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Effects of African cassava mosaic geminivirus on the yield of cassava

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Abstract *This review considers studies performed over many years in 12 countries on the effects of African cassava mosaic geminivirus (ACMV) on yield. Some experiments compared the yield of plants raised from ACMV-infected cuttings with equivalent uninfected controls in formal replicated trials. In others, yield data were obtained from plants selected in experimental plantings or farmers' fields according to the type and severity of symptoms expressed or the date when they first appeared. Such studies have shown that the effects of ACMV on yield depend on variety and stage of infection but are usually substantial. Plants grown from infected cuttings are much more seriously affected than those infected later by the whitefly vector* (Bemisia tabaci) *and plants infected at a late stage of crop growth are almost unaffected. Positive relationships have been established between the extent and severity of the leaf symptoms and yield loss, but losses can be considerable, even in varieties designated as resistant. The limitations of these studies are discussed and emphasis is placed on the need for additional information on the effects of ACMV on the yield of the improved virus-resistant varieties now available. Data are also required on possible competition and compensation effects within mixed stands of infected and uninfected plants at different sites, spacings and levels of soil fertility.*

Keywords: African cassava mosaic virus disease, geminivirus, whitefly vector, *Bemisia tabaci*, yield loss, competition, compensation, Cameroon, Congo, Côte d'Ivoire, Kenya, Madagascar, Malawi, Nigeria, Tanzania, Togo, Uganda, Zaire, Zanzibar.

Introduction

African cassava mosaic geminivirus (ACMV) occurs in all the important cassava-growing areas of Africa and it is so prevalent in many countries that it was considered to be the most damaging vector-borne pathogen of any African crop in a recent economic assessment (Geddes 1990). However, despite its undoubted importance there is little reliable information on the magnitude of the losses caused by ACMV in the many African countries where cassava is cultivated. This is because few data are available on the incidence of infection in different regions and on the effects

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Table 1. Experiments on the effects of ACMV on yield

Reference	County	Varieties*	Experiment type	Comparison†
Muller (1931)	Congo	L		
Golding (1936)	Nigeria	L	B	C/W/H
Tidbury (1937)	Zanzibar	L	B	C/W/H
Briant and Johns (1940)	Zanzibar	L	B	C/W/H
Cours (1951)	Madagascar	L	B	S
Beck and Chant (1958)	Nigeria	L	A	C/H
Jennings (1960)	Tanzania	L	A	C/H
Bock and Guthrie (1976)	Kenya	L/I	A	C/H
Bock and Guthrie (1978)	Kenya	L/I	A	C/H
Anon, (1979)	Nigeria	L/I	A	C/H
Anon. (1980)	Nigeria	L/I	A	C/H
Terry and Hahn (1980)	Nigeria	L/I	A	C/H
Hahn *et al.* (1980a)	Nigeria	I	A	C/H
Dengel (1980)	Togo	L	B	C/H
Anon. (1981)	Nigeria	L/I	A	C/H
Chapola (1981)	Malawi	L	A	S
Seif (1982)	Kenya	L	A	C/H
Terry (1982)	Nigeria	L/I	A	C/W/H
Bock (1983)	Kenya	L/I	A	C/H
Muimba (1984)	Zaire	L	A	C/H:S
Ng and Chukwuma (1986)	Nigeria	I	A	C/H
Fargette *et al.* (1988)	Côte d'Ivoire	L	A+B	C/W/H:S
Raffaillac and Nedelec (1988)	Côte d'Ivoire	L	B	C/W/H
Otim-Nape *et al.* (1992)	Uganda	L	B	C/W/H:S
Tankou and Lyonga (1994)	Cameroon	L	B	C/H
Nyirenda *et al.* (1993)	Malawi	L	A	C/H

*L, local; I, improved.
†Comparisons made between plants infected by ACMV as cuttings (C) or by whiteflies (W), or unaffected and assumed to be healthy (H). Also between plants with leaf symptoms of different degrees of severity (S).

of ACMV on the yield of the wide range of varieties grown (Thresh *et al.*, this volume, p. 3). Evaluations of yield effects are considered in this review, which discusses the methods adopted in previous studies, the results obtained and the need for further research.

Previous experiments on the effects of ACMV on yield

The effects of ACMV on yield have been assessed at different times and in at least twelve countries (Table 1). Two main experimental approaches have been adopted.

Type A Cuttings were established from ACMV-affected and unaffected plants in formal trials.

