REVIEW ARTICLE

Strategies for controlling cassava mosaic virus disease in Africa

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Cassava mosaic disease (CMD) is caused by whiteflyborne viruses of the genus *Begomovirus* (family *Geminiviridae*). The disease has long been regarded as the most important of those affecting cassava in sub-Saharan Africa, and has been the subject of much research, especially since the onset of the current very damaging pandemic in eastern and central Africa. This review considers the main features of CMD and the various possible means of control. The main emphasis to date has been on the development and deployment of virus-resistant varieties. These are widely adopted in countries where CMD has caused serious problems, and provided a powerful incentive for farmers to abandon some of the most susceptible of their traditional varieties. Only limited use has been made of phytosanitation involving CMD-free planting material and the removal (roguing) of diseased plants. Cultural methods of control using varietal mixtures, intercrops or other cropping practices have also been neglected, and there is a need for much additional research before they can be deployed effectively. Nevertheless, the severe losses now being caused by CMD in many parts of sub-Saharan Africa could be greatly decreased through the application of existing knowledge.

Keywords: begomovirus, *Bemisia tabaci*, cassava, cultural control, insecticides, *Manihot esculenta*, mild-strain protection, phytosanitation, resistant varieties, whitefly vector

Introduction

Cassava (*Manihot esculenta*) is a major staple food crop in many parts of the tropics. It is particularly important in sub-Saharan Africa, which currently accounts for *c.* 54% of total world production (FAO, 2004). Important attributes of cassava are that it can be grown in a wide range of environments and withstands long periods of drought. Another feature of the crop is that growth is indeterminate and the tuberous roots can be left in the ground for many months until required for consumption or processing. Moreover, cassava is not dependent on fertile soils and will produce at least some yield, even in very unfavourable conditions where it can play a key role in food security.

Cassava can be expected to become even more important as human populations and pressure on the available land continue to increase and soil fertility declines (Cockcroft, 2004). However, the productivity of cassava in sub-Saharan Africa is generally low, in part due to the deleterious effects of pests and diseases. Cassava brown streak virus disease in coastal areas of eastern and southern Africa and cassava mosaic virus disease in all regions, are two of the most important biotic constraints and greatly decrease yields (Calvert & Thresh, 2002).

Cassava mosaic disease (CMD) is prevalent in many parts of Africa, India and Sri Lanka, and causes serious losses (Geddes, 1990; Calvert & Thresh, 2002; Sseruwagi *et al*., 2004). The geminiviruses responsible and their whitefly vector (*Bemisia tabaci*) have been studied extensively and much attention has been given to possible control measures and their deployment. This review summarizes the main features of CMD and considers the various control strategies that have been, or could be, adopted in Africa and the opportunities for their use on a large scale. Substantial additions and changes have been necessary since the previous assessment completed in 1993 (Thresh & Otim-Nape, 1994). It is notable that 127 of the 210 papers on cassava cited in this review have been published since 1993, whereas only 39 were published during the previous decade. This reflects the greatly increased research and extension activities in recent years, which have been largely a direct consequence of the 1990s epidemic of CMD in Uganda that has spread to other countries of eastern and central

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Africa and become a regional pandemic (Otim-Nape & Thresh, 1998; Legg, 1999; Otim-Nape *et al*., 2000; Legg & Thresh, 2000, 2004).

Cassava mosaic disease

History

The symptoms of CMD were first reported more than 100 years ago in what is now Tanzania (Warburg, 1894). The disease was later identified during the early decades of the 20th century in many other countries of sub-Saharan Africa (Fauquet & Fargette 1990). At the time it was particularly prevalent in Gold Coast (now Ghana), Nigeria, Cameroon, Madagascar and several of the former French and Belgian colonial territories of West and Central Africa. This led to studies on the means of spread and control. It also became apparent that some of the varieties of cassava being grown were less affected than others by CMD, and resistance breeding programmes began in the 1930s or 1940s in Ghana, Madagascar, Tanzania and elsewhere.

In recent decades there have been major projects on the aetiology, epidemiology and control of CMD in Nigeria, Kenya, Ivory Coast and, most recently, Uganda (Thresh *et al*., 1994b). Studies in Uganda followed the first reports of a particularly damaging epidemic there in the late 1980s (Thresh *et al*., 1994c; Otim-Nape & Thresh, 1998), the latest and most fully documented of those to have affected cassava in Africa at different times and places during the 20th century. This explains why CMD has featured so prominently, and for so long, in the literature on cassava. Indeed, CMD had received more attention than any other disease of an African food crop, even before the greatly increased research effort on the disease in recent years (Thresh, 1991; Legg & Thresh, 2004).

Symptoms

CMD causes characteristic leaf symptoms (Fig. 1a) that can usually be recognized without difficulty by farmers and extensionists after basic training by pathologists. The symptoms are very variable in type, extent and severity, but it is convenient to make a broad distinction between 'green mosaic' and 'yellow mosaic' (Storey & Nichols, 1938a). Plants affected by 'green mosaic' have leaves with contrasting sectors of dark and light green tissue. These symptoms are apparent only when diseased plants are examined closely and are not usually associated with an obvious decrease in leaf area, leaf number, plant size, or yield of tuberous roots. Plants affected by 'yellow mosaic' are much more conspicuous, as they have leaves with contrasting areas of normal green and yellow tissue. Moreover, the chlorotic areas may expand less than other parts of the leaf lamina, which can lead to distortion of the leaflets and rupturing of the tissues. Severe chlorosis is often associated with premature leaf abscission, a characteristic S-shaped curvature of the petioles of the remaining leaves and an obvious decrease in vegetative growth and yield of tuberous roots (Cours, 1951). The most severely affected plants are so stunted that they produce virtually no yield of roots or stems for further propagation.

Cassava is usually grown from stem cuttings and those collected from CMD-infected plants usually develop shoots that express symptoms from the outset. In contrast, plants infected by the viruliferous whitefly vector develop symptoms later and the earliest leaves are symptomless (Fig. 1a). Consequently, close inspection during the early months of growth and before the earliest leaves abscise will usually reveal which plants were infected as cuttings. This information is important in epidemiology and has been obtained in the most recent surveys, as discussed by Sseruwagi *et al*. (2004).

CMD-resistant varieties express much less severe symptoms than susceptible ones (Fig. 1b), especially during the late stages of crop growth, when resistant varieties may become virtually symptomless (Jennings, 1957). Symptom expression is also influenced by environmental factors and leaves produced during periods of cool weather tend to be affected more than those produced under hotter conditions (Gibson, 1994). Symptoms are also enhanced when plants regenerate after being cut back to stimulate shoot development (Verhoyen, 1979), by grazing animals, or when detopped (Childs, 1957) to provide leaves for consumption (Lutaladio & Ezumah, 1981; Ariyo *et al*., 2003). Moreover, some strains of virus cause more severe symptoms than others and have greater effects on growth and yield (Owor *et al*., 2002, 2004).

There is no evidence for consistent differences between the symptoms caused by the different cassava mosaic geminiviruses (CMGs) that have been distinguished thus far. Each of these viruses can occur as severe or less severe strains. However, dual infection with two different CMGs causes more severe symptoms than either virus alone, as reported by studies in Uganda and Cameroon (Harrison *et al*., 1997; Fondong *et al*., 2000a; Pita *et al*., 2001). The main difficulties that arise in recognizing CMD symptoms occur when the leaves of plants being examined are affected by arthropod pests or nutrient deficiency. The cassava green mite (*Mononychellus tanajoa*) and zinc deficiency (Asher *et al*., 1980) cause particular problems in diagnosis. However, the damage they cause is usually similar on the different leaflets of each affected leaf, whereas CMD has less uniform effects and the two halves of a leaflet on either side of the midrib are often affected differently. This asymmetry is an important distinguishing feature of CMD that should be stressed when training staff and farmers in disease recognition. However, severely damaged or poorly growing plants cannot be examined effectively for virus symptoms and whenever possible inspections for CMD should be made when plants are growing vigorously and unaffected by drought, pests or nutrient deficiency.

In recording experiments and in screening for resistance to CMD, much use has been made of simple numerical scoring systems based on the extent and severity of the symptoms expressed. Following the pioneering work of Cours (1951) and Dulong (1971) in Madagascar, scales of 0 or 1 (symptomless) to 4 or 5 (most severe symptoms)

Figure 1 Cassava mosaic disease. (a) Severely affected cassava grown from a healthy cutting and subsequently infected during growth by viruliferous whiteflies; (b) landraces of cassava, susceptible (left) and resistant (right) when exposed to infection by CMGs; (c) severe CMD in an initially healthy planting of cassava during the 1997 epidemic in Uganda; (d) an abandoned planting of cassava established with cuttings from plants infected in the previous year.

have been used widely to quantify differences in symptom expression due to host genotype, season, stage of crop growth and virus strain, and in assessing the relationship between symptom severity and yield loss (Terry & Hahn, 1980; Muimba-Kankolongo & Phuti, 1987; Fauquet & Fargette, 1990). Such scales have been used to categorize individual leaves or whole plants and, less satisfactorily, for whole plots in field trials and resistance screening.

A recurring problem in handling data on symptom severity has been the treatment of scores for symptomless plants. In many publications these are included when calculating 'mean symptom severity', which has the effect of decreasing severity scores according to the proportion of symptomless plants. For this reason it has been argued that there should be a clear distinction between *disease incidence* (percentage or proportion of plants affected) and *disease severity* based solely on the scores of plants with symptoms (Sseruwagi *et al*., 2004).

Distribution and prevalence

CMD occurs in all the cassava-growing areas of Africa and on the adjacent islands, including Cape Verde in the Atlantic Ocean to the west and Zanzibar, Seychelles, Mauritius and Madagascar in the Indian Ocean to the east. The disease also occurs in Sri Lanka and southern India, but it has not been confirmed elsewhere in Asia, or in the Americas (Calvert & Thresh, 2002). There are big differences between African countries in the date when CMD was first reported (Fauquet & Fargette, 1990). This is partly related to the importance of cassava in the different regions, which has influenced the amount of attention given to the crop by plant pathologists.

In many African countries there is general agreement that CMD is the most important disease of cassava (Geddes, 1990), although in some areas it is regarded as less damaging than cassava bacterial blight caused by *Xanthomonas axonopodis* pv. *manihotis* or cassava brown streak virus disease. Until recently there were few data to support these assumptions. The situation changed in the 1990s, and the incidence and severity of CMD have been assessed on one or more occasions in representative plantings in 18 important cassava-growing countries of Africa (Table 1). Such surveys are expensive and time-consuming, and inevitably the number of plantings sampled has been small in relation to the total amount of cassava grown. Nevertheless, surveys were undertaken in Uganda following the onset of the recent epidemic (Fig. 1c,d) (Otim-Nape *et al*., 1998b) and subsequently in 17 other countries to monitor the progress of the 1990s pandemic, or as part of more comprehensive assessments of pest and disease problems of cassava (Sseruwagi *et al*., 2004). The results summarized in Table 1 indicate the prevalence of CMD and the sometimes large differences that occur between and within particular countries.

The overall incidence of CMD exceeded 50% in 11 of the 18 countries surveyed, including the three leading producers: Democratic Republic of Congo (DCR), Nigeria and Ghana, which collectively account for *c*. 57% of total production in Africa (FAO, 2004). The incidence of infection also exceeded 50% in Benin, Cameroon and Uganda and in some parts of Malawi and Tanzania, and currently the situation is known to be deteriorating in Tanzania, Rwanda and Burundi due to the continued progress of the very damaging pandemic in the region. These results emphasize the current prevalence of CMD and the need for effective control.

Based on the survey results, three contrasting situations have been distinguished, referred to as 'epidemic', 'endemic' and 'benign' (Thresh *et al*., 1997). In epidemic areas CMD is being spread rapidly by the whitefly vector (*B. tabaci*) and the symptoms of the disease are usually prevalent and severe. Farmers experience such serious losses that food security is threatened, and it may be necessary to switch at least temporarily from cassava to sweet potato or other alternative staple food crops. Remedial measures are essential if cassava production is to be restored and there is an urgent need for the increased use of CMD-resistant varieties, as developed and supplied through official programmes, or selected by farmers from those already available and being grown. The epidemic situation, as encountered in the 1990s in much of Uganda, spread to adjacent areas of western Kenya and north-west Tanzania and later into Rwanda and Burundi (Legg & Thresh, 2000; Otim-Nape *et al*., 2000; Legg *et al*., 2001; Bigirimana *et al*., 2004; Sseruwagi *et al*., 2005). Similarly, unstable epidemic situations were encountered previously in the 1930s in Madagascar (Cours *et al*., 1997) and later in the Cape Verde Islands (Anonymous, 1992) and Akwa Ibom State of Nigeria (Anonymous, 1993).

