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CASSAVA MOSAIC VIRUS DISEASE IN EAST AND CENTRAL AFRICA: EPIDEMIOLOGY AND MANAGEMENT OF A REGIONAL PANDEMIC

J. P. Legg,[*,†] B. Owor,[‡] P. Sseruwagi,[§] and J. Ndunguru[¶]

[*]International Institute of Tropical Agriculture, Dar es Salaam, Tanzania
[†]Natural Resources Institute, University of Greenwich, Central Avenue
Chatham Maritime, Kent ME4 4TB, United Kingdom
[‡]Department of Molecular and Cell Biology, University of Cape Town
Private Bag, Rondebosch 7701, South Africa
[§]International Institute of Tropical Agriculture, Kampala, Uganda
[¶]Plant Protection Division, Mwanza, Tanzania

In recent years, the cassava mosaic virus disease (CMD) pandemic in Africa has developed to become one of the most economically important crop diseases. By 2005, it had affected nine countries in East/Central Africa, had covered an area of 2.6 million sq km and was

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causing estimated losses of 47% of production in affected countries equivalent to more than 13 million tonnes (mt) annually, out of an Africa-wide total estimated annual loss of 34 mt. Strategic research investigating the cassava mosaic geminiviruses (CMGs) responsible, their whitefly vector (*Bemisia tabaci*) and interactions with their cassava host have provided the vital insights necessary to monitor the pandemic through regional epidemiological studies. Monitoring and forecasting studies have enhanced the effectiveness of host-plant resistance as a principal component of regional management efforts. Efficient movement of CMD-resistant germplasm into affected countries and regions, using an open quarantine procedure, has been key to the successes achieved to date in mitigating the effects of the pandemic. Novel control tactics, the most important of which is the use of transgenic varieties transformed for virus resistance, offer promise for the future, although transformed plants have yet to be evaluated under field conditions. Set against the promise of current and future control initiatives is the rapidly evolving nature and continued progress of the CMD pandemic. Important new threats include sustained super-abundant populations of *B. tabaci* causing physical damage to cassava and the emergence of cassava brown streak virus disease (CBSD) as a serious problem in Uganda. In conclusion, it is argued that the effective deployment of the whole range of potential control tactics will be required if the CMD pandemic is to be managed effectively and that management efforts should aim to restore the largely benign equilibrium that has characterized the interaction between CMGs and their cassava host for the greater part of their more than century-old shared history.

I. Introduction

Cassava (*Manihot esculenta*) is an important root crop in many parts of the tropics, most particularly in sub-Saharan Africa (SSA). Of the more than 18 million ha of cassava cultivated worldwide, approximately two-thirds are in Africa, producing 110 million tonnes (mt) of tuberous roots annually (FAO, 2006). Cassava is particularly valued both for its diverse potential uses, with both tuberous roots and leaves consumed, and its ability to provide acceptable yields in soils of poor fertility and in areas prone to drought. As such, it plays a vital food security role. Cassava has a relatively recent history in Africa, having been introduced through the Gulf of Guinea region of West Africa in the 16th century by Portuguese seafarers, and to the east coast two centuries later (Jones, 1959). Early cultivation was relatively sparse, however, and the crop did not become

more widely grown until early in the 20th century following its active promotion for food security. The earliest report of a disease affecting the crop was made from what is now Tanzania (Warburg, 1894) in which the yellow chlorotic mosaic together with leaf deformation and rugosity were described. However, reports of the occurrence of this disease did not become more widespread until the 1920s, when it was referred to as cassava mosaic disease (CMD). Early epidemics were reported from diverse locations across Africa in the 1920s and 1930s, including Sierra Leone (Deighton, 1926), Uganda (Hall, 1928), Cameroon (Dufrenoy and Hédin, 1929), Ghana (formerly Gold Coast (Dade, 1930)), Ivory Coast (Hédin, 1931), Nigeria (Golding, 1936) and Madagascar (François, 1937). The impact of CMD was so great that large-scale control operations were introduced in several countries. In Uganda, a region-wide programme of phytosanitation was implemented, incorporating bye-laws mandating growers to uproot diseased plantings before disease-free material of partially resistant varieties was introduced after a crop-free period (Jameson, 1964). Breeding programmes were launched independently in both Tanzania (Jennings, 1957) and Madagascar (Cours, 1951; Cours *et al*., 1997). Considerable success was achieved, and the East African breeding programme formed the basis for the later and more extensive continent-wide efforts to develop and deploy host-plant resistance to CMD.

The breeding work of Jennings and colleagues at Amani in Tanzania followed the earliest comprehensive scientific studies of CMD, its causal pathogen and insect vector led by H. H. Storey (Storey, 1936; Storey and Nichols, 1938). Zimmermann (1906) had earlier proposed that CMD was caused by a viral pathogen. This conclusion was supported by the experimental work of Storey, who also provided the first epidemiological characterization of the disease, confirmed earlier experiments (Kufferath and Ghesquière, 1932) demonstrating the vector to be the whitefly now known as *Bemisia tabaci* (Homoptera: Aleyrodidae) and noted the occurrence of both mild and severe symptom variants of the disease (Storey and Nichols, 1938). Early work on CMD in East Africa was followed by a series of studies in Federal Nigeria on whitefly transmission (Chant, 1958), yield loss and the effects of CMD on metabolism (Chant *et al*., 1971) and some of the earliest assessments of resistant germplasm introduced from the Amani-based programme in East Africa (Beck, 1982). During the 1970s and 1980s, an ORSTOM-led research programme in Ivory Coast conducted extensive studies on CMD aetiology, epidemiology, yield loss and management, and many of the results were summarized by Fauquet and Fargette (1990). There was little evidence during this period, however, for significant changes in the status of CMD. Although isolated epidemics of severe CMD were reported in the 1990s from parts of Cape Verde and Nigeria (Anon, 1992; Calvert and Thresh, 2002),

cassava scientists focused more closely on three pests that had been introduced inadvertently from Latin America in the early 1970s: the cassava mealybug (*Phenacoccus manihoti*), the cassava green mite (*Mononychellus manihoti*) and cassava bacterial blight (*Xanthomonas axonopodis* pv. *manihoti*). Nevertheless, progress was made during this period in confirming the viral aetiology (Bock and Woods, 1983), identifying the principal causal viruses now known as *African cassava mosaic virus* (ACMV) and *East African cassava mosaic virus* (EACMV) (both of Genus: *Begomovirus*; Family: *Geminiviridae*) (Hong *et al*., 1993) and describing their largely non-overlapping geographic distributions (Swanson and Harrison, 1994). EACMV was mainly restricted to coastal East Africa, while ACMV occurred in all other cassava-growing areas of the continent. Concurrently, progress was made in describing the characteristics of the transmission of the cassava mosaic geminiviruses (CMGs) by their *B. tabaci* whitefly vector (Dubern, 1979, 1994).

This apparently stable disease situation ended in the latter half of the 1980s with the first reports, from north-central Uganda, of an unusually severe and rapidly spreading form of CMD (Otim-Nape *et al*., 1994a). It was initially thought to be a local phenomenon associated with favourable environmental conditions for the vector. However, it became apparent during the early 1990s that the CMD associated with this epidemic was distinct from that occurring elsewhere in Uganda and the wider East African region (Gibson *et al*., 1996), and that the epidemic was spreading (Legg, 1995; Legg and Ogwal, 1998; Otim-Nape *et al*., 1997). By 2005, what had become a pandemic had spread to affect much of the cassava-growing area of East and Central Africa. This chapter provides a detailed description of the character, pattern of spread and impact of the pandemic and reviews management initiatives implemented to mitigate against its effects. This concludes with an assessment of the status of the pandemic and recommendations for its improved management.

II. Development and Spread of the Cassava Mosaic Disease (CMD) Pandemic in East and Central Africa

A. Biological Characteristics of the Pandemic

1. The Virus

The characteristics and pattern of spread of the severe CMD pandemic have been described in several reviews (Legg, 1999; Legg and Fauquet, 2004; Otim-Nape and Thresh 1998; Otim-Nape *et al*., 1997,

2000). The most significant early finding was that a novel recombinant virus, referred to as *East African cassava mosaic virus*-Uganda (EACMV-UG), was detected in cassava in the epidemic-affected region of Uganda (Deng *et al*., 1997; Zhou *et al*., 1997) and associated with the severely diseased plants that predominated in this region. Recombination of this kind had hitherto not been known for geminiviruses and so this finding represented a significant breakthrough in the understanding of the biology of this virus group. More significant for cassava in East Africa, however, was the fact that the symptoms elicited by the recombinant virus were more severe than those of the previously occurring ACMV, although plants infected with both EACMV-UG and ACMV showed the most severe symptoms (Harrison *et al*., 1997). The enhanced severity was shown to be the result of a synergistic interaction between ACMV and EACMV-UG (Harrison *et al*., 1997; Pita *et al*., 2001a). Subsequent studies have shown that mixed ACMV + 'EACMV-like' virus infections are frequent wherever the severe form of CMD occurs (Berry and Rey, 2001; Ogbe *et al*., 2003; Were *et al*., 2004). Synergism between an EACMV-like virus and ACMV has also been reported from Cameroon (Fondong *et al*., 2000). However, an association between mixed CMG infections and an expanding pandemic of severe CMD has only been demonstrated in East Africa.

2. The Vector

A second major distinguishing biological feature of the CMD pandemic is the super-abundance of the *B. tabaci* whitefly vector, particularly at the epidemic 'front' between severely affected and relatively unaffected areas (Colvin *et al*., 2004; Legg, 1995). Legg and Ogwal (1998) described the spread of the severe CMD epidemic through central and eastern Uganda and noted that *B. tabaci* populations on cassava in the northern epidemic-affected parts of the study area were significantly more abundant than those occurring in the southern as yet unaffected areas. Furthermore, peak populations were recorded at the locations affected by the severe form of CMD. This pattern seems to be a general feature of the CMD pandemic, and it has been hypothesized that numbers of *B. tabaci* decline in areas affected a number of years previously due to a general reduction in the cultivation of cassava that occurred (Legg and Thresh, 2000). There is no definitive evidence to explain why *B. tabaci* populations are boosted in pandemic-affected areas, although both the occurrence of distinct *B. tabaci* genotypes (Legg *et al*., 2002) and synergistic interactions between *B. tabaci* and severely CMD-diseased cassava hosts (Colvin *et al*., 2004, this

volume, pp. 419–452) have been advanced as possible contributing factors, as discussed in Section V.

3. Cassava Germplasm

A considerable diversity of cassava germplasm exists in East and Central Africa, and before the appearance of the CMD pandemic this was almost entirely composed of local farmer-selected cultivars. Surveys in Uganda recorded 129 cultivars in farmers' fields in 1990–92 and 126 in 1994 (Otim-Nape *et al.*, 2001). Virtually all of these proved to be both susceptible and sensitive to the severe CMD of the epidemic, however, and major yield losses led to the widespread abandonment of cassava cultivation in large areas of eastern and central Uganda (Otim-Nape *et al.*, 1997; Thresh *et al.*, 1994b). Local cultivars were readily infected at a very early stage of growth. Symptoms of infection included the previously described chlorotic mosaic, distortion in shape and reduction in size of the leaves together with a general stunting of plant growth. However, additional symptoms that are particularly characteristic of infected local cultivars in pandemic-affected areas include the 'S' shape and down-turning of petioles immediately above the point of inoculation, the presence of lesions and discoloration on these petioles as well as the drying out and premature abscission of severely infected leaves below affected apices (Fig. 1). The combination of these features in an infected plant has commonly led to the use of the term 'candlestick' or 'paint brush' to describe the overall appearance of the plant. Very high virus titres develop in susceptible local cultivars following dual CMG infection with its concomitant synergistic interaction (Harrison *et al.*, 1997; Pita *et al.*, 2001a). This enhances the further dissemination of these viruses between plants.

B. Cassava Mosaic Geminiviruses in Africa and the CMD Pandemic

1. The CMGs Causing CMD in Africa

It has been recognised for many years that CMD is caused by a number of CMGs. In some of the earliest detailed virological studies conducted in Kenya, two strains with distinct patterns of behaviour in herbaceous test plant hosts were recognised (Bock *et al.*, 1981) and these were shown subsequently through sequence analyses of their DNA-A to be two distinct CMG species and given the names: ACMV and EACMV (Hong *et al.*, 1993). A third species recognised at this time was reported from India and designated as *Indian cassava mosaic virus* (ICMV). Using serology-based

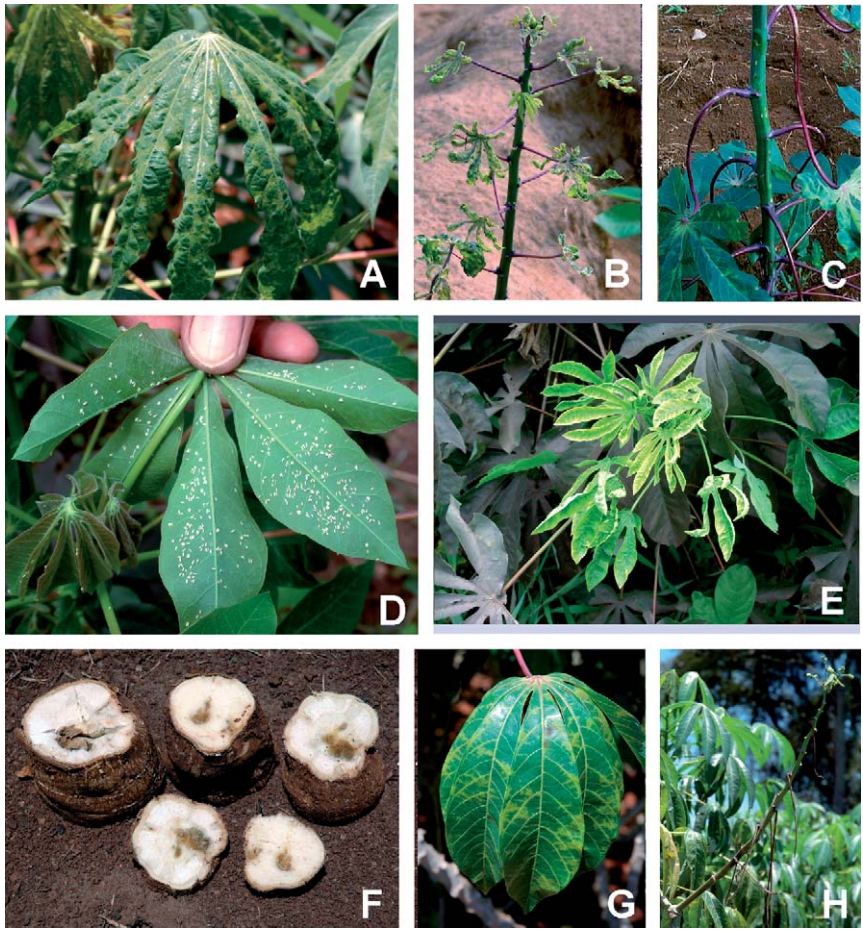

FIG 1. Symptoms of cassava mosaic and cassava brown streak diseases and direct damage caused by the whitefly vector (*B. tabaci*) of the viruses responsible. (A) Moderate leaf mosaic characteristic of ACMV infection, Sangmelima, Cameroon; (B) Severe symptoms caused by mixed EACMV-UG + ACMV infection, Franceville, Gabon; (C) Downturned petioles, stem and petiole lesions associated with EACMV-UG + ACMV infection, Bukoba, Tanzania; (D) Super-abundant *B. tabaci* adults, Namulonge, Uganda; (E) Chlorosis on shoot tip caused by *B. tabaci* adult feeding and sooty mould growth on lower leaves resulting from nymph honeydew secretion; and (F–H) *Cassava brown streak virus* infection in variety TME 204, Namulonge, Uganda ((F) Dry brown necrotic rot in roots; (G) Leaf symptoms; (H) Shoot dieback associated with severe response).

diagnostics through enzyme-linked immunosorbent assay (ELISA), Swanson and Harrison (1994) provided the first distribution map of ACMV and EACMV in Africa. This showed the largely non-overlapping distributions of the two species. ACMV occurred across West Africa, through Central Africa to Uganda and southwards as far as South Africa, whereas EACMV was almost entirely confined to East Africa west of the Rift Valley as well as Malawi and Madagascar.

