Chapter 5

Viruses affecting African crops and their vectors

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1 Introduction

1.1 The importance of plant virus disease in Africa and elsewhere

Viruses and the diseases that they cause are one of the major constraints to global agricultural production. In Africa, problems are particularly acute since control methods are either not available or not readily accessible to farmers. Surprisingly, the first steps towards researching crop virus diseases in Africa were taken more than a century ago. Towards the end of the nineteenth century, the disease condition 'Kräuselkrankheit' was recorded, which was later shown to be caused by the viruses causing cassava mosaic disease (CMD). Around the same time, in South Africa, Claude Fuller made reference in his 'First Report of the Government Entomologist. 1899-1900. Natal' to a variegated 'mealie' (= maize) condition. Although at the time he misinterpreted the cause of this, it was subsequently recognized as the first published observation of maize

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streak disease (MSD). Although the first crop virus was described as early as 1898 (Beijerinck, 1898), it was not until the 1920s/30s that the first reports were made of viruses as the causal agents of plant disease in Africa (Storey, 1936a - MSD; Storey, 1939b - CMD; Jones and Mason, 1926 - Cotton leaf curl disease, CLCuD). Also, at around this time, researchers began to conduct the earliest experiments to confirm that the plant viruses causing these diseases were transmitted by insect vectors (Kufferath and Ghesquière, 1932 - CMD; Kirkpatrick, 1931 - CLCuD; Storey, 1939a - MSD).

In more recent years, the magnitude of importance of many of the viruses affecting crops grown in Africa has been demonstrated. In a recent review of the 'top ten viruses' with respect to their global impact (Rybicki, 2015), it can be noted that many on the list either only occur in Africa or have their major impacts in Africa. This list includes the cassava mosaic begomoviruses (CMBs), maize streak virus (MSV), banana bunchy top virus (BBTV), banana streak virus (BSV) and sugarcane mosaic virus (SCMV, which affects maize). In addition, the major impact of cassava brown streak disease (CBSD) caused by cassava brown streak ipomoviruses (CBSIs), particularly since 2004, was recognized as Pennisi (2010) included this in a report in *Science* as one of the seven greatest plant disease threats to food security in the world.

1.2 Progress in research into major African crop viruses

IITA has since its inception in 1967 aimed to contribute to the reduction of poverty in Africa through research for development targeting several major crop staples. These 'mandate' crops comprise banana/plantain, cassava, cowpea, maize (in the lowlands of West Africa), soybean and yam. All of these crops are affected by several viruses, although the effects range from major losses with occasional localized devastation, to symptomless infections that have no detectable effect on yield. In this chapter we will discuss primarily the most important of the viruses and the diseases that they cause. Our discussion is not intended to be a technical examination of the viruses affecting IITA's mandate crops, but rather a review of the progress that IITA and its partners have made in enhancing understanding of these virus diseases and delivering effective control measures to farmers. The pathosystems that have been selected include:

- Banana/plantain: banana streak virus - mealybug vector; banana bunchy top virus - aphid vector
- Cassava: cassava mosaic and cassava brown streak viruses - whitefly vector
- Legumes: cowpea aphid-borne mosaic virus and soybean mosaic virus - aphid vectors
- Yam: yam mosaic virus - aphid vector

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During the 50 years that IITA has been working towards its mission, there has been significant progress made in improving knowledge of these important viral pathogens. This is illustrated with the results of searches on Elsevier's Scopus database, which is one of the largest repositories for published articles (Fig. 1). The largest number of published documents available for five viruses/virus groups are: BBTV, BSV, CMBs, MSV and SMV (Fig. 1a), whilst those for which there are relatively less published articles are CBSIs, CABMV, the viruses causing MLN and YMV (Fig 1b). What is evident in all cases, however, is the

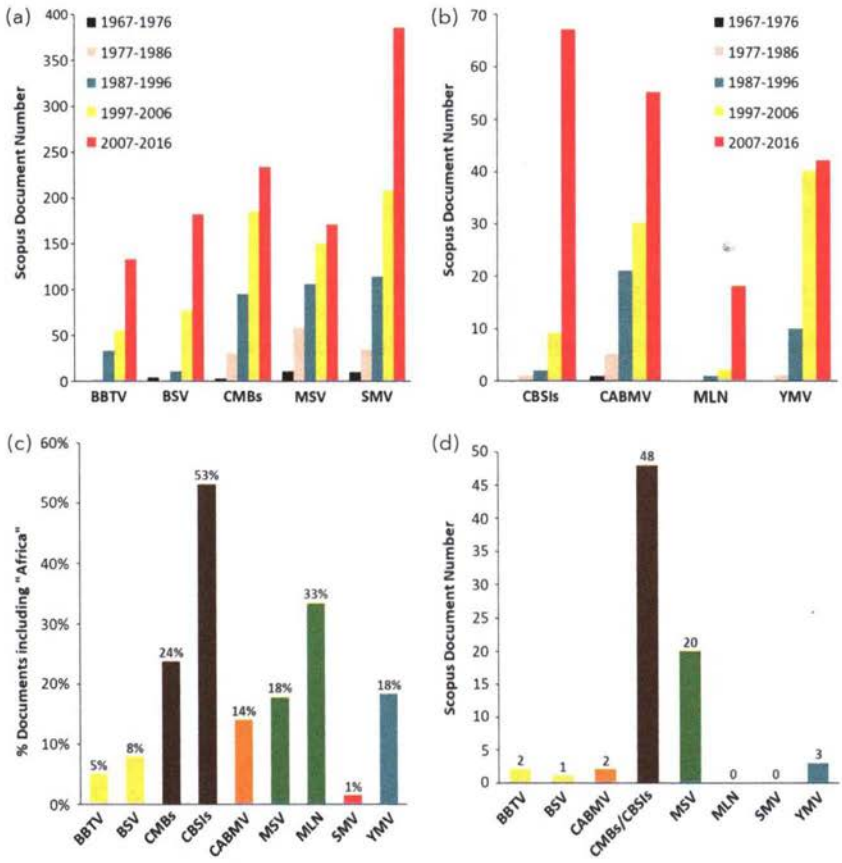


Figure 1 Number of publication references in the Scopus (Elsevier) database for selected important plant viruses. Searches queried for title, abstract and keywords. (a) Five viruses with most published documents. (b) Four viruses/virus diseases with least published documents. (c) Proportion of documents referencing each of the nine viruses/virus diseases in which the term 'Africa' was included for the period 1960–2017. (d) Number of published documents for each of the viruses/virus disease where the terms 'Africa' and 'Vector' were both included: a measure of the amount of vector research on each of the pathosystems.

large increase in the volume of published research, decade-on-decade, from 1967 to 2016. The most rapid increases in publishing frequency over the last decade (2007–16) have been recorded for MLN and CBSIs, both of which are notable in having experienced rapid epidemiological expansions in recent years. Since the documentary records of publications are not restricted to Africa, an additional set of searches was run incorporating 'Africa' in the search query. The results generated through this (Fig 1c) highlight a strong Africa focus for publications on CBSIs, MLN, CMBs, MSV and YMV. All of these viruses/virus disease conditions either occur exclusively in Africa, or are of much greater importance in Africa than elsewhere. BSV and BBTD occur almost worldwide where bananas are grown, and SMV is of major importance in the Americas where most soybean production is concentrated. Finally, database searches using terms for the vector groups responsible for transmitting each of these virus groups reveal a heavy emphasis on research into the whitefly *Bemisia tabaci* (Genn.) (Hemiptera; Aleyrodidae), which transmits the two groups of cassava viruses, as well as the *Cicadulina* leafhoppers (Hemiptera; Cicadellidae) that transmit MSV (Fig 1d).

1.3 Structure of the chapter

As these observations demonstrate, the last 50 years has seen substantial change in the 'landscape' of plant virus research in Africa. In the following sections, which focus on specific pathosystems, we will further highlight the nature of these changes, and will emphasize the ways in which research methods and control measures have been adapted to cope with the strongly dynamic plant virus situation.

2 Cassava virus diseases

2.1 Introduction

Several groups of viruses have been recorded from cassava in Africa, and these have been described in detail in reviews (Calvert and Thresh, 2002; Legg et al., 2015). In this chapter we will consider only two groups, which are by far the most important. These groups are the CMBs and the CBSIs. The CMBs are from the genus *Begomovirus* and family *Geminiviridae*, while CBSIs are from the genus *Ipomovirus* and family *Potyviridae*. Nine species of CMBs have been recorded from Africa (Legg et al., 2015) but all are closely related and elicit the same mosaic symptoms in infected plants, which is why the disease caused is known as CMD. CMD has been reported from all territories of continental Africa where cassava is cultivated, and in part due to the extent of this distribution, is responsible for losses which have been estimated at more than US$1 billion annually (Legg et al., 2006). There are two species of CBSIs: *Cassava brown*

streak virus and *Ugandan cassava brown streak virus* (Mbanzibwa et al., 2011). Both species produce similar symptoms, which comprise a blotchy vein-associated chlorosis on lower leaves, occasional stem lesions, as well as areas of brown, dry, necrotic rot in mature tuberous roots (Nichols, 1950). CBSD was for many years confined to coastal East Africa and the shores of Lake Malawi, but since 2004 has spread more widely through East and Central Africa (Alicai et al., 2007; Legg et al., 2011). Losses due to CBSD have been estimated at US$ 75 million annually (Manyong et al., unpublished).