In endemic areas there is a generally high incidence of CMD, but the symptoms are not usually very severe. The overall disease situation is stable and changes little from year to year. Infected stem cuttings are used extensively as planting material and crop yields are undoubtedly impaired. Nevertheless, the losses have seldom been quantified and are either largely ignored by farmers or considered acceptable. Control measures are not regarded as essential, although they are likely to bring substantial benefits. This is the situation in much of Ivory Coast, Ghana, Nigeria and the lowland forest areas of Cameroon, and may extend into other areas of West and Central Africa.

Where CMD is benign, incidence is generally low and seldom exceeds 25%. Infection is mainly due to the use of infected cuttings, and there is little or no evidence of spread by whiteflies. Symptoms are usually inconspicuous and are not associated with obvious deleterious effects on plant growth or root yield. Losses are not substantial, control measures are not considered necessary and even if implemented would bring little or no immediate benefit. This was formerly the situation in much of Uganda, Rwanda, Burundi and western Kenya and is encountered currently in parts of coastal Kenya and large areas of Tanzania and Mozambique, and also in the mid-altitude agroecologies of Nigeria, Malawi, South Africa and parts of Zambia.

There is an urgent need for additional information on the current incidence and severity of CMD in the pandemic-affected areas and in the DCR and other countries of Central Africa where the disease is known to be prevalent and appears to be causing increasing problems (Neuenschwander *et al*., 2002; Legg *et al*., 2004). Information is also required on other important cassava-growing areas of sub-Saharan Africa not yet assessed, including Sierra Leone, Liberia, southern Sudan and Angola. It will then be possible to identify the areas that should receive priority in any attempts at control. Meanwhile, it should be appreciated that the situation can change dramatically and within only a few years. This is apparent from early experience in Madagascar and elsewhere (Cours *et al*., 1997). More recently, in Uganda and neighbouring countries the situation changed rapidly from benign to epidemic, and is now changing to endemic as the original equilibrium that occurred between host and disease is being restored (Otim-Nape *et al*., 2000).

Aetiology

For many years CMD was assumed to be caused by a virus because the disease was transmissible by grafts and by the whitefly now known as *B. tabaci*. However, no visible pathogen was detected in infected plants. The situation changed in the 1970s when a virus was transmitted mechanically by sap inoculations with extracts from the leaves of CMD-affected cassava to the herbaceous test plant *Nicotiana clevelandii* (Bock, 1975). The status of the virus isolated was unclear at first because it was not detected in CMD-affected cassava sampled in coastal Kenya (Bock *et al*., 1978). Hence the virus was initially referred to as cassava latent and this name continues to

Table 1 Summary of surveys of the incidence of cassava mosaic disease in 18 African countries

Country	Regions	Year	Reference/s	No. sites	CMD inc. (%)
Benin	Countrywide	1994	Yaninek *et al.* (1994); Wydra & Msikita (1998)	31	53
	Transition forest, wet and dry savannah	1997/98	B. Gbaguidi *et al.*, unpublished	60	39
Cameroon	Countrywide	1994	Yaninek *et al.* (1994); Wydra & Msikita (1998)	61	67
	South-west, north-west and centre-south	1997/98	N. Ntonifor *et al.*, unpublished	70	61
Congo Rep.	–	2002	P. Ntawuruhunga, unpublished	105	79
DRC	Nine regions	2002/03	INERA/IITA, unpublished	236	60
Chad	–	1992	Johnson (1992)	48	40
Ghana	Countrywide	1994	Yaninek *et al.* (1994); Wydra & Msikita (1998)	40	72
	Countrywide	1997/98	A. Cudjoe *et al.*, unpublished	80	72
Guinea	Countrywide	2003	G. Okao-Okuja, unpublished	60	62
Kenya	Western and Nyanza	1993	Legg (1999)	13	20
	Western and Nyanza	1996–98	Legg (1999)	112	56–84
	Southern Nyanza	1998	Legg (1999)	15	5
	Coast, Western and Nyanza	1998	J. Kamau *et al.*, unpublished	50	51
	Coastal	2000	Munga & Thresh (2002)	29	60
Madagascar	Countrywide	1998	S. Ranomenjanahary *et al.*, unpublished	111	47
Malawi	Countrywide	1993	Nyirenda *et al.* (1993)	450	21
	Three regions	1994	Sweetmore (1994)	34	17
	Central and Northern Lakeshore, Central	1997/98	M. Theu *et al.*, unpublished	41	42
Mozambique	Two provinces	1999–2002	Thresh & Hillocks (2003)	377	40
Nigeria	Countrywide	1994	L.C. Dempster, unpublished	93	55
	Countrywide	1994	Yaninek *et al.* (1994); Wydra & Msikita (1998)	111	82
	Four regions	1997/98	T. Echendu *et al.*, unpublished	80	54
Rwanda	Five regions	2000	Legg *et al.* (2001)	26	26
	Countrywide	2001	P. Sseruwagi, unpublished	120	30
Senegal	Western	2003	G. Okao-Okuja, unpublished	20	83
South Africa	Three regions	1998	Jericho *et al.* (1999)	20	31
Tanzania	Countrywide	1993/94	Legg & Raya (1998)	242	27
	Lake Victoria Zone	1998 (Jan)	Legg (1999); Legg *et al.* (1999)	35	35
	Zanzibar	1998	Thresh & Mbwana (1998)	13	71
	Lake Victoria Zone, Mtwara and Tanga	1998 (May)	J. Ndunguru *et al.*, unpublished	60	34
	Eight regions	1998 (Jun)	Legg (1999)	60	21
	Lake Victoria Zone	1999 (Jul)	J. Ndunguru *et al.*, unpublished	89	72
	Kagera region	1999	Legg (1999)	19	65
Uganda	28 districts	1990–2002	Otim-Nape *et al.* (1998b)	1350	57
	27 districts	1994	Otim-Nape *et al.* (2001)	1215	65
	12 districts	1997/98	Legg *et al.* (1999)	80	68
	Five districts	1997/98	IITA/NARO, unpublished	450	75
	Masaka and Rakai	1998	IITA/NARO, unpublished	90	67
	Six districts	1999–2001	IITA/NARO, unpublished	810	74
	21 districts	2003	Bua *et al.* (2005)	1007	46
Zambia	Countrywide	1996/97	Muimba *et al.* (1997, 1999)	62	45

appear occasionally in the literature. However, the name became inappropriate when an additional test plant species (*Nicotiana benthamiana*) was used to detect and distinguish between different virus isolates that caused typical symptoms of CMD when inoculated to cassava (Bock & Woods, 1983). The different isolates were initially referred to as strains of African cassava mosaic virus (*sensu lato*), and three groups or 'clusters' of strains were distinguished serologically (Bock & Harrison, 1985). These were later regarded as constituting three separate viruses (Hong *et al*., 1993; Swanson & Harrison, 1994) which are now ascribed to the genus *Begomovirus*, family *Geminiviridae* (Fauquet & Stanley, 2003). Two of these viruses [*African cassava mosaic virus* (ACMV) and *East African cassava mosaic virus* (EACMV)] have not been found outside Africa, whereas the third [(*Indian cassava mosaic virus*, (ICMV))] appears to be restricted to the Indian subcontinent.

From the results of serological tests using a panel of monoclonal antibodies, ACMV and EACMV were considered originally to have distinct and largely nonoverlapping distributions in Africa (Swanson & Harrison, 1994). However, subsequent studies revealed a more complex situation. EACMV was at first assumed to be restricted to coastal East Africa, Malawi and Madagascar, whereas it has since been detected elsewhere in western districts of Kenya and Tanzania and also in parts of Zambia, Ghana, Nigeria and Cameroon, where previously only ACMV had been reported (Ogbe *et al*., 1996, 1997, 1999; Fondong *et al*., 1998; Offei *et al*., 1999). Additional CMGs have also been detected in South Africa (Berrie *et al*., 1998), Zanzibar (Maruthi *et al*., 2002a), elsewhere in East Africa (Fauquet & Stanley, 2003; Were *et al*., 2004) and Sri Lanka (Saunders *et al*., 2002). Moreover, what is considered to be a hybrid recombinant virus has been distinguished in Uganda, Tanzania, southern Sudan, Cameroon, DCR and elsewhere in Africa. It has some of the genomic properties of both ACMV and EACMV (Deng *et al*., 1997; Harrison *et al*., 1997; Zhou *et al*., 1997; Berry & Rey, 2001; Neuenschwander *et al*., 2002; Legg & Fauquet, 2004) and has been designated EACMV-UG.

The strain of EACMV-UG that occurred at the height of the epidemic in Uganda was particularly damaging, especially when present together with ACMV, which was the only CMG reported in the country before the epidemic. EACMV-UG is also associated with the pandemic affecting other countries of the region and is regarded as the main cause of the problem. However, the occurrence of EACMV-UG does not explain the large increase in vector populations which is another feature of the pandemic.

The full biological and epidemiological significance of the great diversity in biochemical properties of the different CMGs that is now apparent in Africa and the Indian subcontinent has not been determined and requires further study. Nevertheless, there is already evidence that dual infection with the hybrid recombinant virus and ACMV, or with EACMV and ACMV, is more damaging than either virus of the pair occurring alone (Harrison *et al*., 1997; Fondong *et al*., 2000a; Pita *et al*., 2001). Moreover, the occurrence of different viruses or virus combinations in different regions could complicate and may even undermine the effectiveness of resistance breeding programmes, quarantine controls on the movement of cassava material between different parts of Africa and Asia, and any attempts to exploit mild-strain protection. Until these issues are resolved it is important to avoid moving infected cassava plants or vegetative propagules between different countries or regions and especially from areas affected by a severe form of CMD. It is particularly important to avoid the transfer of CMGs by transporting plant material from Africa to the Indian subcontinent or *vice versa* and from these regions to the Neotropics.

Effects on growth and yield

There is an extensive literature on the effects of CMD on the growth and yield of cassava. Data have been collected at different times and places on a wide range of cassava cultivars using two main approaches (Thresh *et al*., 1994a). Comparisons have been made in formal experiments established with cuttings collected from CMD-affected and unaffected plants. Moreover, naturally infected and uninfected plants have been identified and assessed within larger plantings at experimental stations or in farmers' fields.

Some of the main findings are as follows. (i) Cassava varieties differ greatly in their response to CMD. Some are severely stunted and produce little or no yield of foliage, stem cuttings or tuberous roots, whereas other varieties are relatively unaffected and sustain little or no damage. (ii) There is a general relationship between symptom severity and the decrease in vegetative growth and yield of tuberous roots caused by CMD (Cours, 1951). (iii) Plants grown from CMD-infected cuttings are more severely affected than those of the same variety infected at an early stage of crop growth by whitefly; plants infected late sustain little or no damage (Fargette *et al*., 1988). (iv) Competition and compensation effects can occur within stands of cassava. Both CMD-affected and unaffected plants grow and yield more alongside diseased neighbours than alongside unaffected ones (Otim-Nape *et al*., 1997b). Consequently, differences between the growth and yield of healthy and diseased plants are less when comparisons are made between healthy and diseased plants each having neighbours of similar health status, than between plants each having neighbours of dissimilar status. (v) Some virus strains or strain combinations cause more severe symptoms and decrease growth and yield more than others. (vi) CMD affects the performance and sustainability of varieties by influencing the number, viability and growth of stem cuttings available for vegetative propagation. (vii) The identity of the CMG(s) present in CMD-affected plants has been determined in only the most recent crop-loss studies (Owor, 2003; Owor *et al*., 2002, 2004), and additional information is required on the effects of specific virus strains when present alone and in different combinations.

Overall crop loss

The results of yield comparisons have been used to estimate the overall losses caused by CMD in localities, regions or countries. However, for definitive estimates to be made detailed information is required, not only on the incidence and severity of the disease in different areas, but also on the prevalence, type, productivity and sensitivity to infection of the main varieties being grown. Such details are not available, so published estimates of yield loss provide only a general indication of the damage sustained.