Type B Established plants in experimental plantings or farmers' fields were selected and marked according to the type and severity of symptoms expressed or

Table 2. Effect of ACMV on Zanzibar varieties

	Root yields (as percentage of uninfected controls)	
Variety	Cutting infection	Whitefly infection
Msitu	16	77
Mpezaze	25	85
F279	38	71
Kilele	44	99
F100	33	104
Binti	16	80
Mshele	29	92
Kajayeye	30	111
Mean	**29**	**90**

From Briant and Johns (1940).

the date when symptoms first appeared. These plants were later harvested, together with equivalent unaffected plants as controls.

The results are summarized here by country and are followed by a critique of the work to date and suggestions for further studies.

Zanzibar

In an early 'Type B' experiment, wholly or partially diseased plants of three local varieties were selected and compared with symptomless plants of similar size and branching habit and with other symptomless plants selected entirely at random (Tidbury 1937). Wholly affected plants yielded significantly less than plants of any other category and produced only 31% of the yield of the randomly selected symptomless controls. The yields of partially infected plants were not significantly smaller than those of the paired or random controls.

'Type B' observations were also made on a more comprehensive range of unimproved local and introduced varieties (Briant and Johns 1940). Three groups of plants were distinguished of each variety:

- those showing symptoms from the outset and assumed to be infected as cuttings;
- those developing symptoms more than 2 months after planting and assumed to be infected by the whitefly vector (*Bemisia tabaci* Genn.); and
- those that remained symptomless throughout the growing period.

For several varieties there were too few plants in some categories for valid comparisons to be made. However, plants of 10 varieties infected as cuttings were severely damaged and produced 5–44% of the yield of equivalent uninfected controls (overall mean 29%). The yields of plants infected later were affected much less than the controls, or not at all (Table 2).

Madagascar

The important and comprehensive studies of Cours (1951) merit detailed consideration here as they are not well known and are seldom quoted. Presumably this is because they were presented in a 197-page paper in a journal that is not readily available.

Cours assessed a range of local varieties and studied the interrelationships between symptom severity, leaf area, yield and virus incidence (which he termed 'the degree of contamination'). A simple symptom scoring system was devised to give numerical 'severity index' (SI) values ranging from 0 (no symptoms) to 5·0 (death of plant), with nine intermediate points. The system was described in detail and illustrated by colour plates, and was an early example of a quantitative approach that has since become commonplace in crop loss studies on a wide range of pathosystems (Zadoks and Schein, 1979).

Cours' results are summarized in Figure 1, which indicates that severe symptoms ($SI \geqslant 3$) were associated with restricted leaf area, low yields and a high incidence of infection. By comparison, varieties which developed relatively mild symptoms had a low incidence of infection, grew satisfactorily and in some instances outyielded those that were unaffected. This suggests that only plants with severe symptoms should be discarded in breeding programmes and that slight symptoms have no serious detrimental effects. However, a more precise interpretation of the results is difficult because the comparisons were between different varieties and not between infected and uninfected plants of each variety.

Despite this limitation Cours' results are of great importance and raise many issues, some of which have still not been adequately addressed. For example, Cours suggested that slight symptoms may be beneficial because they are associated with an improved partitioning of assimilates between the tuberous roots and aerial parts. Others have since made similar suggestions (Raffaillac and Nedelec 1988; Otim-Nape *et al.*, this volume, p. 43). Cours was also concerned with the extent to which the losses caused by ACMV are related to effects on leaf area and soil fertility and analysed affected and unaffected leaves to assess differences that might influence their performance, as done in later studies in Nigeria (Chant and Beck 1959; Chant *et al.* 1971). The apparent relationship established by Cours between symptom severity and virus incidence is of even greater significance for resistance screening and in relation to current studies on the various components of resistance. This has led to the concept of a dynamic equilibrium between new infections caused by whitefly vectors and recovery due to the failure of ACMV to become fully systemic in resistant varieties, which tend to be those that develop slight symptoms (Jennings, this volume, p. 110; Fargette *et al.*, this volume, p. 123).

Kenya

Bock and Guthrie (1978) compared the yields of infected and uninfected plants of four varieties in 'Type A' experiments. Yields of infected plants (expressed as percentages of uninfected controls) were 33% and 29% for two local varieties, 14%