As is apparent from these figures, and the background provided in the introduction to this chapter, these are two of the most important groups of viral pathogens, not just in Africa, but in the global context. In the following three sections we discuss some of the key stages of research on cassava viruses in Africa.

2.2 'The resistance-breeding years'

Following the first reports of cassava viruses from East Africa at the outset of the twentieth century, there was a period during the 1920s and 1930s during which there was a 'flurry' of new disease reports for CMD in particular, throughout Africa. It was at this time that the first organized research was initiated into CMD in several parts of Africa, and CBSD in East Africa. First reports were made of the viral cause of CMD and CBSD (Storey, 1936b) and of the whitefly transmission of pathogens causing CMD (Kufferath and Ghesquière, 1932). A concerted breeding effort was launched by Storey and colleagues in Tanzania in 1937 to identify sources of resistance to cassava viruses (Nichols, 1947), and this gave rise to the 'Amani breeding programme'. This initiative, directed from the Amani Research Station, in Tanga Region, north-eastern Tanzania, aimed to introgress resistance into cultivated cassava (*Manihot esculenta* Crantz) from wild relatives. The most important of these turned out to be ceará rubber (*M. glaziovii* Müll.-Arg.). Third backcrosses to cultivated cassava from *M. esculenta* × *M. glaziovii* hybrids demonstrated high levels of resistance to both CMD and CBSD. Seed taken from resistant genotypes produced in this way was introduced to Nigeria where seedling and clonal evaluations were conducted which eventually resulted in the identification of the CMD-resistant clone TMS 58308 – selected in 1958.

It was this clone that provided the basis for the first significant research programme launched by IITA with a major focus on CMD, which was led by S. K. Hahn. Since TMS 58308 had poor quality roots and low yield, an initial task was to cross TMS 58308 with other genotypes with high yield potential and/or improved quality characteristics. In order to do this, Hahn and colleagues used a recurrent selection approach (Hahn et al., 1980). Although CMD work at IITA during this time was primarily focused on breeding for resistance, important

supporting research was conducted on other aspects of the pathosystem. Vector entomological studies demonstrated that the abundance of the whitefly vector – *B. tabaci* – was a key factor driving seasonal patterns of CMD spread (Leuschner, unpublished), and pathology research described the yield impacts of CMD and related the severity of CMD symptoms to components of yield (Terry and Hahn, 1980). One of the most straightforward but useful outputs of this period of research was the development of the 1-5 severity scoring system for CMD (Hahn et al., 1980), which continues to be universally used to this day. Some of the CMD-resistant cassava genotypes generated during this period continue to be the most widely disseminated and grown varieties. One important example is TMS 30572; first cloned in 1972, but still widely cultivated and continuing to retain an effective level of resistance to CMD. The proportion of IITA germplasm contributing to variety release in the national research programmes of African countries increased from 55% during the 1970 to 1979 period to almost 80% between 1980 and 1989, illustrating the scale of the Africa-wide impact of this resistance breeding effort.

2.3 'The surveillance and epidemiology years'

The second major 'era' of IITA's research on cassava viruses began following the shocking stories of cassava production collapse that emerged from Uganda during the early 1990s. Reports were received of CMD so severe, that plants became stalks, yields were reduced to almost nothing and people in northern Uganda were suffering from food shortages and localized famine (Otim-Nape et al., 1997; Thresh et al., 1994). At this time, only two species of CMB were known – based on serological studies – and these were *African cassava mosaic virus* (ACMV) and *East African cassava mosaic virus* (EACMV) (Swanson and Harrison, 1994). However, the arrival of new nucleic acid-based diagnostics using the polymerase chain reaction (PCR), together with affordable sequencing meant that it became possible to 'look inside' viruses and make comparisons between their genetic material. Although serological methods suggested that the usual ACMV was associated with the severe CMD occurring in northern Uganda, when PCR and sequencing methods were employed, it was demonstrated that an EACMV-ACMV recombinant hybrid virus was always present in areas affected by severe CMD (Zhou et al., 1997). Furthermore, the severest symptoms were the result of mixed infections of both ACMV and the new recombinant, which became known as EACMV-UG, or the 'Uganda Variant' (Harrison et al., 1997).

In spite of initial scepticism within the IITA breeding community about this new form of CMD, the institute initiated a new programme of research in partnership with Uganda's National Agricultural Research Organisation (NARO) to characterize, monitor and mitigate the impacts of this rapidly expanding epidemic of severe CMD. The programme was housed at IITA's Eastern and Southern Africa Regional Centre (IITA-ESARC), which was based at NARO's

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Namulonge Research Station, about 25 km north of Kampala. It soon became apparent that the severe CMD, which was associated with both EACMV-UG and unusually high populations of *B. tabaci*, was spreading through Uganda and into the neighbouring countries of Kenya to the east and Tanzania and Rwanda to the west.

In response, IITA launched a regional CMD pandemic mitigation effort, in partnership with NARS in each of the affected countries. This had the aims of monitoring the regional spread of severe CMD, forecasting future patterns of spread, identifying worst-affected regions, evaluating the best available CMD-resistant germplasm and working with NARS and local NGOs to multiply and disseminate planting material of CMD-resistant varieties to farmers. During this period, an extensive set of published data was compiled, including important contributions from Advanced Research Institutes in Europe and the United States, NARS researchers in affected countries, as well as IITA scientists. The extent and speed of the pandemic spread were characterized (Otim-Nape et al., 1997; Legg and Ogwal, 1998), regional risk maps were developed (Legg, 1999), the nature of virus-virus interactions causing severe disease were described (Pita et al., 2001), mild strain protection was demonstrated (Owor et al., 2004) and new studies characterizing CMBs were initiated in neighbouring countries, such as Tanzania (Ndunguru et al., 2005) and Kenya (Were et al., 2004).

As the pandemic spread through East and Central Africa, and the monitoring activities of IITA and partners tracked it, a series of 'first reports' were generated for countries newly affected (Legg et al., 2001 - Rwanda; Neuenschwander et al., 2002 - Republic of Congo; Legg et al., 2004 - Gabon; Bigirimana et al., 2004 - Burundi; Lava Kumar et al., 2009 - Angola; and Akinbade et al., 2010 - Cameroon). Major steps were made in pandemic mitigation during this period, and progress was facilitated by carefully managed germplasm introduction programmes to countries in the region using 'open quarantine' procedures. These sources of CMD-resistant varieties would provide the basis for massive multiplication and dissemination programmes which gradually increased in scale from the mid-1990s through to the end of the 2000s. A further crucial feature of the CMD research work of IITA during this period was capacity building at postgraduate level. Between 2000 and 2005, nine MSc and five PhD students from within the affected region were supervised specifically on cassava viruses and their whitefly vector. Several of these trained researchers have gone on to take up positions of considerable responsibility within their national research systems, which means that their training is having a transformative impact on agricultural research for development in this part of Africa.

2.4 *'The building quality seed system years'*

For seven decades, CBSD had been a problem of minor importance in Africa, being confined to the eastern coastal areas and the shores of Lake Malawi.

The situation changed dramatically, however, following reports of a new outbreak in 2004 in southern Uganda, at altitudes (>1000 masl) (Alicai et al., 2007) hitherto considered to be inimical to the survival and spread of CBSD (Nichols, 1950). In the years immediately following, the emerging pandemic of CBSD spread to Kenya, Tanzania, Rwanda, Burundi and eastern Democratic Republic of Congo (Bigirimana et al., 2011; Legg et al., 2011; Mulimbi et al., 2012). This spread was associated with large-scale losses in newly affected regions, an effect that was exacerbated by the fact that most of the locally available varieties were highly susceptible to this disease that had never previously been encountered.

In response, there was a rapid increase in the level of human and financial investment directed towards improving understanding of the disease and controlling the pandemic. For the first time this had become a truly African problem, as westwards spread threatened the major cassava production centres of Central and West Africa. Several of the young researchers who had been trained during the period of the CMD pandemic were able to transfer their newly acquired knowledge and skills to tackling this new challenge. The consequence was an unprecedented level of research output. This is clearly demonstrated by the Scopus publication data (Fig. 1b) which reveal that whilst there were only two publications on CBSD in the period 1987–96 (0.02/month), this number increased to 9 between 1997 and 2006 (0.08/month) and reached as high as 67 for 2007 and 2016 (0.6/month). Moreover, in the first ten months of 2017, there were 19 new CBSD publications in the Scopus database (1.9/month). It is significant to note that of these 19 papers, roughly half include authors who are students and half include either IITA scientists or NARS researchers who did their postgraduate training with IITA. These points highlight the research impact that is being realized through previous and ongoing capacity development efforts within the region.