Following the discovery that the developing pandemic in East Africa was associated with the novel recombinant virus, EACMV-UG, there was increased research interest in CMGs and an extensive series of new surveys was undertaken in different parts of the continent. Significantly, surveys in western Kenya (Ogbe *et al*., 1996) and north-western Tanzania (Ogbe *et al*., 1997) provided the first evidence that both ACMV and EACMV can occur in the same region. The nucleic acid-based diagnostic techniques that had facilitated the identification of EACMV-UG in 1997 were subsequently applied more widely and most significantly enabled the detection of mixed CMG infections. This was particularly important for West Africa, where most EACMV-like virus infections were in mixtures with ACMV (Ariyo *et al*., 2005; Fondong *et al*., 2000; Ogbe *et al*., 2003). EACMV-like viruses were identified in this way from several West African countries, although sequence-based characterizations have shown these West African isolates to be a distinct CMG species, *East African cassava mosaic Cameroon virus* (EACMCV) (Fondong *et al*., 2000). Like EACMV-UG, sequence analyses of both genome components (DNA-A and DNA-B) revealed the presence of recombined portions (in the AC2–AC3 region and in BC1), a feature that seems to be frequent with viruses of the genus *Begomovirus* (Padidam *et al*., 1999; Pita *et al*., 2001b). Six species of CMG are recognised from Africa to date (Fauquet and Stanley, 2003). In addition to ACMV, EACMV, EACMCV and EACMV-UG (which is considered to be a strain of EACMV), there are: *East Africa cassava mosaic Malawi virus* (EACMMV) (Zhou *et al*., 1998), *East African cassava mosaic Zanzibar virus* (EACMZV) (Maruthi *et al*., 2004a) and *South African cassava mosaic virus* (SACMV) (Berrie *et al*., 2001). Based on these findings and summarizing existing survey data, Legg and Fauquet (2004) developed an updated distribution map for CMGs in Africa. From the 22 countries included in the dataset, ACMV occurred in 20, EACMV in 10, EACMV-UG in 11, EACMCV in 5, SACMV in 2, EACMZV in 2 and EACMMV in 1. There are also records of SACMV in Madagascar (Ranomenjanahary *et al*., 2002) and EACMCV in southern Tanzania (Ndunguru *et al*., 2005a). Senegal and Guinea in West Africa are unique in being the only countries for

which extensive surveys have been conducted and where only one virus species has been reported (i.e. ACMV) (Okao-Okuja *et al.*, 2004). This does, however, reflect the generally more limited diversity of CMGs in West Africa compared with eastern and southern Africa.

Sequence characterizations of 13 CMG isolates from Tanzania revealed the occurrence of three species, clear evidence for recombination in at least two of the species (EACMV-UG and EACMCV), and an unprecedented level of diversity based on both sequencing and restriction fragment length polymorphism (RFLP) analyses (Ndunguru, 2005). Based on these findings, East Africa has been proposed as a centre of diversity for CMGs in Africa and a probable source of the begomoviruses that infected cassava and provided the key components for both the historical and evolutionary change in this group of viruses (Ndunguru *et al.*, 2005a). Evolutionary processes have been influencing the function and interactions of CMGs with their plant hosts, whitefly vector and co-infecting CMGs for millenia, including the prolonged period before the first introduction of cassava. The CMD pandemic, however, provides an excellent example both of the relative speed with which CMG evolution can occur and major consequences on plant disease that can arise.

C. Sub-Genomic DNAs and the CMD Pandemic

A number of cassava plants in the pandemic-affected area of northwestern Tanzania were observed with unusual virus-like symptoms during a countrywide CMG survey (Ndunguru, 2005). Detailed laboratory investigation of samples of this material revealed the presence of two novel DNA molecules. These 'small' DNA molecules have been shown to be dependent on geminiviruses for replication and movement within the plant, confirming their status as satellite DNAs (Ndunguru, 2005). Their sizes are 1.0 and 1.2 kbp, respectively, and they are distinct from each other sharing only 23% nucleotide sequence homology. They possess no significant homology with other sequences published in searchable databases, including those of geminiviruses. This clearly raises questions as to their evolutionary origin and the mechanisms underlying their *trans*-replication (Ndunguru, 2005). When these satellite molecules occurred in co-infections with geminiviruses, the satellites caused increased viral accumulation and novel, severe disease symptoms. Moreover, high resistance to geminiviruses in the West African cassava landrace TME 3, which has become an important component of cassava improvement programmes, including the CMD pandemic mitigation effort, can be

broken by the satellites. This has raised concern about the impact of these satellites on cassava production and their possible role in the current pandemic of CMD, a question currently under investigation. Most importantly, information is required on their respective distributions and whether or not one or both are consistently associated with the severe symptoms typical of the pandemic. Regardless of whether such an association is found, there is an obvious need to increase understanding of these unusual molecules and how they interact with each of the six African CMG species in order to ensure that control approaches are effective against all potential virus and virus-satellite infections.

D. PCR-Based Diagnostics Aid the Tracking of Pandemic-Associated CMGs

Although ELISA-based diagnostics continue to be useful for detecting many plant viruses, the occurrence of recombinations involving the coat protein and the relatively high frequency of mixed infections for CMGs in Africa mean that this group of viruses is best detected and identified using nucleic acid-based techniques. Specific oligonucleotide primers have been developed for all CMG species known in Africa and they facilitate diagnosis through the polymerase chain reaction (PCR). Zhou *et al*. (1997) developed primers for detecting the principal pandemic zone viruses (ACMV and EACMV-UG) and these have been used widely in subsequent studies. An alternative method combines the use of universal primers to produce near full-length amplicons of DNA-A followed by endonuclease digestion of these amplicons to give RFLPs. This method has been used extensively to enable the diagnosis of single and mixed CMG infections and also to detect unusual virus variants (Ndunguru, 2005; Okao-Okuja *et al*., 2004; Sseruwagi *et al*., 2004a,b, 2005a).

Many of the CMD diagnostic surveys conducted between 1997 and 2005 in East and Central Africa have used one or both of these approaches to monitor the spread of the pandemic-associated virus, EACMV-UG (Table I). Surveys conducted over a number of years in similar locations have provided a very clear picture of the pattern of change in virus occurrence as the CMD pandemic spreads through a previously unaffected region or country. Data for Uganda provide the first and one of the clearest examples of this (Table I). In the first surveys (1995 and 1996) conducted during the early period of the epidemic in central-southern Uganda (Harrison *et al*., 1997; Otim-Nape *et al*., 1997), ACMV was more frequent than EACMV-UG,

TABLE I

VIRUS SURVEYS IN CMD PANDEMIC-AFFECTED REGIONS OF SUB-SAHARAN AFRICA

Country	Region	Year	Epidemic status	Methods	Number of samples	ACMV	EACMV-UG	ACMV+ EACMV-UG	EACMV	Other	No result	Reference
Uganda	Central	1995	Early epidemic	SP	32	12 (38)	6 (19)	14 (43)	–	–	–	Harrison *et al*., 1997
	Country	1996	Epidemic	SP	68	22 (32)	21 (31)	25 (37)	–	–	–	Harrison *et al*., 1997
	Country	1997	Late epidemic	SP	129	36 (31)	62 (53)	19 (16)	–	–	12	Pita *et al*., 2001a
	Country	2002	Post-epidemic	SP/RFLP	152	28 (18)	97 (64)	27 (18)	–	–	–	Sseruwagi *et al*., 2004b
Kenya	Western	1999	Late epidemic	SP	>200	(22)	(52)	(17)	3 (n.i.)	1 (n.i.)	–	Were *et al*., 2004
	Western	2003	Post-epidemic	SP/RFLP	107	6 (6)	75 (74)	8 (8)	12 (12)	–	6	Obiero, H., unpublished data
Tanzania	Northwest	2000	Early epidemic	SP/RFLP	44	26 (59)	11 (25)	7 (16)	–	–	–	Jeremiah, S., unpublished data
	Northwest	2002	Epidemic	SP/RFLP	42	6 (14)	27 (64)	3 (7)	5 (12)	1 (2)	–	Jeremiah, S., unpublished data
Rwanda	Country	2000	Early epidemic	SP	52	26 (79)	6 (18)	1 (3)	–	–	19	Legg *et al*., 2001
	Country	2001	Early epidemic	SP/RFLP	76	69 (91)	7 (9)	–	–	–	–	Sseruwagi *et al*., 2005a
	Country	2004	Epidemic	SP	88	32 (38)	35 (41)	18 (21)	–	–	3	Okao-Okuja, G., unpublished data
Burundi	Country	2003	Early epidemic	SP/RFLP	55	34 (62)	17 (31)	3 (5)	1 (2)	–	–	Bigirimana *et al*., 2004
	Country	2004	Epidemic	SP/RFLP	94	51 (55)	21 (22)	22 (23)	–	–	1	Bigirimana, S., unpublished data
Gabon	Country	2003	Epidemic	SP/RFLP	110	92 (84)	1 (1)	16 (14)	1 (1)	–	–	Legg *et al*., 2004

Virus data indicate numbers and (percentages) of particular virus species/strains in samples tested.

Abbreviations: SP, specific primers; RFLP, restriction fragment length polymorphism; n.i., not included in percentage calculations.

although there was an increase in the proportion of plants infected with both ACMV and EACMV-UG. During later surveys, however, the proportion of CMD-diseased plants infected with ACMV alone was much reduced while the proportion infected with EACMV-UG alone increased. It was also significant that the proportion of mixed infections decreased over time. Patterns of change over time in virus occurrence are virtually identical for other pandemic-affected countries for which data are available (Table I). These data reveal a general temporal progression in the evolution of CMG-infection patterns associated with the spread of the CMD pandemic, as follows:

1. The virulent EACMV-UG spreads to areas where previously cassava was only infected with ACMV at generally low incidences.
2. Synergistic interactions between EACMV-UG and ACMV in dual-infected plants lead to rapid increases in the incidence of mixed EACMV-UG + ACMV infections.
3. Farmers select vigorous plants to provide cuttings for new planting and reject very severely diseased stems of dual-infected plants. It is then hypothesized that this leads to a reduction in the frequency of dual-infected plants with a concomitant increase in the frequency of single EACMV-UG infected plants. Even if farmers do not select, the trend towards more vigorous single EACMV-UG infected plants is enhanced because mild infections produce many more cuttings than severe ones.

The net result of these processes is the competitive exclusion of ACMV by EACMV-UG, a phenomenon whose validity seems to be confirmed by the CMG survey data (Table I).

The extensive use of monitoring and diagnostic surveys to determine the pattern of distribution of the pandemic-associated EACMV-UG has facilitated the tracking of the spread of this virus over time. Based on results of these and other surveys, efforts have been made at various times to map the extent of coverage of the pandemic (Anon, 1998a,b; Dixon *et al*., 2003; Legg, 1999; Legg and Fauquet, 2004; Legg and Thresh, 2000). Drawing on these earlier efforts and records of the geographical pattern of spread of EACMV-UG obtained from published data, a diagrammatic representation of the pattern of development of the pandemic from 1997 to 2005 is presented in Fig. 2 and years of first pandemic infection for affected countries are indicated in Table II. It is notable that while the map represents an estimation of the historical behaviour of the pandemic, in many areas it has not been possible to obtain data. This point is most pertinent for the large areas of eastern

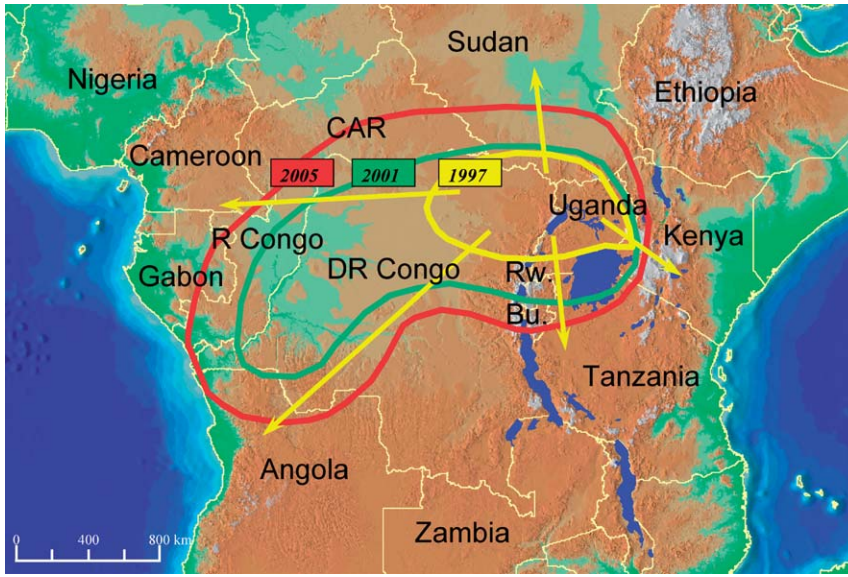

FIG 2. Estimated extent of the epidemic of the CMD pandemic in SSA in years 1997, 2001 and 2005. DR Congo, Democratic Republic of Congo; R Congo, Republic of Congo; Rw., Rwanda; Bu., Burundi.

and central Democratic Republic of Congo (DRC), which are both extremely difficult to access and have been disturbed by internal civil conflict. As such, estimations made for these regions are speculative. This contrasts with the southern and eastern parts of the pandemic-affected zone which have been mapped intensively, particularly since 1998. Using the maps developed in Fig. 2 and by applying simple geographical information system-based techniques, it is possible to estimate that the area affected by the pandemic increased from 520,000 sq km in 1997, when only Uganda and parts of Kenya were affected, to 1,710,000 sq km in 2001 and 2,650,000 sq km in 2005. This information is of considerable importance in estimating the likely impact of the pandemic on cassava production in Africa and targeting control efforts based on knowledge of the proximity of important cassava-growing areas to zones of expected new EACMV-UG spread. These data have been used to develop risk maps which provide an important management tool for pandemic CMD, as discussed in Section III.