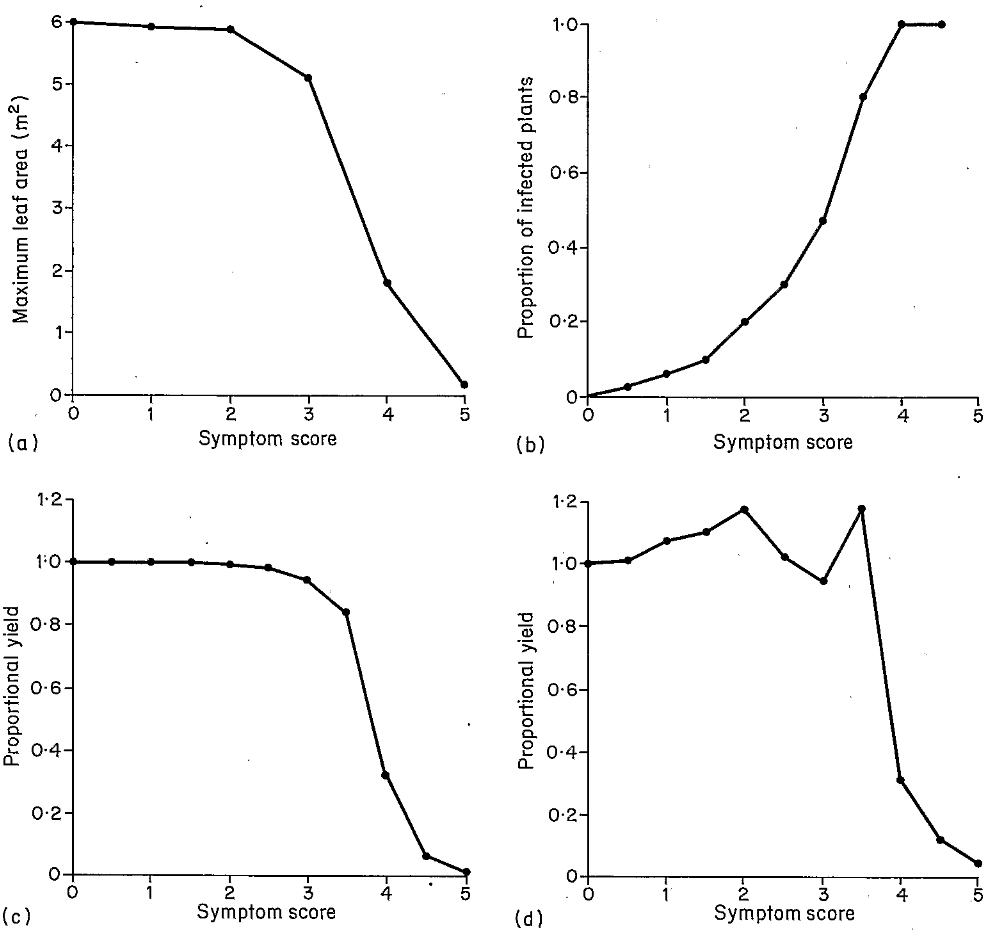

Figure 1. The relationship between symptom severity score and (a) maximum leaf area, (b) proportion of plants infected, (c) yields of tuberous roots at site of low fertility and (d) yields of tuberous roots at site of high fertility. Data from Cours (1951) for different Madagascan varieties. Yields are expressed as proportions of data for uninfected varieties (symptom severity score 0).

for a susceptible Indonesian variety and 31% for a Tanzanian variety that was reported to be resistant and having at least some degree of tolerance.

Robertson (1987) reported other 'Type A' experiments with local and introduced varieties in which the yields of infected plants ranged from 56% to only 14% of those of uninfected controls.

Seif (1982) described a 'Type A' experiment that is unique in that ACMV was introduced by grafts from a standard infected source. The yield of infected plants (expressed as a percentage of equivalent uninfected controls) was only 25% for a local susceptible variety and 30% for a moderately susceptible one that had originated in the Tanzanian breeding programme. Two other resistant Tanzanian varieties were less severely affected (59% and 56%) and a third, regarded as highly resistant, produced

76% of the control yield. All the decreases in yield were statistically significant, even though some of the symptoms were slight and the most resistant variety was eventually symptomless. It is notable that the Tropical Manihot Series (TMS) of varieties from the International Institute of Tropical Agriculture (IITA) were derived from the Tanzanian material and display only very limited symptoms as they grow and tend to recover.

Nigeria

Golding (1936) reported early 'Type B' observations on an experimental planting of two local varieties near Ibadan soon after ACMV was first reported in Nigeria. Totally affected plants with symptoms on all branches produced 66% and 57% of the yield of unaffected controls selected at random. No effect on yield was apparent in plants with symptoms on only one branch that were attributed to recent infection by whiteflies.

Beck and Chant (1958) described a 'Type A' experiment with a local low-yielding variety. The yields of plants that were infected by whiteflies during the trial were omitted from the analysis. Plants infected as cuttings produced 83%, 66% and 71% of the yield of uninfected controls when harvested 4, 6 and 8 months after planting, respectively. The decreases in yield were highly significant on the second and third occasions.

