished)	INERA/IITA	236	60	4	56	3.1	15.0	P
Ghana	Countrywide	1994	Yaninek et al. (1994); Wydra and Msikita (1998)	ESCaPP	40	72	–	–	–	–	–
Ghana	Countrywide	1997/8	Cudjoe et al. (2004)	SP-IPM	80	72	–	–	2.3	3.7	P
Guinea	Countrywide	2003	G. Okao-Okuja (unpublished)	IITA/National	60	62	10	52	2.4	1.0	P
Kenya	Western and Nyanza	1993	Legg et al. (1999a)	NRI/KARI	13	20	2	18	–	–	–
Kenya	Western and Nyanza	1996	Legg et al. (1999a)	NRI/KARI	43	57	22	35	3.8	–	P
Kenya	Coast and Western	1996	Ogbe et al. (1996)	NRCRIU/KARI	[160]	–	–	–	–	–	E
Kenya	Western and Nyanza	1997	Legg et al. (1999b)	NRI/IITA/KARI	50	70	37	33	3.3	–	P
Kenya	Western and Nyanza	1998	Legg et al. (1999b)	IITA/KARI	17	84	14	70	2.9	0.2	P
Kenya	Southern Nyanza	1998	Legg et al. (1999b)	IITA/KARI	15	5	1	4	2.1	0.6	P
Kenya	Coast, Western and Nyanza	1998	Kamau et al. (2004)	SP-IPM	50	51	–	–	2.5	1.2	P
Kenya	Coastal	2000	Munga and Thresh (2002)	NRI/KARI	29	60 ⁺	–	–	2.6	–	–
Madagascar	Countrywide	1998	Ranomenjanahary et al. (2004)	SP-IPM	111	47	–	–	3.2	5.0	P
Malawi		1993	Nyirenda et al. (1993)	National	450	21	–	–	–	–	–
Malawi	Three regions	1994	Sweetmore (1994)		34	17	<1	17	–	–	–
Malawi		1997	Ogbe et al. (1997)		[36]						E
Malawi	Central and Northern Lakeshore, Central	1997/1998	Theu and Sseruwagi (2004)	SP-IPM	41	42	–	–	2.8	1.3	P
Mozambique	Two provinces	1999	Hillocks et al. (2002)	NRI/INIA/WV	[4163]	25 ⁺	–	–	–	–	–
Mozambique		1999–2002	Thresh and Hillocks (2003)	NRI/INIA/WV	377	40 ⁺	–	–	–	–	–
Nigeria	Countrywide	1994	L.C. Dempster, unpublished	IITA	93	55	–	–	–	–	–
Nigeria	Countrywide	1994	Yaninek et al. (1994); Wydra and Msikita (1998)	ESCaPP	111	82	–	–	–	–	–

Table 3 (Continued)

Country	Regions	Year	References	Institutions/ project	No. sites (no. of plants)	Cassava mosaic disease					CMBs identified
						Inc. (%)	W. Inf. (%)	C. Inf. (%)	Sev. 1–5	Wf. (Ave)*	
Nigeria	Four regions	1997/1998	Echendu et al. (2004)	SP-IPM	80	54			2.3	1.8	P
Rwanda	Three regions	1997	Legg (2000)	IITA/ISAR	22						P
Rwanda	Five regions	2000	Legg (2000); Legg et al., 2001	IITA/ISAR	26	26	5	21	2.7	–	P
Rwanda	Countrywide	2001	P. Sseruwagi (unpublished)	IITA/ISAR	120	30	13	17	3.5	0.4	P
South Africa	Three regions	1998	Jericho et al. (1999)	National	20	31			2.4		–
Senegal	Western	2003	G. Okao-Okuja, unpublished	IITA/National	20	83	12	71	2.4	3.2	P
Tanzania	Countrywide	1993–1994	Legg and Raya (1998)	NRI/TRTCP	242	27 ⁺	3	24	–	5.0	–
Tanzania	Countrywide	1997	Ogbe et al. (1997)		[138]						E
Tanzania	Lake Victoria Zone	1998 (January)	Legg et al. (1999a)	IITA/TRTCP	35	~35					P
Tanzania	Zanzibar	1998	Thresh and Mbwana (1998)	NRI/TRTCP	13	71 ⁺					P
Tanzania	Lake Victoria Zone, Mtwara and Tanga	1998 (May)	Ndunguru et al. (2004)	SP-IPM	60	34	15	19	3.0	3.0	P
Tanzania	Eight regions	1998 (June)	Legg (2000)	OFDA	60	21					P
Tanzania	Lake Victoria Zone	1999 (July)	Ndunguru and Jeremiah (1999)	TRTCP/IITA	89	72	36	36	3.2	49.0	P
Tanzania	Kagera region	1999	Legg (2000)	IITA	19	65					P
Uganda	28 districts	1990–1992	Otim-Nape et al. (1998a)	NARO/NCP	1350	57					–
Uganda	27 districts	1994	Otim-Nape et al. (2001)	NARO/NCP	1215	65					–
Uganda	Countrywide	1996	Otim-Nape et al. (1997)	NARO/NCP	1215						–
Uganda	12 districts	1996	Ogbe et al. (1996)		[157]						E
Uganda	12 districts	1997/1998	Sseruwagi et al. (2004)	SP-IPM	80	68	22	46	2.9	3.9	P
Uganda	Five districts	1997	IITA/NARO (unpublished)	PL-480	225	74	15	59	2.9	3.9	P
Uganda	Five districts	1998	IITA/NARO (unpublished)	PL-480	225	76	3	73	3.1	6.3	P
Uganda	Six districts	1999	IITA/NARO (unpublished)	PL-480	270	83			3.5		P
Uganda	Six districts	2000	IITA/NARO (unpublished)	PL-480	270	74	15	59	3.2	8.5	P
Uganda	Six districts	2001	IITA/NARO (unpublished)	PL-480	270	66	22	44	3.0	3.7	P
Uganda	Masaka and Rakai	1998	IITA/NARO (unpublished)	OFDA	90	67	19	48	3.3	2.0	P
Zambia	Countrywide	1994	Muimba-Kankolongo et al. (1999)	RTP-Zambia	62	45	–	–	–	50.5	–
Zambia		1997	Ogbe et al. (1997)		[100]						E