CBSD produces symptoms that are not easily recognized, and infected plants may sometimes be completely asymptomatic. The practical consequence of this is that this disease is much more readily spread through infected planting material than CMD, which usually presents clear symptoms. In view of the potential for rapid hidden spread of the viruses causing CBSD through infected planting material, a key focus of CBSD pandemic management efforts has been to strengthen systems for the production, exchange and dissemination of near virus-free planting material. A 'Quality Management Protocol' was developed that prescribed tolerance levels for the major pests and diseases of cassava, as well as other quality characteristics for planting material. This was extensively applied through the USAID-funded Crop Crisis Control Project (C3P) in the six target countries of Burundi, Democratic Republic of Congo, Kenya, Rwanda, Tanzania and Uganda. Application of the protocol ensured that cassava multiplication

and dissemination work carried out through the project from 2006 to 2007 conformed to high quality standards and minimized the chance of inadvertent virus spread.

The need for these types of approaches became much more acute, however, during the period of operation of the larger Great Lakes Cassava Initiative (GLCI), which ran from 2007 to 2012. It was during this period that rapid new spread of CBSD was taking place through the Great Lakes region of East and Central Africa, which largely matched the target zone of the GLCI project. New virus testing protocols were introduced based on real-time PCR (Adams et al., 2013) and a zero-tolerance plan for CBSIs was initially recommended for movements of planting material from one multiplication site to other multiplication sites or farmers' fields. Eventually the impracticality of this extreme approach was recognized as large-scale virus testing was simply not feasible nor affordable and farming areas being served were in most cases so much worse affected than multiplication sites that it made no practical sense to ban movements of planting material from multiplication sites where there were very low levels of CBSIs.

A new model was therefore developed through the New Cassava Varieties and Clean Seed to Combat CMD and CBSD (5CP) project in which stringent yet pragmatic tolerance levels were set for each of the major cassava pests and diseases, including the CMBs and CBSIs. Most importantly, these levels were set in a consultative way with the involvement of the full range of cassava seed sector stakeholders, including farmers. Additionally, the process was managed by the national agency responsible for seed certification, which in Tanzania was the Tanzania Official Seed Certification Institute (TOSCI). With the twin aims of enhancing the quality of cassava planting material production and facilitating the emergence of commercially viable cassava 'seed' business within Tanzania, TOSCI succeeded in officially appending the new certification guidelines to the Government of Tanzania Seed Act on 17 January 2017. This provides specified tolerance levels for disease and other quality parameters for pre-basic, basic and certified levels of seed production, as well as specifying virus testing requirements and service charges payable by seed producers. Significantly, virus testing is only required for CBSIs at the pre-basic level. In view of the success of this programme, as well as parallel efforts implemented by NARO in Uganda, concerted efforts are currently being made by IITA, NARS and seed certification agencies in several other countries (Burundi, DRC and Rwanda) to deliver similar cassava virus management outcomes through high quality seed systems. An approach that combines the deployment of cassava virus-resistant varieties with effective systems for the management of seed health offers great promise for the sustainable management of cassava viruses in East/Central Africa and beyond.

3 Maize virus diseases

3.1 Introduction

Numerous viral diseases of maize occur in Africa, but that caused by *Maize streak virus* (MSV; genus *Mastrevirus*; family *Geminiviridae*) has been by far the most important and widespread (Thottappilly et al., 1993) since it was first reported more than a century ago. In more recent years, however, Maize lethal necrosis (MLN), also known as Corn lethal necrosis, has spread through East and Southern Africa following the introduction through infected seed of *Maize chlorotic mottle virus* (MCMV; genus *Machlomovirus*; family *Tombusviridae*). The MLN condition results from the synergistic interaction of MCMV with *Sugarcane mosaic virus* (SCMV; genus *Potyvirus*; family *Potyviridae*). SCMV is endemic in Africa, but MCMV seems to have been recently introduced, most probably from the Far East.

3.2 The period of research into MSV (1980s-1990s)

Early years of research at IITA on MSV examined the epidemiology of the virus, interactions with its leafhopper vectors (*Ciccadulina* spp.) and managing the disease through resistance breeding. Vector aspects are examined in detail in the subsequent section on virus vectors. In this section we discuss epidemiology and control through host plant resistance.

MSV is widely distributed in sub-Saharan Africa (SSA) and adjacent islands (Thottappilly et al., 1993). Symptoms of MSV in maize first appear as small, spherical, chlorotic spots. As leaves expand streaks develop along the veins on most of the leaf but since the virus is systemic, symptoms appear only on the inoculated and subsequent leaves (Thottappilly et al., 1993). Symptom severity depends on genotype susceptibility and plant age at the time of infection (Bosque-Pérez et al., 1998). In highly sensitive varieties, chlorosis of the entire leaf lamina might be observed, followed by progressive necrosis and plant death, particularly if infection has occurred at an early plant growth stage. MSV reduces yield and growth of maize and in susceptible varieties yield reductions often exceed 70% (Bosque-Pérez et al., 1998).

MSV is a new encounter disease, which emerged after maize was introduced to Africa from the Americas over 400 years ago. It is believed that only some of the original isolates of this African virus were capable of naturally infecting maize plants (Bosque-Pérez, 2000). A shift from native grasses to maize would have required that both virus and leafhopper vectors expand their host ranges. Possibly, infection events occurred independently in various locations in Africa, from where further virus spread took place (Bosque-Pérez and Buddenhagen, 1999). With the expansion of maize cultivation across SSA, outbreaks then ensued and continue to occur sporadically.

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Epidemiological and ecological studies of MSV and its vectors were done by IITA scientists in the 1980s and 1990s. Characterization of 24 isolates originating from grasses and cereal crops in Nigeria revealed differences in virulence among the MSV isolates tested. Some of them caused mild symptoms similar to the original symptoms in grasses and were transmissible to maize only at low rates (Mesfin et al., 1992). Isolates from maize, *Brachiaria lata* (Schumach.), *Axonopus compressus* (Sw.) P. Beauv., *Dactyloctenium aegyptium* (L.) Willd., *Digitaria horizontalis* Willd. and *Setaria barbata* (Lam. Kunth) (all Poaceae) were identified as the most virulent in maize (Mesfin et al., 1992). Of the isolates studied by Mesfin et al. (1992), nine could not infect the maize cultivar Pool 16, which was known for its susceptibility to MSV in farmers' fields in West Africa. The authors concluded that some MSV isolates appear to be adapted to their grass hosts and that many grasses in West Africa would not be a source of maize-infecting isolates in the field (Mesfin et al., 1992).

Understanding the survival of the grasses that harbour vectors and MSV isolates capable of infecting maize during the dry season (November to March), particularly in low-lying hydromorphic soils (i.e. fadamas) was deemed critical for understanding MSV ecology and epidemiology (Bosque-Pérez and Buddenhagen, 1999). Perpetuation of MSV and its vectors during the dry season in West Africa appears to occur mostly in riverine areas and low-lying fields where there is residual moisture, and both maize and grass weeds are present. MSV outbreaks appear to occur only when favourable weather conditions allow vector survival and population build-up, and where MSV isolates capable of causing disease in maize occur in grass hosts (Bosque-Pérez, 2000). Based on host range, serological tests and symptom severity of isolates tested, Mesfin et al. (1992) concluded that weeds of importance in perpetuating epidemiologically competent MSV in Nigeria include the native annuals *S. barbata* and *B. lata* and the introduced perennial *A. compressus* (Asanzi et al., 1994). These weeds harbour MSV under field conditions, are prevalent in many areas of the country and in the humid forest zone are frequently found in hydromorphic areas (Mesfin et al., 1992). Additionally, leafhoppers were commonly found in farmers' fields on *S. barbata* and *B. lata*, but no indigenous perennial grass has been found in West Africa harbouring a maize-competent MSV strain (Bosque-Pérez, 2000).

In addition to ecological zone, incidence of MSV has been found to vary according to variety and planting date (Asanzi et al., 1994; Bosque-Pérez et al., 1998). Late season plantings (July to October) had higher virus incidence than early season ones (March to May) (Fajemisin et al., 1976). Additionally, maize cultivars differ in their ability to sustain virus disease. For example, the susceptible cultivar TZB-Gusau had a higher incidence of MSV in the field than the resistant hybrid 8321-21, which showed a relatively low incidence across locations, planting dates and years (Asanzi et al., 1994; Bosque-Pérez et al., 1998). Low field incidence in 8321-21 is in part due to non-preference for feeding by vectors (Mesfin and Bosque-Pérez, 1998).

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experienced extensive or complete crop loss (Wangai et al., 2012b). Infected plants are frequently barren and the ears formed are small, deformed and set little or no seeds, drastically reducing the yield. Maize grain yield losses ranging from 23% to 100% have been reported in Kenya (De Groote et al., 2016). The monetary value lost to MLN annually has been estimated at US$ 261 million in Ethiopia and US$ 198 million in Kenya (Marenya et al., 2018).