Several Type A experiments have been performed with local and improved varieties at IITA, although some may be duplicate reports (Table 3). Terry and Hahn (1980) reported the results of an experiment using transplanted cuttings of a local variety (Isunikakiyan) and TMS 30395, which is an improved IITA variety rated as highly resistant to ACMV. The yields of plants infected as cuttings were 31% of adjoining paired controls for Isunikakiyan and 68% for TMS 30395 when harvested 7 months after planting. However, the effects of ACMV on Isunikakiyan were probably under-estimated because all the controls were infected during the experiment by whiteflies. In percentage terms the effect of ACMV on the yield of TMS 30395 was greater at 2 months than at 7 months, but plants are not usually harvested so soon after planting.

Isunikakiyan and TMS 30395 were also included in a further 'Type A' experiment, together with a second improved variety TMS 30211 (Terry 1982). Almost all the initially uninfected plants of Isunikakiyan and TMS 30211 became infected during the trial. As in the previous experiment, plants infected during the experiment by whiteflies significantly outyielded those infected as cuttings and the difference was greater for Isunikakiyan than for TMS 30211, which was more tolerant of infection than the local variety. This may have been associated with the limited expression of symptoms in TMS 30211 which reached a peak 5 months after planting and then declined to zero after 7 months.

Other 'Type A' comparisons have been made with several other IITA varieties (Anon. 1980, 1981). The yields in two trials of plants infected as cuttings (expressed as percentages of uninfected controls) were 52% and 69% for TMS 30572, 65% and 64% for TMS 30555 and 68% and 69% for TMS 30040. Yields of 40% were recorded for TMS 30835 compared with plants infected during growth by whiteflies.

Table 3. IITA experiments in Nigeria on the effects of ACMV on yield

Variety	Duration of trial (months)	Yield* (%)	Reference
Isunikakiyan	7	31†	Terry and Hahn (1980)
	7	31†	Anon. (1979)
	7	31†	Terry (1982)
TMS 30001	12	49	Ng and Chukwuma (1986)
TMS 30040	7	68	Anon. (1980)
	7	69	Anon. (1981)
TMS 30157	7	76	Anon. (1981)
TMS 30211	7	{ 42†	Anon. (1979)
	7	{ 42†	Terry (1982)
	7	53	Anon. (1981)
TMS 30395	7	73	Anon. (1981)
	7	68	Terry and Hahn (1980)
	7	{ 68	Anon. (1979)
	7	{ 70	Terry (1982)
TMS 30555	7	65	Anon. (1980)
		64	Anon. (1981)
TMS 30572	7	52	Anon. (1980)
	7	69	Anon. (1981)
TMS 30835	7	{ 40†	Anon. (1980)
	7	{ 40	Anon. (1981)
TMS 4(2)1425	12	90	Ng and Chukwuma (1986)
TMS 60444	12	256†	Ng and Chukwuma (1986)

*Expressed as a percentage of uninfected controls.
†Compared with plants infected during the experiment by vectors.
In some cases, what appears to be the same experiment has been reported in separate publications. These are bracketed together.

The results for TMS 30572 are of particular significance because it is the most widely grown of the IITA varieties in Nigeria and the incidence of infection can be as high as 90% under high inoculum pressure (Hahn *et al.* 1980b, 1989; Anon. 1981).

The most recently reported experiments included ACMV-free clones derived from meristems, but involved few plants and the results were not analysed statistically (Ng and Chukwuma 1986). This makes it difficult to assess the significance of the near three-fold increase in yield of infected TMS 4(2)1425 over uninfected plants.

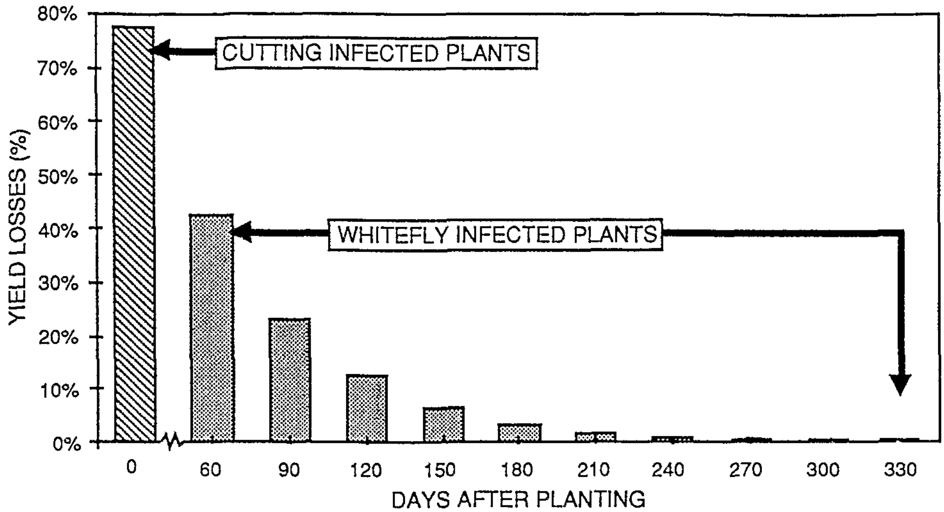

Figure 2. Relationship between the loss of yield in the Côte d'Ivoire cultivar CB and the time and mode of infection with ACMV. Data from Fauquet and Fargette (1990).