TABLE II

First Records of Pandemic Infection for Countries in East and Central Africa

Country	Severe CMD first report	Location	Reference
Uganda	1988	Northern Luwero district	Otim-Nape *et al.*, 1994a
Kenya	1995	Busia district, Western Province	Gibson, R., unpublished
Sudan[a]	1997	Equatoria region, south	Harrison *et al.*, 1997
Rwanda	1997	Umutara prefecture, northeast	Legg, J., unpublished
Tanzania	1998	Kagera region, northwest	Legg, 1999
Republic of Congo	1999	Plateaux region, central	Neuenschwander *et al.*, 2002
Democratic Republic of Congo	2000	Kinshasa Province, southwest	Neuenschwander *et al.*, 2002
Burundi	2003	Kirundo and Muyinga Provinces, northeast	Bigirimana *et al.*, 2004
Gabon	2003	Haute-Ogooué and Ogooué-Ivindo Provinces, east	Legg *et al.*, 2004

[a] Record of EACMV-UG and severe CMD in a single sample.

E. Epidemiology of CMD and the Pandemic

There is extensive literature describing the epidemiology of CMD. Important developments have included:

- The early demonstration of the link between seasonal environmental factors and rates of CMD spread at a locality in Tanzania (Storey, 1938)
- Descriptions of the association between vector abundance and rates of CMD spread (Dengel, 1981; Fargette *et al*., 1993; Fishpool *et al*., 1995)
- The occurrence of environmental gradients associated with CMD spread and the primary importance of external inoculum sources compared with internal sources (Fargette *et al*., 1985, 1990)
- The status of temperature and rainfall as key determinants of cassava growth, vector population increase and subsequent virus spread (Fargette *et al*., 1993; Fishpool *et al*., 1995)
- The value of resistant varieties in both delaying and reducing rates of virus spread (Colon, 1984; Hahn *et al*., 1980; Otim-Nape *et al*., 1998; Sserubombwe *et al*., 2001)
- The potential to predict final CMD incidence through a combined assessment of inoculum and the abundance of early vector immigrants (Legg *et al*., 1997).

The behaviour of CMD at higher-epidemiological levels, as it spreads between fields, regions and countries, has received much less research attention, however, due in part to the inherently greater difficulty of undertaking such extensive studies. Another important reason for the limited treatment of these levels of epidemiology has been that there have been few reports of macro-scale CMD spread over more than a century of the disease's history in Africa, as mentioned in Section I. Two early qualitative descriptions of regional spread were, however, made from Nigeria (Golding, 1936) and Madagascar (Cours, 1951). By contrast, detailed information has been presented describing the regional spread of the CMD pandemic. Much of this relates to Uganda, where the pandemic was first reported. Otim-Nape *et al*. (1997, 2000) and Otim-Nape and Thresh (1998) used qualitative terms to describe the regional dynamics of the CMD epidemic in Uganda. Six zones were defined, representing both a spatial series, running from areas ahead to those behind the 'front' of the epidemic, as well as a temporal series, describing changes in the epidemic as it passed through a given location. 'Zone 1' was defined as the area ahead of the epidemic front in which CMD incidence was low, symptoms were generally mild and

where there was little or no disease spread. Whitefly populations were low and local cassava cultivars were being grown sustainably. This zone was referred to as '*Pre-epidemic*'. The '*Epidemic zone*' or 'Zone 3' corresponded to the 'front' of the epidemic where increased whitefly populations were causing rapid spread of CMD, symptoms were severe and local cultivars were becoming entirely diseased. In the '*Recovery zone*' (Zone 5), production of severely diseased local cultivars was being abandoned following the failure of crops where farmers had attempted to replant using cuttings from already severely diseased mother plants. As the intensity of cassava cultivation declined, inoculum levels and whitefly numbers dropped, leading to a general amelioration in the situation that was enhanced by the apparent increase in frequency of plants infected by mild strains.

Legg and Ogwal (1998) used quantitative data collected along two north–south transects in central and eastern Uganda to characterize the changes in CMD and whiteflies between 1992 and 1993. The key variables used to describe these changes were whitefly abundance, CMD incidence and severity and, perhaps most importantly, the relative amounts of cutting and whitefly-borne infection. Current season whitefly-borne infection was recognised by the absence of symptoms on the first-formed leaves at the base of the plant being assessed, whereas cutting-borne infection was apparent from the occurrence of symptoms on first-formed leaves. The relative proportions of these two infection categories allow inferences to be made about the epidemiological situation.

A combined analysis of CMD incidence and infection type using georeferenced data gathered from surveys in the Lake Victoria Basin zone of East and Central Africa was used to map the distributions of different epidemic zones and to highlight threatened areas immediately ahead of the epidemic (Legg *et al*., 1999a). The '*Zone of epidemic expansion*' was defined as the area where incidence was greater than 70% and the percentage of whitefly-infected plants was commonly more than three times the percentage of cutting-infected plants. At this time, two such zones were identified, the first of which covered Western Province in western Kenya, and the second, the southern Ugandan districts of Masaka and Rakai, just north of the border with Tanzania. Using a similar approach, patterns of change in the epidemiological zones in space and over time within the East and Central African regions were tabulated for the period 1990–1999 (Legg, 1999). An updated and slightly modified analysis of this type is presented in Tables III and IV, which summarizes the pandemic's zones in 2005. It is notable that

TABLE III

STATUS OF CMD-PANDEMIC ZONES IN SUB-SAHARAN AFRICA, 2005 (ADAPTED FROM LEGG, 1999)

Zone	Designation	CMD incidence	Mean CMD severity	Type of infection	*B. tabaci* abundance	Cassava cultivation
1	Pre-epidemic zone	<30%	Low (<2.5)	Mainly cutting	Low (0–1)	Normal
2	Zone of epidemic expansion	30–70%	High (>3)	Mainly whitefly	High (>5)	Normal
3	Mature epidemic zone	>70%	High (>3)	Whitefly and cutting	High (>5)	Sustained but yields reduced
4	Post-epidemic zone	>50%	Moderate (2.5–3)	Mainly cutting	Moderate (1–5)	Reduced or abandoned
5	Zone of recovery	<50%	Low (<2.5)	Mainly cutting	Moderate (1–5)	Being re-established

TABLE IV

EPIDEMIOLOGICAL ZONATION OF PANDEMIC-AFFECTED COUNTRIES IN 2005 (BASED ON ZONES DESCRIBED IN TABLE III)

Country	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5
Uganda	–	–	–	North, south, west	East, centre
Kenya	East, centre	–	South Nyanza Province	North Nyanza Province	Western Province
Rwanda	Southwest	–	Centre, south	Northeast	–
Tanzania	East, centre, south	Kigoma, Mara, Shinyanga regions	Mwanza region	Kagera region	–
Republic of Congo	–	–	–	Entire country	–
Democratic Republic of Congo	Southeast	East	Northeast	Centre	Southwest
Burundi	–	South, west	Centre, north	Northeast	–
Gabon	North, south, centre, west	East	–	–	–

"–": not present.

while five countries have been newly reported as CMD pandemic-affected since 1999, only parts of Uganda, Kenya and the DRC have progressed to Zone 5. The reasons for this apparently limited progress in the management of the pandemic will be discussed in Section IV. However, the comparison between the 1999 and 2005 datasets does highlight the magnitude of the extent of 'new' spread of the pandemic and the scale of the problem that it poses.

An alternative approach that can be taken to collating epidemiological data collected from CMD surveys across Africa is to combine the principal variables affecting CMD epidemiology to develop an '*Epidemic Index*', which gives an overall estimate of the acuteness of the CMD problem in a region. The key variables are indicated in Table V, and in each case three levels or categories have been defined from 'low' (category '1') to 'high' (category '3'). For the three directly scored quantitative measures, higher levels (CMD incidence and CMD-symptom severity) or greater numbers (whitefly abundance) gave higher-category levels. For the CMD-infection factor, derived by dividing the whitefly-borne infection by the incidence of cutting infection, greater values similarly gave higher-category levels. For the virus-diversity factor, two aspects were considered to enhance epidemic severity. The first of these was the presence of EACMV-UG, since it typically has high virulence and the second was the presence of more than one virus species or strain, as virus–virus synergism is known to be a key factor in enhancing CMG spread.

Using country survey data, mean values are calculated for each of the quantitative variables and for each of the regions considered within the survey. The '*Epidemic Index*' value for each of these regions is then calculated by summing the index-category values for each of the five factors. Values can range from a minimum of $5 \times 1 = 5$ (lowest/weakest) to a maximum of $5 \times 3 = 15$ (highest/strongest). Available survey data collected between 1998 and 2003 have been analysed in this way for the 17 countries in SSA shown in Fig. 3, and *Epidemic Index* values obtained have been mapped and are presented in the same figure. Assuming that a region or country with an *Epidemic Index* value of 11 or above is in an '*acute epidemic*' state, the analysis yields 30 regions in 7 countries so affected. On superimposing the region of coverage of the CMD pandemic over this map (Figs. 2 and 3), 28 of the 30 acute zones are within the pandemic-affected area, highlighting this as the only major part of the cassava-growing region of Africa in which CMD is a severe and spreading problem.

TABLE V

FACTORS AND CATEGORIES USED IN CALCULATING THE 'EPIDEMIC INDEX'

	Index category		
Factor	1	2	3
CMD incidence	0–33%	33–67%	67–100%
CMD severity (1–5 scale)	2.0–2.75	2.75–3.5	3.5–5.0
CMD infection[a]	0–0.33	0.33–1.00	>1
Whitefly abundance	0–1	1–5	>5
Virus diversity	Single sp., no EACMV-UG	EACMV-UG present	Mixed spp. + EACMV-UG

[a] CMD infection = ratio of whitefly to cutting infection.

Whitefly infection is the percentage of plants infected by the whitefly vector during the current season and is distinguished by the absence of CMD symptoms on the lowermost first-formed leaves.

Cutting infection is the percentage of plants infected through planting CMD-infected cuttings and is distinguished by the presence of symptoms on the lowermost first-formed leaves.

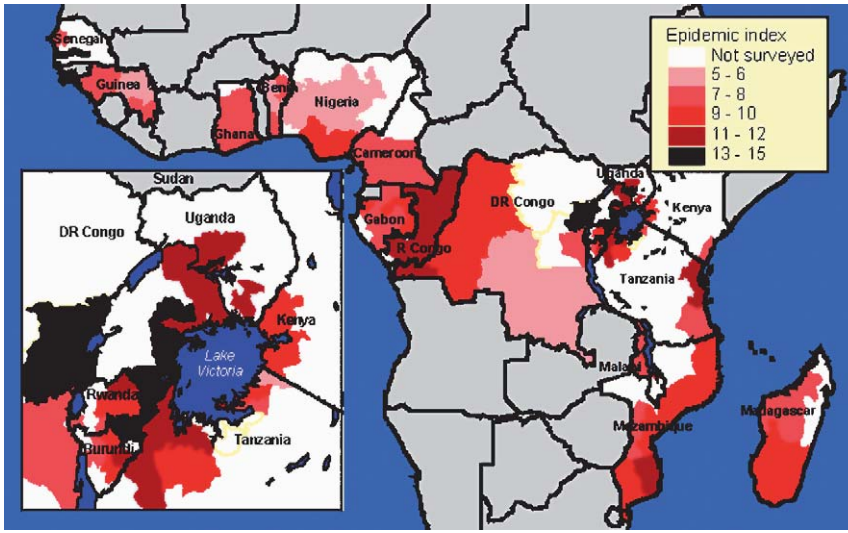

FIG 3. Epidemic index values for cassava mosaic disease in regions of SSA surveyed between 1998 and 2003.

III. ECONOMIC AND SOCIAL IMPACT OF THE CMD PANDEMIC

A. Introduction and Field-Level Yield Loss Studies

Because of the severe damage that pandemic CMD has caused to the largely susceptible and sensitive local cultivars grown across the major production zones of East and Central Africa, it is not surprising that there have been diverse impacts both on the production of the crop and, as a consequence of this, on producers and consumers. Considering the basic unit of the plant, losses have been particularly severe where cassava stems from plants infected for the first time by the viruses causing severe pandemic CMD have been used to provide the following season's crop. In Uganda, yield loss estimates for local cultivars measured prior to the pandemic's spread ranged from 20% to 40% (Otim-Nape *et al.*, 1994b). A later study, by collecting planting material from a location within the pandemic-affected zone, quantified losses in tuberous root yield of 66% in CMD-diseased plants of what was then the most commonly grown local cultivar, 'Ebwanateraka' (Byabakama *et al.*, 1999). Similar assessments made during the pandemic in Bukoba district, Kagera region, Tanzania in 2001 and 2002 gave yield losses for three of the most widely grown local cultivars as

72% for Msitu Zanzibar, 85% for Rushura and 90% for Bukalasa Ndogo (=Bukalasa 11 or F279), giving a mean loss of 82% (Ndyetabura, I., unpublished data). Comparable results were obtained for CMD-susceptible varieties in Siaya district, western Kenya, where losses for two local cultivars were estimated at 72% for Karemo and 63% for Bukalasa 11 (mean = 68%) (Mallowa, 2006). However, none of these studies considered the nature of the virus infection in plants whose yields were measured. The only study to date that has attempted to measure yield losses attributable to specific virus infections was in western Uganda from 1999 to 2000 and considered the yield effects of infection by mild and severe forms of EACMV-UG, ACMV and mixed ACMV + EACMV-UG infections on the local cultivar Ebwanateraka (Owor *et al.*, 2004a). As anticipated, losses were greatest for mixed infected plants (82%), intermediate for plants infected with EACMV-UG severe alone (68%) or ACMV alone (42%) and least for EACMV-UG mild infections (12%).