Inc., Total incidence; W. Inf., whitefly infection; C. Inf., cutting infection; Sev., severity (1–5 scale), where 1 = no disease symptoms and 5 = very severe symptoms; Wf.: whitefly adult population; CMBs: Cassava mosaic begomoviruses, (–) data absent; E, ELISA-based diagnostics; P, PCR-based diagnostics. *Abbreviations:* DGRST, General Delegation for Scientific Research and Technology; INERA, Institut de l'Environnement et de Recherches Agricoles; INIA, Institut Nacional Investigaciones Agricole; ISAR, Institut des Sciences Agronomiques du Rwanda; KARI, Kenya Agricultural Research Institute; NRCRIU, Nigerian Root Crops Research Institute, Umudike; NRI, Natural Resources Institute, UK; OFDA, US Office for Foreign Disaster Assistance; TRTCP, Tanzania Root and Tuber Crops Programme; USAID, United States Agency for International Development; WV, World Vision.

* Mean of values for maximum whitefly count on top five leaves.

+ The incidence of cassava brown streak disease was also assessed in these surveys.

Senegal (83%) and Uganda (up to 83%). The lowest incidences were in Chad, Malawi, Madagascar, Rwanda, South Africa and the parts of Tanzania not yet affected by the current pandemic.

4.1. *The collaborative study of cassava in Africa (COSCA)*

This was a multi-million dollar project funded by the Rockefeller Charitable Foundation and involved several research organisations. Phase I of the project was in six countries: Uganda, Tanzania, Ivory Coast, Nigeria, Ghana and Zaire (now Democratic Republic of Congo) between 1989 and 1990. The project considered production factors affecting cassava, including CMD incidence and symptom severity and assessed yields using a random sampling method. However, the results for CMD were of limited value as too few plants were assessed in each country and no distinction was made between C and W infections (Nweke, 1994a,b; Thresh et al., 1994a). For these reasons the results are omitted from Table 3.

4.2. *The ecologically sustainable cassava plant protection project (ESCaPP)*

This was a collaborative initiative executed by IITA and involved the national root crop programmes in Benin, Ghana, Nigeria and Cameroon. In each country there was a comprehensive survey of pests and diseases of cassava, including CMD (Wydra and Msikita, 1998). As in the COSCA survey, a random grid system was used in selecting areas to be sampled. Assessments were made of CMD incidence and severity and adult whitefly populations in the main dry and wet seasons of 1994.

4.3. *The systemwide programme for integrated pest management (SP-IPM)*

Surveys were made in nine African countries on whiteflies as vectors of viruses in cassava and sweet potato in 1997 and 1998 (Anderson and Markham, 2004). The main objective was to identify the whiteflies and whitefly-transmitted viruses of cassava and sweet potato. Moreover, additional information was gathered on the natural enemies of whiteflies, which were not considered in the earlier COSCA or ESCaPP surveys. This project has obtained the most detailed and recent sets of data on the incidence and severity of CMD in the countries assessed (Legg et al., 1998; Anderson and Markham, 2004) (Table 3). An important feature of the assessments was the use of molecular techniques to identify the CMGs present in each country (Legg and Okao-Okuja, 1999; Markham et al., 2004).

4.4. *National surveys*

The results of surveys for CMD by the National Agricultural Research Services (NARS) together with local or in-

ternational partners in eighteen countries are summarised in Table 3.

4.5. *Overall estimates of crop loss in Africa*

Thresh et al. (1997) estimated the overall yield loss due to CMD in Africa using a conservative estimate for incidence of 50–60%, based on the survey data then available from eight countries, and assuming a yield loss of 30–40% for affected plants. On these assumptions, Africa-wide yield losses were estimated to be 15–24%, equivalent to 12–23 million tonnes in relation to actual production at the time of 73 million tonnes Legg and Thresh (2003) used a similar approach to update this estimate based on an expanded and updated set of survey data for 17 countries which together represented almost 90% of total African production. FAOSTAT production data for 2002 (FAO, 2003) were used together with the 30–40% CMD loss estimate adopted previously and actual incidence figures to calculate an estimated loss range for each country. National losses were summed and added to estimated losses for unsurveyed producer countries which were calculated using the average incidence for those surveyed. Total losses in Africa were estimated to be 19–27 million tonnes, compared to actual production of 97 million tonnes. (FAO, 2003). Such calculations are simplistic and markets in Africa could not readily absorb such a big increase in productivity. Nevertheless, the estimates indicate the ineffective way in which land, labour and resources are currently being used in cassava production. Control of CMD would greatly increase productivity, release land and labour for other crops and permit extended periods of fallow to restore soil fertility.

Regional studies have also used survey data combined with yield loss approximations to estimate yield loss, most notably for the pandemic-affected area of East Africa (Legg et al., 1999a). Based on the assumptions of a 40% yield loss in pandemic-affected areas, a 13% yield loss in unaffected areas (Sserubombwe, 1998) and a value for cassava of US\$ 100 per tonne, total monetary losses in pandemic-affected areas of Uganda and Kenya were put at US\$ 74 million, whilst those in areas of Kenya and Tanzania which were unaffected at that time were estimated to be US\$ 19 million.