Côte d'Ivoire

In a trial with many different local and introduced varieties there was a negative correlation between yield and the severity of the leaf symptoms caused by ACMV (Vandevenne 1975). Fargette *et al.* (1988) later described 'Type B' experiments with the local variety CB planted on two different dates in 1983. Plants that showed symptoms from the outset were assumed to have been infected as cuttings and produced only 45% and 23% of the yield of uninfected plants in the two trials. Later symptoms were attributed to infection by whiteflies and were associated with less drastic effects on yield. The earlier an infection occurred, the greater the yield loss, which was not significant in plants that developed symptoms later than 4 months after planting (Figure 2).

In a third experiment, plants infected as cuttings sustained a 37% yield loss in relation to uninfected controls when grown in separate batches, compared with a 69% loss when infected plants were surrounded by uninfected neighbours. This result suggests that competition effects within stands are important.

Raffaillac and Nedelec (1988) describe detailed 'Type B' observation on the early growth of plants of the variety CB and compared uninfected plants with others infected as cuttings or later by whiteflies. Big effects of ACMV on branching and on leaf and root production were recorded, especially when infection occurred early. However, these authors stressed that a decrease in leaf area or in aerial growth does not necessarily lead to decreased yields because of possible internal competition effects between the aerial parts and roots. Reference was made to the studies of Cours (1951) in Madagascar, who noted that plants with inconspicuous symptoms outyielded uninfected plants, especially at a fertile site where there was prolific leaf production.

Table 4. Effect of ACMV on Malawi varieties

	Root yields*	
Symptom severity	cv. Gomani	cv. Mbundumali
Mild	93	77
Moderate	49	28
Severe	34	18

*Expressed as a percentage of uninfected controls.
From Chapola (1981).

Togo

In a 'type B' experiment Dengel (1980) established negative correlations between the severity of the symptoms caused by ACMV and total leaf area 6 months after planting. Moreover, there was a positive relationship between leaf area and the dry weight of tuberous roots, stems and whole plants. In a series of experiments with three local varieties the yields of ACMV-infected plants ranged from 50 to 85%, 59 to 66% and 34 to 62% of equivalent uninfected controls.

Malawi

Chapola (1981) presented a brief summary of 'type A' experiments with two local varieties, in which the cuttings used were selected from symptomless plants and others with symptoms of three different degrees of severity. The variety Mbundumali was more severely affected than Gomani, and in each variety there was a negative relationship between yield and symptom severity (Table 4). Further experiments have been undertaken with those and two other local varieties at five different sites (Nyirenda *et al.* 1994). Infected plants of Gomani produced less than 10% of the yield of uninfected controls at four sites. However, yields were 56% of the uninfected controls at the fifth site where overall yields in all varieties were much greater than elsewhere. This suggests that soil fertility or other factors that affect growth may influence the response to infection.

Uganda

'Type B' assessments have been made of many different local varieties in farmers' fields in three districts of western Uganda (Otim-Nape *et al.* 1992; this volume, p. 43). Uninfected plants were more vigorous and more productive than infected ones and the decreases in yield were positively correlated with the severity and extent of the symptoms expressed. ACMV decreased several components of yield including root number, root size and harvest index.

Limitations of the studies

Many previous studies on the effects of ACMV on yield have been undertaken, but several serious limitations are evident.