B. Regional-Level Assessments of Production Losses Due to CMD

Several regional-level assessments of pandemic-associated cassava production losses have been made. Annual losses in the mid-1990s in Uganda were estimated as being equivalent to the total production of four districts each year, which amounted to an estimated 600,000 t annually, equivalent to a financial cost of US$ 60 million (Otim-Nape *et al.*, 1997). Similar calculations were used to produce an estimated annual loss for western Kenya of US$ 14 million (Legg *et al.*, 1999a). Thresh *et al.* (1997) provided an approximation for continental level losses due to CMD. Their calculation assumed an overall incidence of 50–60% and losses for infected plants of 30–40% and gave a range of 15–24% for losses due to CMD in Africa as a whole. New incidence data allowed this estimate to be updated in 2003, with a revised figure for Africa-wide losses of 19–27 mt (Legg and Thresh, 2004).

Here, we review existing data for pandemic recovery (Uganda), pandemic-affected and as yet unaffected countries and parts of countries (Table VI). The mean loss for CMD-infected plants in pandemic-affected countries has been calculated as 72%, which is the mean value of the loss estimates presented previously of 66% for widely grown cultivars in Uganda (Byabakama *et al.*, 1999), 82% for Tanzania (Ndyetabura, I., unpublished data) and 68% for Kenya (Mallowa, 2006). The comparable mean loss for CMD-infected plants in countries not yet affected by the pandemic is that used previously (Legg and Thresh, 2004; Thresh *et al.*, 1997) of 30–40%, although here we have used the single mean value of 35%.

TABLE VI

CMD-Infection Characteristics, Cassava Production and Estimated Losses for 17 Cassava-Producing Countries in Africa

Country (reference)	Year	Cassava mosaic disease: Cutting infection (%)	Cassava mosaic disease: Whitefly infection (%)	Cassava mosaic disease: Total incidence (%)	Cassava mosaic disease: Mean symptom severity	*B. tabaci* (no. per shoot)	CMGs detected	Actual production (1000 t)	Estimated loss (1000 t)
Recovery[a]									
Uganda (Okao-Okuja, G., unpublished data; Owor *et al*., 2004a; Sseruwagi *et al*., 2005b)	1998, 2003	44	16	60	2.9	25.0	ACMV, EACMV-UG	5500	1048 (16%)
Pandemic-affected[b]									
Western Kenya (Kamau *et al*., 2005; Obiero, H, unpublished data)	1998, 2005	36	27	63	2.8	6.6	ACMV, EACMV, EACMV-UG	420[2/3,d]	349
Northwestern Tanzania (Jeremiah, S., unpublished data; Ndunguru *et al*., 2005b)	1998, 2002	18	35	53	3.0	30.6	ACMV, EACMV, EACMV-UG	2333[1/3]	1440
Rwanda (Sseruwagi *et al*., 2005a)	2001, 2004	27	23	50	3.6	2.4	ACMV, EACMV-UG	782	440
Burundi (Bigirimana *et al*., 2004; Bigirimana, S., unpublished data)	2003, 2005	36	25	61	3.4	18.3	ACMV, EACMV-UG	710	556
Northern, eastern and western DRC (Tata-Hangy, A., unpublished data)	2002–2003	56	11	67	3.1	41.1	ACMV, EACMV-UG	9982[2/3]	9303
ROC (Ntawuruhunga, P., unpublished data)	2003	82	4	86	3.3	2.0	ACMV, EACMV-UG	900	1464
Eastern Gabon (Legg *et al*., 2004; Legg, J., unpublished data)	2003	77	7	84	2.8	<1	ACMV, EACMV-UG	29[1/8]	44
Average–pandemic-affected		47	19	66	3.1	14.5			
Total–pandemic-affected								**15,156**	**13,596 (47%)**
Pandemic-unaffected[c]									
Eastern and central Kenya (Kamau *et al*., 2005; Obiero, H., unpublished data)	1998	24	10	34	2.4	<1	EACMV, EACMZV	210[1/3]	28

Eastern and southern Tanzania (Jeremiah, S., unpublished data; Ndunguru *et al*., 2005b)	1998	16	10	26	2.9	<1	EACMV, EACMCV	4667[2/3]	467
Southern and central DRC (Tata-Hangy, A., unpublished data)	2002–2003	34	0	34	2.8	<1	No diagnoses	4991[1/3]	674
Western, northern and southern Gabon (Legg *et al*., 2004; Legg, J., unpublished data)	2003	79	0	79	2.3	1.4	ACMV	201[7/8]	77
Cameroon (Ntonifor *et al*., 2005)	1998	55	7	62	2.3	3.3	ACMV, EACMCV	1950	538
Nigeria (Echendu *et al*., 2005)	1998	54	2	56	2.3	2.1	ACMV, EACMCV	38,179	9225
Benin (Gbaguidi *et al*., 2005)	1998	34	2	36	2.1	2.9	ACMV, EACMCV	3100	447
Ghana (Cudjoe *et al*., 2005)	1998	56	15	71	2.3	2.3	ACMV, ACMCV	9739	3232
Guinea (Okao-Okuja *et al*., 2004)	2003	52	10	62	2.4	1.0	ACMV	1350	379
Senegal (Okao-Okuja *et al*., 2004)	2003	71	12	83	2.3	3.2	ACMV	402	165
Malawi (Theu and Sseruwagi, 2005)	1998	25	17	42	2.8	1.3	EACMV, EACMMV	2600	448
Mozambique (Toko, M., unpublished data)	2003	9	16	25	2.6	17.9	ACMV, EACMV, EACMV-UG	6150	590
Madagascar (Ranomenjanahary *et al*., 2005)	1998	41	6	47	3.1	5.0	ACMV, EACMV, SACMV	2191	435
Average–pandemic-unaffected		42	8	50	2.5	3.3			
Total–Pandemic-unaffected								**75,730**	**16,705 (18%)**
Unsurveyed area (18% loss estimate)								14,034	3081
Overall Total								**110,420**	**34,430 (24%)**

[a] Yield losses for the recovery country (Uganda) calculated based on an estimated overall production loss due to CMD of 16% (see text for details).

[b] Yield losses for pandemic-affected countries calculated based on a mean loss for CMD-infected plants of 72%.

[c] Yield losses for pandemic-unaffected countries calculated based on a mean loss for CMD-infected plants of 35%.

[d] For countries for which data have been divided between affected and unaffected areas, fractions indicate the estimated proportion of total production in that area.

Uganda has been placed in a distinct pandemic 'recovery' category in view of the extensive dissemination of CMD-resistant varieties (Sserubombwe *et al*., 2005a) and the post-epidemic amelioration of CMD in local cultivars. The virus survey data show mild and severe strains of EACMV-UG to be the predominant viruses causing CMD (Sseruwagi *et al*., 2004b). Combining an average for yield losses in a local cultivar infected by EACMV-UG mild (12%) and EACMV-UG severe (68%) (Owor *et al*., 2004a) with a local cultivar prevalence of 67% (Sserubombwe *et al*., 2005a) and a CMD incidence of 60% (Okao-Okuja, G., unpublished data), gives an overall estimate for production loss to CMD in Uganda of 16%. This makes the reasonable assumption that losses in CMD-resistant varieties are negligible. For those countries only partially affected by the pandemic (Tanzania, Kenya, DRC and Gabon), loss estimates have been made for affected and unaffected areas. For affected areas, the 72% figure has been used for losses in infected plants, while for unaffected areas, the 35% figure has been used. The regional coverage of the pandemic zone has been used to estimate the fraction of cassava production affected in Tanzania (1/3), DRC (2/3) and Gabon (1/8). In Kenya, the pandemic-affected fraction has been estimated as 2/3, since approximately two-thirds of Kenya's cassava production is in the pandemic-affected western part of the country.

Production loss estimates have been calculated for pandemic-affected and unaffected countries and parts of countries using figures for CMD incidence, percentage loss for infected plants (either 35% or 72%) and the overall production figures for 2005 obtained from the Food and Agriculture Organization (FAO) database (FAO, 2006). The total production of all surveyed countries represents *c.* 87% of total African production. The production loss for the remaining 13% was calculated using the mean percentage loss calculated for non-pandemic countries (=18%). Using this analysis, overall losses for pandemic-affected areas are estimated at 47%, between two and three times the value for those countries not yet affected (18%) and the recovering Uganda (16%). The estimate for total loss due to CMD in Africa of more than 34 mt (equivalent to 24% of total production) is comparable but slightly greater than the previous estimates of Thresh *et al*. (1997) and Legg and Thresh (2004). This is a consequence of the increased figure for yield loss due to CMD in the pandemic zone and the greater area affected. It is recognised that there are deficiencies in the approach used here to estimate yield losses. For countries in the pandemic zone, estimates of the proportion of cassava production affected are imperfect and there is considerable variation in effects on yield depending on the varietal response, stage of infection and the mix of CMG species or strains present. In addition, some countries known

to be affected by the pandemic have not been surveyed and, therefore, are not included in the analysis in Table VI (Sudan). Other countries are almost certainly affected but they have not yet been surveyed (Central African Republic (CAR) and Angola). Despite these deficiencies, the results provide a reasonable and relatively conservative reflection of the actual situation, and are probably the best that could be achieved with the data currently available.

C. Social Impact of the CMD Pandemic

The social consequences of the CMD pandemic differed considerably between regions and countries, with the primary determining factor being the importance of cassava to the livelihoods of the affected populations. While the pandemic represents an 'inconvenience' in the high-potential farming areas of parts of southern Uganda, northwestern Tanzania and western Kenya, it poses a significant threat to the survival of more vulnerable communities in drier, less-fertile farming areas such as northeastern Uganda, the Kenya shore of Lake Victoria, the southern and eastern shores of Lake Victoria in Tanzania and eastern areas of both Rwanda and Burundi. In large parts of the humid forest zone of Central Africa, encompassing central and northern DRC, Republic of Congo (ROC) and Gabon, cassava is often the only crop grown, and large quantities of leaves as well as the tuberous roots are consumed. In all such areas, the social impact of the pandemic has been acute.

Otim-Nape *et al*. (2000) listed eight key facets of the pandemic's impact on cassava cultivation in vulnerable farming communities of eastern Uganda. These were: a drastic reduction in cassava production, large decreases in the area of cassava being cultivated, marked increases in market prices for cassava food products and planting material, changes in the relative importance of cassava cultivars being grown, increased trade in cassava planting material as farmers seek out improved varieties, increased cultivation of alternative crops, a rise in thefts of cassava roots and stems (particularly of improved resistant varieties following their introduction) and widespread demands from farmers, farmer groups, local officials and ultimately from politicians for the implementation of urgent mitigation measures. These demands peaked in the early stages of the pandemic's spread through eastern Uganda, which coincided with a sustained drought in the 1993–1994 season and led to widespread food shortages, localized famine and reports of hundreds of hunger-related deaths (Thresh and Otim-Nape, 1994).

Similar situations have continued to occur as the pandemic has spread through East and Central Africa, one of which was a severe food shortage in the provinces of Kirundo and Muyinga in northeastern Burundi in 2004/2005. The combined effects of the CMD pandemic exacerbated by drought led to more than 100 famine-related deaths and threats to thousands more (Anon, 2005a). In an attempt to address the crisis, the Government of Burundi introduced an emergency tax on the salaries of all civil servants and collected one-off payments from all other workers (Anon, 2005b). This was to provide emergency support to 1-million people in the affected provinces. Governments may or may not provide support for affected communities, but individuals impacted have to find ways to cope with the lost cassava production. Some of the most prominent means have included the substitution of cassava by alternative crops, most importantly sweet potato, and search for employment on the farms of more prosperous neighbours. Affected families immediately cut back on all non-essential expenditure, one of the most important of which is the payment of education expenses for children. Other slightly longer-term responses have included migration to urban centres or the removal of some family members to other locations, which are either less severely affected and, therefore, better suited for farming or where there are more opportunities for employment. These negative impacts also have adverse effects on relationships within families which in turn further exacerbate the crisis. At a higher level, the negative social effects of the pandemic have affected politics at both local and national levels. These effects have sometimes been negative, as politicians or political groups have sought to apportion blame for the harmful socio-economic effects of the pandemic rather than making more constructive contributions to addressing the crisis. In some situations, however, awareness amongst national politicians has led to increased governmental commitments to solving the problem. The example of this is Burundi, where the ruling party, whose flag bears an image of a cassava plant, made it a national priority to deal with the production losses arising from the CMD pandemic, following its election victory in mid-2005.

IV. Management of the CMD Pandemic

A. Introduction: Virus Management Strategies

A broad range of techniques is known to be of value for the management of plant virus diseases, such as CMD. These have been reviewed extensively (Fauquet and Fargette, 1990; Guthrie, 1988; Thresh and

Cooter, 2005; Thresh and Otim-Nape, 1994; Thresh *et al*., 1998). As for other plant virus diseases, the strategy for managing CMD focuses on preventing infection, delaying the time of infection, minimizing the effects of infection once it has occurred, or ideally combinations of the three. The key elements of control strategies include the use of phytosanitation (primarily involving the uprooting of diseased plants (roguing) and selection of disease-free stems for new planting) and the development and deployment of host-plant resistance. Largely as a consequence of the success that has been achieved in breeding for resistance to CMGs in cassava, this has been the primary tactic exploited in CMD management programmes. Phytosanitation has mainly been used within the framework of schemes for the multiplication of resistant varieties. Cross protection, which makes use of mild or attenuated virus strains that decrease the effects of infection by related but more virulent strains, has been used for some viruses/virus diseases, but until recently, there was no evidence for the potential value of this approach in controlling CMGs. Various crop management strategies may be used to hinder the spread of CMGs into initially CMD-free crops. These include isolation, field disposition and orientation with respect to inoculum sources, inter-cropping and varietal mixtures in which resistant varieties are used to 'protect' susceptible local cultivars. All of these have their limitations and there is little experimental evidence demonstrating significant benefits, although the varietal mixture approach has been shown to provide some degree of protection for CMD-susceptible material in Uganda (Sserubombwe *et al*., 2001, 2005b).

Although the CMD pandemic has arisen and spread through the interaction of virus, vector and host plant, surprisingly, little attention has been given to the possible scope and value of vector management. This is in part a result of earlier findings from West Africa in which there was shown to be a weak relationship between field resistance (proportion of infected plants) and vector resistance (Fauquet and Fargette, 1990). However, concern about super-abundant populations of the CMG vector, *B. tabaci*, particularly on CMD-resistant varieties, has led to a renewed interest in possible whitefly-control measures and investigations into both host-plant resistance against whiteflies and biological control through natural enemy augmentation have been initiated. Virus resistance has traditionally been developed using conventional breeding approaches, however, there is an increasing trend towards the development of virus resistance through genetic engineering. Conventional intra- and inter-species crossing is an imprecise means of introgressing resistance genes into a target genotype.