Watts Padwick (1956) used information from regional plant pathologists to estimate the losses caused by CMD in the former British Colonial territories of Africa. He concluded that total production at the time was 12% less than would have been achieved in the absence of the disease. Fargette *et al*. (1988) later estimated the annual losses in Ivory Coast to be 500 000 tonnes, compared with actual production at the time of 800 000 tonnes. They assumed that all plants in the country were affected and sustained losses in tuberous root yield of 38%, as recorded in their experiments with one of the main Ivorian varieties. On similar assumptions, losses in Africa were estimated to be 30 million metric tonnes (Mt), compared with actual production at the time of 51 Mt (FAO, 1985).

It then became apparent that these assumptions were inappropriate because CMD is less prevalent than had been assumed and incidence is moderate or low in some important cassava-growing areas of Africa (Table 1). Moreover, some widely grown varieties are much less severely affected than the variety assessed in Ivory Coast. These considerations led Thresh *et al.* (1997) to estimate total losses in Africa as 12–23 Mt, based on the plausible assumptions of an overall CMD incidence of 50–60% and a loss of 30–40% in the yield of diseased plants. Estimated losses were later revised to 19–27 Mt to take account of the latest survey findings (Legg & Thresh, 2004). This led to the conclusion that CMD is one of the more damaging, if not the most damaging, of plant virus diseases in the world (Legg & Fauquet, 2004).

Estimates have also been made of losses in particular areas, as in Uganda at the height of the 1990s pandemic (Otim-Nape *et al.*, 2000). It was assumed that each year an area equivalent to four whole districts was rendered totally unproductive. This was regarded as being equivalent to a loss of 60 000 ha of cassava, which could have been expected to produce 600 000 t tuberous roots worth US$60 million at a conservative valuation of US$100 t^{-1}. Similarly, losses due to the epidemic in western Kenya were estimated to exceed US$10 million in 1998 alone (Legg, 1999). It is inevitable that losses in the region have since become much greater, as Rwanda, Burundi and additional areas of western Kenya and north-west Tanzania have been severely affected.

Transmission by the whitefly *Bemisia tabaci*

The putative virus assumed to cause CMD in Africa was one of the first pathogens to be transmitted experimentally by whiteflies. Studies began in the 1920s when it became evident that the virus was spreading naturally and that whiteflies were the only sap-sucking insects on cassava that were likely to be vectors. The first successful transmissions were reported from Congo using adults of a species referred to as *Bemisia mosaicivecta* (Ghesquière, 1932), which was later regarded as a misprint for *B. mosaicivectura* (Storey & Nichols, 1938a). The species was also referred to as *B. gossypiperda* var. *mosaicivectura* (Mayné & Ghesquière, 1934). Adults of the same or a closely related species referred to as *B. nigeriensis* were used in successful transmission experiments in Nigeria (Golding, 1936) and later in Tanzania (Storey & Nichols, 1938a), where infection was achieved by transferring infective whiteflies to the youngest leaves and shoots of cassava test plants, but not to older leaves.

Subsequent experiments on the mode of transmission by whiteflies were carried out in Nigeria (Chant, 1958), Ivory Coast (Dubern, 1979, 1994) and Kenya (Seif, 1981), using what seems to have been the whitefly species used earlier, but referred to as *Bemisia tabaci*, as in all subsequent studies. Based on current knowledge it is likely that the transmission experiments in coastal East Africa (Storey & Nichols, 1938a; Seif, 1981) were with EACMV and those in Congo and West Africa were with ACMV (Ghesquière, 1932; Mayné & Ghesquière, 1934; Golding, 1936; Chant, 1958; Dubern, 1979, 1994). There are recent reports of whitefly transmission studies with the Ugandan variant (EACMV-UG) associated with the current pandemic in East Africa (Maruthi *et al.*, 2002b).

The East and West African virus isolates are transmitted in a persistent manner, and the minimum (and optimum) acquisition access, inoculation access and latent periods for successful transmission are 3 h (5 h), 10 min and 3–4 h (6 h), respectively. Virus is retained by adult whitefly for at least 9 days. It persists during moulting, but is not transmitted transovarially (Dubern, 1979, 1994). Nymphs can transmit, although they are not of epidemiological importance because of their immobility. Up to 1·7% of adult whiteflies were shown to be infective when collected in severely diseased fields of cassava in Ivory Coast and transferred to young test seedlings of cassava (Fargette *et al.*, 1990). Infectivities of up to 10% were demonstrated in subsequent trials with whiteflies collected in an epidemic area of southern Uganda (Colvin *et al.*, 2004).

Epidemiology

The whiteflyborne viruses that cause CMD in Africa have not been reported in the neotropics and are assumed to have spread from indigenous African plant species to cassava some time after the crop was first introduced to the continent from South America in the 16th century (Swanson & Harrison, 1994). Several indigenous host species have been identified, including *Jatropha* spp., but it is uncertain whether they are the original host(s) from which CMGs spread to cassava. Wild hosts certainly seem to be of little or no current importance epidemiologically as initial sources of inoculum (Fargette & Thresh, 1994).

Cassava is usually propagated vegetatively from hardwood stem cuttings, and CMD is disseminated widely in infected planting material. Any subsequent spread that occurs is attributed to viruliferous whiteflies moving between or within plantings, having acquired virus from cassava plants grown from infected cuttings or infected by whiteflies during crop growth. This is consistent with the findings of epidemiological trials in Ivory Coast, Kenya and Uganda, that the spread into and within experimental plantings is directly related to the number of adult whiteflies recorded, and also to the incidence of CMD as determined in the locality or administrative district in which the trials were carried out (Legg *et al.*, 1997; Legg & Ogwal, 1998; Otim-Nape *et al.*, 1998a). New plantings are soon colonized by immigrant whiteflies moving from older stands of cassava in the area. The immigrants then reproduce to reach peak populations within a few months, before populations decline and adults disperse to other, younger cassava, as reported by studies in several countries of East and West Africa (Dengel, 1981; Robertson, 1987; Fishpool & Burban, 1994; Legg, 1994; Fishpool *et al.*, 1995).

The distribution of immigrant whiteflies and of plants newly affected by CMD is influenced by the direction of the prevailing wind and by the effects of wind turbulence around and within crop stands. The incidence of whiteflies and CMD tend to be greatest at the field margins, especially along the windward and leeward edges, and environmental gradients have been observed within fields in which both whitefly populations and virus incidence decrease with increasing distance from the perimeter (Fargette & Thresh, 1994; Fargette *et al*., 1985; Colvin *et al*., 1998). Incidence is also increased around breaks or discontinuities in the crop canopy that facilitate the alighting and establishment of viruliferous vectors (Fargette *et al*., 1985, 1993; Fargette & Thresh, 1994).

Possible control measures

There is considerable information on the incidence and severity of CMD and the effects of the disease on growth and yield, but this relates only to some of the many African countries where cassava is grown widely. Nevertheless, there is an overwhelming case for controlling the disease, especially in areas where infection is prevalent and severe. However, an important proviso is that the measures used should be simple, inexpensive, and within the limited capacity of the farmers concerned. The measures should also be sustainable and involve little or no use of pesticides so as to avoid damage to human health, natural enemies or the environment. Effective control measures used on a large scale would increase productivity per unit area and lead to greater production of cassava, or release land and labour for other uses and permit longer periods of fallow to restore soil fertility. These are important benefits, given the need to increase food production to feed the burgeoning human population, and to do so without adverse side effects and despite decreased availability of rural labour as a consequence of urbanization and the ravages of AIDS/HIV (Cockcroft, 2004).

In general terms, there are three possible approaches to decreasing the losses due to a virus disease: (i) decrease the proportion of plants that become infected; (ii) delay infection to such a late stage of crop growth that losses become unimportant; (iii) decrease the severity of damage sustained after infection has occurred. These objectives can be achieved in diverse ways (Thresh, 2003) and the main possibilities for controlling CMD are phytosanitation, disease-resistant varieties, cultural practices, vector control and mild-strain protection.

Phytosanitation

This term is used in a general sense for the various means of improving the health status of cassava planting material and for eliminating sources of inoculum from which further spread of CMD can occur through the activity of the whitefly vector.

There are three main features of phytosanitation for the control of CMD: (i) crop hygiene involving removal of all diseased cassava or other host plants from within and immediately around sites to be used for new plantings; (ii) use of CMD-free stem cuttings as vegetative planting material; (iii) removal (roguing) of diseased plants from within crop stands.

Crop hygiene

This is a basic means of facilitating control of many pests and diseases by removing the debris and surviving plants of previous crops to decrease the risk of carry-over of pests or pathogens to any new plantings at the site or nearby. Little attention has been given to adopting this approach with cassava and CMD, and the benefits to be gained have not been demonstrated. They could be substantial because cassava plants, including those affected by CMD, regenerate readily from stems left in or on the ground at harvest. Moreover, farmers often harvest piecemeal from the most vigorous plants within a stand, then establish new cuttings in the gaps created. Consequently, young plants often develop beneath or immediately alongside older, infected ones that are potential sources of virus inoculum and also of other pathogens and pests including cassava green mite (*M. tanajoa*) and cassava mealybug (*Phenacoccus manihoti*). There is a need to assess the risks involved and devise appropriate management practices to improve the current unsatisfactory situation. This is because the only relevant information on the spread of CMD from foci of inoculum within plantings was obtained in experiments in which the cassava plants introduced as sources of infection were planted at the same time as those being exposed (Bock, 1983; Fargette *et al*., 1990; Otim-Nape, 1993; Byabakama *et al*., 1999).

Information is also lacking on the significance of tree cassava (*Manihot glaziovii*), *Jatropha* spp. and other alternative hosts as sources of inoculum. Infected plants of these species occur quite commonly within or alongside cassava plantings and are sometimes infested with whiteflies. However, the extent to which they contribute to spread to cassava or to the diversity of CMGs is not known and it is unclear whether there are substantial advantages to be gained from their removal.

CMD-free planting material

A basic approach to disease control is to use uninfected propagules for all new plantings. The benefits to be gained with cassava and CMD are considerable because healthy stem cuttings establish more readily and grow more quickly than infected ones. The subsequent yields of initially healthy plants are also substantially greater, even if they are infected during growth by whitefly (Fargette *et al*., 1988; Thresh *et al*., 1994a). Moreover, the use of healthy cuttings together with crop hygiene means that initially there are no foci of infection within or alongside new plantings from which spread can occur. This avoids, or at least delays, the onset of CMD and decreases the period over which spread can occur during the early, most vulnerable stages of crop growth.

The feasibility and effectiveness of sanitation depend on the availability of adequate stocks of CMD-free cuttings of suitable varieties at prices farmers can afford and also on the rapidity with which such material is infected by whitefly. Herein lie the difficulties, as only some farmers have ready access to planting material of improved varieties and even fewer can obtain stocks that are known to be largely or entirely free of CMD. Moreover, even if such stocks become available in quantity there may be problems due to latent infection or subsequent infection by vectors. Latency is not usually a problem, except with resistant genotypes, or if plants have been severely affected by drought or arthropod pests and have shed many of the symptom-bearing leaves. However, unless there is little spread by whiteflies it would be necessary to introduce CMD-free cuttings at prohibitively frequent intervals, or to adopt very stringent selection procedures to ensure that only unaffected plants are used to provide cuttings for further plantings. These are serious limitations and add to the difficulty and expense of developing simple, acceptable and sustainable measures for use by farmers.

There are no technical difficulties in producing basic stocks of cassava that are free of CMD. This has been done simply by careful visual selection from the source plants already available, as in Zanzibar (Tidbury, 1937); what is now the DCR (Opsomer, 1938a, 1938b); Tanzania (Storey, 1936; Childs, 1957); Uganda (Jameson, 1964; Otim-Nape *et al*., 1998a, 2000); Malawi (the late R.F.N. Sauti, unpublished data); Kenya (Bock, 1982, 1988); and Ivory Coast (Fauquet *et al*., 1988a, 1988c). From these and other studies it is apparent that several factors influence the effectiveness of selection based on the absence of the characteristic leaf symptoms of CMD. Moreover, epidemiological factors influence the proportion of cuttings that are latently infected, even when collected solely from symptomless plants. The proportion can be substantial in cuttings taken from symptomless plants of a susceptible variety growing under epidemic conditions, where rapid spread is occurring and many nearby plants are already expressing symptoms. The amount of latent infection is less for resistant varieties and least for cuttings collected from within stands in which there is a low incidence of infection and little or no spread by vectors.