Each of the viruses associated with MLN can cause symptoms when present in a single infection. Symptoms depend upon genotype, age of infection and environmental conditions (Mahuku et al., 2015a). Symptoms are much more severe where there are mixed infections of MCMV together with a *Potyvirus*, the most commonly occurring of which is SCMV. This synergistic condition is what characterizes MLN and what makes it so damaging to the plant. The maize plant is susceptible to MLN infection at all stages of plant growth; the earlier the plant becomes infected, the greater the damage and the entire crop can frequently be killed before tasselling (Niblett and Claflin, 1978; Uyemoto et al., 1980, 1981; Wangai et al., 2012b; Makone et al., 2014).

MLN was first identified in the United States in 1976 (Niblett and Claflin, 1978). In Africa, the first outbreak of MLN was reported in 2011 in Bomet County in the Southern Rift Valley Region in Kenya (Wangai et al., 2012a). The disease subsequently spread to several other countries in East and Central Africa (Mahuku et al., 2015a,2015b; Lukanda et al., 2014; Adams et al., 2014). Some projections based on the current situation indicate that MLN could spread and intensify across Africa by 2020 which would result in a more significant impact on food security in the region (Isabirye and Rwomushana, 2016).

MCMV is transmitted mechanically and is also spread by several insect vectors including maize thrips (*Frankliniella williamsi* Hood) (Thysanoptera; Thripidae) (Cabanas et al., 2013; Jiang et al., 1992), maize rootworms (*Diabrotica undecimpunctata* (L.), *Diabrotica longicornis* (Say) and *Diabrotica virgifera* LeConte) (Coleoptera; Chrysomelidae), cereal leaf beetles (*Oulema melanopus* (L.)) (Coleoptera; Chrysomelidae), corn flea beetle (*Systena frontalis* (Fabricius)) (Coleoptera; Chrysomelidae) and *Chaetocnema pulicaria* F.E. Melsheimer (Coleoptera; Chrysomelidae) (Nault et al., 1978; Jensen, 1985; Reyes and Castillo, 1988). SCMV is spread by maize aphids. Also, seed transmission of MCMV has been reported (Jensen et al., 1991).

The best approach for the management of MLN is to employ integrated pest management practices encompassing the implementation of sound quarantine and phytosanitary measures, cultural control (such as a closed season, crop rotation and crop diversification), vector control using seed treatment followed by foliar sprays with contact insecticides, and host plant resistance, all supported by appropriate policy measures.

The use of seed that is free of the viruses that cause MLN is an effective strategy for managing MLN. All seed coming into a country should be certified

as MCMV-free, and there should be no movement of commercial seed from MLN endemic to unaffected countries. National plant protection organizations may also need to apply internal quarantine restrictions. Combining the enforcement of such regulations with measures to raise awareness amongst the public and within farming communities can help to reduce the spread of the disease.

Crop rotation and maize-free windows can be used to contain MLN (Uyemoto, 1983; Wangai et al., 2012b; Kiruwa et al., 2016). Rotating maize crops with a non-grass crop or non-cereals reduces the virus inoculum of both MCMV and SCMV. It is necessary to use good field sanitation methods, including weed control and burning grasses around the field to eliminate alternative hosts for potential vectors (Wangai et al., 2012b). Seeds should not be recycled; farmers should use clean and certified seeds. Furthermore, crop debris should not be moved around, as it represents a potential source of inoculum (Samson et al., 2014).

Reduction of vector populations through insecticide application is unlikely to have any impact on the disease unless applied consistently and over large areas. These conditions are difficult to achieve in the dense patchworks of smallholder plantings found in Africa. In Hawaii, chemical spraying at early establishment was deemed successful in mitigating MLN spread (Nelson et al., 2011). However, seed dressing can be effective, as this prevents secondary transmission of the viruses, but this is only practical in seed production fields.

The use of tolerant or resistant varieties is probably the most effective means of managing MLN. Superior resistance to MCMV is widely available in tropical maize seed stocks and provides the best control for this disease (Nelson et al., 2011). Ultimately, resistant varieties need to be developed for all agro-ecological zones because most maize producing areas are either affected or are vulnerable (Isabirye and Rwomushana, 2016). Although resistance to both MCMV and SCMV is available, no complete immunity has been observed. Preliminary studies on the inheritance of MCMV resistance suggest a polygenic control of the disease, with resistance being partially dominant (Gowda et al., 2015). A similar situation has been observed for SCMV and other potyviruses (Jones et al., 2011). This encourages the commercial production of hybrids only if both parents are resistant to the pathogen. As the symptoms of MLN are due to co-infection with two viruses, resistance against any one of the viruses can substantially reduce the damage due to the disease. In the long run, deployment of varieties that are resistant to both MCMV and SCMV will be the best means of managing MLN. Through breeding, resistance to MCMV can be incorporated into susceptible maize varieties within a 4-year period. National and international programmes should intensify efforts to introgress MLN resistance into the commercial genetic pools in all countries including those that are not yet affected by MLN.

MLN continues to be a major threat to maize production in Africa. Effective management of the disease will require a rigorous surveillance system for MCMV, awareness creation of farmers and seed producers of the impending threat and policy regulations to minimize movement of seed from MCMV endemic areas. Research is needed on vectors of MCMV, vector biology, epidemiology, ecology, molecular biology and effective management strategies. Levels of resistance to the viruses among all varieties of maize grown in the region and the available germplasm are also low. Continued efforts are therefore required to understand the mechanisms of resistance to MCMV and to develop MLN-resistant maize varieties, and to have these deployed in both affected and threatened regions.

4 Banana and plantain virus diseases

4.1 Introduction

Banana virology at IITA commenced in the 1990s at around the time of reports of the integration of *Banana streak virus* (BSV; genus *Badnavirus*; family *Caulimoviridae*) genomic sequences into the genome of *Musa* and its implications on international germplasm distribution and banana breeding programmes (Harper et al., 1999). Of about 20 different viruses reported to infect *Musa* worldwide, the bulk of the IITA virology work was focused on BSV, responsible for 'leaf streak', and *Banana bunchy top virus* (BBTV; genus *Babuvirus*; family *Nanoviridae*) responsible for bunchy top (Kumar et al., 2015). Details of achievements on BSV and BBTV are presented in Chapter 10. In this section, a synthesis of the IITA banana virology programme is presented to highlight the focus based on the emerging priorities and future directions.

The objectives of the banana virology programme have changed over the course of time. Initial research was focused on the diagnosis of banana viruses to support the production of virus-free tissue culture clones for international distribution. The discovery of BSV genomic sequence integration into the *Musa* genome led to an increase in the scale and coverage of banana virus research at IITA from the mid-1990s to 2005. This involved a focus on several key elements of BSV research. These included understanding the biological significance of BSV integration on plant performance, breeding and banana micropropagation, as well as the development of reliable tools for detection of episomal (replication form) BSV infections in banana. The discovery of BSV genome integration halted the distribution of *Musa* germplasm in the 2000s, especially newly bred synthetic banana and plantain hybrids, as well as the BITA and PITA series clones developed by the IITA *Musa* breeding programme in West Africa. This situation restricted the progress of *Musa* improvement for several years. After 2008, however, IITA adopted a new strategy to distribute *Musa* clones within Africa based on the African Union

Inter-African Phytosanitary Council (AU-IAPSC) guidelines that allowed the distribution of clones with integrated BSV, with informed consent. This step provided momentum and reinvigorated banana improvement efforts. The IITA protocol was later adopted at global level in 2015 for the international distribution of *Musa* clones (Thomas et al., 2015). Subsequent to this work on BSV, the research focus shifted to BBTV, which emerged as a serious threat to *Musa* production in Southern and Central Africa. The research work on BBTV since 2008 has represented the core of banana virology research at IITA. Banana virus diagnostics and the production of virus-free planting material continue to be key components of the virology programme, and these also enable IITA to fulfil its role as an internationally recognized source of *Musa* germplasm.

Objectives of the current programme are to map the distribution and diversity of BBTV in Africa, to understand virus-host-vector interactions, to characterize the diversity of the banana aphid (*Pentalonia nigronervosa* (Coquerel) (Hemiptera; Aphididae)) that vectors BBTV, to elucidate the role of endosymbionts in banana aphid biology, to design biocontrol approaches for banana aphid management, to develop versatile diagnostic tools for application under lab and field conditions, to establish improved procedures for the production of virus-free *Musa* planting material and to develop BBTV-resistant clones using conventional and transgenic approaches. The virology programme is well equipped to diagnose all viruses reported to infect banana around the world and endowed with excellent capacity to develop new diagnostics and conduct virus discovery research using next-generation sequencing-based approaches.

4.2 Future prospects

Of about 20 different viruses reported to infect *Musa* worldwide, BBTV, BSV and *Cucumber mosaic virus* (CMV; genus *Cucumovirus*; family *Bromoviridae*) are known to occur in all or several *Musa*-producing countries in Africa, whereas *Banana bract mosaic virus* (genus *Potyvirus*; family *Potyviridae*) is confined to a few countries in Asia and has not been reported from Africa (Kumar et al., 2015). IITA research work has mainly focused on BSV and BBTV owing to their importance to banana and plantain production systems in Africa. An important achievement has been to break the decade-old impasse on *Musa* germplasm distribution through advocating for a pragmatic approach, which was supported by the AU-IAPSC guidelines for *Musa* germplasm distribution and which was eventually accepted as the global standard. This work has had the important spin-off benefit of reviving the *Musa* improvement programme at IITA, whose success and relevance hinged on having a safe but effective system for the international distribution of clones.