Genetic transformation offers the potential to provide a much more precise method of introducing genes conferring specific beneficial traits. As knowledge of the genomes of crops such as cassava is gained, the prospect increases of 'cut and paste' technologies that will allow the insertion of sets of desirable genes into farmer-preferred local cultivars, thereby assuring acceptability. Experience with the distribution of improved varieties has shown that such a route towards rapid acceptance is highly desirable, as quality characteristics of conventionally bred CMD-resistant materials often differ from those of local farmer-preferred yet CMD-susceptible cultivars, and this mismatch can result in poor uptake of the improved material.

The magnitude of the problems caused by the CMD pandemic has been such that virtually all possible approaches to controlling the disease have been used, including many 'local' methods used by farmers. The following sections detail the characteristics and methods of implementation of the most important of these approaches.

B. Targeting Control Through Monitoring the CMD Pandemic

1. Rationale for Pandemic Monitoring

The CMD pandemic has been unique, in relation to the history of the disease in Africa, in being dynamic and spreading through a number of countries. This has important implications for the management strategy. Epidemiology has provided information on the rate at which the pandemic is spreading and about the contrasting characteristics of CMD in different 'zones' of the pandemic, and how these change both in space and time. Since the characteristics of CMD at a given location and time determine the most appropriate control approach, detailed epidemiological information is a vital pre-requisite for effective management. Most importantly, epidemiological data, when gathered sufficiently frequently, can identify the areas of real crisis, such as the two examples provided in Section III, namely, eastern Uganda in the early 1990s and northeastern Burundi in 2004/2005. Monitoring and diagnostic surveys have, therefore, become a key component of CMD pandemic mitigation programmes throughout the affected countries and regions (Sseruwagi *et al.*, 2004a).

2. Qualitative and Quantitative Monitoring Assessments

The first attempts to monitor the CMD pandemic were undertaken in Uganda in the early 1990s as spread occurred through the central

southern part of the country. Observations were made along transects running north–south across the epidemic front and elements of the epidemic assessed included severity, incidence and infection type (by cutting or by whitefly), farmer responses and overall cultivation intensity (Otim-Nape *et al.*, 1997, 2000). From information gathered during these surveys, the zonal characteristics of the spreading epidemic were described and the first attempts were made to estimate rates of spread. Concurrent with the wide-ranging qualitative monitoring surveys, a quantitative study provided further evidence for an annual spread rate of 20–30 km (Legg and Ogwal, 1998), and this information led to the first concerns about spread to neighbouring areas of western Kenya and northwestern Tanzania.

3. Forecasting Pandemic Spread

Through the mid-1990s to late 1990s, consistent patterns of CMD spread through Uganda and into the neighbouring countries of Kenya and Tanzania made it clear that patterns of expansion from year to year were predictable. Epidemiological data obtained from surveys in Uganda, Kenya and Tanzania were used to make a forecast of 'threatened' areas in the late 1990s (Legg *et al.*, 1999a) and this approach was modified subsequently to propose a zone, surrounding the known limits of the CMD pandemic, that was expected to be affected within 5 years (Legg, 1999). At this time, monitoring and diagnostic surveys became a routine component within CMD pandemic management programmes (Anon, 1999). Typically, these were conducted annually in the extensive geographical areas in and around the pandemic-affected zone. The most important elements of these surveys were assessments of changes in CMD incidence, symptom severity and pattern of infection and tests for the pandemic-associated virus, EACMV-UG. The principal outputs of these surveys were regional maps that plotted the pattern and speed of spread of the pandemic. Thus, it was possible to delineate newly affected areas and those most severely impacted by the pandemic, with a view to preferentially targeting control activities towards them.

4. Forecasting Examples from East and West Africa

Diagnostic survey data have been used to develop risk maps for East Africa. The first step in the construction of such maps is to determine the administrative areas (typically districts or provinces) already affected by the pandemic. Risk to administrative regions beyond the limits of the pandemic-affected zone is then assessed based on the cassava cultivation intensity in the region and the distance of

the region from the boundary of the pandemic. Three levels are defined for each of the two factors and combined to determine the level of risk, which can be low, medium or high (Table VII). A risk map is then generated using the results obtained. Figure 4 is a risk map developed in 2001 for use within a regional CMD pandemic mitigation programme. By 2005, all 14 of the regions identified as at high risk in 2001 had been affected by the pandemic, 12 of the 17 regions in the medium-risk category and 6 of the 10 in low-risk regions. The fact that so many of even the lowest risk category regions were affected within 4 years, highlights both the rapidity with which the pandemic has spread in East Africa and the need to increase the distances used in defining the three levels in the distance-based factor used in the risk assessment.

An alternative approach used to locate severe CMD in a previously unsurveyed country for which no data were available was attempted in Gabon in West/Central Africa. Earlier survey work had shown that EACMV-UG occurred in the open, hilly grassland environment of Plateaux Region in central ROC (Neuenschwander *et al.*, 2002). Experience from East Africa had also shown that pandemic spread occurred most readily in open savannah-like environments, such as those of eastern Uganda (Otim-Nape *et al.*, 2000). Vegetation maps of West/Central Africa (Fig. 5) showed clearly that the savannahs of central ROC extended to the east into the eastern part of Gabon. Consequently, it was predicted that EACMV-UG and the pandemic had already

TABLE VII

Combinations of Factors Giving the Different Risk Levels Plotted on the Risk Assessment Map (Fig. 4)

Distance from pandemic front (km)	Cassava cultivation intensity	Threat/risk level
<50	H	H
	M	H
	L	M
50–150	H	H
	M	M
	L	L
>150	H	M
	M	L
	L	L

Abbreviations: L, low; M, medium; H, high.

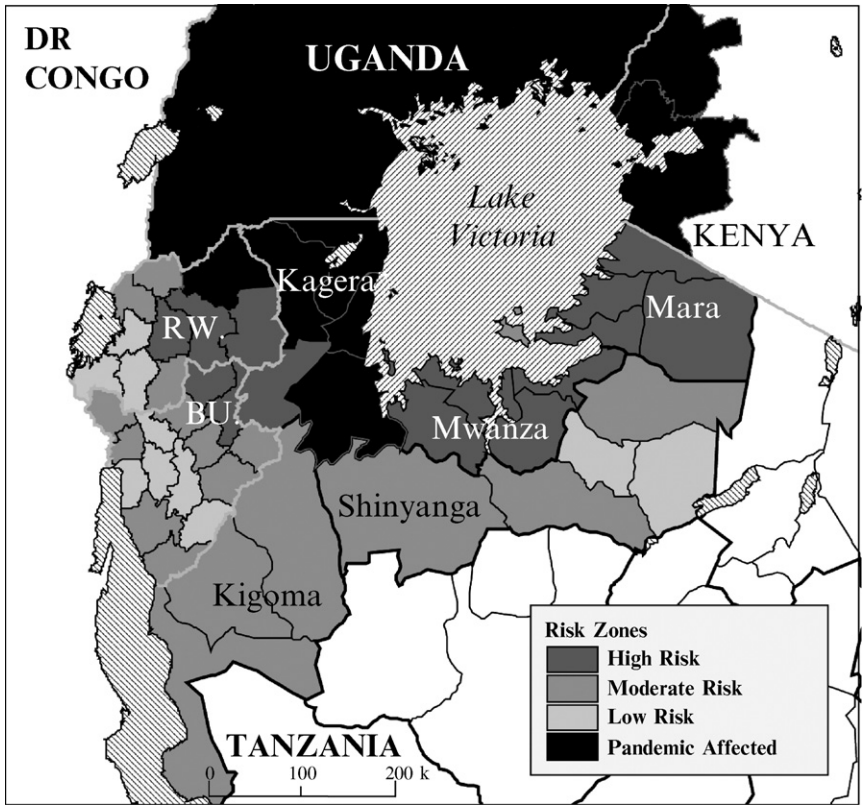

FIG 4. Risk assessment map for the CMD pandemic in East/Central Africa, 2001.

spread into eastern Gabon and that the affected area would be in the grassland zone of central eastern Gabon near to the town of Franceville (Fig. 5). Subsequent surveys confirmed both predictions (Legg *et al*., 2004) and these findings led directly to the development of recommendations to limit spread of the pandemic through Gabon. This was particularly valuable because at the time of the survey, the incidences of EACMV-UG and severe CMD were very low, offering the possibility of initiating control measures at an early stage of epidemic development. Despite the relative remoteness of this location, the recognition of spread into Gabon represented the earliest stage at which this had been diagnosed in any of the countries affected by the pandemic.

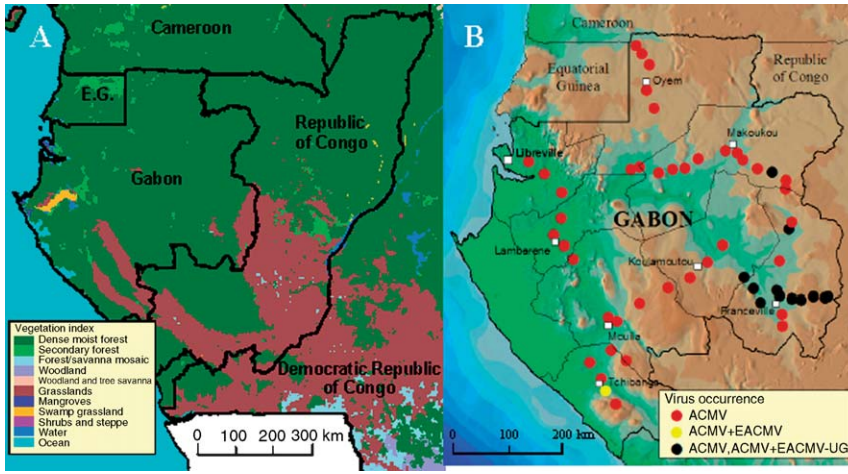

FIG 5. (A) Vegetation map for Central/West Africa used to predict spread of EACMV-UG into Gabon (Anon, 2005d). (B) Occurrence and distribution of cassava mosaic geminiviruses in Gabon, 2003 (Legg *et al.*, 2004).

5. Monitoring Surveys and Impact Assessment

Another key function of monitoring surveys is to collect data that can serve as a pre-intervention baseline, which subsequently can be compared with data collected from the same area in an attempt to assess the impact of control programmes. The most successful example of this is central southern Uganda, where a CMD management programme based on the multiplication and distribution of resistant varieties was accompanied by an annual set of cassava pest and disease assessment surveys between 1998 and 2001 (discussed further in Section H).

C. Host-Plant Resistance Development and Deployment

1. Early Resistance Breeding Initiatives in Tanzania and Madagascar

From the earliest research into CMD, it was recognised that some cassava cultivars were more readily and more severely affected than others. Moreover, there was an understanding that wild relatives of crops are very often more resistant to pest and disease problems than the cultivated forms. With this background, cassava improvement programmes were initiated separately in the 1930s in Madagascar and in what is now Tanzania. Both programmes utilized existing

knowledge of breeding to attempt to introgress resistance from both wild cassava relatives and cultivated cassava into target cassava germplasm (Cours, 1951; Jennings, 1957). In the East African regional cassava-breeding programme in what is now Tanzania, greatest success was achieved with crosses with *Manihot glaziovii* that were then triple back-crossed with cultivated cassava to produce progeny that combined the CMD-resistance trait of *M. glaziovii* with the edible storage roots of *M. esculenta*. Although this programme ended in the 1950s, some of the materials produced were carried to Nigeria, where resistance breeding continued under the Federal Research Programme in the 1960s (Beck, 1982). This work was expanded in the major new cassava germplasm development programme launched by the Nigeria-based International Institute of Tropical Agriculture (IITA) from the early 1970s (Hahn *et al*., 1980).

2. Africa-Wide Breeding Programme of IITA

During the early period of the IITA breeding programme in the 1970s, efforts were focused on extending the Amani (Tanzania) work to develop varieties that were resistant to CMD, and also to some of the other key pest and disease constraints, the most important of which at the time was cassava bacterial blight (CBB) (*X. axonopodis* pv. *manihotis*) (Hahn *et al*., 1980). Significant successes were achieved in deploying resistant germplasm in Nigeria, but progress was slower elsewhere, although many countries received sets of CMD-resistant germplasm in tissue culture form through IITA's continental distribution programme (Manyong *et al*., 2000). Significantly, resistant varieties had been sent to Uganda in 1984, although this had coincided with a period when pest and disease constraints there were only of moderate importance.

3. Host-Plant Resistance and the 1990s Epidemic of CMD in Uganda

As the CMD epidemic first began to affect cassava production in Uganda in the early 1990s, initial attempts were made to address the problem by distributing uninfected material of 'local improved' cultivars, notably 'Ebwanateraka', 'Bao' and 'Aladu Aladu' (Otim-Nape *et al*., 1997), although it quickly became apparent that these genotypes were susceptible to the severe epidemic CMD. Small collections of IITA-developed varieties were available, however, and these were multiplied rapidly and evaluated with farmers in epidemic-affected areas. Three varieties were selected and released officially in 1994 (Otim-Nape *et al*., 1994a): TMS 60142 (released as Nase 1), TMS

30337 (Nase 2) and TMS 30572 (Migyera or Nase 3). A rapid programme of multiplication and distribution followed with considerable early success, and Nase 3 in particular was widely adopted by farmers, particularly in the eastern and northwestern districts, where cassava is primarily processed into flour. The Ugandan National Agricultural Research Organization (NARO) released six other varieties in 1999, which were IITA-derived genotypes or locally developed half-sib progeny obtained through seed from CMD-resistant maternal parents. The most important variety from this second release was named SS4 (released as Nase 4), and in view of its very high level of CMD resistance and generally low cyanogenic glucoside content, it was widely promoted in parts of the country where cassava is usually eaten following simple boiling rather than being processed into flour. Based on the successes of TMS 30572 and SS4 in Uganda, these became the main varieties multiplied and distributed in neighbouring Kenya and Tanzania following pandemic spread to these two countries.

4. Nature and Mechanisms of Resistance to CMD

Few quantitative studies of CMD resistance were available prior to the surge in interest in the disease that occurred following the outbreak of the epidemic in Uganda. However, exceptions were the studies of Colon (1984) in Ivory Coast, who assessed a wide range of genotypes, and Hahn *et al*. (1980) in which the performance of IITA-bred germplasm was contrasted to that of local material. Key facets of CMD resistance identified at this time included a reduction in the rate of infection and an overall reduced level of infection. A characteristic feature of the *M. glaziovii*-derived resistance was incomplete systemicity of the virus in infected plants, which led to the observed phenomena of recovery and reversion (Fargette *et al*., 1994; Pacumbaba, 1985), both of which appeared to be enhanced by high temperatures (Gibson, 1994). Fargette *et al*. (1996) recognised a series of components of resistance to CMG infection. These included: resistance to the vector before infection, reduction in virus replication, inhibition of virus movement within the plant and decreased response of the plant to a given virus content as assessed serologically. Little is known about the molecular processes that underlie these mechanisms of resistance, although there is increasing evidence that other crop plants have developed defence responses to geminivirus infection that involve post-transcriptional gene silencing of virus gene products (Lucioli *et al*., 2003).