The importance of these factors was evident from experience in Uganda in the 1990s. Initially, stocks of healthy cuttings could be selected without difficulty in pre-epidemic areas of southern districts bordering Lake Victoria, where there was a generally low incidence of CMD at the time and little spread was occurring (Otim-Nape *et al*., 1998a). In such circumstances only 1–2% of cuttings were infected, whereas 20–30% were infected when cuttings were collected concurrently from symptomless plants of the same varieties growing in epidemic areas to the north (Otim-Nape *et al*., 2000). This emphasizes the need to select cuttings from stands in which there is a low incidence of CMD and ideally from stocks grown in relative isolation and subject to frequent and stringent inspection to find and remove all diseased plants.

In selecting healthy stocks, it is possible to exploit the phenomenon referred to as 'reversion', when uninfected plants develop from cuttings derived from CMD-infected source plants. This is attributed to the failure of CMGs to become fully systemic, especially in the most resistant cassava cultivars (Verhoyen, 1979; Pacumbaba, 1985; Rossel *et al*., 1988; Fauquet *et al*., 1988c; Njock *et al*., 1994; Fargette *et al*., 1994b, 1996; Thresh *et al*., 1998a). Stem cuttings collected from infected plants are least likely to be infected if they are short, collected from the symptomless shoots of recently infected plants and from the upper portions of the shoots rather than the base (Cours, 1951; Cours-Darne, 1968; Atiri & Akano, 1995; Fondong *et al*., 2000b). Reversion has an important 'self-cleansing' effect, as demonstrated by field trials and the results of modelling studies on sustainability (Fargette *et al*., 1994b; Fargette & Vié, 1995; Holt *et al*., 1997). These have shown that the health status of stocks does not necessarily deteriorate during successive cycles of vegetative propagation and, in some circumstances, may be expected to improve or reach a state of dynamic equilibrium, depending on the resistance of the variety and the conditions under which it is grown.

Heat and meristem-tip therapy can be used to develop CMG-free plants of clones that are totally infected (Chant, 1959; Fereol, 1978; Kaiser & Teemba, 1979; Adejare & Coutts, 1981; Kaiser & Louie, 1982; Frison, 1994). Originally, freedom from CMGs was inferred if no symptoms developed throughout prolonged periods of observation. Quick, sensitive serological and biochemical tests are now available for CMGs and also for other pathogens of cassava, including *Cassava brown streak virus* which occurs in Tanzania, Mozambique and some other parts of eastern and southern Africa (Calvert & Thresh, 2002; Legg & Thresh, 2004; Thottappilly *et al*., 2004).

Once virus-free 'foundation' plants have been identified and made available, they can be multiplied rapidly by micropropagation, single-node cuttings, mist propagation or other standard techniques. Initially this can, if necessary, be done in insect-proof structures to provide a protected, favourable, year-round environment and to preclude infection by viruliferous whiteflies. However, stocks can be produced in the large quantities required for distribution to farmers only by using extensive outdoor propagation sites. The plants may then be at risk of contamination by vectors and it is important to utilize carefully selected sites where inoculum pressure is low and there is known to be a low probability of infection by incoming whitefly vectors.

There are advantages in propagating selected stocks with at least some degree of isolation at experimental stations or state farms that are under official control and sound management, and away from the main areas of cassava production. Such sites have been identified in both mid-altitude and lowland areas of East Africa (Storey, 1936; Bock, 1982; Otim-Nape *et al*., 1998a) and in the Guinea savannah regions of Ivory Coast and Nigeria (Fauquet *et al*., 1988a, 1988b; Akano *et al*., 1997). However, the use of remote sites can create management and distribution problems and also add to the costs of transporting large quantities of bulky planting material into the main cassava-producing areas. It has also become apparent that the overall epidemiological situation can change dramatically and quickly, as reported in Uganda during the 1990s (Otim-Nape *et al*., 2000) and more recently elsewhere. Epidemics occurred in southern areas of Uganda where previously there had been so little spread that healthy stocks of susceptible varieties could be produced without difficulty for distribution to farmers. Conversely, it has become possible to raise healthy stocks in areas to the north, where previously there had been rapid spread. This emphasizes the need to monitor the labile, continually changing epidemiological situation so that selection and propagation procedures, and the 'safe' areas suitable for use as multiplication sites, can be adjusted in response to any changes that occur.

The fate of CMG-free cuttings when released to farmers and exposed in the field depends on their inherent susceptibility to infection and on the overall inoculum pressure encountered. The concept of 'inoculum pressure' is an important one and indicates the degree to which plants of a susceptible variety are at risk of infection. This is determined by the magnitude, activity and infectivity of whitefly vector populations. These are, in turn, influenced by seasonal and other environmental factors and by the size, proximity, distribution and potency of sources of infection, especially older CMD-affected cassava plantings located upwind and nearby, as demonstrated in Ivory Coast (Fauquet *et al*., 1988a) and later in Uganda (Legg *et al*., 1997).

Additional information on the factors influencing infection pressure has been obtained in Uganda. In three separate studies, the positive but statistically weak relationships between numbers of adult whitefly recorded on cassava during the early months of growth, and the amount of virus spread that occurred, were improved by incorporating into the regression analysis an additional variable to provide a measure of the amount of inoculum available. This was done from assessments of CMD incidence in older plantings within 250 m of the trials (Legg *et al*., 1997); or in the administrative districts in which the trials were located (Otim-Nape *et al*., 1998a); or in the planting material used by farmers hosting the trials (Legg & Ogwal, 1998).

The interaction between varietal susceptibility and infection pressure was evident from experience in the lowland forest areas of Ivory Coast and Nigeria and later at mid-altitude localities in Uganda. Susceptible varieties were almost totally infected within a few months of planting at sites of high infection pressure, whereas there was relatively little spread to very resistant varieties (Hahn *et al*., 1980; Fauquet *et al*., 1988a; Fargette *et al*., 1990; Byabakama *et al*., 1997; Otim-Nape *et al*., 1998a). In contrast, there was little or no spread to either susceptible or resistant varieties when grown at sites of low infection pressure. Thus the greater the inoculum pressure, the greater the need for resistant varieties and the greater the difficulty in maintaining the health status of nonresistant ones, or in achieving control by other means. This emphasizes the importance of obtaining information on inoculum pressure and rates of spread in the many other parts of sub-Saharan Africa, and on the relative susceptibility to infection of the main varieties being grown in the different agroecologies (Thresh *et al*., 1994b; Legg *et al*., 1997). Only then will it be possible to determine the minimum degree of resistance required of the varieties to be recommended for use in each area, and on the prospects of exploiting CMD-free material and other approaches to control.

The merits of using CMD-free material have long been apparent. They were first discussed by Storey (1936), who noted that farmers in the Morogoro Region of what is now Tanzania obtained cuttings for new plantings from upland areas where there was a generally low incidence of CMD. Official schemes for the release of CMD-free material were first introduced in Zanzibar (Briant & Johns, 1940). A similar approach was adopted later in Uganda, where attempts were made to establish plots of healthy propagation material in each chiefdom of the areas worst affected by CMD (Tothill, 1940; Jameson, 1964).

In several countries the CMD-free material that was released was of improved varieties of cassava that had greater resistance to infection, or other advantages compared with the farmer-selected varieties grown previously. For example, special arrangements were made in Tanzania to release uninfected material of two CMD-resistant, high-yielding hybrids (Childs, 1957). Cuttings for distribution were raised at isolated sites, or by arrangement with selected farmers and the aim was to produce sufficient material to displace the local CMD-affected varieties from entire localities within 2–3 years.

A similar policy was adopted in the former Teso Region (now Soroti and Kumi Districts) of Uganda following the severe drought of 1943–44, when there was a large increase in the incidence of CMD due to the widespread and inadvertent use of infected cuttings (Jameson, 1964). Uninfected material of CMD-resistant varieties was introduced to Teso in attempts to displace the infected stocks being grown. The uninfected stocks were raised initially at the Serere Experiment Station at an isolated 'quarantine' site. Secondary multiplication on prison farms soon produced sufficient cuttings to supply complete administrative units, each *c*. 300 ha. Farmers were advised to remove all existing cassava before replanting and were assisted if food shortages occurred before the new crops of cassava were sufficiently mature to be harvested. This approach was highly successful and was extended later to other areas by adopting a systematic 'advancing front' plan, which involved clearing all cassava from whole areas before replanting began, to decrease the opportunity for infection to occur. By 1951 Teso Region had sufficient planting material to meet the demand and legislation was introduced to enforce the destruction of any remaining CMD-affected cassava. The Ugandan scheme operated very effectively for over a decade, but it lapsed during the 1970s period of political instability and civil unrest.

A similar scheme was operated in the 1980s in parts of Malawi, where CMD was almost entirely displaced from some northern areas, including islands in Lake Malawi (the late R.F.N. Sauti, personal communication). Replies to a 1987 questionnaire addressed to staff of each of the many national cassava programmes in Africa (Anonymous, 1988) indicate that CMD-free planting material was also being used at the time in several other countries, including Liberia, Cameroon, Burundi and Benin. However, few details were provided, and there is a need for up-to-date assessments of the production and distribution procedures now being used to supply planting material in different countries, the problems encountered, the results achieved and the response of farmers.

In each locality, much will depend on the extent to which cassava is being grown and on the overall infection pressure encountered. There are obvious advantages in adopting a systematic approach to the deployment of CMD-free material, with the emphasis on supplying entire districts to avoid any carryover of inoculum and to ensure all infected material is replaced expeditiously. However, there are likely to be difficulties in areas where it is necessary to obtain the participation and cooperation of many individuals, each farming mainly small, contiguous land holdings. There are also likely to be problems in producing sufficient CMD-free material, unless enough propagation sites are available in low-risk areas, or the varieties grown are so resistant to infection that much reversion occurs and there is little subsequent spread by vectors.

Roguing

Roguing is a well known means of virus disease control of wide applicability (Thresh, 1988). It has been recommended repeatedly to control CMD. For example, Guthrie (1990) advised that cassava plantings should be inspected at least weekly for the first 2–3 months of growth, to find and remove immediately any diseased plants that occur. More recently, Colvin *et al.* (1999) stressed the importance of adopting strict phytosanitation following their finding that whiteflies breed more rapidly on CMD-affected than on healthy cassava. Thus, unless diseased plants are removed promptly, they can be expected to make a disproportionately large contribution to the overall flux of vector activity in the area. Despite these recommendations, there is little experimental or other evidence to indicate the effectiveness and feasibility of roguing, or the most appropriate procedure to follow. This emphasizes the scope for additional research and the need to involve farmers in more detailed socioeconomic assessments of the approach than any yet undertaken.

There is general agreement that roguing should be adopted as an essential feature of official schemes for selecting and maintaining virus-free stocks to provide cuttings for release to farmers, as discussed earlier. In such circumstances the health status of the material is paramount, and it is accepted that some losses due to roguing CMD-affected plants are inevitable and acceptable. Stringent roguing regimes are justified and it is appropriate to follow the exacting recommendations of Guthrie (1990).

The situation is very different in farmers' plantings, where other considerations apply and there is a general and understandable reluctance to remove any plants that might contribute at least some yield. Frequent roguing is certainly not justified where there is little spread of CMD between or within plantings by whitefly. Moreover, roguing is inappropriate and ineffective and leads to a progressive and unacceptable decrease in plant populations in areas of high inoculum pressure where much spread occurs to susceptible varieties. This was demonstrated in each of the only two experiments on roguing yet reported. At a site in the lowland forest zone of Ivory Coast, the spread of CMD was rapid and the final incidence of infection exceeded 75% in rogued and unrogued plots of a range of varieties (Colon, 1984). Rapid spread also occurred in a second experiment in the same locality where 67% of plants became infected in rogued plots established with CMD-free cuttings of a local Ivorian variety, compared with 87% in equivalent unrogued plots (Fargette *et al.*, 1990).

A cogent argument against roguing is based on evidence from Kenya, Ivory Coast and Uganda that the spread of CMD is mainly between cassava plantings, and not from internal foci of infection within them (Bock, 1983; Fargette *et al.*, 1990; Otim-Nape, 1993; Byabakama *et al.*, 1999). This suggests that roguing is likely to have little effect in reducing spread within treated fields, and so is of little or no immediate benefit to those adopting the practice, although it can be expected to decrease the risk of spread to other younger plantings nearby. From this it can be inferred that roguing is likely to be most effective when practised by groups of farmers and throughout whole localities, as recommended and adopted in Uganda in the 1940s and 1950s.