5. **Monitoring the spread and distribution of cassava mosaic begomoviruses (CMBs)**

Only the most recent surveys of CMD in Africa have considered the identity and distribution of the CMBs present. ELISA and usually small numbers of samples per country were first used by Swanson and Harrison (1994) to map the distribution of ACMV and EACMV. Ogbe et al. (1996, 1997) adopted a similar approach, albeit with larger numbers of samples for more restricted geographical areas of eastern, southern and western Africa (Table 3). PCR and RFLP analyses were then introduced. They facilitated compar-

isons of the DNA of virus isolates collected from different locations in Uganda in 1996–97, distinguished between ACMV, EACMV and EACMV-UG (Zhou et al., 1997) and provided evidence of an association of EACMV-UG with the severe epidemic occurring in the country (Harrison et al., 1997). Consequently, the techniques have been used widely to detect ACMV, EACMV, EACMV-UG and other CMBs in virus samples collected during recent diagnostic surveys (Table 3), and to map the distribution and spread of EACMV-UG and mixtures of CMBs in East and Central Africa (Legg et al., 1999b, 2001; Legg and Okao-Okuja, 1999; Markham et al., 2004; Neuenschwander et al., 2001) and in Nigeria (Ogbe et al., 2003).

6. Forecasting future spread of cassava mosaic disease

Information from CMD surveys can be used to forecast the future spread of the severe form of the disease that is causing the current pandemic and this is of vital importance in control. Forecasting future spread requires regular diagnostic surveys in key cassava growing areas to establish:

- the spread of CMD both in space and time;
- the epidemic characteristics of CMD, i.e. the amount and relative proportion of W and C infections;
- the identity and distribution of the different CMBs present;
- the population and distribution of the whitefly vector (*B. tabaci*);
- the occurrence, frequency, amount and type (resistant/susceptible) of cassava cultivars being grown.

Using this information, the rate of spread of the disease can be monitored over time and computer-generated maps can be produced. By mapping CMD epidemic-affected zones, establishing the prevailing epidemic characteristics, CMB identity and distribution, whitefly populations and the rate of spread of the epidemic, it is possible to map the areas at risk and predict when they are likely to be affected (Legg, 1999). Using this information, a model could be produced to forecast future spread of the epidemic and to provide a decision support system for disease management.

7. Management of cassava mosaic disease

Data obtained from CMD field surveys are vital in devising appropriate control measures to manage the disease in severely affected areas and to make adequate preparations in threatened areas. A number of CMD control measures are available including the use of phytosanitation involving selection of cuttings for propagation solely from symptomless plants (Fauquet and Fargette, 1990; Otim-Nape, 1993; Thresh and Otim-Nape, 1994; Thresh et al., 1998a), the removal ('roguing') of diseased cassava from partially infected stands (Otim-Nape, 1993; Thresh and Otim-Nape, 1994; Thresh et al., 1998a), and proper disposal and burn-

ing of crop debris to decrease the risk of infection (Fargette et al., 1985; Otim-Nape, 1993). It is also possible to adjust the disposition of crops and cropping practices to decrease the risk of infection (Fargette et al., 1985; Otim-Nape, 1987; Thresh and Otim-Nape, 1994) and to use virus-resistant cultivars (Nichols, 1947; Jennings, 1957, 1994; Otim-Nape, 1993; Mahungu et al., 1994; Thresh and Otim-Nape, 1994; Thresh et al., 1998a).

Although these methods are available for use either singly or in combination, host plant resistance is the most widely used approach in both national and regional CMD management programmes. In Uganda and other areas already affected by the current pandemic the strategy has been to select, multiply and distribute CMD-resistant cultivars to farmers. This has helped to restore cassava production in areas where the crop had been largely abandoned. The incidence and severity of CMD has been considerably decreased in these areas depending on the extent to which the CMD-resistant cultivars were adopted (Legg et al., 1999b; Otim-Nape et al., 1998a, 2000, 2001).

The approach in recently affected and threatened areas includes:

- germplasm introduction of CMD-resistant material using an 'open quarantine' procedure in recently affected areas and as specially prepared in vitro plantlets in threatened areas;
- development of a 'fast-track' approach to evaluate new CMD-resistant germplasm through on-station and on-farm trials including targeted evaluation in CMD 'hot spot' areas;
- participatory evaluation of new germplasm at technology transfer centres and within farmer field schools and other farmer research/development groups;
- training of agricultural workers and farmers in cassava pest and disease control using formal training courses and in-field practical exercises to promote an integrated approach;
- 'early warning systems' to inform researchers, agricultural workers and farmers of the impending epidemic through media, bulletins, workshops, field days, open days. etc.;
- networking through consultative project planning and implementation by both national and regional steering committees.

A weakness in the current approach is over-reliance on host resistance. For the future, adoption of an integrated approach including phytosanitary and cultural measures to complement host resistance offers the prospect of more effective control.

8. Conclusion

CMD has been known for more than 100 years and for much of this period it has received at least some attention

from researchers and extensionists in one or more African countries. However, past activities have been sporadic, limited to few of the many countries where the disease occurs and seldom sustained for a sufficiently long period (Thresh et al., 1994c). Consequently, the overall effort has been inadequate in relation to the magnitude of the losses sustained. The situation has changed considerably in recent years following the onset of the serious epidemic in Uganda in the late 1980s (Otim-Nape and Thresh, 1998; Otim-Nape et al., 2000). This has since become a major pandemic that is affecting other countries in the region and the full extent of the problem posed by CMD in sub-Saharan Africa has only recently become apparent (Legg, 1999). These developments have provided a powerful incentive for increased research on all aspects of CMD and its control and for crop improvement projects based on the release of improved virus-resistant cultivars (Legg and Thresh, 2003).