Through germplasm development work at IITA in the early 1990s, it became apparent that many of the local landraces represented in

IITA's germplasm collection, from various parts of West Africa (and designated the Tropical *Manihot esculenta* or TME group) had some resistance to CMD (Mignouna and Dixon, 1997). Significantly, these resistant materials also had many of the quality characteristics preferred by farmers (upright growth habit, 'sweet' taste, mealyness) that were absent in the *M. glaziovii*-derived material (within the bred tropical *Manihot* species or TMS group). Subsequent studies linked resistance in TME genotypes, the type example of which was TME 3, with the presence of a single dominant CMD resistance gene, referred to as *CMD2* (Akano *et al*., 2002). Much of the breeding work of IITA and its national partners over the last decade has, therefore, involved developing germplasm that has a combination of *CMD2* and *M. glaziovii*-derived resistance (Dixon *et al*., 2003). Additional sources of resistance continue to be discovered, however, and molecular marker techniques have been used to show that TME 7 has a CMD resistance gene or genes different from, but related to *CMD2* (Lokko *et al*., 2005). Genomics approaches involving the development of expressed sequence tag (EST) libraries (Anderson *et al*., 2004) and ultimately the complete sequencing of the cassava genome offer much promise for the identification of further CMD resistance genes and should open up the potential for resistance gene 'pyramiding'. Conventional breeding approaches have and will continue to be used in identifying and combining resistance genes, but increasingly transgenic approaches are likely to be pursued, as discussed further in Section IV.F.

D. Phytosanitation

Phytosanitation describes a number of primarily field-applied techniques that are used to reduce the incidence of disease in a crop. Three of these have been widely applied for the management of CMD in Africa, namely, the use of tissue culture, selection of disease-free stems for new plantings and removing diseased plants from within a crop stand (usually referred to as roguing). The value as well as the potential drawbacks of these methods have been discussed extensively (Thresh and Cooter, 2005; Thresh and Otim-Nape, 1994; Thresh *et al*., 1998), but there is little published information either confirming or refuting their effectiveness. The main points of concern are that where inoculum pressure is high and susceptible cultivars are being grown, roguing can lead to almost complete removal of the crop, yet where a resistant variety is being grown, the slight yield losses suffered when plants are infected may mean that the losses incurred through roguing would exceed those resulting from infection. Because

of these concerns, and the fact that persuading farmers to change their cultural practices is inherently difficult, use of phytosanitation measures has largely been confined to formal germplasm exchange and 'clean stock' multiplication programmes. Tissue culture, involving meristem tip excision, thermotherapy and virus indexing, provides a means to produce virus-tested plantlets that can then be transported across international boundaries without presenting a quarantine hazard (Frison, 1994). This approach has been used by IITA to move virus-tested plantlets of CMD-resistant varieties to CMD-affected countries. The broader strategic use of this method in CMD management programmes is discussed further in Section IV.G. Roguing and selection of CMD-free stems for planting have been widely used in resistant variety multiplication in all of the countries affected by the CMD pandemic (Legg *et al.*, 1999b). Although roguing and selection of planting material by farmers appear to have little role to play in areas affected by the pandemic, evidence from a post-epidemic situation in western Kenya (Mallowa, 2006) suggests that selecting planting material of local cultivars can provide yields that are similar to those of resistant varieties grown under similar conditions. Such a result is of particular significance since resistant variety multiplication programmes typically require 5–10 years before the majority of farmers have access to such planting material. Moreover, where material is available, farmers very often prefer to retain a proportion of their own local cultivars since these have specific desirable quality traits that are absent in the resistant material.

E. Mild Strain Protection and Virus–Virus Interference

1. Mild Strain Protection

A feature of the post-epidemic condition in parts of East and Central Africa, affected by the CMD pandemic, is the resurgence of local cultivars and a general reduction in the severity of CMD symptoms expressed. Three factors contributing to this effect are: the previously described reduction in frequency of mixed virus infections (Table I), the increased cultivation of more CMD-tolerant local cultivars and decreased virulence of EACMV-UG as mild strains have become frequent (Sseruwagi *et al.*, 2004b). Pita *et al.* (2001a) first demonstrated the occurrence of both mild and severe strains of EACMV-UG in Uganda, and showed that the differences in disease phenotype were due to sequence differences of only a few nucleotides. The practical importance of these differences was confirmed through the virus-specific yield loss studies of Owor *et al.* (2004a) in which EACMV-UG severe

infection led to losses of 68% compared with 12% for EACMV-UG mild. Although mildly diseased cassava plants infected with EACMV-UG were frequent in post-epidemic Uganda (Sseruwagi *et al*., 2004b), it was also noted that initially healthy plants typically expressed severe symptoms when they became infected. This observation suggested that EACMV-UG mild infection provides some kind of cross protection against severe strains that are, by contrast, readily able to infect healthy plants. Early studies on cassava had reported the inability of mild strains to protect against severe strains (Dade, 1930; Storey and Nichols, 1938). To determine if indeed mild strains of EACMV-UG were providing a form of cross protection, an experiment was carried out in central Uganda. Plants grown from initially CMD-free parents and plants initially infected with mild EACMV-UG were grown, and subsequent patterns of infection, symptom expression and tuberous root production were assessed (Owor *et al*., 2004b). Plants grown from initially CMD-free parents developed more severe disease and yielded less than plants derived from mildly diseased parents. These results were complemented by screenhouse-based studies in which whitefly transmission tests were used to confirm the cross protection effect of mild strains of EACMV-UG (Owor, 2002). These results help to explain the resurgence of local cultivars in post-epidemic areas and also indicate that cross protection could offer an important novel approach for the management of CMGs. An important consideration in implementing such an approach, however, will be to determine where mild strain protection works and where it does not, in view of the diversity of virus occurrence. Further study will also be required to acquire an understanding of the molecular basis for the cross protection effect.

2. Defective Interfering Molecules

Defective interfering (DI) sub-genomic DNAs that arise primarily through initial or serial *in vitro* passage of geminiviruses in test plants such as *Nicotiana benthamiana* can moderate viral damage of the wild-type virus. A naturally occurring truncated form of CMG DNA-A (1525 nts), which upon sequence analysis has been shown to be a defective (df) form derived from EACMV, has been isolated and characterized in Tanzania (Ndunguru *et al*., 2006). The 'missing' portions include the *AC2* and *AC3* genes on the complementary-sense strand, and the C-terminal portions of *AC1* as well as *AV2* and over 80% of the *AV1* (coat protein gene) on the virion-sense strand. The sub-genomic DNA has, nevertheless, retained all the *cis*-acting elements necessary for its maintenance. Phylogenetic comparisons placed the molecule close to mild and severe isolates of EACMV-UG2 (>95% nucleotide

sequence identity). Biolistic inoculation of the infectious df DNA-A clone 15 (df DNA-A 15) with EACMCV showed symptom amelioration as compared to the plants singly infected with EACMCV and there was an accumulation of the df DNA-A 15 in systemically infected leaves 14 days after inoculation. The data indicate that 1.5 kbp df DNA-A 15 is a defective DNA that can modulate symptoms of the wild-type geminivirus. Investigation of a possible trans-encapsidation and transmission of the df DNA-A 15 under field conditions as well as its mechanism of symptom modulation could shed light on its possible role in symptom variability associated with the CMD pandemic and also on any involvement in the mild strain protection phenomenon described previously. Even where these effects are not attributable to sub-genomic molecules, mechanisms of symptom amelioration are likely to be shared, and further study of the molecular mechanisms behind these responses is warranted.

F. Cassava Transformation

In several crops, transgenic plants resistant to an infective virus have been developed by introducing a sequence of the viral genome into the target crop by genetic transformation. Virus-resistant transgenics have been developed in many crops by introducing either viral coat protein or replicase gene-encoding sequences, which interfere with one or more essential steps in the replication cycle of the virus. Replicase (Rep) protein-mediated resistance against a virus in transgenic plants was first shown in tobacco against *Tobacco mosaic virus* in plants containing the 54 kDa putative *Rep* gene (Golemboski *et al*., 1990). Geminiviruses have been used to study fundamental aspects of RNA interference (RNAi) and virus-induced gene silencing (Chellappan *et al*., 2005; Turnage *et al*., 2002). Proof of the concept that RNAi can be engineered to target geminiviruses effectively has been documented in transient assays for ACMV. Vanitharani *et al*. (2003) reported successful generation of a transgenic cassava (line Y85) resistant to ACMV and two other related CMGs. Detection of the transgene-derived siRNAs and extremely low levels of the transgene product (the truncated Rep protein from ACMV) in this line suggested that RNA silencing accounts for the broadly active resistance.

The greatest resistance recorded in experiments done in containment facilities with artificial methods of inoculation has been obtained using the so-called *Rep* gene of ACMV (Chellappan, P., unpublished data). The susceptible genotype TMS 60444 was transformed and near-immune plants were regenerated. In addition, these plants are

resistant to other CMG species, including EACMCV and *Sri Lankan cassava mosaic virus* (SLCMV), indicating a wide range of protection, which is a key requirement in view of the molecular variability of known CMGs. Furthermore, these plants have shown a very high level of resistance to the synergistic mixture of ACMV and EACMV-UG, indicating that the strategy employed is very effective against the natural mixture causing the pandemic. It appears that the most resistant plants are using the post-transcriptional gene silencing mechanism and the broad spectrum of protection to other virus species is attributed to common short sequences between their respective Rep protein genes (Chellappan *et al*., 2004). Plants so transformed are currently being tested under screenhouse conditions in western Kenya.

An alternative approach used anti-sense RNA technology (Zhang *et al*., 2005) in which targets for the anti-sense interference were the mRNAs of *C1*, *AC2* and *AC3* of ACMV. Assays of virus accumulation in transgenic plants revealed reduced or inhibited replication of ACMV. In a third approach, a hypersensitive response to infection is elicited by transforming TMS 60444 with the bacterial *barnase* and *barstar* genes from *Bacillus amyloliquefaciens*, controlled by the ACMV A bi-directional promoter (Zhang *et al*., 2003). Reductions of viral replication of 86–99% were demonstrated, when comparing leaves of untransformed and transgenic plants. While this strategy is still at the greenhouse testing stage, both the *Rep* and anti-sense RNA strategies have yielded successfully regenerated cassava lines ready for field testing in areas devastated by the CMD pandemic.

In another development, a toxin gene, *dianthin*, was placed downstream of a transactivatable geminivirus promoter from ACMV. When transgenic *N. benthamiana* plants were inoculated with ACMV, *dianthin* was synthesized only in the virus-infected tissues, where it inhibited virus multiplication (Hong *et al*., 1996). This approach also warrants further consideration for its potential value in CMD management. Although further refinements of the group of transgene-derived CMG-resistance strategies are required before effective field implementation, these tactics offer great promise. Most importantly, they could provide a valuable complement to conventional control tactics and could effectively allow farmers to continue to grow locally preferred cultivars (albeit transformed for virus resistance). In view of the difficulties that have been experienced in some pandemic-affected areas in addressing farmer quality preferences, this represents a very important development. Biosafety of newly developed transgenic crops remains a concern in much of SSA, however, and legislation governing the introduction, testing and release of transgenic plants is still being

developed in many of the pandemic-affected countries. Kenya is currently the only African country to have tested transgenic CMG-resistant varieties of cassava under screenhouse conditions, but even here, field testing of such material has yet to be approved. Despite this initial caution, however, trends in the larger developing countries suggest that early concerns will be overcome and that transgenic technologies will be widely adopted. These novel approaches to CMD management appear, therefore, to have much potential in the near future, a prospect that certainly justifies further investment in the technology.

G. Integrated Management Programmes

1. Early Successes in Uganda

Management of any major disease epidemic covering a large area requires considerable logistical organization and the participation of diverse stakeholders. The first country-level model for the approach to managing the CMD pandemic was developed in Uganda and co-ordinated by the National Cassava Programme (NCP) of NARO. An informal network of partners was established, including the NCP research team, government extension officers, agricultural workers from non-governmental organizations and farmer groups (Otim-Nape *et al.*, 1994a). Following on-farm evaluations, the best-performing CMD-resistant varieties were identified and multiplied, firstly at institutional sites (mainly comprising research stations, district farm institutes, prisons and other government institutions) and then closer to farming communities at collective multiplication sites. Various approaches were used in different projects that targeted CMD management, and there were varying degrees of success (Otim-Nape *et al.*, 2000). Programmes that focused on the multiplication of CMD-resistant varieties were generally effective, although the degree of adoption by farmers was influenced greatly by the way in which cassava is utilized; results were much better in areas where traditionally cassava is processed to make flour. During the early years of CMD management in Uganda, the TMS varieties were emphasized but some of these were limited in their acceptability by quality issues, and from the late 1990s there has been a greater focus on the promotion of TMS $\times$ TME crosses or TME landraces. Widely promoted TME clones include TME 14 and TME 204, while some of the most popular TME $\times$ TMS crosses are I92/0067 (=Akena) and I92/0057 (=Omongole). Although these varieties combine the qualities of local farmer-preferred cultivars with good levels of resistance, drawbacks include their apparent attractiveness

to whiteflies and the vulnerability of some of them (notably TME 204) to the other main cassava-infecting virus in Africa, *Cassava brown streak virus* (Genus: *Ipomovirus*; Family: *Potyviridae*). These concerns are discussed further in Section V. In addition to the resistant variety multiplication programmes, training of extension workers and farmers and awareness-raising through printed materials and the media (radio and television) were important components of CMD management in Uganda, as described in detail by Otim-Nape *et al*. (2000). The approaches developed there were of crucial importance in developing control programmes elsewhere.