Such drastic measures are no longer appropriate or acceptable to farmers and cannot be enforced by legislation. Consequently, the current approach being considered in Uganda and Tanzania is to develop simple, less exacting procedures that can be used by farmers to sustain the health status of the material being grown, at little inconvenience or expense. One possibility is to rogue once or twice soon after planting, as the cuttings begin to sprout, when any infected ones usually develop shoots expressing conspicuous symptoms. Roguing can be done quickly and easily at this early stage of crop growth and there is still time to fill the gaps created by planting additional cassava or other crop plants. Any later infections that occur are allowed to remain, which avoids creating gaps and the decrease in yield that is otherwise likely to occur because of the reduced stand. This is because plants infected by whiteflies during growth sustain little or no reduction in yield, although it is important to avoid propagating from such plants as the cuttings obtained would be affected more severely (Fargette *et al.*, 1988; Thresh *et al.*, 1994a). Thus a standard recommendation in India is to mark CMD-affected plants with paint so that they are not used at harvest to provide cuttings, even if they are collected when plants are leafless and so not expressing symptoms (Malathi *et al.*, 1988).

The merits of this approach have not been assessed in Africa. However, a possibility currently being investigated in Uganda, Kenya and Tanzania is to compare selection of healthy planting material and roguing to determine their effectiveness in maintaining the health status of plantings when used singly and also in combination. It is already apparent from experience in Uganda that, in some circumstances, farmers will adopt such techniques if provided with sufficient training and justification (Otim-Nape *et al.*, 2000). However, the situation in many parts of Uganda during the 1990s was unusual in that the CMD epidemic had caused such severe damage that prices of cassava and other foodstuffs were exceptionally high, resistant varieties were not readily available and farmers were desperate to maintain cassava production from their susceptible varieties by whatever means available. Consequently, they were willing to make considerable effort to safeguard the crop, which provided their main staple food. It is doubtful whether farmers will respond similarly in endemic areas where CMD is a long-standing and so less obvious problem, and where acceptable, albeit substandard, yields are obtained without any evident need to change variety, or to adopt roguing or other specific control measures.

Use of CMD-resistant varieties

Early resistance breeding in Tanzania and Madagascar

The use of resistant or tolerant varieties has obvious advantages in seeking to decrease the losses due to viruses (Russell, 1978). This was appreciated by early workers on CMD in Africa in the 1920s and 1930s, when cassava production expanded rapidly in many areas and CMD became increasingly important (Lefèvre, 1935; Opsomer, 1938a, 1938b). It was then recognized that some varieties of cassava were more severely affected by the disease than others and attempts were made to increase the range of CMD-resistant varieties available by introducing genotypes from other regions and through resistance breeding programmes. One of the most influential of these was in East Africa, where attitudes were influenced by the great success of efforts in many parts of the tropics and subtropics to breed and release sugarcane varieties resistant to *Sugarcane mosaic virus* (Storey, 1936). Local and introduced varieties of cassava (*M. esculenta*) and the progeny of intraspecific crosses between cassava varieties were soon found to be insufficiently resistant to CMD. Attention then turned to hybrids between cassava and other species, including *Manihot melanobasis* and Ceara rubber (*M. glaziovii*), which were shown to be the most suitable parents (Nichols, 1947). There was no evidence of immunity to infection, but *M. esculenta* × *M. glaziovii* hybrids were shown to have considerable resistance. This is also expressed in progenies obtained by backcrossing such hybrids to cassava to restore and enhance the yield and quality of the tuberous roots produced.

Initially, resistance was assessed by exposing batches of cloned plants to infection and recording the number of months before each plant developed symptoms. Selection procedures were later simplified and resistance to infection was assessed more rapidly, but less precisely, from the number of months before the first plant of each clone developed symptoms. However, it was appreciated that the response of plants to infection is also important and that resistant varieties are of limited value if they do not yield satisfactorily when infected.

From subsequent experience in Tanzania, it became apparent that selections that are resistant to infection tend to develop inconspicuous symptoms when infected. Moreover, symptoms are sometimes ephemeral and restricted to parts of only one or two shoots of an affected plant (Jennings, 1957). Consequently, recording procedures were revised to take account of both the incidence of CMD and the severity of symptoms. Some of the varieties selected for resistance in this way proved suitable for East African conditions and were released to farmers (Doughty, 1958; Jameson, 1964). Seeds from promising selections were also sent to Nigeria in the 1950s for use in the national breeding programme. Nigerian clonal selection 58308, which originated from East African seed, has since featured prominently as a parent in resistance breeding at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria (Jennings, 1976, 1994; Beck, 1982; Nweke *et al*., 2002).

Whilst the East African breeding programme was in progress there was a similar but independent project in Madagascar. CMD was first reported there in 1932, and by 1937 it was causing serious problems and threatening the whole future of the crop on the island (Cours *et al*., 1997). As in mainland East Africa, local and introduced cassava varieties were evaluated and cassava was crossed with *M. glaziovii* (Cours, 1951). Varieties with a high level of resistance to CMD and with roots having a satisfactory starch content were obtained by backcrossing *M. esculenta* × *M. glaziovii* hybrids to cassava.

The new Madagascan cultivars were first multiplied at experimental sites and the most appropriate selections were propagated on commercial plantations before being distributed more widely. This soon led to an almost complete replacement of the genotypes being grown previously and to a decrease in both CMD incidence and yield loss. The vulnerable landraces (referred to as *manioc du pays*) were replaced first by intra- and later by interspecific hybrids and much of the original cassava gene pool was lost. However, some local genotypes survived in the few isolated areas that remained largely free of CMD and some of the desirable characteristics of these cassavas were reproduced in progenies derived by backcrossing interspecific hybrids with local varieties.

The wholesale and quick replacement of susceptible varieties by resistant ones led to a large increase in yield, and productivity in Madagascar was restored and eventually exceeded 30 t ha^{-1}. Resistant varieties were less infected in the field than those grown previously and suffered only slight losses when infected (Cours, 1951; Cours-Darne, 1968). Furthermore, a significant proportion of cuttings derived from infected plants were virus-free and this reversion 'self-cleansing' effect was recognized and exploited. Many CMD-free cuttings of resistant varieties were produced from multiplication plots, each of some tens of hectares. Cuttings were selected from the upper portions of the stems, as experience had shown that these are less likely to be infected than those collected from the lower portions (Cours, 1951; Cours-Darne, 1968). Any diseased plants that occurred later were removed (rogued) as they were observed. Further multiplication was by the farmers and the overall incidence of CMD in their plantings remained low, even though sanitation was not practised subsequently. This reflected the equilibrium reached between pathogen and host, leading to a generally low incidence of infection and little yield loss. The equilibrium depended also on the environment: cultivars that had been abandoned on the coast because of their vulnerability to infection could be grown successfully at mid-altitude sites where inoculum pressure was relatively low.

Subsequent resistance breeding at IITA and elsewhere in Africa

Since the 1970s, the most comprehensive and influential cassava breeding programme in Africa has been at IITA where, from the outset, resistance to CMD was one of the main attributes sought (Hahn *et al*., 1980; Mahungu *et al*., 1994; Nweke *et al*., 2002). Progenies were exposed to infection and individual plants were evaluated using a scale ranging from no symptoms (score 1) to severe leaf mosaic and distortion (score 5). Mean symptom severity scores were then calculated for breeding lines or trial plots. A limitation of this approach is that virus incidence and symptom severity are not clearly distinguished and symptomless plants could be CMD-free 'escapes', or they could be infected and extremely tolerant. Moreover, a low average score for a progeny or selection could mean that a few plants are infected and show severe symptoms, or that many succumb but are only slightly affected. Consequently, some breeders use the maximum symptom severity score recorded on diseased plants in evaluating a breeding line or selection. This provides a more satisfactory indication of the response of a particular genotype to infection than the overall mean score derived from a mixture of healthy and diseased plants (Mahungu *et al*., 1994).

Several of the first IITA selections of the Tropical Manihot Series (TMS) derived from crosses with *M. glaziovii* were categorized as 'highly resistant', 'resistant' or 'moderately resistant' to CMD. These have been released for use by farmers in Nigeria and for assessment and possible adoption elsewhere. IITA clones and seed stocks have also been widely distributed for use as parents, or for further evaluation in national breeding programmes. Clones TMS 30337, TMS 30395 and TMS 30572 were raised at IITA in 1973. They are three of the first improved varieties that were shown to be resistant to CMD, yet they may sustain a substantial loss of yield when infected (Terry & Hahn, 1980; Terry, 1982). The most resistant of the TMS varieties, notably TMS 30001, are even more difficult to infect and, when infected, develop inconspicuous symptoms of restricted distribution. Virus is incompletely systemic in such varieties and tends to be localized at the base of the main stem, as described initially in Madagascar and Tanzania (Cours, 1951; Jennings, 1960, 1988; Cours-Darne, 1968) and later at IITA (Rossel *et al*., 1988; Njock *et al*., 1994).

There is only limited information available on the relative performance of infected and uninfected plants of many of the TMS varieties released by IITA and designated as CMD-resistant to some degree (Thresh *et al*., 1994a). Nevertheless, it is apparent that an important feature of these varieties is their ability to grow and yield satisfactorily, even in areas where CMD is prevalent and causes serious losses in traditional farmer-selected varieties. Some of the IITA varieties, including TMS 4(2)1425 and TMS 60142, usually develop conspicuous symptoms during the early stages of crop growth and then tend to recover. Other varieties, including TMS 30572, TMS 30395 and TMS 30001, also show a strong tendency to revert. Consequently, stocks of such varieties never become totally infected, even when grown for years in conditions of intense infection pressure. However, the overall loss in yield caused by CMD in mixed stands of infected and uninfected plants of representative TMS varieties has not been determined. Nor has it been established whether there is any advantage in roguing such varieties and deploying only CMD-free stocks. A further deficiency is the limited amount of information available on the potency of resistant varieties as sources of inoculum to whitefly vectors. The limited systemicity of virus in resistant varieties and the generally low virus content, detected by serological assays (Fargette *et al*., 1996; Ogbe *et al*., 2002), suggest limited potency. However, evidence for this has not been sought in vector transmission studies.

In the latest phase of the IITA resistance breeding programme, considerable use has been made of cassava landraces collected in Nigeria and elsewhere in West Africa (Raji, 1995; Mignouna & Dixon, 1997; Fregene *et al*., 2001; Raji *et al*., 2001). Some of these tropical *M. esculenta* (TME) types are very resistant to infection and are seldom infected, even when exposed at sites of very high inoculum pressure. Moreover, the high resistance of some TME clones is attributed to a single dominant gene that was designated *CMD2* and linked with a specific marker sequence (Akano *et al*., 2002). The TME resistance differs from that of TMS varieties, which is considered to be polygenic and associated with gene *CMD1* derived from *M. glaziovii* (Fregene *et al*., 1997; Fregene, 2000). Thus the two types of resistance are complementary in their effects, and can be combined by intercrossing TME and TMS parents at sites specially selected to ensure that flowering occurs (Lokko *et al*., 2001a, 2001b). Following these developments, marker-assisted selection can now be used in South America to introduce the *CMD1* and *CMD2* genes to local populations, although CMD is not present and so cannot be utilized in the standard screening procedures used for many years in sub-Saharan Africa. This is an important development in making CMD-resistant varieties available in the neotropics, should the need arise.

Several of the TME × TMS hybrids produced in the IITA breeding programme have given very high yields, and additional attributes of many landraces and their progeny are that they have the erect growth habit preferred by many farmers and the tuberous roots are of good taste and quality. Several of the landraces and progenies derived from crosses with TMS clones are already being grown in Nigeria. They have also been introduced to parts of eastern and southern Africa, where they are being evaluated in on-station and on-farm trials in several countries including Kenya, Madagascar, Rwanda, Tanzania and Uganda. The most suitable of the recent CMD-resistant selections are now being released to farmers, and it is likely that they will soon make a substantial contribution in the various cassava-improvement projects, especially in areas affected by the current pandemic.

The identification and deployment of the TME type of resistance to CMD, which complements and supplements that derived from *M. glaziovii*, is an important development in relation to the potential problems caused by resistance-breaking strains of virus, as reported with some other viral pathosystems (Thresh, 1989). Such resistance-breaking strains have not yet been reported with CMD and the *M. glaziovii*-type resistance identified more than 50 years ago in Tanzania and Madagascar, and since deployed in the IITA TMS series of varieties and in other breeding programmes, has remained effective in East Africa even during the current pandemic (Otim-Nape *et al*., 1998a, 2000). Moreover, the resistance is also effective in West Africa and India (Hahn *et al*., 1980), where different CMGs predominate. This suggests that the *M. glaziovii* resistance is robust and durable. It remains to be seen whether the TME-type major gene resistance will be as successful, and whether the combined resistances are more effective than either used alone.