The surveys considered in the foregoing sections have played an important role in establishing the importance of CMD in Africa and in identifying the nature of the problem and the areas at greatest risk from the current pandemic. The data obtained have also been used to justify the allocation of additional funds for research and extension projects on CMD and to demonstrate the benefits that have been gained from past activities. Surveys have been only a small part of the overall effort and have not led to a major diversion of resources and personnel. Nevertheless, at least some information is available on the status of CMD in 18 of the 38 countries where cassava is grown in Africa. There is also information on the CMBs present in representative samples collected in 13 of the countries surveyed. It is important to initiate surveys in additional countries, including the important cassava-growing areas of Angola, Burundi, Liberia and Sierra Leone, although this will be difficult because of continuing civil unrest and chronic insecurity. Surveys should also be repeated or extended in countries where the assessments were incomplete or done several years ago and where there is little or no information on the identity and distribution of the CMBs present. A further requirement is to refine the current procedures and address the issue of sample size and some of the limitations identified in this review. The effectiveness with which C and W infections are being distinguished should be assessed and the extent to which survey results are reproducible when carried out by different personnel and in different seasons. Information is also required on the relationship between symptom severity and yield loss in farmers' plantings so that survey results can be used more effectively to indicate the overall economic and social impact of CMD in different regions.

References

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

- Ahohuendo, B.C., Sarkar, S., 1995. Partial control of the spread of African cassava mosaic virus in Benin by intercropping. *Z. Pflanzensch.* 102, 249–256.
- Anderson, P.K., Markham R.H., 2004. Whiteflies and whitefly-borne viruses in the tropics: building a knowledge base for global action. Centro Internacional de Agricultura Tropical, Cali, Colombia, in press.
- Avidov, Z., Harpaz, I., 1969. *Plant pests of Israel*. Israel University Press, Jerusalem, 549 pp.
- Bock, K.R., 1994. Studies on cassava brown streak virus disease in Kenya. *Trop. Sci.* 34, 134–145.
- Bock, K.R., Harrison, B.D., 1985. African cassava mosaic virus. AAB Descriptions of Plant Viruses No. 297. Associated of Applied Biologists, Wellesbourne, Warwick, UK, 6 pp.
- Butt, D.J., Royle, D.J., 1980. The importance of terms and definitions for a conceptually unified epidemiology. In: Palti, J., Kranz, J. (Eds.), *Comparative Epidemiology: A Tool for Better Disease Management*. Centre for Agricultural Publishing and Documentation, Wageningen, pp. 29–45.
- Byabakama, B.A., Adipala, E., Ogenga-Latigo, M.W., Tusiime, G., Otim-Nape, G.W., 1997. The resistance of improved cassava varieties to cassava mosaic disease in Uganda. *Afr. J. Plant Prot.* 7, 45–57.
- Calvert, L., Thresh, J.M., 2002. The viruses and virus diseases of cassava. In: Hillocks, R.J., Thresh, J.M., Bellotti, A.C. (Eds.), *Cassava: Biology, Production and Utilization*. CAB International, Wallingford, UK, pp. 237–260.
- Chant, S.R., 1959. A note on the inactivation of mosaic in cassava (*Manihot utilissima* Pohl) by heat treatment. *Emp. J. Expt. Agric.* 27, 55–58.
- Cours, G., 1951. Le Manioc à Madagascar. *Mémoires de l'Institut Scientifique de Madagascar. Série B, Biologie Végétale* 3, 203–400.
- Cudjoe, A., James, B., Gyamenah, J., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Ghana. In: Anderson and Markham.
- Dubern, J., 1994. Transmission of African cassava mosaic geminivirus by the whitefly *Bemisia tabaci*. *Trop. Sci.* 34, 82–91.
- Echendu, T.N.C., Ojo, J.B., James, B.D., Gbaguidi, B., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Nigeria. In: Anderson and Markham.
- Fargette, D., 1985. *Epidémiologie de la Mosaïque Africaine du Manioc en Côte d'Ivoire*. University Thèse de la Faculte des sciences des Montpellier, 203 pp.
- Fargette, D., Fauquet, C., 1988. A preliminary study on the influence of intercropping maize and cassava on the spread of African cassava mosaic virus by whiteflies. *Asp. Appl. Biol.* 17, 195–202.
- Fargette, D., Fauquet, C., Thouvenel, J.-C., 1985. Field studies on the spread of African cassava mosaic. *Ann. Appl. Biol.* 106, 285–294.
- Fargette, D., Fauquet, C., Thouvenel, J.-C., 1988. Yield losses induced by African cassava mosaic virus in relation to the mode and date of infection. *Trop. Pest Man.* 34, 89–91.
- Fargette, D., Thouvenel, J.-C., Fauquet, C., 1987. Virus content of leaves of cassava infected by African cassava mosaic virus. *Ann. Appl. Biol.* 110, 65–73.
- Fargette, D., Fauquet, C., Fishpool, L.D.C., Thresh, J.M., 1992. Ecology of African cassava mosaic virus in relation to the climatic and agricultural environment. In: Martelli, R. (Ed.), *Viruses, Vectors and the Environment*. Abstracts of the 5th International Plant Virus Epidemiology Symposium, Valenzano (Bari), Italy, 27–31 July, 1992, pp. 107–108.
- Fargette, D., Jeger, M., Fauquet, C., Fishpool, L.D.C., 1994. Analysis of temporal disease progress of African cassava mosaic virus. *Phytopathology* 84, 91–98.
- Fauquet, C., Fargette, D., 1990. African cassava mosaic virus: etiology, epidemiology and control. *Plant Dis.* 74, 404–411.
- Fauquet, C.M., Stanley, J., 2003. Geminivirus classification and nomenclature: progress and problems. *Ann. Appl. Biol.* 142, 165–189.
- Fishpool, L.D.C., Burban, C., 1994. *Bemisia tabaci*: the whitefly vector of African cassava mosaic geminivirus. *Trop. Sci.* 34, 55–72.