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While BSV posed technical challenges, the real impact on *Musa* production has been caused by BBTV, an aphid-transmitted virus that has now spread to 16 countries in Central, Southern and West Africa. IITA initiatives have contributed to the establishment of the status of the disease and factors contributing to its spread (Kumar et al., 2011), which eventually led to the development of a continental strategy to contain BBTV spread and restore banana production. This approach termed the 'ALLIANCE against BBTV in Africa', which is co-led by IITA, Bioversity International and CIRAD, is an important priority R4D theme for the Roots, Tubers and Bananas Programme of the CGIAR (CRP) (www.bbtvalliance.org). A multi-pronged approach is being used to tackle BBTV together with a range of national and international partners in SSA.

An important component of this approach is the search for durable host resistance. Recent advances in *Musa* genomics and new phenotyping methods are ushering in new hope for sustainable alternatives to current management approaches which involve cultural methods such as the eradication and replanting of infected mats with clean planting material obtained from virus-indexed source material. IITA and the ALLIANCE team are poised to achieve these milestones in the near future. Capacity development, especially training in the application of diagnostics, clean planting material production and surveillance procedures, remains a key requirement for the strengthening of future banana virus management efforts. Postgraduate students and national research programmes remain key partners with the banana virology programme for collaborating in research as well as disseminating knowledge and technologies to partners. Finally, in order to achieve the greatest improvements to banana productivity and the optimum use of limited resources, IITA needs to develop an integrated banana disease management strategy. In addition to tackling viral pathogens and the vectors that spread them, this should also address the major bacterial (banana *Xanthomonas* wilt) and fungal (*Fusarium oxysporum* f. sp. *cubense* Tropical Race 4) diseases.

5 Yam viruses

5.1 Introduction

Several species of yams are cultivated by farmers for their edible starchy tubers. The white yam (*Dioscorea rotundata* Poir.) dominates production in the West African yam belt, followed by water yam (*D. alata* L.) and several other less important species such as *D. cayenensis*, *D. esculenta* (Lour.) Burkill, *D. dumetorum* (Kunth) Pax and *D. bulbifera* L. Yams are propagated vegetatively using tubers. Mosaic disease caused by virus infection of yam is one of the leading contributors to low tuber yields in the yam belt which is the main target area for IITA's yam improvement programme. The yam belt, stretching from the

west of Cameroon to Ivory Coast is the world's largest food yam production zone, accounting for about 95% of the global production (FAO, 2016). Research into yam viruses began at IITA in the 1980s and focused on characterization of viruses, development of diagnostic tools for virus detection and breeding for *Yam mosaic virus* (YMV) resistance in *D. rotundata*.

5.2 Yam virus disease aetiology, epidemiology and effects on yield

Various survey studies since the 2000s have revealed that the viruses causing disease in yams in the West African yam belt belong to three genera. The virus species and their genera are YMV and *Yam mild mosaic virus* (YMMV) (previously known as *Dioscorea alata virus*) (genus *Potyvirus*); CMV; and a complex of several yam badnaviruses (YBVs) belonging to the genus *Badnavirus* (Eni et al., 2008; Turaki et al., 2017). All of these viruses have insect vectors. The vectors are aphids for members of the genus *Potyvirus* and *Cucumovirus* and mealybugs for members of the genus *Badnavirus*. The significance of vector transmission is yet to be elucidated.

YMV is most prevalent and known to reduce yields by up to 60% in most of the yam varieties. Vegetative propagation, sequential re-use of farmer-saved seed yams, farmer-to-farmer seed exchange and the informal seed trade have contributed to the wide dissemination of virus-infected seed yams and consequent spread of yam viruses in West Africa. Surveys conducted in the 2000s confirmed a virus incidence of >80% in white yam and an overall prevalence of >90% in the yam belt (Eni et al., 2008). Virus infection therefore is a threat to both plant and seed health. Durable virus resistance was not available in cultivated yam landraces. The production and supply of virus-free seed yams was prioritized as a tactic to control virus diseases in West Africa. In support of this effort, a major thrust was placed on the development of reliable diagnostic tools for yam viruses necessary for seed health indexing and certification. This work was implemented through the Yam Improvement for Income and Food Security in West Africa (YIIFSWA) Project. Since 2012 this work has resulted in the development of a range of diagnostic tools for the detection of viruses in the field and lab, including conventional PCR-based assays as well as isothermal methods such as Loop-mediated Isothermal Amplification (LAMP) (Nkere et al., 2018) and Recombinase Polymerase Amplification (RPA) (Silva et al., 2018) methods for the detection of YMV, YMMV and CMV. The rolling circle amplification method has been used for the detection of badnaviruses whose genomes are known to be integrated into the yam genome (Bömer et al., 2016). Methods for the production of virus-free plants were also established to support the production of clean seed (Balogun et al., 2017). More details about clean seed systems are given in Chapter 9.

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5.3 Seed degeneration

Seed degeneration is one of the major challenges to clean seed systems. Virus-free seed introduced to the field gets re-infected by viruses as all the released cultivars are susceptible to viruses. To help improve the situation various on-farm management approaches such as 'positive selection' are being implemented, by selectively harvesting seed from healthy plants for replanting. This approach is effective but laborious and not readily practised by farmers. Therefore, increasing efforts are being made to augment host resistance through breeding. Systematic screening of yam landraces conserved in the IITA Genebank identified promising YMV-resistant sources which are being exploited as parents for breeding (Mignouna et al., 2002). This work is being continued as part of the AfricaYam Project.

5.4 Future prospects

There has been significantly less donor investment in yam research and development than for other African food staples such as bananas, cassava and maize. This has resulted in relatively less progress in virus research on this crop. Core support in the early years focused on breeding initiatives, although interest in screening germplasm for the major pests and diseases did generate valuable knowledge on the relative importance of viruses and their impact on yield reduction, prompting a stakeholder consultation in the West African sub-region and subsequent baseline studies in the 2000s. These efforts have demonstrated the high value and importance of yams to West African livelihoods and led to major new project investments such as the YIIFSWA and AfricaYam Projects, which have in turn led to strong progress in the development and application of state-of-the-art diagnostics and new breeding approaches. However, all ongoing efforts on yam viruses are focused on West Africa, and Nigeria in particular. Although, yam production is less significant in other parts of the world, a basic understanding of virus threats is necessary for surveillance and to support clean seed production programmes.

6 Cowpea viruses

6.1 Introduction

Cowpea (*Vigna unguiculata* (L) Wallp.) is an annual legume that was first domesticated in Africa and is widely cultivated in semi-arid tropical West Africa for its protein-enriched seed for human consumption and the haulms that are used as fodder for livestock (Boukar et al., 2013). Although the crop is grown in all parts of the tropics and sub-tropics, the most intensive cultivation is confined to Nigeria, Niger and Burkina Faso, which collectively represent 81% of the

total global production of 12.3 million ha (FAO, 2016). Viral diseases in cowpea have been recorded wherever it is cultivated (Hema et al., 2014). IITA initiated virus research on cowpea in the late 1970s with a focus on (i) distribution and diversity of viruses infecting cowpea in West Africa, (ii) breeding for virus disease resistance and (iii) development of diagnostic tools, especially for virus indexing and production of virus-free seed stocks for conservation and international distribution of cowpea genetic resources.

6.2 Understanding the diversity of viruses infecting cowpea in the field

Surveys of cowpea virus diversity confirmed the occurrence of at least ten virus species belonging to seven genera in West Africa among the more than twenty viruses recorded in cowpea around the world (Atiri et al., 1984; Biemond et al., 2013; Shoyinka et al., 1997; Thottappilly and Rossel, 1992; Hema et al., 2014). All the cowpea-infecting viruses detected in West Africa are known to have broad host ranges and infect other cultivated legumes, weeds and wild plants. Natural spread of these viruses in the field is through insect vectors and seed. However, exceptions are CGMV and SHMV, which are not seed-transmitted and SHMV which is not known to have any insect vector. The same insect vectors are involved in the transmission of diverse cowpea viruses albeit with different transmission mechanisms. CMMV, CYMV (genus *Comovirus*; family *Secoviridae*), CpMoV (genus *Carmovirus*; family *Tombusviridae*) and SBMV (genus *Sobemovirus*; family unassigned) are transmitted by leaf beetles (*Chrysomelidae* family), whereas the whitefly (*Bemisia tabaci*) transmits CGMV (genus *Begomovirus*; family *Geminiviridae*) and CPMMV (genus *Carlavirus*; family *Betaflexiviridae*), and aphids (*Aphis craccivora* Koch) are involved in the transmission of BCMV-BlCMV and CABMV (genus *Potyvirus*; family *Potyviridae*) and CMV.