Transgenic resistance

The concept of pathogen-derived resistance was developed in the 1980s (Sanford & Johnston, 1985) and led to the possibility of genetically engineering cassava to induce resistance to CMGs. This was one of the original objectives of the 'cassava-trans' project in California (Fauquet & Beachy, undated). An advantage of this approach is that it could provide a means of introducing resistance to CMD-susceptible varieties that are, in other respects, very satisfactory and popular with farmers. Studies have continued at laboratories in the USA and Europe and some success has been achieved in engineering resistance to CMGs in herbaceous host plants and, more recently, in cassava (Fregene & Puonti-Kaerlas, 2002; Legg & Fauquet, 2004). However, transgenic cassavas have yet to be evaluated and exposed to inoculum in the field – and even when they are available, there are likely to be formidable difficulties in obtaining the government approvals and public acceptance necessary for their use on a large scale. This suggests that there is no immediate prospect of utilizing genetically engineered resistance, although this remains a possibility for the future.

Dissemination and adoption of CMD-resistant varieties

A 1980s survey in Nigeria established that TMS varieties, including some that are highly resistant to CMD, accounted for *c*. 20% of all plantings in Ondo State (Akoroda *et al*., 1987, 1989; IITA, 1986). The results of a later questionnaire (Anonymous, 1988) established that IITA varieties were much less widely grown outside Nigeria, except in the Republic of Benin, where they were said to account for over 60% of all plantings. By 1998 it was estimated that improved varieties accounted for *c*. 22% of the overall total of 9 million ha of cassava grown in Africa (Manyong *et al*., 2000). The area of improved varieties was 23% of the total in Nigeria and exceeded 30% in Tanzania, Uganda and Cameroon. Uptake was limited in several other countries and various problems were cited by respondents to the 1988 questionnaire. They included a shortage of planting material and of information on the overall performance and suitability of the TMS varieties. There were also concerns about the flavour, bitterness, texture or cyanide content of the tuberous roots, the branched spreading growth habit, poor root storage characteristics and lack of adaptation to local conditions. Some of these limitations have also been apparent from on-farm trials and farmer participatory research in Uganda and several other countries in recent years (Otim-Nape *et al*., 1994). Another problem is that some countries lack the resources to establish, multiply and distribute the improved varieties that have been introduced in very small quantities as virus-free plantlets in nutrient culture. There may also have been limited staff and facilities to grow and assess the seed material distributed from IITA for local evaluation and selection.

These are serious constraints that are not easily resolved, although cassava is propagated so readily that a shortage of planting material should not be a problem, given adequate funding and a suitable degree of commitment by researchers, extensionists and farmers. This is apparent from experience in Nigeria and, more recently, in Uganda and other East African countries. IITA varieties that are resistant to CMD and also possess other desirable attributes first became available for use in Nigeria in the mid-1970s. However, there were initial delays in their dissemination because of the shortage of planting material and the lack of an effective means of distribution to farmers (Akoroda *et al*., 1987). The Nigerian situation changed for several reasons (Nweke *et al*., 1996). There was an increased demand for cassava for processing and to meet the requirements of the rapidly increasing urban population. Moreover, government agencies and large international commercial companies were required to allocate substantial funds to improve access to rural areas and for large-scale agricultural extension activities (Osagie, 1998). Cassava featured prominently in many of these projects. For example, one in Ondo State released sufficient planting material of TMS 30572 to establish 26 000 ha in 1986 alone. Moreover, the Cassava Programme of the Nigerian National Seed Service began operations in 1987 and by the end of 1990 it had supported the establishment of 283 420 small demonstration plots of the improved varieties distributed throughout the main cassava-growing areas. Thus improved CMD-resistant varieties became widely distributed and accounted for 35% of all the cassava grown in the subhumid areas of Nigeria and for an even greater proportion in the humid and nonhumid areas (60 and 40%, respectively). The overall resistance of the TMS varieties to CMD and their generally superior performance compared with the varieties grown previously made a substantial contribution to the large increase in cassava production and in yields per hectare that have occurred in recent years in Nigeria (Nweke *et al*., 2002).

In Uganda, the need to introduce CMD-resistant varieties became apparent in the early 1990s, when many of the local landraces that predominated at the time were severely damaged during the epidemic that eventually affected much of the country (Thresh *et al*., 1994c; Otim-Nape *et al*., 2000). Initially, three of the IITA varieties from Nigeria (TMS 60142, TMS 30337 and TMS 30572) were shown to withstand infection by CMD, performed well in both on-station and on-farm trials, and were accepted readily by farmers. Moreover, TMS 30572 is widely adaptable and also resistant to bacterial blight (Zinsou *et al*., 2005). Accordingly, these varieties and others released later were multiplied in large quantities for general distribution. This was done using the substantial funds made available by governmental and nongovernmental organizations (NGOs) to alleviate the crisis in food security due to the drastic decrease in cassava production caused by CMD.

The different cassava rehabilitation projects in Uganda, the methods adopted and the results achieved are detailed in several publications (Otim-Nape *et al*., 1994, 1997a, 2000; Anonymous, 1997; Cooter *et al*., 1999; Thresh, 2002). Three main approaches were used for multiplication: on institutional farms; by groups of farmers; and by individual farmers. Each method has advantages and disadvantages, and considerable experience has been gained on the implications, costs and other socioeconomic issues involved. By 1993 an estimated 468 ha of improved CMD-resistant material were available to supply cuttings for distribution to farmers. The amount has since increased greatly as farmers have continued to multiply the new material for their own use, for distribution to neighbours and for sale to NGOs for use in cassava rehabilitation projects. Improved varieties were recorded in nine of the 16 districts of Uganda that were surveyed in 1997; in all six districts recorded annually between 1998 and 2001; and in 20 of the 21 districts assessed in 2003 (Bua *et al*., 2005). Improved varieties predominated in 34% of all plantings assessed in the 2003 nationwide survey. These varieties have a substantial yield advantage and a much lower incidence and severity of CMD compared with the locals. CMD incidences were particularly low (<10%) in TMS 30572 (Nase 3), which predominated in several districts, and also in the resistant Ugandan selection Nase 4 (SS4). These results indicate the extent to which improved varieties have contributed to the recovery in cassava production that has occurred in Uganda since the 1990s epidemic. However, local varieties continue to be widely grown and still predominate in some districts, and it is apparent that farmers have become increasingly fastidious in their varietal preferences and requirements as the losses due to CMD have decreased and the need to grow resistant varieties has become less compelling. This emphasizes the need for more rigorous selection of CMD-resistant varieties for any further distribution and also the scope for using varieties having the new TME landrace source of resistance and other favourable attributes.

Socioeconomic factors in Nigeria, and the devastating epidemic of CMD in Uganda and neighbouring countries, provided powerful stimuli for farmers to change the varieties being grown. They also led to the release of donor or other funds to facilitate this on a scale and with a rapidity that would otherwise have been impossible. There are now equally strong incentives to adopt CMD-resistant varieties in western Kenya, north-west Tanzania, Burundi and Rwanda, areas that were affected by the epidemic later than Uganda. In these areas, and also in parts of Central Africa, there is a need to make greater use of any CMD-resistant genotypes already available and to introduce or develop new varieties with resistance and all the other desirable attributes required by farmers. The general use of resistant varieties is an essential component of any disease-control strategy in areas of high infection pressure. It may then become possible to exploit the benefits of CMD-free planting material and roguing in areas where such measures are otherwise inappropriate or ineffective. Alternatively, it may be possible to develop varieties that are so difficult to infect, or in which the reversion characteristic is so marked that roguing or other control measures become unnecessary.

Cultural practices and crop disposition

Experience with many virus diseases is that planting date, cultural practices and crop disposition can greatly influence vector populations and virus spread (Thresh, 1982). This has been demonstrated in studies on CMD that may ultimately be of considerable practical relevance. Only limited information has been obtained, however, and additional research is required before farmers can be given definitive advice on the most appropriate cropping practices to adopt to facilitate control of CMD. Even then, there are likely to be great difficulties in implementation due to the small size of many farms and the limited availability of suitable sites, which impose serious constraints on field size, shape and disposition. Moreover, there is the need to produce continuous supplies of cassava for use locally, or for processing and transport to urban markets. This necessitates the sequential planting of mainly small plots that are often established in close proximity and in overlapping sequence, greatly facilitating the spread of CMD from old to young plantings nearby. Such problems are less acute on large commercial farms, or at official establishments used to produce CMD-free cuttings for distribution to farmers. Much can be done in such circumstances by adopting cropping schedules and spatial arrangements that provide at least some degree of spatial or temporal isolation and so decrease spread and facilitate control.

Field size and shape

Whitefly numbers and CMD incidence tend to be greatest in the outermost rows of plantings, especially those oriented across the direction of the prevailing wind. This suggests that it is advantageous to plant in large, compact blocks. If this is not possible, elongated plots should be oriented along rather than across the direction of the prevailing wind to decrease the proportion of plants in the most vulnerable peripheral areas. It may also be appropriate to discard the outermost rows of propagation plots being used to raise CMD-free cuttings for distribution, or to plant a CMD-resistant variety of cassava around the field margins. An alternative approach may be to plant windbreaks, or a suitably tall crop other than cassava, to intercept and impede the movement of incoming whitefly vectors and so restrict the spread of CMD. However, little attention has been given to such possibilities and, in the only experiment reported, there was considerable infection along the windward edge of a plot surrounded by rows of sugarcane, even though these ultimately reached a height of 2·5 m (Fargette *et al*., 1985).

Crop disposition

The main spread of CMD is into and not within plantings. This emphasizes the importance of crop disposition and the opportunity to facilitate control by selecting sites where there is only limited risk of infection from outside sources. In practice this means using suitably isolated sites, but there is scant information available on the minimum isolation distance that is likely to be effective and on the decrease in probability of infection to be expected with increasing distance from the source. Information is required on the slope and extent of the disease gradients that occur from infected plantings of different size, shape and potency. Studies in Ivory Coast have provided evidence of spread by windborne adult whiteflies over distances of several kilometres (Fauquet *et al*., 1988a), however, nearby sources of infection, especially those located upwind, are particularly important (Fargette *et al*., 1985, 1990; Fauquet *et al*., 1988a; Legg *et al*., 1997). Thus new plantings tend to be at serious risk where sources of infection are upwind and nearby, but not when the nearest sources are downwind and remote. Spread is also likely to be decreased by establishing sequential plantings in an upwind direction from the source and not downwind, and also by orientating plantings to restrict the length of the interfaces along which spread is most likely to occur.

The opportunity for utilizing such information is obviously influenced by the overall patterns of wind direction, land use and land ownership, and by the willingness of farmers to cooperate. The greatest scope is in areas where cassava is not widely grown and there is already considerable separation between plantings, and also where cassava is grown on large estates and established synchronously in large, uniform blocks of similar age that are given at least some degree of isolation. However, this is seldom the situation in the main areas of cassava production in sub-Saharan Africa.

Planting date

Cassava establishes so readily from stem cuttings that farmers usually have considerable latitude in the choice of planting date, especially in the humid lowland equatorial rainforest zones of West and Central Africa where there is adequate rainfall to enable planting throughout much of the year. The aim should be to facilitate the control of CMD by not exposing vulnerable young plants to serious risk of infection at times when the whitefly vector is likely to be most abundant. There are good prospects of increasing yields in this way by decreasing the incidence of CMD, and because plants not infected until a late stage of growth are not seriously affected.

In coastal districts of Kenya, the main spread of CMD by vectors occurs during the early rains from mid-May to mid-July and there are likely to be advantages in planting later in the year provided conditions are not so dry that crop establishment and subsequent growth are impaired (Robertson, 1987). There is a somewhat similar situation in the forest areas of Ivory Coast, where virus spread occurs throughout the year, but is most rapid from March to July and least rapid from August to November during the latter part of the rainy season (Fargette *et al*., 1994a).

Additional evidence on the effects of planting date has been obtained in Tanzania (Storey & Nichols, 1938b), Cameroon (Ambe, 1993), Nigeria (Okogbenin *et al*., 1998) and Uganda (Adipala *et al*., 1998). However, the full implications, practicability and likely benefits of this approach to control have not been studied. Hence the need for additional information from the various agroecological zones before attempts are made to persuade farmers to change traditional practices, which usually involve planting soon after the onset of each main rainy season. Such studies merit high priority because they could bring substantial benefits at no great inconvenience or expense by improving the health status of the planting material available to farmers. Moreover, major shifts in the attitude of farmers are possible if there is sufficient incentive and justification, as demonstrated in parts of Central America where cassava planting is delayed to facilitate control of bacterial blight (Lozano, 1986).