- Fishpool, L.D.C., Fauquet, C., Fargette, D., Thouvenel, J.-C., Burban, C., Colvin, J., 1995. The phenology of *Bemisia tabaci* (Homoptera: Aleyrodidae) populations on cassava in southern Côte d'Ivoire. *Bull. Entomol. Res.* 85, 197–207.
- Fondong, V.N., Pita, J.S., Rey, M.E.C., de Kochko, A., Beachy, R.N., Fauquet, C.M., 2000. Evidence of synergism between African cassava mosaic virus and a new double-recombinant geminivirus infecting cassava in Cameroon. *J. Gen. Virol.* 81, 287–297.
- Fondong, V.N., Thresh, J.M., Zok, S., 2002. Spatial and temporal spread of cassava mosaic virus disease in cassava grown alone and when intercropped with maize and/or cowpea. *J. Phytopathol.* 150, 365–374.
- Food and Agriculture Organization of the United Nations, 2003. Cassava production data 2002. (<http://www.fao.org>).
- Fulton, M.C., Asher, C.J., 1997. Zinc treatments applied to cassava (*Manihot esculenta* Crantz) sets changes early growth and zinc status of plants. *Austr. J. Expt. Agric.* 37, 825–830.
- Gameel, O.I., 1977. *Bemisia tabaci*. In: Kranz, J., Schmutterer, H., Kock, W. (Eds.), *Diseases, Pests and Weeds in Tropical Crops*. Paul Parey, Berlin, pp. 320–322.
- Gbaguidi, B., James, B., Saizonou, S., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Benin. In: Anderson and Markham.
- Gibson, R.W., 1994. Long-term absence of symptoms in heat-treated African cassava mosaic geminivirus-infected resistant cassava plants. *Trop. Sci.* 34, 154–158.
- Gibson, R.W., Legg, J.P., Otim-Nape, G.W., 1996. Unusually severe symptoms are a characteristic of the current epidemic of mosaic virus disease of cassava in Uganda. *Ann. App. Biol.* 128, 479–490.
- Golding, F.D., 1936. *Bemisia nigeriensis* Corb., a vector of cassava mosaic in Southern Nigeria. *Trop. Agric.* 13, 182–186.
- Hahn, S.K., Terry, E.R., Leuschner, K., 1980. Breeding cassava for resistance to cassava mosaic disease. *Euphytica* 29, 673–683.
- Harrison, B.D., Zhou, X., Otim-Nape, G.W., Liu, Y., Robinson, D.J., 1997. Role of a novel type of double infection in the geminivirus-induced epidemic of severe cassava mosaic in Uganda. *Ann. App. Biol.* 131, 437–448.
- Hillocks, R.J., Raya, M.D., Thresh, J.M., 1999. Distribution and symptom expression of cassava brown streak disease in southern Tanzania. *Afr. J. Root Tuber Crops* 3, 57–62.
- Hillocks, R.J., Thresh, J.M., Tomas, J., Botao, M., Macia, R., Zavier, R., 2002. Cassava brown streak disease in northern Mozambique. *Int. J. Pest Man.* 48, 179–182.
- IITA, 1979. Thermotherapy. In: Annual Report 1978, IITA Root and Tuber Improvement Programme. IITA, Nigeria, p. 59.
- Jennings, D.L., 1957. Further studies in breeding cassava for virus resistance. *East Afr. Agric. J.* 22, 213–219.
- Jennings, D.L., 1994. Breeding for resistance to African cassava mosaic geminivirus in East Africa. *Trop. Sci.* 34, 110–122.
- Jericho, C., Thompson, G.J., Gerntholtz, U., Viljoen, J.C., 1999. Occurrence and distribution of cassava pests and diseases in South Africa. In: Akoroda, M.O., Teri, J.M. (Eds.), *Proceedings of the Scientific Workshop of the Southern African Root Crops Research Network (SARRNET)*, Lusaka, Zambia, 17–19 August 1998, pp. 252–262.
- Johnson, A., 1992. Report: Lake Chad Farmer Training and Agricultural Development Project: American Organizations for Rehabilitation Through Training, U.S. Agency for International Development.
- Kamau, J., Sseruwagi, P., Aritua, V., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Kenya. In: Anderson and Markham.
- Kartha, K.K., Gamborg, O.L., 1975. Elimination of cassava mosaic disease by meristem culture. *Phytopathology* 65, 826–828.
- Khalifa, A., El-Khider, E., 1965. Biological Study on *Trialeurodes lubia* and *Bemisia tabaci* (Aleyrodidae). *Bull. Soc. Entomol. Egypte* 48, 115–129.
- Legg, J.P., 1995. The ecology of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) vector of African cassava mosaic geminivirus in Uganda. Ph.D. Thesis. University of Reading, UK, 183 pp.
- Legg, J.P., 1999. Emergence. *Crop Prot.* 18, 627–637.