- Several of the 'Type A' experiments were small and omitted guard rows or provided inadequate separation between infected and uninfected plants. Thus edge, competition and compensation effects could have been important and may have influenced the results obtained.
- In 'Type B' experiments it is not always possible to select a sufficient number of plants of each of the categories required for statistical comparison. Moreover, because there is no guarding the growth and yield of the plants selected is likely to be influenced by competition or shading from their immediate neighbours, which will depend on their health status and overall vigour.
- 'Type B' experiments have been used to determine the effects of ACMV introduced by whiteflies at different stages of crop growth. However, insect vectors do not alight indiscriminately on plants within a stand and those plants that do become infected with ACMV may be an unrepresentative sample. Edge effects are known to be important from studies in Côte d'Ivoire in which whitefly populations and virus incidence were greatest around patches of bare ground and at the margins of plantings, especially those across the direction of the prevailing wind (Fargette *et al.* 1985, 1990). Moreover, vectors may alight preferentially on the largest plants within a stand (for example, plants may be larger than average in localized areas or near the margin of the planting). There is no evidence of this for *B. tabaci*, but other whitefly species in South America that are not known to be vectors of ACMV occur in greatest numbers on large, vigorously growing plants (Gold *et al.* 1990).
- Only few, and mainly small, unguarded experiments of limited duration have been performed with the improved ACMV-resistant types now being promoted in many African countries. Information is limited or entirely lacking on several of the TMS varieties that are being released in quantity to farmers or for use as parents in national breeding programmes.
- No information whatsoever has been published on the effects of ACMV on populations of plants containing different proportions of infected individuals, even though this is the usual field situation. This is a serious omission because on *a priori* grounds competition and compensation effects are likely to be important, as discussed later.
- Several workers have related the decrease in yield caused by ACMV to a reduction in leaf area (Cours 1951; Beck and Chant 1958; Vandevenne 1975; Dengel 1980). However, the extent to which other factors are involved is unclear. Some of the deleterious effects are probably associated with the impaired efficiency of leaves affected by mosaic and varicus changes have been reported in chloroplast structure, chloroplast number, chlorophyll content and rates of photosynthesis (Chant and Beck 1959; Chant *et al.* 1971; Ayanru and Sharma 1982).

- The analysis and interpretation of the results of 'Type A' experiments can be complicated if many of the control plants are infected with ACMV by whiteflies that move into or within the experimental area, as described in several of the Nigerian trials (Beck and Chant 1958; Anon. 1979, 1980, 1981; Terry and Hahn 1980; Terry 1982).
- In only one experiment (Seif 1982) has there been any attempt to standardize the virus strain used in the study. All other trials have used plants already infected as cuttings or those infected naturally by whiteflies. Whether these plants were infected with strains of the East or West African forms of ACMV was not determined as this distinction has only recently been made (Hong *et al.* 1993).
- No attention has been given to possible differences in virulence between the two ACMVs or virus isolates or to the possibility that some isolates are much more damaging in their effects on yield than others.
- Experiments have not been undertaken at different spacings to determine whether increasing the plant population is a means of decreasing or avoiding the losses caused by ACMV. This is possible because there is some evidence from physiological studies that optimum yields of cassava per unit area of land are dependent on the establishment of a continuous crop canopy, which is difficult to achieve quickly using infected plants at conventional spacings.
- Little attention has been given to the effects of soil fertility and nutrient status on the losses caused by ACMV.
- All the experiments reported have involved monocultures, regular spacing and weed control, whereas cassava is usually grown in Africa at irregular spacings and intermixed with various other crops in which weeds occur. The presence of other crops and weeds is likely to modify the effects of ACMV on growth and yield depending on such factors as spacing, planting date, the timing and efficiency of the weed control measures adopted and overall soil fertility. In some circumstances the impaired growth of ACMV-infected plants could be unimportant or even beneficial if associated with enhanced yields from other components of the cropping system.
- Previous studies have not considered possible interactions with other pathogens such as bacterial blight (*Xanthomonas campestris* p.v. *manihotis* Berthet & Bondar: Dye) or arthropod pests of cassava of which cassava mealybug (*Phenacoccus manihoti* Mat.-Ferr.) and cassava green mites (*Mononychellus tanajoa* Bondar and others) are the most important. This is a serious omission because there are indications that the deleterious effects of cassava mealybug and green mites are greatly influenced by the vigour of their host, which is seriously impaired by ACMV. Moreover, a correlation has been reported between resistance to ACMV and to bacterial blight so that the two diseases tend to occur together and are most severe on a similar range of varieties (Hahn *et al.* 1980a).
- Little attention has been given to the effects of ACMV on leaf number, size and palatability, even though leaves are used widely for human consumption in many African countries. Indeed, in several countries (including Zaire) leaves are the

main source of dietary protein and crops grown for their leaves can be worth much more than those used solely to produce tuberous roots (Lutaladio and Ezumah 1981; Almazan and Theberge 1989). ACMV is likely to decrease leaf production and leaf quality, especially in sensitive varieties in which leaf area is greatly decreased and the most severely damaged leaflets are little more than expanded mid-ribs.