Crop spacing

There is evidence from Ivory Coast and Uganda that the spread of CMD is influenced by host-plant population density. Disease incidence, expressed as a percentage of the total stand, was greatest at the widest spacing adopted and alongside footpaths or around gaps in otherwise continuous stands of cassava (Fargette *et al*., 1990; Fargette & Thresh, 1994; Egabu *et al*., 2001). These findings are of obvious practical importance and can be utilized immediately by farmers, who should be encouraged to establish uniform dense stands rather than the irregular widely spaced ones commonly adopted.

Soil fertility and nutrient status

With many virus diseases there is evidence that the nutritional status of host plants influences vector populations, and also susceptibility and response to virus infection (Bawden, 1950). Such effects have been considered with CMD, but seldom in experiments with healthy planting material using a recording procedure that makes the important distinction between CMD incidence and severity (Ekpe & Chinaka, 2000; Sseruwagi *et al*., 2004). Moreover, whitefly vector populations have usually been assessed per shoot and not per plant, which makes it difficult to interpret the results obtained because of differences in plant size due to variations in soil fertility

(Sseruwagi *et al.*, 2003). These are serious limitations, and additional research is required to clarify the influence of soil fertility and nutrient status on vector populations, virus spread, crop growth and yield loss. Such studies are particularly important because one of the merits of cassava is that it will tolerate unfavourable environments, and many plantings are made in poor soils and after other, more nutrient-demanding crops have been grown (Nweke, 1994). This may enhance the damage caused by CMD, as suggested by the experience of many farmers during the 1990s epidemic in Uganda. The effects of the disease were most severe in the northern areas, where soil conditions and rainfall regimes are generally less favourable than in the south (Otim-Nape *et al.*, 2000). However, this difference in behaviour could be because diseased plants at fertile sites still produce a harvestable yield, whereas a similar proportionate reduction in the yield of impoverished plants at infertile sites renders plants virtually worthless.

Important evidence on the role of soil fertility has been obtained in studies on Pemba Island, Zanzibar, where cassava grown on fertile land recently brought into cultivation from fallow was less affected by CMD than at less fertile sites where fields had been cultivated for more than 10 years (Spittel & van Huis, 2000). There was a clear negative relationship between yield and CMD symptom severity score at the less fertile site, but not at the fertile site where CMD had no obvious deleterious effects. Moreover, the greatest yield response of cassava to the application of a green mulch was by the most severely diseased plants at the infertile site. These results are consistent with those of an earlier study in Tanzania in which the extent to which improved CMD-resistant selections outyielded local CMD-affected varieties was greater at a low-fertility than at a high-fertility site (Childs, 1957). Clearly there is a need for additional studies, and until these are done there is little scope and insufficient evidence to consider ameliorating the effects of CMD by influencing soil fertility. However, this may eventually be possible as increased attention is given to methods of sustaining or even enhancing cassava yields through fertilizer application or improved cultural practices.

Intercropping

There is only limited evidence on the spread of CMD in plantings of cassava grown with other crop species, as compared with sole stands of cassava. This is a serious omission: in many parts of sub-Saharan Africa cassava is usually grown with other crops in mixed or relay cropping systems (Gold *et al.*, 1989; Mutsaers *et al.*, 1993; Gold, 1994; Nweke, 1994). These involve many other crop species including banana, sweet potato, cereals and legumes that may have beneficial effects through improving overall land productivity and by decreasing whitefly vector populations, whitefly activity and virus spread.

Preliminary studies on intercropping cassava were made in Ivory Coast with maize at different spacings and sowing dates (Fargette & Fauquet, 1988); in Benin with maize, cowpea and groundnut (Ahohuendo & Sarkar, 1995); and in Cameroon with maize and cowpea used singly or together (Fondong *et al.*, 1997, 2002). In the Ivory Coast trial the incidence of CMD was less in only one of the six intercrop treatments compared with the sole crop control. More consistent beneficial effects of intercropping in decreasing the spread of CMD were obtained in the trials done elsewhere. These results emphasize the scope for further studies, but even at best, intercropping is likely to supplement and not replace other, more effective control measures.

Varietal mixtures

Another general feature of cassava production in many parts of Africa is that numerous varieties are grown, often in the same locality and within the same plantings. This is evident from the results of the Collaborative Study of Cassava in Africa (Nweke, 1994; Nweke *et al.*, 1994) and from surveys of farms in Uganda (Otim-Nape *et al.*, 2001) and Mozambique (Hillocks *et al.*, 2002). The use of varietal mixtures enables farmers to extend the harvest period and also to meet the requirements of consumers for different types of cassava. It also contributes to the merits of cassava as a robust, versatile crop that is resilient and able to grow satisfactorily in very diverse environments, even when exposed to a wide array of damaging pests and diseases. Vulnerable varieties that grow poorly are discarded, whereas relatively resistant ones are retained so that farmers can soon adapt to any problems that arise. This occurred during the 1990s epidemic of CMD in Uganda, where losses were much less in districts where many varieties were being grown than where there was almost complete reliance on the susceptible variety Ebwanateraka (Otim-Nape *et al.*, 2001). Nevertheless, little attention has been given to the role of varietal diversity as a means of decreasing the losses caused by CMD, or to the ability of resistant varieties to protect susceptible ones within a varietal mixture, or to compensate for their impaired growth. In the two experiments reported, the incidence of CMD in a susceptible variety was greater when it was grown alone than when mixed with resistant varieties (Sserubombwe *et al.*, 2001). The differences were statistically significant, even though the experiments were done under epidemic conditions of exceptionally high inoculum pressure that led to considerable multiple infection (*sensu* Gregory, 1948). This suggests that the differences would have been even greater under less exacting conditions and emphasizes the need for additional experiments done in collaboration with farmers on the scope for using varietal mixtures and to assess any possible yield benefits.

Vector control by insecticides or other means

Insecticides

A possible means of controlling arthropod-borne viruses is by using pesticides against the insect or mite vectors (Satapathy, 1998; Thresh, 2003). There are several reasons why this approach has seldom been adopted to control CMD, quite apart from toxicological and environmental considerations. The most cogent reason is that pesticides are least effective in controlling arthropod-borne viruses if the main spread is into and not within crops. CMGs are of this type and so insecticides are unlikely to kill incoming viruliferous whiteflies before they have had an opportunity to introduce inoculum.

Moreover, experience with cotton and several other crops is that whiteflies are not easily controlled by insecticides and tend to be killed less readily than their natural enemies (Eveleens, 1983; Dittrich *et al*., 1985). This can lead to a rapid resurgence of whitefly populations soon after insecticides have been applied and any initial benefits of the treatment tend to be short-lived. Furthermore, subsistence farmers in sub-Saharan Africa can seldom afford to purchase or otherwise gain access to spray machines and insecticides, even if these are available. Thus there is little immediate prospect that insecticides will be used to control CMD, except for field trials in which it is important to prevent the spread of CMD to uninfected controls (Owor *et al*., 2004). The situation could change if more effective insecticides or repellents become available and subsidies are provided to farmers, or if there is a need to increase productivity as crop production becomes concentrated in larger and more profitable farming units.

Biological control

From studies in several different African countries, it has been concluded that cassava is not a very favourable host plant for *B. tabaci*, as adult population densities on cassava tend to be low and mainly restricted to the young, expanding leaves (Fargette *et al*., 1987; Fishpool & Burban, 1994; Legg, 1994). Consequently, it was assumed that there was limited scope for implementing biological control of whitefly vectors by natural enemies and that the main biological control effort with cassava will continue to be against green mites and mealybug. As recently introduced pests from South America, they are regarded as being more amenable to biological control by exotic parasitoids than *B. tabaci*, which has occurred in Africa for many years and may be indigenous (Bellotti, 2002).

A reappraisal of the role of natural enemies has been necessitated by the recent occurrence of unusually large populations of *B. tabaci* on cassava and direct feeding damage in areas of Uganda and neighbouring countries affected by the current CMD pandemic (Colvin *et al*., 2004). Large populations have also occurred in Uganda on the cassava variety Nase 4 (also known as SS4) and on some of the other recently introduced CMD-resistant varieties. These developments have led to studies on possible changes in the predominant biotype of *B. tabaci* occurring on cassava in Uganda; on the role of natural enemies in regulating populations; and on the scope for augmenting their numbers by new introductions of parasites or predators.

Vector-resistant varieties

A possible approach to decreasing whitefly vector populations and the spread of CMD is to breed varieties of cassava that are less susceptible to *B. tabaci* than those being grown. This possibility was considered by Leuschner (1977), who emphasized the difficulties likely to be encountered in developing and exploiting such varieties. Later studies identified cassava genotypes that are somewhat resistant to *B. tabaci* and showed that resistance to the vector and to CMD are separate inherited attributes that could be combined to give a very advantageous combination of features (Fauquet *et al*., 1988d; Fargette *et al*., 1996). If such varieties are developed they may have an important role in future CMD control strategies. Moreover, there may be scope for utilizing the sources of resistance to whitefly that have been identified recently in South America, known to be effective against species other than *B. tabaci* that are direct pests of cassava (Gold, 1994; Bellotti & Arias, 2001; Bellotti, 2002). *Bemisia tabaci* seldom occurs on cassava in South/Central America, so its ability to colonize the whitefly-resistant cassava varieties developed there has not yet been determined. This emphasizes the importance of a project that began recently in Uganda on the introduction and evaluation of whitefly-resistant genotypes of cassava from South America (J. Colvin and C. Omongo, personal communication). However, even if resistant to *B. tabaci*, such genotypes are likely to be vulnerable to CMD and so will have to be subject to further breeding and selection before varieties are available for release to farmers.

Mild-strain protection

A possible means of alleviating the effects of virus infection on growth and yield is by prior inoculation with a mild strain of the same virus. The ability of mild strains to protect plants from the damaging effects of closely related virulent ones has long been recognized, and the phenomenon was used extensively by early virologists to assess the relationships between viruses and virus strains (Bawden, 1950). However, there were several reasons for an initial reluctance to consider this approach as a possible means of control. There was concern that mild strains might mutate to more virulent forms, or that they would spread and cause damage to other, more virus-sensitive crops. It was also feared that mild strains might have synergistic effects in combination with other, unrelated viruses. Moreover, the deliberate dissemination of mild strains was incompatible with control strategies based on phytosanitation (Posnette & Todd, 1955).

Despite these reservations, in recent decades stocks infected with mild strains have been disseminated widely and successfully to control *Citrus tristeza virus* and several other viruses that are so prevalent and difficult to control by other means that the deliberate introduction of mild strains poses no additional hazards (Fulton, 1986). This is the situation in the areas worst affected by CMD. The dissemination of cuttings containing a mild strain could be considered in such circumstances, and a potential advantage of this approach is that established, locally adapted varieties could be used. Moreover, cuttings containing the mild strain could be produced in large quantities by using standard methods of propagating from mild strain-infected source plants. No special isolation would be required and an initial release of cuttings would suffice for repeated cycles of crop production. Thus the costs would be less, and the logistics would be simpler and less demanding than for a phytosanitation strategy based on the release of virus-free material.

Currently any consideration of mild-strain protection for cassava is largely hypothetical. Little attention has been given to such an approach, and the precedents from early cross-protection studies with CMGs and another virus of the *Geminiviridae* (*Beet curly top virus*, genus *Curtovirus*) were not encouraging (Bennett, 1971). In early studies on CMD, Storey & Nichols (1938a) failed to demonstrate protection between two Tanzanian virus strains. However, some of their challenge inoculations were made by grafts that are likely to provide a more stringent test of protection than inoculation by the whitefly vector, as would occur in nature. Further difficulties in exploiting mild-strain protection could arise from the increasing number of CMGs now known to occur, and in recent studies combinations of two different CMGs had more damaging effects than either virus alone (Harrison *et al*., 1997; Fondong *et al*., 2000a; Pita *et al*., 2001). The establishment of virulent strains of CMGs may also be facilitated by the restricted and erratic distribution of these viruses in infected plants. However, the prospects for deploying mild strains will not become clear until further comprehensive studies have been undertaken in different agroecologies using combinations of strains of the same and different viruses.