- Legg, J.P., 2000. The cassava mosaic virus disease pandemic in East and Central Africa: past, present and future. Paper presented at the workshop of Management of Cassava virus diseases in Tanzania, 6–8 September, 2000, Kibaha, Tanzania.
- Legg, J.P., James, B., 2004. Summary and Conclusions. In: Anderson and Markham.
- Legg, J.P., Ogwal, S., 1998. Changes in the incidence of African cassava mosaic virus disease and the abundance of its whitefly vector along south-north transects in Uganda. *J. Appl. Entomol.* 122, 169–178.
- Legg, J.P., Okao-Okuja, G., 1999. Progress in the diagnosis and epidemiological characterisation of cassava mosaic geminiviruses in East Africa. Abstracts of the VIIth International Plant Virus Epidemiology Symposium, Aguadulce (Almeria), Spain, 11–16 April, 1999, pp. 74–75.
- Legg, J.P., Raya, M., 1998. A survey of cassava virus diseases in Tanzania. *Int. J. Pest Man.* 44, 17–23.
- Legg, J.P., Thresh, J.M., 2003. Cassava virus diseases in Africa. In: *Proceedings of the First International Workshop on Plant Virology in Sub-Saharan Africa*. IITA, Ibadan, pp. 517–552.
- Legg, J.P., Kapinga, R., Teri, J., Whyte, J.A., 1999a. Pandemic of cassava mosaic virus disease in East Africa: control strategies and regional partnerships. *Roots* 6 (1), 10–19.
- Legg, J.P., Okao-Okuja, G., Mayala, R., Muhinyuza, J.-B., 2001. Spread into Rwanda of the severe cassava mosaic virus disease pandemic and the associated Uganda variant of East African cassava mosaic virus (EACMV-Ug). *Plant Pathol.* 50, 796.
- Legg, J.P., Sseruwagi, P., Aritua, V., 1998. Sustainable integrated management of whiteflies as pests and vectors of plant viruses in the tropics. Progress report of phase I for sub-project 4, Whiteflies as vectors of viruses in cassava and sweetpotato in Africa. ESARC, IITA, Uganda, DANIDA.
- Legg, J.P., Sseruwagi, P., Aritua, V., Kamau, J., Ajanga, S., Jeremiah, S.C., Otim-Nape, G.W., Muimba-Kankalongo, A., Gibson, R.W., Thresh, J.M., 1999b. The pandemic of severe cassava mosaic disease in East Africa: current status and potential future threats. In: Akoroda, M.O., Teri, J.M. (Eds.), *Food security and crop diversification in SADC countries: the role of cassava and sweet potato*. Proceedings of the Scientific Workshop of the Southern African Root Crops Research Network (SARRNET), Lusaka, Zambia, 17–19 August, 1998, pp. 236–251.
- Mahungu, N.M., Dixon, A.G.O., Kumbira, J.M., 1994. Breeding cassava for multiple pest resistance in Africa. *Afr. Crop Sci. J.* 2, 539–552.
- Malathi, V.G., Thankappan, M., Nair, N.G., Nambisan, B., Ghosh, S.P., 1987. Cassava mosaic disease in India. In: *Proceedings of the International Seminar on African Cassava Mosaic Disease and its Control*, Yamoussoukro, Côte d'Ivoire, 4–8 May, 1987. CTA/FAO/ORSTOM/IITA/IAPC, pp. 189–198.
- Markham, P., Briddon, R., Roussot, C., Farquhar, J., Okao-Okuja, G., Legg, J.P., 2004. The diversity of African cassava mosaic disease. In: Anderson and Markham.
- Massala, R., 1987. African cassava mosaic in the Congo, its importance, distribution and methods of control. In: *Proceedings of the International Seminar on African Cassava Mosaic Disease and its Control*, Yamoussoukro, Côte d'Ivoire, 4–8 May 1987. CTA/FAO/ORSTOM/IITA/IAPC, pp. 14–19.
- Mollard, E., 1987. African cassava mosaic among farmers of the lower Ivory Coast. In: *Proceedings of the International Seminar on African Cassava Mosaic Disease and its Control*, Yamoussoukro, Côte d'Ivoire, 4–8 May 1987. CTA/FAO/ORSTOM/IITA/IAPC, pp. 150–160.
- Muimba-Kankalongo, A., Mahungu, N.M., Legg, J.P., Theu, M.P., Raya, M.D., Chalwe, A., Muondo, P.A., Abu, A.A., Kaitisha, G., 1999. Importance of cassava mosaic disease and intervention strategies for its control in southern Africa. In: Akoroda, M.O., Teri, J.M. (Eds.), *Food Security and Crop Diversification in SADC Countries: The Role of Cassava and Sweet Potato*. Proceedings of the scientific workshop of the Southern African Root Crops Research Network (SARRNET), Lusaka, Zambia, 17–19 August, 1998, pp. 212–235.