The involvement of similar vectors in transmission often results in multiple infections in cowpea as revealed in several survey studies. Of the ten viruses, the most economically important ones are BCMV-BlCMV and CABMV which were found to occur in every season and which cause significant yield loss in either single or mixed infection with any other cowpea virus, especially in the presence of CMV. These infections can sometimes result in the premature death of the plant. The incidence of other viruses is known to be sporadic, although infections of these viruses, especially at early stages of growth, can result in significant reduction in yield. A peculiar case is that of CMV and CMMV which in single infection are either asymptomatic or produce only mild mottling symptoms, in spite of high virus titres in the plants. The knowledge of virus diversity has been used for planning strategies to breed for resistance to BCMV-BlCMV and CABMV, and for the development of diagnostic tools for all of the

viruses, regardless of their economic significance. The effective application of diagnostics supports germplasm exchange as well as quality seed production (as described in detail in Chapter 3).

6.3 Several viruses, one disease and the unpredictability of virus diversity in cowpea fields

When cowpea is infected by different viruses, the result is a 'mosaic disease' typified by mild to severe mosaic and yellowing symptoms on leaves. There may also be mild to severe stunting and 20–80% reduction in grain yield. Virus disease symptoms are severe in plants infected at an early stage and result in the most serious losses. Symptom type and severity is influenced by cowpea genotype and time of infection. Considerable variation in incidence and distribution of cowpea viruses were observed within and between seasons and in different cowpea growing areas (Shoyinka et al., 1997). For instance, SBMV incidence and prevalence was highest in Nigeria in surveys conducted in 1991, although this virus was not detected in surveys conducted in 1992, and its incidence was very low in 1993 (Thottappilly and Rossel, 1992). Similar situations were observed for other viruses, complicating the prediction of field virus incidence. Although extensive epidemiological investigations still need to be carried out, the type of virus and incidence observed in cowpea fields seems to depend on the seed-borne virus inoculum, vector spread and alternative hosts or volunteer plants from the previous crop (Biemond et al., 2013; Odedara and Kumar, 2016). Understanding the factors driving virus incidence and diversity is essential for enhancing preparedness to tackle virus disease outbreaks in cowpea.

6.4 Overcoming challenges to cowpea virus diagnosis

Symptoms induced by the different virus infections in cowpea lack distinctiveness to use as virus-specific diagnostic markers. This means that diagnostic tools have to be used for virus identification. As a consequence of this, the knowledge on virus diversity generated is skewed by the availability of diagnostic tests and the ability of those tests to distinguish related viruses. Surveys without the use of diagnostics at best provide incidence and severity of mosaic disease and miss out viruses that do not cause clear symptoms, such as single infections of CPMMV and CMV. These factors have affected the virus reports from various surveys, particularly those during the early years.

Transmission electron microscopy has been used for virus identification based on particle morphology. Another commonly used diagnostic method is host range studies using sap inoculation on a range of herbaceous hosts. Based on host range and particle morphology knowledge, IITA virologists procured

antibodies from other research groups for confirmation of virus identity or embarked on virus purification procedures to produce antibodies which were subsequently used for diagnostics. This approach was reliable but also led to the misidentification of certain viruses. For instance, BlCMV and CABMV were initially considered as distinct serotypes of the same species. However, it was later clarified that they were separate species in the genus *Potyvirus* (Huguenot et al., 1993). Another example is the case of *Blackeye cowpea mosaic virus* (BlCMV), initially considered to be a separate species. Later work, however, revealed that it is identical to the previously described *Bean common mosaic virus* (BCMV), leading to its renaming as a cowpea strain of BCMV (BCMV-BlCMV) (Khan et al., 1993). This taxonomic confusion was effectively addressed with the better understanding of virus properties made possible by advances in virus purification, gene cloning and PCR. Current diagnosis at IITA is based on serological methods such as enzyme-linked immunosorbent assay and reverse transcription-PCR. All the important viruses have been characterized by genomic sequencing to assign them to exact taxonomic groups. This improved understanding of diversity has led directly to improved diagnostics.

6.5 Cowpea virus control through resistant varieties

Breeding for virus resistance has been the main approach used by IITA for cowpea virus disease control. Although virus resistance breeding was not the primary target, the evaluation of germplasm and breeding lines for virus response was considered as part of the process of variety development and any promising lines selected were advanced. Considering their widespread occurrence, BCMV-BlCMV and CABMV were identified as priority targets (Boukar et al., 2013). Inconsistencies in infection rate encountered during field screening experiments led to IITA establishing protocols for screenhouse-based screening for targeted viruses. This improvement led to the identification of several highly resistant cowpea lines that were used in breeding programmes to incorporate resistance to potyviruses (e.g. IT98K-1092-1). However, recent studies have shown that resistance selected against potyviruses is compromised in co-infection with other viruses (e.g. CMV) due to the phenomenon known as synergistic interaction. This finding led to the modification of the screening procedure to include simultaneous testing of genotypes under single and mixed infections for selected lines with the most promising levels of resistance.

6.6 Future prospects

Despite excellent progress, cowpea remains vulnerable to virus epidemics as most of the popular landraces and improved varieties lack durable resistance to even the most commonly occurring viruses. It is fortunate that there are no

records of cowpea virus disease epidemics in West Africa or elsewhere in Africa. However, it is unlikely that this situation will remain the same given the rapid changes occurring within farming systems including crop intensification. These changes contribute to breaking the natural seasonal barriers that check the perpetuation of disease cycles. Additionally, it seems likely that anthropogenic climate change will make conditions increasingly conducive for vectors and disease establishment. In order to counter these threats, it is important for IITA to perform scenario analysis by considering various risk situations. This should improve understanding of the likely impact of virus diseases on cowpea production and enable the preparation of informed mitigation strategies. Also, efforts should be made to conduct comprehensive baseline studies on the status of viruses in Southern Africa, where cowpea is fast emerging as a dual-purpose legume for food and fodder use. Cowpea collections along with wild relatives need to be phenotyped in order to select robust resistance to multiple virus infections and investments should be made to tap advanced technologies for cowpea virus disease surveillance, diagnostics, phenotyping and the development of genomic markers for accelerated breeding for virus resistance.

7 Soybean viruses

7.1 Introduction

Soybean (*Glycine max* L. Merr.) is widely grown in Nigeria and several countries in Southern Africa. The industrial potential of this crop is making it attractive for farmers and as a consequence the soybean production area in many countries is rapidly increasing. From 2006 to 2016 land area under soybean increased 32.5% in Africa (FAO, 2016). Soybean virology has not been strongly prioritized at IITA, and research activities have been limited primarily to seed health testing.

7.2 Occurrence, diversity and incidence of soybean viruses

Although virus symptomatic plants have been noted in many soybean fields, the incidence and severity of such plants has often been regarded as being below the economic threshold. The first comprehensive surveys for soybean viruses were conducted in Nigeria between 2008 and 2010 (Time et al., 2010). This study revealed a very low incidence of viruses in most soybean production areas in Nigeria. However, in Benue State, which was the first state to commercialize soybean cultivation over 45 years ago, and where soybean cultivation is most intense, a high incidence and diversity of viruses was recorded. This suggests that endemic viruses have adapted to African soybean production systems, perhaps due to the movement of vectors between crops. Over 15 viruses were detected in soybean in Nigeria, including two novel begomoviruses,

Soybean mild mottle virus (SbMMV) (genus *Begomovirus*; family *Geminiviridae*) and *Soybean chlorotic blotch virus* (SbCBV) (genus *Begomovirus*; family *Geminiviridae*) (Alabi et al., 2010), and the first report of ACMV on soybean (Mgbechi-Ezeri et al., 2008).

Several viruses detected in soybean are known to infect cowpea as well, and they are transmitted by aphids, beetles and whiteflies. Virus infection results in foliar symptoms such as mosaic and mottling, leaf distortion, severe reduction in leaf size and stunting of plants. Mixed infection with more than one virus is common under field conditions. *Cowpea mild mottle virus* (CPMMV) was the most frequently detected virus in soybean. Unlike in cowpea, CPMMV causes severe mosaic symptoms similar to *Soybean mosaic virus* (SMV). Evaluation of over 30 soybean cultivars, released or part of advanced yield evaluation trials for release, revealed high susceptibility to CPMMV (Time et al., 2010).

7.3 Future prospects

Future efforts should focus on breeding for CPMMV resistance because of its widespread occurrence and the ability of this virus to cause serious yield reduction. Future priorities for soybean virology are similar to those indicated for cowpea. Although virus epidemics in soybean have not yet been recorded anywhere in Africa, studies have shown the widespread susceptibility of soybean germplasm to endemic virus infections in Africa. Changes in soybean farming systems associated with agricultural intensification and climate change could alter the balance, exposing the crop to a greater risk of damage from viruses. Currently, there are no measures in place to tackle such an eventuality. This should be addressed by performing scenario analyses considering various levels of risks with the aim of developing soybean virus disease risk control strategies.