Such research is now in progress, and in the first trials in Uganda plants grown from cuttings infected with a mild strain grew better and were less affected by CMD under conditions of high inoculum pressure than plants grown from initially uninfected cuttings. The latter soon became infected with virulent strains and then expressed severe symptoms (Owor *et al*., 2002, 2004; Owor, 2003). It remains to be determined whether the protection is effective elsewhere in Uganda and in other countries, and also whether it is durable if cuttings are collected from mildly affected plants and used for further cycles of propagation.

Cassava research and development

From this and previous reviews (Fauquet & Fargette, 1990; Thresh & Otim-Nape, 1994; Thresh *et al*., 1994b, 1998c; Legg & Thresh, 2000, 2004; Calvert & Thresh, 2002; Thottappilly *et al*., 2004) it is evident that CMD has been studied in many countries and to at least some extent throughout the 20th century, and much information is available on the aetiology and epidemiology of the disease and its control. Nevertheless, the overall scale of the research effort has been totally inadequate in relation to the huge importance of cassava in Africa and to the enormity of the CMD problem. Moreover, there has been a serious lack of continuity. Several different approaches to control have been considered, but they have not been fully evaluated to determine their effectiveness when used singly or in different combinations and seasons in the very diverse agroecologies in which CMD occurs. There has also been inadequate attention to socioeconomic issues and the factors influencing the attitudes of farmers to the varieties of cassava available and to CMD and its control.

These considerations largely explain the current prevalence of CMD and why only limited and intermittent progress has been made in decreasing the losses sustained, even before the onset of the current pandemic that has caused such devastation in East and Central Africa and now threatens other regions of sub-Saharan Africa. There are several reasons for this unsatisfactory situation. One is that cassava is particularly important in many of the most impoverished countries of Africa where there has been a long history of political unrest and instability, culminating in civil war. This has occurred in more than 11 countries in recent decades, including Angola, DCR, Ivory Coast, Liberia, Mozambique, Sierra Leone, Sudan and Uganda, which are all major cassava producers. Cassava has been particularly important in sustaining human populations during such times of crisis because it can be left in the ground until it can be harvested during any lull in the fighting. In these circumstances, CMD poses a particularly grave threat to food security. There is evidence from Uganda (Otim-Nape *et al*., 2000) that the disease situation was aggravated in the 1980s when the vigorous, healthy plants were harvested preferentially during periods when the fighting was less intense, leaving only the weaker, infected ones to provide cuttings for subsequent propagation.

Another unsatisfactory aspect of civil strife is that agricultural research and extension activities are curtailed and may even become impossible due to limited access to rural areas and to the loss of trial sites, facilities and personnel, as occurred in Uganda in the 1980s (Anonymous, 1997) and later in Rwanda and Sierra Leone. Moreover, emergency food relief programmes become necessary, and in some instances these have led to the distribution of infected planting material and to the introduction of unsatisfactory varieties from elsewhere that proved particularly vulnerable to infection, or deficient in other respects.

Even in regions where conditions are relatively stable, cassava research and development have long been neglected and receive inadequate support, despite the dietary importance of the crop and its potential for export, and it being a source of starch, animal feed, fuel and other commercial products. Cassava in Africa has had a generally low status as a crop because it is grown mainly for consumption or sale locally by subsistence farmers. It has not received the attention given to the main African export crops, or those grown extensively by influential landowners or commercial companies on large, mechanized farms.

Another consideration is that since the 1970s there has been a major diversion of the overall limited research effort on cassava to combat cassava green mite, cassava mealybug and cassava bacterial blight. In some countries these have caused acute damage that was more obvious than the chronic and often relatively insidious effects of CMD on growth and yield. Consequently, except when particularly severe epidemics occur, CMD tends to be accepted as almost inevitable by many farmers and even by some advisers, researchers and those responsible for agricultural policy and budget allocations. Growth and yield are generally considered to be satisfactory, even though they are demonstrably substandard and could be greatly improved through effective disease control.

A further constraint to the adoption of control measures is that in the DCR and also in many other parts of sub-Saharan Africa, cassava leaves are consumed as a nutritious vegetable (Lutaladio & Ezumah, 1981; Lutaladio, 1984; Ariyo *et al.*, 2003), and it is claimed that there is a strong consumer preference for leaves expressing symptoms of CMD (Almazan & Theberge, 1989). This view has, at times, been used to justify a failure to implement disease control measures or for official inertia. Moreover, it led cassava breeders in DCR to select genotypes that express mild CMD symptoms, rather than those that remained symptomless in screening trials (Mahungu *et al.*, 1994). However, the claim that consumers prefer infected leaves to healthy ones has not been verified using tasting panels and appropriate blind-testing protocols and procedures designed to avoid subjectively biased assessments. It is important that such tests are done and subjected to rigorous statistical analysis, to compare not only CMD-affected and symptomless leaves, but also leaves expressing symptoms of different type and severity. Leaves with very different symptoms are likely to differ considerably in fibre content and texture, palatability, and possibly also chemical composition, cyanogen content and taste (Chant *et al.*, 1971; Mahungu *et al.*, 1996).

Particular problems will arise in the many countries of Africa where the extension and advisory services are limited by a grave shortage of financial resources, facilities and personnel, and where any need to control CMD must be considered in relation to the more obvious losses caused by other pests or diseases of cassava, and also to the requirements of other important subsistence or export crops. Farmers should, ideally, have access to cassava varieties with resistance not only to CMD and its vector, but also to other pests and diseases. Moreover, the control measures used against CMD must be fully compatible with the overall crop protection strategy being implemented and also with recommended cropping practices.

Towards an integration of control measures

Despite the limitations of the available information and the need for more research on many aspects of CMD, sufficient is known about the disease to achieve satisfactory control. This is apparent from experience gained in Madagascar, Nigeria and, more recently, Uganda, where very damaging epidemics were brought under control mainly by deploying CMD-resistant varieties. The problem is to reproduce this success elsewhere and on a much larger scale, including areas where CMD is endemic and poses a less obvious threat to production than in epidemic areas that are in crisis. There is also a need to exploit the whole range of possible control measures as an overall integrated crop and disease management strategy.

Only limited attention has been given to developing integrated approaches to the control of cassava arthropod pests and diseases and to cassava production (Thresh *et al.*, 1994), although considerable progress has been made with bacterial blight (Wydra *et al.*, 2003). One possible crop protection strategy is to rely mainly on resistant varieties, and routine screening tests against pests and diseases feature prominently in the cassava breeding programme at IITA and also in many national programmes in Africa (Mahungu *et al.*, 1994). Much attention has also been given to the biological control of cassava green mite and the cassava mealybug (Bellotti, 2002). However, the contrasting approaches to pest and disease control by resistant varieties and by exploiting natural enemies have not been closely integrated. Moreover, the role of sanitation, including the use of planting material free of the various arthropod pests and pathogens of cassava in the overall context of the cropping systems employed, has also received only limited attention in sub-Saharan Africa (Porto & Asiedu, 1993). There is obvious scope for developing improved practices and cassava is one of the target crops being considered by the Inter-Center Initiative to Promote Integrated Pest Management in the Tropics (Oliveira *et al.*, 2001).

Apart from the problems of mounting effective crop improvement and integrated pest and disease control programmes for cassava, there are likely to be difficulties due to the very diverse agroecological conditions in which the crop is grown in Africa (Carter *et al.*, 1992). Cassava is planted over a wide altitudinal and climatic range, as a major or minor crop and in areas having very different growing seasons and patterns of crop production. Consequently, there are sometimes big differences in whitefly populations, virus strains and virus spread between and also within regions yet control measures or varieties that are appropriate in one situation may be ineffective or inappropriate elsewhere.

From the foregoing account it will be apparent that there is no immediate prospect of using insecticides, biological control, mild-strain protection or genetically engineered forms of resistance to control CMD. Instead, in all regions the basic approach in the foreseeable future will involve resistant varieties, together with at least some use of phytosanitation and crop deployment. Unfortunately, a fully integrated approach along these lines is not yet feasible. CMD-resistant varieties are not always available with the necessary combination of attributes required by farmers and consumers, or they are released in insufficient quantity, or the level of host plant resistance required for use in the region has not been determined. Furthermore, farmers may be unwilling to select healthy planting material or to rogue diseased plants, or they have not been encouraged to do so. They seldom have much latitude in the choice of site, because of the limited land available. Also, they usually have little or no control over the activities of their neighbours, who may use infected planting material or prefer to grow nonresistant varieties.

Despite these constraints, the available evidence suggests that CMD can be controlled effectively in large areas of Africa by releasing virus-free material of local or improved varieties and by persuading farmers to adopt basic measures of phytosanitation and crop deployment. Experience suggests that there are no intrinsic difficulties in adopting such an approach, provided that suitably resistant varieties are used and farmers are sufficiently informed, motivated and receptive.

Circumstances in large tracts of eastern and southern Africa are generally propitious, as currently the overall inoculum pressure appears to be low in many areas. Whitefly populations and spread of CMD appear to be limited by prolonged dry periods and also at mid-altitude sites exceeding 1000 m above sea level. Moreover, in many areas the crop is not grown widely compared with the humid lowland forest zones of West and Central Africa and there is usually at least some spatial separation between plantings. This suggests that the main problems likely to be encountered in controlling CMD in such areas will relate to the logistics of producing and distributing CMD-free cuttings of suitable varieties on the huge scale required, and to the need to change the current attitudes and practices of vast numbers of subsistence farmers.

Conditions in the lowland forest zones of West Africa are very different, as they facilitate whitefly reproduction and rapid spread of CMD throughout much of the year. Cassava is widely grown in the region and the infection pressure seems to be high. Moreover, both ACMV and EACMV occur in Cameroon, Ghana, Ivory Coast and Nigeria, which may lead to serious damage due to dual infection and to the appearance of virulent recombinant viruses of the type associated with the East African pandemic. Thus it is hardly surprising that there appears to be little prospect of control by sanitation using many of the susceptible varieties now being grown. However, control will become feasible once suitably acceptable varieties with substantial resistance to infection are available and widely grown. This is apparent from experience with the most resistant of the varieties deployed in Nigeria, Benin and Uganda and from trials with the introduced variety Aipin Valenca in Ivory Coast (Colon, 1984; Nweke *et al*., 2002).

The situation in the lowland forest zones, where currently there is a high incidence of CMD, could be transformed once highly resistant varieties become generally available and are acceptable to farmers, processors and consumers. Meanwhile, the use of CMD-free planting material, deployment and roguing with susceptible varieties is likely to be successful only on large, commercial farms isolated from outside sources of infection. Sanitation is likely to be more effective in the adjoining southern Guinea savannah areas where cassava is not yet widely grown and where infection pressure is correspondingly low (Fauquet *et al*., 1988b; Akano *et al*., 1997). It is unclear whether a similar approach would be successful in the important cassava-producing areas of the DCR and other countries of Central Africa, especially following recent reports of severe problems caused by CMD in the DCR and the Congo Republic (Neuenschwander *et al*., 2002), and even more recently in Gabon (Legg *et al*., 2004) and the Central African Republic (J.P. Legg, personal communication). CMD is known to be prevalent in these areas, but whether this is due mainly to the dissemination of infected cuttings, or to rapid spread by whiteflies, has not been determined. Thus the current scope for using CMG-free planting material and the way in which it should be deployed is uncertain.

Conclusions

Much could be achieved by utilizing the existing information on CMD and research has in some respects outstripped the ability to apply the results obtained. However, the control measures now advocated depend on the availability of CMD-free cuttings and of suitably resistant varieties, and also on the willingness of farmers to adopt this material and to practise at least some degree of phytosanitation and crop deployment. This emphasizes the importance of developing additional varieties and adopting them on an adequately large scale. There is also a need for detailed studies on the socioeconomic issues involved and on the attitudes of farmers to CMD, their choice of varieties and their different approaches to control. Moreover, much additional information is required on the epidemiology and control of CMD and on the prevalence of the different CMGs and the interactions between them, especially in the many parts of Africa where there have been no previous studies.

It has still to be determined whether the present approaches to control are appropriate in all circumstances. One of the crucial unresolved issues is whether phytosanitation is advantageous and appropriate if the varieties being grown are sufficiently resistant to infection (Thresh *et al*., 1998b). Whatever the strategies developed, it will be necessary for the extension services and other agencies to adopt greatly improved methods to ensure the measures advocated are widely understood and adopted. This will not be achieved quickly or easily, but a successful outcome will bring great benefits to the millions of farmers and their dependants now affected by CMD in Africa.

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