- Munga, T., Thresh, J.M., 2002. Incidence of cassava mosaic and cassava brown streak virus diseases in coastal Kenya. *Roots* 8 (1), 12–14.
- Ndunguru, J., Jeremiah, S., 1999. Incidence of severe CMD and severity scores in Kagera and Mara regions. In: Emergency programme to combat the cassava mosaic disease pandemic in East Africa. Fourth Quarterly Technical Report (July–September 1999), November 1999 issue, pp. 27–30.
- Ndunguru, J., Sseruwagi, P., Jeremiah, S., Kapinga, R., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Tanzania. In: Anderson and Markham.
- Neuenschwander, P., Hughes, J.d'A., Ogbé, F., Ngatse, J.M., Legg, J.P., 2001. Occurrence of the Uganda Variant of East African cassava mosaic virus (EACMV-Ug) in western Democratic Republic of Congo and the Congo Republic defines the westernmost extent of the CMD pandemic in East/Central Africa. *Plant Pathol.* 51, 384.
- Nichols, R.F.W., 1947. Breeding cassava for virus resistance. *E. Afr. Agric. J.* 12, 184–194.
- Ntonifor, N., James, B., Tumanteh, A., Gbaguidi, B., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Cameroon. In: Anderson and Markham.
- Nweke, F.I., 1994a. Cassava pest and disease diagnostic survey protocols, International Institute of Tropical Agriculture, Plant Health Management Division (IITA-PHMD).
- Nweke, F.I., 1994b. Farm level practices relevant to cassava plant protection. *Afr. Crop Sci. J.* 2, 563–582.
- Nweke, F.I., Dixon, A.G.O., Asiedu, R., Fodayan, S.A., 1994. Cassava varietal needs of farmers and the potential for production growth in Africa. Working Paper 10. Collaborative Study of Cassava in Africa. IITA, Ibadan, Nigeria, 239 pp.
- Nyirenda, G.K.C., Munthali, D.C., Phiri, G.S.N., Snati, R.F.N., Gerling, D., 1993. Integrated pest management of *Bemisia* spp. Whiteflies in Malawi. Report: Makoka Research Station, Thondwe, Malawi.
- Ogbé, F.O., Legg, J.P., Raya, M.D., Muimba-Kankalongo, A., Theu, M.P., Kaitisha, G., Phiri, N.A., Chalwe, A., 1997. Diagnostic survey of cassava mosaic viruses in Tanzania, Malawi and Zambia. *Roots* 4 (2), 12–15.
- Ogbé, F.O., Songa, W., Kamau, J.W., 1996. Survey of the incidence of African cassava mosaic and East African cassava mosaic viruses in Kenya and Uganda using a monoclonal antibody based diagnostic test. *Roots* 3 (1), 10–14.
- Ogbé, F.O., Thottappilly, G., Dixon, A.G.O., Atiri, G.I., Mignouna, H.D., 2003. Variants of East African cassava mosaic virus and its distribution in double infections with African cassava mosaic virus in Nigeria. *Plant Dis.* 87, 223–229.
- Ohnesorge, B., Sharaf, N., Allawi, T., 1980. Population studies on the tobacco whitefly *Bemisia tabaci* Genn. (Homoptera: Aleyrodidae) during the winter season. I. Spatial distribution on some host plants. *Z. Angew. Entomol.* 90, 226–232.
- Otim-Nape, G.W., 1987. Importance, production and utilization of cassava in Uganda. In: Proceedings of the International Seminar on African Cassava Mosaic Disease and its Control, Yamoussoukro, Côte d'Ivoire, 4–8 May, 1987. CTA/FAO/ORSTOM/IITA/IAPC, pp. 203–218.
- Otim-Nape, G.W., 1993. Epidemiology of the African cassava mosaic geminivirus disease (CMD) in Uganda. Ph.D. Thesis, University of Reading, UK, pp. 252.
- Otim-Nape, G.W., Thresh, J.M., 1998. The current pandemic of cassava mosaic virus disease in Uganda. In: Gareth Jones, D. (Ed.), *The Epidemiology of Plant Diseases*. Kluwer Academic, Netherlands, pp. 423–443.
- Otim-Nape, G.W., Alicai, T., Thresh, J.M., 2001. Changes in the incidence and severity of cassava mosaic virus disease, varietal diversity and cassava production in Uganda. *Ann. Appl. Biol.* 138, 313–327.
- Otim-Nape, G.W., Shaw, M.W., Thresh, J.M., 1994. The effects of African cassava mosaic virus on the growth and yield of cassava in Uganda. *Trop. Sci.* 34, 43–54.
- Otim-Nape, G.W., Thresh, J.M., Fargette, D., 1996. *Bemisia tabaci* and cassava mosaic virus disease in Africa. In: Gerling, D., Meyer, R.T. (Eds.), *Bemisia* 1995: Taxonomy, Biology, Damage, Control and Management. Intercept, UK, pp. 319–350.
- Otim-Nape, G.W., Thresh, J.M., Shaw, M.W., 1998a. The incidence and severity of cassava mosaic virus disease in Uganda: 1990–1992. *Trop. Sci.* 38, 25–37.
- Otim-Nape, G.W., Thresh, J.M., Bua, A., Baguma, Y., Shaw, M.W., 1998b. Temporal spread of cassava mosaic virus disease in a range of cassava cultivars in different agro-ecological regions of Uganda. *Ann. Appl. Biol.* 133, 415–430.
- Otim-Nape, G.W., Bua, A., Thresh, J.M., Baguma, Y., Ogwal, S., Ssemakula, G.N., Acola, G., Byabakama, B., Colvin, J., Cooter, R.J., Martin, A., 2000. The current pandemic of cassava mosaic virus disease in East Africa and its control. NARO, NRI, DFID. Chatham Maritime, UK, 100 pp.
- Owor, B., 2003. Effect of cassava mosaic geminiviruses (CMGs) on growth and yield of cassava mosaic disease (CMD) susceptible cultivar in Uganda and cross protection studies. M.Sc. thesis, Makerere University, Kampala, Uganda, 134 pp.
- Pita, J.S., Fondong, V.N., Sangaré, A., Kokora, R.N.N., Fauquet, C.M., 2001. Genomic and biological diversity of the African cassava geminiviruses. *Euphytica* 120, 115–125.
- Ranomenjanahary, S., Ramelison, J., Sseruwagi, P., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Madagascar. In: Anderson and Markham.
- Rossel, H.W., Asiedu, R., Dixon, A.G.O., 1992. Resistance of cassava to African cassava mosaic virus: what really pertains. *Tropic. Root Tuber Crops Bull.* 6 (1), 2.
- Seif, A.A., 1981. Seasonal fluctuation of adult population of the whitefly, *Bemisia tabaci*, on cassava. *Insect Sci. Appl.* 1, 363–364.
- Spittel, M.C., Van Huis, A., 2000. Effect of cassava mosaic disease, soil fertility, plant spacing and their interactions on cassava yields in Zanzibar. *Int. J. Pest Man.* 46, 187–193.
- Sserubombwe, W.S., 1998. Progress of cassava mosaic virus disease (CMD) and its effects on growth and yield in different cassava varieties under epidemic conditions in Uganda. M.Sc. Thesis, Makerere University, Kampala, Uganda.
- Sserubombwe, W.S., Thresh, J.M., Otim-Nape, G.W., Osiru, D.O.S., 2001. Progress of cassava mosaic virus disease and whitefly vector populations in single and mixed stands of four cassava varieties grown under epidemic conditions in Uganda. *Ann. Appl. Biol.* 135, 161–170.
- Sserubombwe, W.S., Thresh, J.M., Sseruwagi, P., Otim-Nape, G.W., 1999. Assessing the effects of cassava mosaic virus disease on growth and yield: critical considerations. In: Cooter, R.J., Otim-Nape, G.W., Bua, A., Thresh, J.M. (Eds.), *Proceedings of the Workshop on CMD Management in Smallholder Cropping Systems, Jinja-Uganda, 7–9 December, 1998*, pp. 23–40.
- Sseruwagi, P., Legg, J.P., Otim-Nape, G.W., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Uganda. In: Anderson and Markham.
- Sseruwagi, P., Otim-Nape, G.W., Osiru, D.S.O., Thresh, J.M., 2003. Influence of NPK fertiliser on populations of the whitefly vector and incidence of cassava mosaic virus disease. *Afr. Crop Sci. J.* II, 171–179.
- Storey, H.H., Nichols, R.F.W., 1938. Studies of the mosaic diseases of cassava. *Ann. Appl. Biol.* 25, 790–806.
- Swanson, M.M., Harrison, B.D., 1994. Properties, relationships and distribution of cassava mosaic geminiviruses. *Trop. Sci.* 34, 15–25.
- Sweetmore, A., 1994. Adaptation and development of diagnostic reagents for cassava brown streak virus for use in less-developed countries. Technical report to Natural Resources Institute (NRI) on Malawi survey. Kent, UK, 21 pp.
- Theu, M.P.K.J., Sseruwagi, P., 2004. Whiteflies as vectors of plant viruses in cassava and sweetpotato in Africa: Malawi. In: Anderson and Markham.
- Thomas, J.E., Massalski, P.R., Harrison, B.D., 1986. Production of monoclonal antibodies to African cassava mosaic virus and differences in their reactivities with other whitefly-transmitted geminiviruses. *J. Gen. Virol.* 67, 2739–2748.