2. Regional CMD Pandemic Mitigation Programme

As the CMD pandemic expanded to cover large parts of the cassava-growing areas of the Lake Victoria Basin of East Africa during the second half of the 1990s, it became apparent that a co-ordinating programme was required that would help to transfer some of the lessons learnt in Uganda, provide a regional forum for sharing experiences and information on CMD management and create 'leverage' to seek external support. It was recognised that various forms of such support were needed, including cassava germplasm (through IITA, Nigeria), finance (from donors) and technical 'backstopping' (from centres with specialist expertise). Sustained donor support was essential, and a regional team co-ordinated through IITA, was successful in attracting financial backing for a regional pandemic mitigation programme from the Office of United States Foreign Disaster Assistance (OFDA), which still continues. The regional programme complemented other country-focused CMD management initiatives financed by United States Agency for International Development (USAID), the Crop Protection Programme (CPP) of the UK's Department for International Development (DFID), the Gatsby Charitable Foundation, the Canadian International Development Research Centre (IDRC) and the Rockefeller Foundation. The regional team that was established through the OFDA-supported project linked researchers, extensionists, plant protection and quarantine staff, NGOs and farmers from the participating countries of Uganda, Kenya and Tanzania, although the participation later broadened to include both the ROC in 2001 and Burundi in 2002. The overall strategy of this on-going programme comprises the following principal components: monitoring and forecasting CMD pandemic expansion, germplasm diversification and exchange, multiplication and distribution of CMD-resistant varieties; and training of researchers, extension workers and farmers in CMD management techniques. Country and regional representatives

participate in a stakeholder group that co-ordinates the regional CMD mitigation programme through consultative reviews and planning. Within countries, activities are co-ordinated similarly through national steering committees, which have a comparable make-up of participating institutions.

a. Monitoring and Forecasting CMD Pandemic Expansion The programme has been the first to implement a regional CMD-monitoring system. The technical approaches were described earlier (Section IV.B). An important facet of the organization has been the regional-network structure developed, as described in the previous paragraph. This has facilitated the rapid transfer of information, the provision of technical support, where required, to country-level monitoring teams and the channels for the communication of results of the work. This final step has been particularly important, since the early provision of information on newly threatened areas or new problems is vital to the success of controlled implementation work. Efforts were made to use a different approach to monitoring pandemic spread in which farmer groups in advance of the epidemic 'front' were trained in what to expect and asked to provide information on any new spread into their farming areas. Weaknesses in the communication systems from farm, through extension and up to researchers, however, meant that this approach was unworkable. Any future attempt on these lines must pay particular attention to improving communication pathways.

b. Germplasm Diversification and Exchange The rapid provision of appropriate CMD-resistant germplasm for areas affected by the pandemic is key to successful management. The spread of EACMV-UG into countries neighbouring Uganda immediately made this task more complex since known resistant stocks were present in Uganda and movement of germplasm across borders raised phytosanitary concerns. The first affected country to face this issue was Kenya. It was soon realized that the simplest, quickest and most effective way to address pandemic spread there was to introduce the CMD-resistant varieties being used in Uganda in sufficient quantity to facilitate a multiplication and dissemination programme. An 'open quarantine' protocol was developed to introduce substantial quantities of these varieties and yet avoid the risk of inadvertently introducing quarantine pests/pathogens (including EACMV-UG). This enabled the introduction of substantial quantities of cuttings of TMS 30572 and SS4 to a 2 ha fenced open quarantine site at Alupe, western Kenya, in 1997. This plot was maintained under regular surveillance for pests and

diseases for a year, after which the stems were harvested and used to initiate the multiplication programme at a series of primary multiplication sites distributed across the pandemic-affected area. This at that time comprised all of Western Province and the northern part of Nyanza Province. The development of the open quarantine site also facilitated the introduction of >600 cassava clones with a background of CMD resistance from the Serere (Uganda)-based regional cassava germplasm development programme of the East African Root Crops Research Network (EARRNET). EARRNET, established as an IITA-executed regional network, subsequently used the Serere-based cassava germplasm collection as the key central 'source' of CMD-resistant germplasm for the entire region, and similar and repeated transfers were made to Tanzania, Rwanda, Burundi and southern Sudan, in addition to Kenya. In addition to the use of open quarantine sites, another key element of the regional germplasm introduction programme was the transport of virus-indexed tissue culture plantlets of CMD-resistant varieties from IITA, Nigeria. As part of this programme:

- Small numbers of tissue-culture plantlets were sent to Kakamega, western Kenya through the Muguga-Nairobi Plant Quarantine Station of the Kenya Plant Health Inspectorate Service.
- 10,000 tissue culture plantlets were sent via Dar es Salaam to Ukiriguru Research Institute, Mwanza, Tanzania, on the southern shore of Lake Victoria, an area ahead of the CMD pandemic.
- 5000 tissue culture plantlets were delivered to Brazzaville, ROC. This represented the first supply of CMD-resistant varieties of known provenance to this country, which by that time was almost entirely affected by severe CMD.

These initiatives had mixed success. The transfer of plantlets to Kenya worked well, although in terms of scale alone, the open quarantine introduction proved to be much more effective and lasting in its impact. Both of the large-scale introductions to Tanzania and ROC suffered substantial losses arising in part from the transport of the fragile plantlets over long distances, and partly also due to difficulties encountered during hardening off and field planting of the plantlets. Nevertheless, where CMD-resistant material was not available previously, as in ROC, the plants that were established provided a vital first set of germplasm for subsequent CMD management.

Following the introduction of CMD-resistant germplasm, evaluation programmes were initiated, starting in many cases from the open quarantine site itself. A few of the best-performing introduced cassava clones were typically then 'fast-tracked' to on-farm evaluations with

farmers to accelerate the germplasm selection process, and identify farmer-acceptable CMD-resistant materials for multiplication and dissemination as quickly as possible. Fourteen clones were fast-tracked in Kenya, 10 in Tanzania, 7 in Burundi, 20 in DRC and 17 in ROC.

c. Multiplication and Dissemination of CMD-Resistant Varieties Efforts to multiply and disseminate cassava germplasm rapidly in pandemic-affected countries of East and Central Africa followed similar approaches to those already implemented successfully in Uganda (Otim-Nape *et al.*, 2000). Typically, a three-tier system was used in which 'nuclear' stocks of resistant material were multiplied initially at primary multiplication sites, before being disseminated to secondary then tertiary sites. Primary sites were mainly at government-owned institutions, such as research stations, district farm institutes and prisons. These sites typically ranged in size from a few to tens of hectares. Secondary sites were commonly established by farmer groups, community-based organizations, or large private farms (usually up to 2 ha in size) and tertiary sites involved individual farmers and tended to be small (<2 ha). Diverse systems were developed for the various components of multiplication, which included the partitioning of costs and labour for management, the handling of planting materials during planting, harvest and distribution, the agronomic methods used and the system of distribution of the harvested cuttings. Although irrigation can be of considerable value in allowing almost continuous production in rapid multiplication systems, this was rarely used because it was seldom available. An exception was the Nyakasanga location near Mwanza, Tanzania, where CMD-resistant germplasm introduced from IITA, Nigeria was multiplied rapidly at an irrigated site. This then enabled the Tanzania team to multiply and disseminate resistant material from a site ahead of the pandemic 'front', while material introduced from Uganda was being multiplied from within the pandemic-affected region.

There are many examples of successful approaches to the multiplication and dissemination of CMD-resistant germplasm, but one of the most effective programmes in Tanzania was that of an NGO, Norwegian Peoples' Aid (NPA) in Ngara District, Kagera Region, bordering Rwanda and Burundi. A 5 ha intensively managed nursery plot has been used to rapidly multiply CMD-resistant material that was then distributed to groups of farmers. Within these groups, up to 20 farmers have planted contiguous multiplication plots of 0.2 ha each and have agreed to contracts with NPA in which they return to NPA two-thirds of the cuttings produced over a two-year period and keep the remaining one-third for themselves. From an initial group of 5 villages in

2003, NPA increased the coverage of the programme to 45 villages by February 2005. The block approach appears to have been more effective than alternatives tried elsewhere, but clearly benefits from the fact that in Ngara suitable land is more readily available than it is in other parts of the region, such as northern Kagera in Tanzania, Burundi and western Kenya.

Multiplication has been greatest in those countries affected earliest. Cassava production in Uganda is currently greater than before the pandemic (FAO, 2006). Similar successes have been achieved in western Kenya, where production in 2004 was only a little less than before the pandemic and almost double that during the worst-affected period in 1997. In Tanzania, more than 1000 ha of resistant varieties had been established by mid-2005. Progress in Burundi, Rwanda and ROC has been slower, however, mainly because activities began later. Problems with civil insecurity initially hindered progress in DRC, but major CMD mitigation programmes being led by IITA and FAO have been operating since 2000, and substantial areas of CMD-resistant varieties have been produced, particularly in the Bas Congo, Kinshasa, Bandundu and South/North Kivu Provinces.

d. Training Increasing the knowledge of all stakeholders affected by the CMD pandemic has been an important component of the regional CMD pandemic management programme. Researchers have been trained in the technical elements of CMD: the ecology of the viruses responsible and their whitefly vector, diagnostic techniques and approaches to CMD management. Practical, field-based training initiatives have been run for agricultural workers of government extension systems and NGOs. Knowledge of affected farmers has also been improved through *in situ* training, typically at multiplication or on-farm evaluation sites, as well as through farmer exchange visits which have involved groups from Uganda, Kenya and Tanzania. Most countries have also attempted to raise awareness by publishing information about the pandemic and ways in which to control the problem via radio and television. Radio has been a particularly important medium since it is almost universally accessible, even in the remotest locations.

3. Pre-Emptive CMD Management Programmes

Much of the CMD pandemic management activity in East and Central Africa has been in response to an existing problem. None of the countries has been successful in disseminating CMD-resistant varieties within communities at risk but as yet unaffected by the pandemic,

despite significant efforts to do so in Kenya and Tanzania. A fundamental limiting factor behind this phenomenon is the fact that the generally conservative farming communities are usually not prepared to switch to different cassava varieties, while those that they already have and are accustomed to using continue to provide acceptable yields. The spread of the pandemic into the western part of Central Africa, however, has given rise to concern in Nigeria, Africa's largest cassava producer, of the potential social and economic consequences of the 'arrival' of the pandemic there. To ensure that resistant germplasm is available before such spread occurs, a major 'pre-emptive' pandemic mitigation programme was initiated in 2003 targeting the 12 states considered to be most vulnerable in the south and southeast of the country. In order to overcome potential unwillingness of farmers to adopt new varieties prior to the impact of the pandemic, this programme aims to develop commercial opportunities for processed cassava products that should lead to expanded markets and increased demand. This effort is being enhanced significantly through major governmental interventions. These include a 'Presidential Initiative', which targets the establishment of cassava industries for export promotion and the introduction of a minimum use of 10% cassava flour by bread producers (Anon, 2005c).

H. Impact of Management Initiatives

Considerable success has been achieved through CMD pandemic mitigation activities, although experience from Uganda has shown that the recovery period is protracted and takes at least 10 years. Despite the evident benefits of CMD management, there is currently no impact assessment in the published literature. An examination of production statistics, such as those of FAO (2006), should provide some indications of declines in production associated with spread of the pandemic, and subsequent increases arising from the uptake of CMD-resistant varieties. Unfortunately, the inadequate systems that exist for collecting these data in East and Central Africa mean that these estimates are unreliable and not suitable for use. Monitoring survey data do provide an alternative means of estimating impact, however, as varieties are recorded from surveyed fields, thereby, allowing assessments to be made of changes in frequency of cultivation of particular varieties, including CMD-resistant materials introduced through management programmes. Using this approach, an estimate was made of the impact of CMD-resistant variety multiplication in six central Ugandan districts that were targeted through a USAID-funded project that ran from 1998 to 2001. During this period, annual surveys

of more than 270 fields in the 6 districts, revealed a series of changes. Intensity of cultivation increased by 16%, equivalent to an increase in area of more than 11,000 ha, and the proportion of farmers' fields in which CMD-resistant material predominated increased from 17% to 35%. On-farm trials conducted in the project districts gave average yields for local cultivars of 7.4 t/ha compared to 15.5 t/ha for resistant varieties, results which are comparable to data collected from a later survey in 2003 (Sserubombwe *et al*., 2005a). Considering the benefit to producers alone, these changes give an estimated benefit of more than US$ 22 million, based on a conservative price for fresh cassava of US$ 100 per tonne.

The degree of impact differs greatly between areas, largely due to differences in the acceptability of introduced CMD-resistant varieties to local farming practices and patterns of cassava utilization. Another important determinant is the relative importance of cassava to the affected community. Where cassava is not the main food crop, as in parts of southwest Uganda, Bukoba district in northwestern Tanzania and the high-potential maize-growing areas of western Kenya, adoption of CMD-resistant varieties is slower and farmers often continue to plant diseased local CMD-susceptible cultivars. This is of concern as sustained high incidences of CMGs and the continued presence of high-whitefly populations provide ideal conditions for the emergence of novel and potentially resistance-breaking virus recombinants, which highlights the importance of a sustained focus on CMD control efforts even after the initial crisis of the epidemic condition has passed.

V. New Threats

A. *Super-Abundant* B. tabaci

Increased populations of *B. tabaci* have been a general feature of the CMD pandemic, as described in Section II.A.2. Initial studies seemed to suggest that populations were particularly high at the 'front' of the pandemic and then declined in areas affected earlier, as the area under cassava was reduced (Legg and Ogwal, 1998; Otim-Nape *et al*., 1997). Experience from Uganda, however, has shown that this decline seems to be temporary, and that subsequently there has been a sustained increase in *B. tabaci* abundance. Data collected from a sequence of 50×50 plant arrays of local cultivar 'Bao', each planted in exactly the same manner over the period 1992–1994 and again in 1998 and 1999, illustrate the magnitude of this population change (Fig. 6). Similar

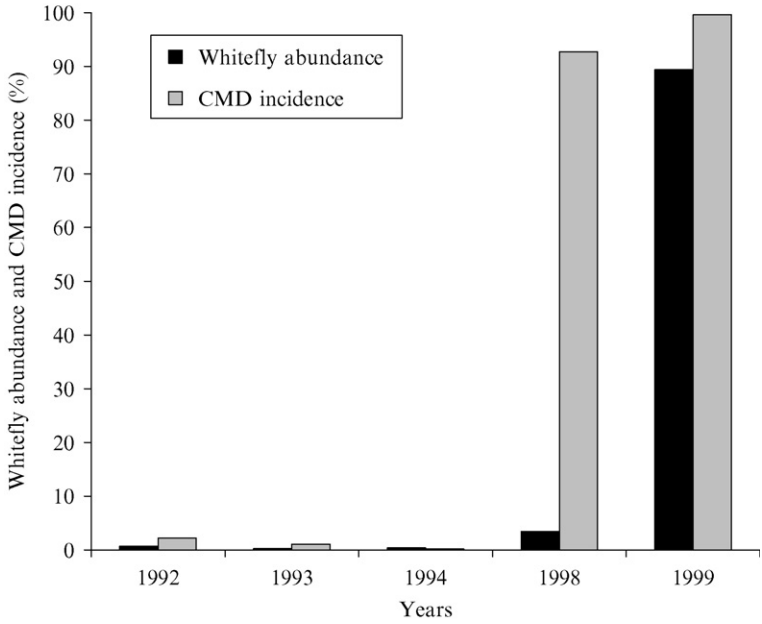

FIG 6. CMD incidence and abundance of *B. tabaci* whiteflies recorded from initially CMD-free plots of the local CMD-susceptible cultivar 'Bao' planted at Namulonge, Uganda from 1992–99 (CMD incidence was the percentage of plants infected with CMD at the end of each trial, 12 months after planting; whitefly abundance was the mean number of *B. tabaci* adults on the top five leaves of a representative shoot of plants sampled weekly over a period of 6 months from 2–8 months after planting).

sustained increases in the abundance of *B. tabaci* have been reported throughout other pandemic-affected parts of East and Central Africa.