8 Virus vectors

8.1 Introduction

Most plant virus species use an arthropod vector as a means of transportation from one host to another. The insect vectors of plant viruses mostly belong to three orders: Hemiptera, Coleoptera and Thysanoptera. Hemiptera comprise the majority of the virus vectors in the families Aphididae (aphids), Aleyrodidae (whiteflies), Cicadellidae (leafhoppers), Fulgoridae (planthoppers), Psyllidae (psyllids), Pseudococcidae (mealybugs) and Coccidae (soft scales). Aphids, whiteflies and leafhoppers transmit more than 80% of plant viruses which represents close to 400 virus species within 39 different genera (Fereres and Moreno, 2009). In this section we provide a short summary of some of the key research findings on two of the most important vector groups affecting

the IITA mandate crops, namely the whitefly vector of cassava viruses and the leafhopper vectors of MSV.

8.2 The whitefly vector of cassava viruses

Both the CMBs causing CMD and the CBSIs causing CBSD are transmitted by the whitefly *Bemisia tabaci* (Storey and Nichols 1938; Dubern 1994; Maruthi et al. 2005; 2017). *Bemisia tabaci* is a cryptic species complex that is currently reputed to have at least 34 morphologically indistinguishable species (De Barro 2012; Tay et al. 2012). The cassava-colonizing species have five major haplogroups SSA1 to SSA5 with SSA1 further divided into five subgroups SSA1-SG1 to SG5 based on partial sequences of the mitochondrial cytochrome oxidase I (mtCOI) gene (Ghosh et al. 2015; Legg et al., 2014a). Recently, these were reclassified into six major haplogroups (SSA-ECA, SSA-ESA, SSA-CA, SSA-WA, SSA2 and SSA4) based on SNP genotyping (Wosula et al. 2017).

Bemisia tabaci has six developmental stages: egg, four nymphal instars and the adult. All but the adult stage and brief, early first instar crawler are functionally immobile (Byrne and Bellows 1991). Reproduction is arrhenotokous; unmated females produce males and mated females produce both males and females (Byrne and Bellows 1991). *B. tabaci* is a multivoltine insect that has no diapause or quiescent stage. As a result, populations are sustained through the continual exploitation of multiple host resources, both wild and cultivated, over the annual cycle (Byrne and Bellows 1991). Mean development duration varies depending on the region, host plant and prevailing conditions (Byrne and Bellows 1991). On cassava, *B. tabaci* completes its life cycle in about 21 days with prevailing temperatures of 26.6°C to 31.5°C (Fishpool et al. 1995).

Bemisia tabaci transmits viruses mostly in the genus *Begomovirus* in a persistent, circulative and non-propagative manner (Rosen et al. 2015). These viruses are acquired through phloem feeding and require a latent period (time interval between acquisition and transmission) to translocate from the insect midgut epithelial cells into the haemolymph, and to the salivary glands from which they are inoculated into the phloem with saliva (Brown and Czosnek 2002). Begomoviruses such as CMBs are thought to be retained in the whitefly vector for its entire life, and whiteflies are capable of inoculating plants in as little as 10 min (Dubern, 1994). *Bemisia tabaci* transmits viruses in the genus *Ipomovirus* such as the CBSIs in a semi-persistent manner (Ng and Falk, 2006; Maruthi et al., 2017).

Severe CMD pandemics in the 1990s led to the inclusion of cassava whiteflies in a major project, The Tropical Whitefly IPM Project, an initiative of the System-wide IPM Programme of the Consultative Group on International Agricultural Research (CGIAR). Under this project IITA was mandated to carry out baseline surveys in SSA to identify whiteflies colonizing cassava and their

parasitoids with the aim of using this information to understand the dynamics of CMD and development of control tactics (Legg 2005; Sseruwagi et al. 2005). In nine major cassava-growing countries that were sampled, the most dominant whiteflies on cassava were *B. tabaci* and *B. afer* (Priesner and Hosny), with the latter not known to transmit cassava viruses. Two major parasitoid groups *Encarsia* spp. and *Eretmocerus* spp. (both Hymenoptera Aphelinidae) were also reported to parasitize *B. tabaci*. The information generated from this project laid the foundation for the numerous studies on genetic diversity of cassava-colonizing *B. tabaci* and its parasitoids, and its role in the spread of cassava virus pandemics.

There are two major groups of *B. tabaci* in Africa that are referred to as cassava-colonizing and non-cassava-colonizing. Studies in East and West Africa in the 1990s showed that *B. tabaci* found colonizing cassava were largely restricted to this plant and its close relatives (Burban et al 1992; Legg 1996). The severe CMD pandemic in the 1990s was driven by super-abundant *B. tabaci* populations (>100 adults per top five leaves) that contributed to rapid disease spread (20–30 km/year) (Legg and Ogwal 1998). MtCOI sequencing of *B. tabaci* specimens collected along transects from CMD pandemic to non-pandemic locations in 1997 revealed the occurrence of two major haplogroups designated Ug1 and Ug2, with the latter found to be abundant in locations with severe disease (Legg et al. 2002), although several years later, Ug2 was not detected, having apparently been displaced by Ug1 (Sseruwagi et al. (2006).

A study on genetic diversity of cassava *B. tabaci* collected from six countries in East and Central Africa from 1997 to 2010 reported the existence of six haplogroups under the SSA group, namely SSA1-SG1 (formerly Ug1), SSA1-SG2, SSA1-IntSG1/2, SSA1-SG4, SSA2 (formerly Ug2) and SSA3 (Legg et al. 2014a). This study demonstrated that although there was an initial association between the CMD pandemic and the SSA2 haplotype (1997–9), the SSA1-SG1 haplogroup eventually replaced SSA2, becoming the primary haplogroup associated with the spread of the pandemic, and expanding its geographical range coincident with the CMD pandemic from 2000 to 2010 (Legg et al. 2014a). Recently, using SNP genotyping, Wosula et al. (2017) reported that mtCOI is not reliable at discriminating between cassava *B. tabaci* genotypes. Based on this finding, cassava *B. tabaci* were reclassified into six major haplogroups (SSA-ECA, SSA-ESA, SSA-CA, SSA-WA, SSA2 and SSA4), and these results will be used to develop robust SNP-based diagnostic tools. There remains a strong geographical association of one of the haplogroups (SSA-ECA) with regions affected by the severe CMD and CBSD pandemics, although it is likely that there are other non-genetic factors associated with the super-abundance phenomenon. Tajebe et al. (2015) noted a low frequency of the bacterial endosymbiont *Arsenophonus* in *B. tabaci* populations occurring

in areas of Tanzania affected by the severe CMD pandemic, and Ghosh et al. (2018) have demonstrated the deleterious effects of *Arsenophonus* infection on both fitness parameters and virus transmission of cassava-colonizing *B. tabaci*.

8.3 Control of Bemisia tabaci

Although insecticides are widely used to control *B. tabaci* in commercial agriculture, their use in cassava systems is confined to experimental trials and large-scale 'clean seed' production sites, but rarely used amongst smallholder farms in Africa (Legg et al. 2014b). At least eleven species of parasitoids, mainly in the *Encarsia* and *Eretmocerus* genera, have been used in attempts to control *B. tabaci* through augmentation (Gerling et al., 2001). Two detailed studies on parasitoids of cassava-colonizing *B. tabaci* in Uganda and Tanzania reported the prevalence of *Encarsia* spp. and *Eretmocerus* spp., with *Encarsia sophia* (Girault and Dodd) and *Eretmocerus mundus* Mercet the most dominant species (Guastella et al. 2015; Otim et al. 2006). Entomopathogen/mycoinsecticide products based on *Lęcanicillium lecanii* R. Zare & W. Gams (order Hypocreales; family *Cordycipitaceae*), *Isaria fumosorosea* Wize (order Hypocreales; family *Clavicipitaceae*) and *Beauveria bassiana* Bals.-Criv. (order Hypocreales; family *Cordycipitaceae*) have been explored and used under greenhouse and field conditions to control whiteflies including *B. tabaci* (Faria and Wraight 2001). So far, no literature is available on identification of entomopathogens and their efficacy against *cassava B. tabaci* in Africa. Host plant resistance against *B. tabaci* has been aggressively pursued in crops such as tomato, soybean, cotton, alfalfa, cucurbits and pepper (Nombela and Muñiz 2010), although there has been little significant progress in identifying sources of resistance to *B. tabaci* on cassava in Africa. Although there are several potential control options for whiteflies on cassava in Africa, none are currently being regularly used. Insecticides are too expensive, whilst there are currently still no practical applications for the use of parasitoids, entomopathogens or host plant resistance. Further research is therefore required to identify solutions that can be effective and practical in the context of SSA, where most cassava producers are smallholder farmers.

8.4 The leafhopper vectors of MSV

Twenty-two species of *Cicadulina* are recognized, of which 18 occur in Africa (Webb, 1987), which is presumed to be the centre of origin of this genus (Rose, 1978). Nine of the species in Africa have been reported as vectors of MSV. Studies in Nigeria demonstrated that *C. mbila* (Naudé) is the most abundant

vector across major ecological zones (forest, southern Guinea savanna and northern Guinea savanna) and seasons (Asanzi et al., 1994).