- Thresh, J.M., 1987. Strategies for controlling African cassava mosaic virus. In: Proceedings of the International Seminar on African Cassava Mosaic Disease and its Control, Yamoussoukro, Côte d'Ivoire, 4–8 May, 1987. CTA/FAO/ORSTOM/IITA/IAPC, pp. 26–35.
- Thresh, J.M., Hillocks, R.J., 2003. Cassava mosaic and cassava brown streak diseases in Nampula and Zambézia provinces of Mozambique. *Roots* 9(1), in press.
- Thresh, J.M., Mbwana, M.W., 1998. Cassava mosaic and cassava brown streak virus diseases in Zanzibar. *Roots* 5 (1), 6–9.
- Thresh, J.M., Otim-Nape, G.W., 1994. Strategies for controlling African cassava mosaic geminivirus. *Adv. Dis. Vector Res.* 10, 215–236.
- Thresh, J.M., Fargette, D., Otim-Nape, G.W., 1994a. The viruses and virus diseases of cassava in Africa. *Afr. Crop Sci. J.* 2, 459–478.
- Thresh, J.M., Fargette, D., Otim-Nape, G.W., 1994b. Effects of African cassava mosaic geminivirus on the yield of cassava. *Trop. Sci.* 34, 26–42.
- Thresh, J.M., Fishpool, L.D.C., Otim-Nape, G.W., Fargette, D., 1994c. African cassava mosaic disease: an under-estimated and unsolved problem. *Trop. Sci.* 34, 3–14.
- Thresh, J.M., Otim-Nape, G.W., Legg, J.P., Fargette, D., 1997. African cassava mosaic virus disease: the magnitude of the problem. *Afr. J. Root Tuber Crops* 2, 13–19.
- Thresh, J.M., Otim-Nape, G.W., Fargette, D., 1998a. The control of African cassava mosaic virus disease: phytosanitation and/or resistance. In: Hadidi, A., Khetarpal, R.K., Koganezawa, H. (Eds.), *Plant Virus Disease Control*. APS Press, St Paul, MN, USA, pp. 670–677.
- Thresh, J.M., Otim-Nape, G.W., Thankappan, M., Muniyappa, V., 1998b. The mosaic diseases of cassava in Africa and India caused by whitefly-borne geminiviruses. *Rev. Plant Pathhol.* 77, 935–945.
- Wydra, K., Msikita, W., 1998. An overview of the present situation of cassava diseases in West Africa. In: Akoroda, M.O., Ekanayake, I. (Eds.), *Root Crops and Poverty Alleviation. Proceedings of the Sixth Triennial Symposium of the International Society for Tropical Root Crops: Africa Branch*, pp. 198–206.
- Yaninek, J.S., James, B.D., Bieler, P., 1994. Ecologically sustainable cassava plant protection (ESCaPP): a model for environmentally sound pest management in Africa. *Afr. Crop Sci. J.* 2, 553–562.
- Zhou, X., Liu, Y., Calvert, L., Munoz, C., Otim-Nape, G.W., Robinson, D.J., Harrison, B.D., 1997. Evidence that DNA-A of a geminivirus associated with severe cassava mosaic disease in Uganda has arisen by interspecific recombination. *J. Gen. Virol.* 78, 2101–2111.