Competition and compensation

The complex situation that can arise in mixed stands of infected and uninfected plants is illustrated diagramatically in Figure 3. The yields of totally infected and uninfected stands are represented by Y_{min} and Y_{max}, respectively. The straight line joining the two points indicates the yields to be expected from mixed stands of infected and uninfected plants in different proportions, *assuming that there is no interference between infected and uninfected plants*. However, this assumption is not justified as the yield of infected plants is likely to be decreased by the presence of uninfected neighbours, because these are more vigorous and so compete more successfully for available water, nutrients, space and light.

If such compensatory growth occurs the line joining Y_{max} and Y_{min} becomes curvilinear and convex, and there will be a critical incidence of infection below which ACMV has negligible effects on the overall yield of the stand. Moreover, the critical incidence is likely to depend on spacing, variety, croppage and growth conditions and will also be influenced by the disposition of infected plants within the stand. Compensation will be most likely to occur with vigorous multistemmed varieties at close spacings and in favourable growing conditions. It will also be most marked if

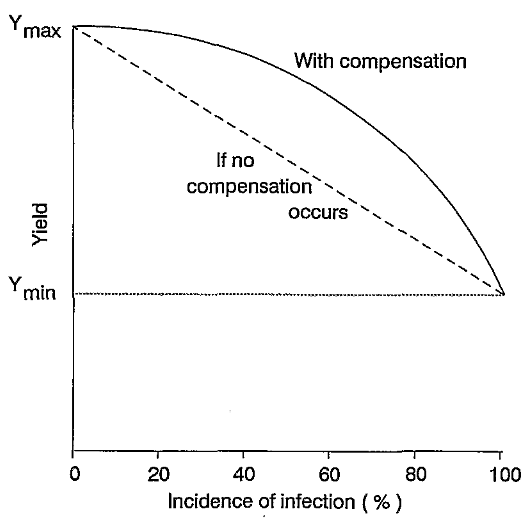

Figure 3. Yield loss in relation to the percentage of infected plants within a stand. A straight line relationship is to be expected if uninfected plants do not compensate for the impaired growth of their infected neighbours, whereas the relationship will be curvilinear and convex if compensation occurs. Redrawn from Reestman (1970).

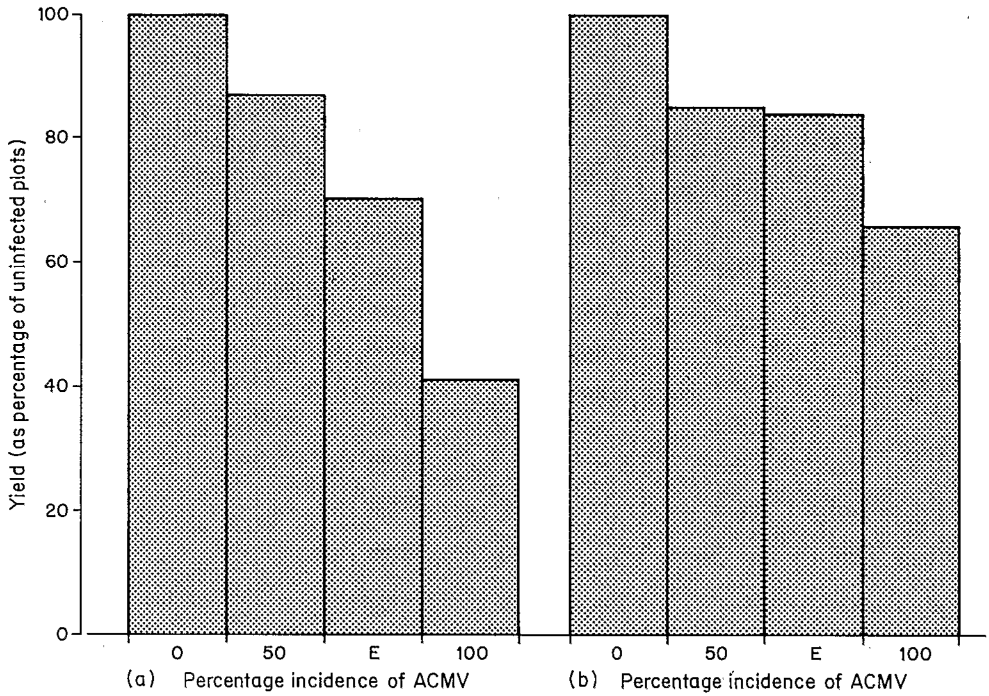

Figure 4. Mean yields of the Ugandan varieties Bao (a) and Bukalasa 11 (b), 15 months after planting in replicated plots with 0% and 100% incidence of ACMV and in 50% plots in which equal numbers of infected and uninfected plants were arranged alternately. The columns marked E indicate the yields to be expected of the 50% plots if the infected and uninfected plants behaved as in pure stands and no competition or compensation effects occurred. All yields are expressed as percentages of uninfected plots. Data from G. W. Otim-Nape (unpublished data).

infected plants are dispersed at random, but not if they are in large groups so that only a small proportion are alongside and influenced by uninfected neighbours.