In addition to causing rapid spread of CMGs to local susceptible cultivars and threatening resistance breakdown for improved CMD-resistant varieties, super-abundant populations of *B. tabaci* are also causing physical damage to cassava. Symptoms (Fig. 1) include a yellow chlorotic mottling on young newly emerged leaves resulting from feeding by *B. tabaci* adults, 'sooty mould' on lower leaves caused by fungal growth on 'honeydew' excreted by whitefly nymphs and a general reduction in plant growth caused by the compound effect of the damage. Preliminary analysis of yield loss trials indicates that losses resulting from whitefly physical damage alone can be 50% for some of the CMD-resistant varieties being promoted (Legg, J., unpublished data). Fortunately, losses appear to differ considerably between varieties, offering

promise for the identification and use within breeding programmes of sources of whitefly resistance.

It is crucial to understand why such a major change has occurred in the numbers of *B. tabaci* on cassava. Experience elsewhere with other pathosystems has shown that increased populations of *B. tabaci* were linked to the appearance of new biotypes or strains of the vector (Bedford *et al*., 1994; Brown and Bird, 1992). This occurred particularly in areas where *Bemisia* whiteflies were previously unimportant. For example, in the southwestern United States, the B biotype of *B. tabaci*, an introduction from the Middle East (Brown, 2000; Costa and Brown, 1991; Costa *et al*., 1993) increased in distribution and abundance, and displaced the 'local' A biotype that occurred previously (Costa *et al*., 1993). The B biotype colonized a large range of plant species (Cock, 1993), leading to outbreaks of previously undescribed begomovirus diseases in the Americas (Brown, 2001; Brown *et al*., 1995; Morales, this volume, pp. 127–162).

It has been recognised for many years in Africa that genetically distinct populations of *B. tabaci* occur and colonize different crops. Burban *et al*. (1992) in the Ivory Coast, used isozyme-based diagnostic tools to demonstrate the occurrence of a cassava-associated biotype of *B. tabaci* that was more or less restricted to that crop. In Uganda, a similar approach was used by Legg *et al*. (1994) to detect polymorphisms amongst cassava-associated whitefly populations from different locations along a CMD epidemic transect using esterase profiles. However, the high degree of genetic variability in the whiteflies precluded the identification of distinct genotypic groups. Further studies of *B. tabaci* collected from cassava in pandemic-affected parts of Uganda have provided definitive evidence on several key questions. It was shown that *B. tabaci* collected from pandemic-affected regions mated readily and produced fertile offspring with *B. tabaci* collected from cassava elsewhere in Africa (Maruthi *et al*., 2001). By contrast, mating was not successful with *B. tabaci* collected on sweet potato, even where these populations were sympatric (Maruthi *et al*., 2004b). Similarly, mating was unsuccessful with *B. tabaci* originating from cassava in India. Furthermore, studies of the transmission of different African CMGs (ACMV and EACMV-UG) by cassava *B. tabaci* populations collected from different parts of Africa revealed relatively minor and insignificant differences (Maruthi *et al*., 2002). However, none of these findings helps to explain the marked increases in *B. tabaci* abundance associated with the pandemic.

Two general hypotheses have been proposed for the change in *B. tabaci* populations in pandemic-affected areas. The first is that

changes in the chemical composition of CMD-infected plants lead to increased populations of whiteflies colonizing them, resulting in more rapid reproduction and a general increase in populations (Colvin *et al.* 2004, this volume, pp. 419–452). Evidence has been adduced for behavioural changes in *B. tabaci* populations on CMD-diseased versus healthy plants (Omongo, 2003), but there is as yet no definitive proof of a causal link between CMD and increased whitefly fitness. This proposal is further confounded by the fact that some of the highest populations of *B. tabaci* are recorded on CMD-free resistant varieties, as observed commonly throughout the pandemic-affected zone. A second hypothesis to explain *B. tabaci* super-abundance is the appearance of a genetically distinct and fitter cassava biotype in pandemic-affected areas. An extension of this view is that the pandemic could be a consequence of the spread of a 'new' fitter *B. tabaci* biotype and that the recombinant virus, EACMV-UG, is simply a fortunate beneficiary. Accordingly, studies were conducted to investigate the genetic variability of *B. tabaci* on cassava in Uganda using the mitochondrial cytochrome oxidase I (mtCOI) marker (Legg *et al.*, 2002). Two genotype clusters were detected along each of three sampling transects that ran north–south across the epidemic 'front'. The clusters were designated Uganda 1 (Ug1) and Uganda 2 (Ug2), and diverged by *c.* 8% (Legg *et al.*, 2002). At the time that Ugandan populations were sampled in 1997, the Ug2 genotypes, which were shown by mismatch analyses to have the characteristics of an 'invasive' population, were associated with the CMD epidemic. The Ug1 genotypes, a non-invasive population that was considered to be indigenous, occurred primarily 'at' and 'ahead' of the epidemic 'front' (Legg *et al.*, 2002). Subsequent observations in 2002 (Sseruwagi, 2005) made after the expansion of the CMD epidemic to all Ugandan cassava-growing areas (Sseruwagi *et al.*, 2004b), confirmed the occurrence of both Ug1 and Ug2 on cassava in the country. Although there had been a distinct epidemic-associated distribution of whitefly genotypes in 1997, this pattern had been lost in 2002, as the two types were more or less randomly distributed with Ug1 predominating, as it made up 83% of the population. The reasons for and mechanisms behind this change remain unclear, although it is recognised that these genotype clusters can interbreed and it is also known that endosymbiotic bacteria can have important effects on *B. tabaci* biology (Zhori-Fein and Brown, 2002), including influencing the pattern of mating success (De Barro, 2005; De Barro and Hart, 2000).

Results indicate that *B. tabaci* genotypes carrying the Ug1 MtCO1 marker now predominate in much of the pandemic-affected zone of East and Central Africa (Legg, J., unpublished data) and retain the

super-abundant 'invasive' characteristic wherever they occur throughout this region. This population is less readily distinguished from neighbouring populations in areas yet to be affected by the pandemic, as Ug1 is closely related to southern African genotypes (Legg *et al*., 2002). However, an important feature retained is the very narrow within-population variability. Collections of *B. tabaci* adults from diverse pandemic-affected locations of Burundi revealed them to be clonal with respect to MtCO1 (Legg, J., unpublished data). Even though genetic uniformity is a consistent feature of super-abundant *B. tabaci* in the pandemic zone, it is difficult to 'track' whitefly genotypes using molecular markers in view of the ready mating and genetic exchange that occurs between populations. This could either be the result of the epidemic-like transfer of a gene or group of genes conferring super-abundance or the consequence of CMD-infected host-plant synergy, or both. Further studies are required to determine which situation pertains.

In view of the major change in the status of *B. tabaci*, control options targeted directly at this whitefly species have become much more important than earlier when populations were relatively low. In Latin America, sources of resistance have been identified against the whitefly, *Aleurotrachelus socialis* (Bellotti and Arias, 2001), which causes direct damage to cassava. Efforts are underway both to test the effectiveness of these resistance sources to African *B. tabaci* and also to introduce wild cassava relatives that may provide new resistance sources. Furthermore, the variability apparent in responses of African cassava germplasm to physical attack from *B. tabaci* suggests that these materials may also have sources of resistance that could be exploited through breeding.

There is also considerable interest in the potential for augmenting existing biological control as a means of reducing *B. tabaci* populations on cassava. A substantial body of knowledge has been generated on the major groups of natural enemies of whiteflies on cassava (Fishpool and Burban, 1994; Legg *et al*., 2003; Otim *et al*., 2004, 2006) and some of the work is examining the behaviour of these groups in order to identify potential interventions that could lead to enhanced natural enemy activity and, therefore, improved whitefly control (Otim, M., and Asiimwe, P., personal communication). Given the abundance of *B. tabaci* populations in pandemic-affected areas, no single whitefly control tactic is likely to be effective in providing sustained reductions in population sizes. This highlights the need for an integrated pest management (IPM) approach to address this dual pest-virus vector problem, which should also complement existing virus control strategies.

The deployment of IPM-oriented approaches is currently being promoted through a multi-institutional project targeting whitefly and whitefly-transmitted virus 'hotspots' in Latin America, Africa and Asia and known as the 'Tropical Whitefly IPM Project' (Anderson, 2005; Anderson and Morales, 2005). The primary focus of this project in Africa is the use of IPM to manage whitefly and CMD (Legg, 2005).

B. Cassava Brown Streak Disease

The only virus of economic importance to cassava production in Africa, other than the CMGs, is *Cassava brown streak virus* (CBSV). This RNA *Ipomovirus* causes a disease of cassava that has been known for many years, having first been described from northeastern Tanzania (Storey, 1936). The most economically important symptom of cassava brown streak disease (CBSD) is a corky brown necrotic rot in tuberous roots (Hillocks *et al*., 1996; Nichols, 1950) (Fig. 1). Surveys conducted in the last decade have confirmed earlier observations that CBSD was largely restricted to coastal East Africa (Tanzania, Kenya, Mozambique) and Malawi (Hillocks *et al*., 1999, 2002; Legg and Raya, 1998) and that the disease did not spread at altitudes of above *c*. 1000 m a.s.l. (Hillocks *et al*., 1999). While the disease causes serious yield loss (Hillocks *et al*., 2001), there was no evidence of the kind of expansion in geographical range that has been such a feature of the current CMD pandemic.

CBSD was first recorded from central Uganda (above 1000 m a.s.l.) in 1935 (Jameson, 1964), but was apparently eradicated through a vigorous phytosanitation campaign and not subsequently observed until 1994 when mild infections at a single location near to Entebbe were reported (Thresh *et al*., 1994a). In the second half of 2004, however, the first informal reports were made of the widespread occurrence of CBSD-like symptoms in Uganda (Alicai, T., unpublished data). Subsequent laboratory tests confirmed the diagnoses. Significantly, symptoms were most apparent in CMD-resistant varieties of the TME group. Worst affected were TME 204, in which both leaf and root symptoms were seen (Fig. 1), and TME 14, but many other CMD-resistant varieties were also affected to lesser degrees and also some local CMD-susceptible cultivars. Extensive surveys through south-central Uganda showed the problem to be widespread, although largely confined to a few improved varieties. Nevertheless, it was considered that infection was spread over too great an area for a zero-tolerance eradication programme to be feasible. The first major consequence of this development is that it seems that CBSD has become established in

Uganda, and will require routine but sustained management, a situation that is complicated by the fact that even in coastal East Africa, effective and stable sources of host-plant resistance have still to be identified. Of greater concern is the increased potential for the wider regional spread of CBSD throughout the mid-altitude cassava-growing areas of East and Central Africa. Research is required to explain how the apparent altitudinal 'ceiling' of 1000 m a.s.l. for CBSD spread has been broken and to determine the implications for possible future spread throughout the extensive mid-altitude (800–1500 m a.s.l.) cassava-growing zones of the region. There is no evidence to suggest any positive interaction with the pandemic-associated EACMV-UG. Although newly introduced CMD-resistant yet CBSD-susceptible germplasm, may in part, have led to the spread of CBSD in Uganda, a much more plausible cause for increased spread would seem to be the increased abundance of the whitefly vector. Transmission studies have confirmed that *B. tabaci*, vector of the CMGs, also transmits CBSV (Maruthi *et al.*, 2005), although the transmission characteristics have yet to be fully determined. The co-occurrence of super-abundant *B. tabaci* populations, CBSV and EACMV-UG, raises the alarming possibility of a 'dual pandemic', although many research questions will need to be addressed before the likelihood of such a development is known.

VI. Conclusions

Although CMD has been an important constraint to cassava production in Africa for more than a century, changes in the nature of the disease during the last two decades have led to losses on a hitherto unprecedented scale. Strategic epidemiological studies which have traced the development and spread of what is now known as the African CMD pandemic have provided vital insights into the mechanisms and pattern through which this disease is spread and the critical interactions with its whitefly vector, *B. tabaci*. Based on this new knowledge, an effective and wide-ranging management programme has been implemented utilizing each of the principal virus management tools, although the primary focus has been on the deployment of host-plant resistance. Substantial impact has been achieved in areas where management programmes have run for several years. The best example of this is Uganda, where more than a third of the cassava crop is under CMD-resistant varieties (Sserubombwe *et al.*, 2005a). Many challenges remain, however. The first relates to the scale of the

problem. Although effective management programmes are running, including innovative 'pre-emptive' control initiatives, the scale of the problem dwarfs the current level of control interventions, and the best current estimate of the affected area exceeds 2.6 million sq km. Of this total, less than a tenth, currently, has adequate control programmes in place (Uganda and western Kenya). In order to improve the management effort significantly, existing programmes must be maintained and expanded, and major programmes are required in more recently affected regions and countries. Particular attention should be given to Central African Republic, Angola and Gabon, where there is currently minimal preparedness for the impact of the pandemic and much needs to be done, if serious losses are to be avoided. A further challenge is the sustained change in abundance of the whitefly, *B. tabaci*, which vectors both CMGs and CBSV. Resurgence of CBSD in Uganda is of considerable concern, raising the possibility of a dual-pandemic throughout the region. The increased interest in controlling *B. tabaci* through both host-plant resistance and biological control is encouraging, but much needs to be done before effective whitefly-management strategies are available for widespread dissemination to pandemic-affected farming communities.

Although the huge scale and continued spread of the African CMD pandemic make it one of the greatest pest/disease challenges now facing agricultural researchers globally, there is considerable hope for successful mitigation. Heightened awareness is leading to increased support from development investors for control programmes. Moreover, experience obtained by multi-stakeholder teams over the past decade has led to the establishment of strong regional networks of personnel active in CMD management. Nevertheless, the CMD pandemic will have a significant negative impact on the continent's cassava production for the foreseeable future. Concerted efforts will be required by researchers, extensionists, farmers and those supporting these groups to ensure that the scale of this impact is minimized, and that in future years CMD reverts to the status of being largely benign. The capacity that the CMGs have demonstrated to 'use' true recombination to exploit new opportunities for spread suggests that elimination is an unrealistic objective, and ambition should, therefore, be restricted to restoring the apparent equilibrium that for long periods seems to have characterized the more than century-old relationship between cassava and CMGs. If this is achieved, it will represent a real success in overcoming what is one of the most pernicious of all crop diseases.

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