MSV is transmitted in a persistent circulative manner. The behaviour of *Cicadulina* on maize varieties exhibiting resistance to the vector in addition to the virus may help reduce MSV spread in the field. For viruses transmitted by aphids in a non-persistent manner, frequent probing is likely to increase virus transmission. However, for a persistent virus such as MSV, short-duration probes that do not reach the phloem would not enhance virus transmission (Bosque-Pérez, 2000).

Cicadulina leafhoppers are generally regarded as grassland species. In West Africa, the greatest numbers of *Cicadulina* leafhoppers were detected on the annuals *Brachiaria deflexa* (Schumach.) (Poaceae), *B. lata*, *Scutellaria barbata* D. Don (Lamiaceae), *D. horizontalis* and *Eleusine indica* (L.) (Poaceae) (Mesfin et al., 1992; Asanzi et al., 1994). Leafhoppers were found also on *Pennisetum* spp. and *Rottboellia cochinchinensis* (Lour.) (Poaceae), but only towards the end of the rainy season in Guinea savanna locations.

Regular surveys of MSV and leafhopper vectors in maize and grasses in farmers' fields and research stations across ecological zones in Nigeria revealed differences in leafhopper species composition (Okoth et al., 1988; Dabrowski et al., 1991). Five *Cicadulina* species, all known to be vectors of MSV were found, although *C. mbila* was the most abundant vector across ecological zones and seasons (Asanzi et al., 1994). In the southern and northern Guinea savannas, leafhopper populations appear to build-up with the rains as grass hosts suitable for feeding and reproduction become available. Compared to northern locations, the humid forest locations in the south often have consistently low leafhopper populations during most of the year (Bosque-Pérez, 2000).

Asanzi et al. (1994) showed that the percentages of viruliferous insects were low at the beginning of the rainy period (0–4%), and higher (15–22%) as the season progressed. As the rainy season progressed and disease incidence increased, the probability of insects feeding on an infected plant and becoming infective increased. In these surveys, however, high percentages of infective leafhoppers did not correspond with high leafhopper densities, but rather occurred immediately following leafhopper population density peaks.

Systemic insecticides have been shown to control leafhopper vectors of MSV, but ongoing influxes of the insects into treated fields from surrounding vegetation mean that repeated applications are required for sustained control (Martin and Shepherd, 2009). Since the majority of affected farmers are smallholders, very few have the means to pay for the expense of chemical vector control. Management of MSV therefore focuses almost entirely on control of the virus through the development and deployment of resistant varieties.

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9 Emerging techniques and future perspectives for plant virus management in Africa

In the past 50 years, conventional approaches have been successfully applied to tackle viral diseases in Africa. In particular, selection of resistant genotypes and improved understanding of the pathosystems have significantly contributed to controlling viral diseases. However, in the last two decades, important technological advances have opened up new possibilities for gaining a deeper understanding of viral diseases at the molecular level. High-throughput sequencing, such as next-generation sequencing (NGS), has become a key technique, essential for innovative research with impact. Nowadays genotyping of hundreds of plants, viruses and their vectors is routine work that can be executed, with the appropriate infrastructure, in as little as two weeks at an affordable cost (Gore et al., 2009). Furthermore, NGS allows highly accurate detection of any known virus and also facilitates the discovery of unknown or unexpected viruses (Carvajal-Yepes et al., 2014). Importantly, NGS technology can be applied reliably to any organism or virus of interest.

The availability of whole-genome sequences coupled with NGS technologies has increased the volume and speed of genetic marker discovery. Functional genomic studies have enabled the identification of loci and sometimes genes responsible for resistance to some of the most severe African viral diseases described above, including the important CMD2 and MSV1 QTLs for resistance to CMD and MSV, respectively (Rabbi et al., 2014; Wolfe et al., 2016; Masumba et al., 2017; Umber et al., 2016; Nair et al., 2015; Welz et al., 1998). This has allowed the development and use of molecular markers leading to the acceleration of breeding programmes as well as the production of resistant transgenic lines (Zhang et al., 2005; Vanderschuren et al., 2012; Shepherd et al., 2007).

Although genetic differences have until now been considered to be the main source of susceptibility/tolerance to variations in both virus and host crop populations, evidence is emerging to support the existence of additional components of heritability linked to epigenetic modification of DNA and chromatin, which operate in parallel with genetics to influence heritable variation, adaptation and defence in plants. There are several examples of this, and one which has been confirmed in cassava is where a loss of resistance to CMD has been shown to be associated with changes in the genomic methylation profile. Other examples involve gene regulation and RNA function.

The involvement of RNA has proved to be central to the potential for heritable genetic and epigenetic variation because, unlike DNA sequences that do not vary, the expression of RNA can change under the influence of biotic

and abiotic stresses and explain some environmental traits in crop selection. Comparative transcriptomics analysis of healthy and virus-infected genotypes or genotypes with different levels of susceptibility to virus infections is proving to be a straightforward strategy to identify genes regulating plant tolerance to viral diseases (Amuge et al., 2017; Anjanappa et al., 2017; Allie et al., 2014). Finally, the discovery of the mechanism of post-transcriptional gene silencing that regulates gene expression by means of small RNA molecules (namely microRNAs and siRNAs) and the elucidation of the central role of such a mechanism in plant-virus-vector interaction during virus infection has opened up new perspectives to addressing viral disease control (Bond and Baulcombe, 2014). An example of this is the siRNA profiling of virus-infected cassava plants that has contributed to clarifying differences in host and viral behaviours during infection (Ogwok et al., 2016; Chen et al., 2015; Wagaba et al., 2017; Xia et al., 2016).

The deeper application of such new knowledge and modern technologies combined with conventional strategies promises to uncover critical aspects of plant-virus-vector pathosystems and to provide new tools to face present and future viral outbreaks.

10 Future trends and conclusion

During the first two decades of virus research at IITA, most of the focus was on providing support to breeders in identifying and incorporating sources of virus resistance into IITA's mandate crops. Great successes were achieved, and many of the virus-resistant varieties developed during this period are still being actively disseminated and grown by farmers today. The development and application of diverse virus diagnostic techniques has provided vital tools to help researchers conduct monitoring and surveillance studies, as well as to assure the production of healthy seeds and vegetatively propagated planting material. During the second part of IITA's 50+ years of virus research, the institute dedicated substantial resources towards the 'fight' against a series of continentally important virus disease pandemics, including severe CMD, CBSD, BBTV and MLN. A key element of several of these efforts has been the establishment of procedures for the production and dissemination of high quality certified seed/planting material of varieties with resistance to each of these major diseases. This work has had a truly transformational effect on the production of cassava, bananas and maize – some of Africa's most important food staple crops.

Key challenges for the future are likely to be the development and application of next-gen technologies for virus characterization and diagnostics development; maximizing the potential for using IT and AI systems for point-of-use disease diagnosis, area-wide surveillance and early warning systems;

releasing the potential for transgenics and gene editing technologies to supplement existing sources of virus resistance obtained through conventional breeding; and putting in place pre-emptive crop virus management strategies to replace the current reactive approaches. Finally, IITA will need to play a lead role within Africa in establishing global networks to develop solutions to virus problems that show an increasing propensity to move between continents. The BBTV Global Alliance is an excellent example of such a network that should serve as a paradigm for similar networks focusing on other crop/virus disease pathosystems.

11 Where to look for further information

There are several books which provide good general coverage of the topic of crop viruses in Africa, and which also feature significant contributions from scientists working at IITA.

Whitefly and Whitefly-borne Viruses in the Tropics: Building a Knowledge Base for Global Action, edited by Anderson, P. K. and Morales, F. J.; with the collaboration of Jones, A. L. and Markham, R. H., Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia, 2005. 351p. - (CIAT publication no. 341) ISBN 958-694-074-8.

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Plant Virology in sub-Saharan Africa: Proceedings of a Conference Organized by IITA, edited by Hughes, J. d'A. and Odu, B. O., 4-8 June 2001, International Institute of Tropical Agriculture, Ibadan, Nigeria. https://books.google.com.ng/books?id=NbLlvMhVxxsC&pg=PA549&lpg=PA549&dq=plant+virology+in+sub-saharan+africa&source=bl&ots=xoOHvTZ65q&sig=hiR8yLBvgJeyxxIVqEfkRsvPS6s&hl=en&sa=X&ved=2ahUKEwjRyZSAxuDeAhVFsaQKHTa4BVIQ6AEwCHoECAgQAQ#v=onepage&q=plant%20virology%20in%20sub-saharan%20africa&f=false

Integrated Pest Management in Tropical Regions, edited by Rapisarda, C. and Massimino Cocuzza, G. E., CAB International, Wallingford, Oxford, UK.

Achieving Sustainable Cultivation of Maize, Volume 2: Cultivation Techniques, Pest and Disease Control, edited by Watson, D., Burleigh Dodds Science Publishing, Sawston, Cambridge, UK, 2017.

Achieving Sustainable Cultivation of Cassava, Volume 2: Genetics, Pests and Diseases, edited by Hershey, C., Burleigh Dodds Science Publishing, Sawston, Cambridge, UK, 2017.

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General websites of relevance to the topic of this chapter:

https://www.iita.org
https://www.plantwise.org/#
https://talk.ictvonline.org/

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