These concepts as illustrated in Figure 3 are well known to crop physiologists and feature in the literature on crop loss assessment due to pests and pathogens including viruses (Reestman 1970; Zadoks and Schein 1979; Bos 1982). However, their applicability to studies on ACMV has not been assessed and the only relevant publication is that of Fargette *et al.* (1988) who noted that the yield of plants infected as cuttings was greater when grown in groups than when grown with uninfected neighbours. This indicates that competition effects occur within partially infected stands of cassava, and evidence of this has been obtained in recent experiments in Uganda (G. W. Otim-Nape, M. W. Shaw and J. M. Thresh, unpublished data). In one of the three varieties studied in two successive experiments, uninfected plants almost completely compensated for the impaired growth of their severely affected neighbours. The yields of plots of the Ugandan variety Bao established with equal numbers of infected and uninfected cuttings planted alternately were little different from plants established solely with uninfected cuttings (Figure 4a). There is an obvious need for further experiments and for collaboration with crop physiologists to establish a comprehensive series of experiments with different varieties and spacings and with different proportions of infected plants ranging from 0 to 100% and in various spatial configurations.

It is particularly important to include virus-resistant varieties in such experiments because of the current uncertainty concerning their ability to withstand the effects of ACMV. These varieties do not all behave in the same way, but collectively they have several attributes which contribute towards their resistance (Rossel *et al.* 1992). For example, they are less readily infected than the usual varieties grown and they develop less severe symptoms, especially during the later stages of crop growth. Virus and symptoms may be localized to certain shoots, the others growing normally. Indeed, some plants recover completely from infection and may give rise to a proportion of uninfected cuttings when used for further propagation. An important consequence of this behaviour is that clones of resistant varieties are never totally infected, even when grown repeatedly in areas of high infection pressure (Fargette *et al.*, this volume, p. 123). Only a proportion of plants within a stand develop symptoms, and these tend to be restricted and inconspicuous. In such circumstances the detrimental effects of ACMV on yield are likely to be much lower than in stands of the usual varieties grown. Indeed, there may be little or no benefit to be gained from adopting ACMV-free planting material or from practising selection and roguing. These control measures have been strongly advocated as being applicable to all varieties but they are not widely adopted by farmers and are difficult to implement on a large scale.

Discussion

There is abundant evidence from the studies summarized here that ACMV greatly decreases the growth and yield of many locally grown African varieties. It is also evident that the losses sustained depend on variety and are greatest when plants are totally infected from the outset as cuttings. However, there is little information on the effects of ACMV in mixed stands of infected and uninfected plants in which compensation and competition effects are likely to be important. Definitive information on the effects of ACMV on the yield of the improved ACMV-resistant varieties now available or being introduced in many countries is also lacking. These are serious deficiencies and make it impossible to provide valid estimates of overall crop losses or to assess whether ACMV-free planting material and other control measures are justified if resistant varieties are adopted.

It would be an important development (and the work of the extension services would be greatly facilitated) if it can be shown that sanitation and other control measures are unnecessary if the varieties grown are suitably resistant. However, such evidence has not been sought and the few experiments performed (with only some of the resistant varieties available) have been small, restricted to few sites and with inadequate separation between plots. They have not considered compensation effects within stands and the possibility that overall yields are unaffected even though the productivity of a proportion of the plants is impaired because of virus infection.

Experiments to consider these effects are long overdue but there are two important constraints, even if the necessary personnel and facilities are available for such studies. One is that the experimental sites must be in areas where there is little or no spread of ACMV by vectors, as this would vitiate the comparison of infected and uninfected material. The other constraint is that adequate stocks of planting material of a wide range of improved and unimproved varieties must be available in ACMV-infected and uninfected condition. Few research centres seem able to meet these requirements, and at IITA in Ibadan rapid spread of ACMV occurs to all but the most resistant varieties and ACMV-free stocks of material are not available in quantity. The situation is more satisfactory in parts of East and Central Africa, including the upland areas of Malawi and the southern area of Uganda, in which the Namulonge Crop and Livestock Research Institute is based. Observations in recent years have shown that there is little spread of ACMV by vectors at Namulonge, where many local and improved varieties are available for study including several of the TMS series (G. W. Otim-Nape, unpublished results). They are now being used in a comprehensive series of experiments on the effects of ACMV on yield. The results will have an important bearing on the most appropriate control strategy to adopt and on the way in which resistant varieties should be deployed – not only in Uganda but also elsewhere.

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