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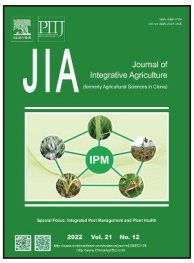

REVIEW

Recent progress in maize lethal necrosis disease: From pathogens to integrated pest management

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Abstract

Maize (*Zea mays*), as a staple food and an important industrial raw material, has been widely cultivated for centuries especially by smallholder farmers. Maize lethal necrosis disease (MLND) is a serious disease infecting maize, which caused devastating damage in the African region recently. MLND is induced by co-infection of maize chlorotic mottle virus and one of several cereal-infecting viruses in the *Potyviridae* family, with the symptoms ranging from chlorotic mottle to plant death at different infection stages. Integrated pest management for MLND needs strengthening detection, focusing on prevention and effective control. Early detection system of MLND has been successfully established by serological methods, nucleic acid-based methods, next-generation sequencing, etc. The practices, such as using certified seeds, sanitary measures, crop rotation, tolerant or resistant varieties etc., have been considered as the effective, economical and eco-friendly way to prevent and control MLND.

Keywords: maize lethal necrosis disease, maize chlorotic mottle virus, integrated pest management

1. Introduction

Maize lethal necrosis disease (MLND) is a serious disease of maize causing severe symptoms, such as leaf necrosis, premature aging, small cobs and even plant death, which dramatically reduce maize (corn) yield (Niblett and Claflin 1978; Wangai *et al.* 2012). In the 1970s and 1980s, MLND was reported in the Americas (Castillo and Hebert 1974; Niblett and Claflin 1978; Uyemoto 1980). In recent years, the outbreaks of MLND in several Asian and African countries caused devastating damage to maize production with large impacts on smallholder farmers (Adams *et al.* 2014; Mahuku *et al.* 2015a). MLND has now been found in more than fifteen countries in the Americas, Asia and Africa, and has become an emerging and catastrophic disease and threat to maize production.

Maize (*Zea mays*) is one of the most widely cultivated cereal crops worldwide, which has provided food and a considerable number of industrial products for centuries. Its capability to grow under diverse climatic conditions makes it a key determinant of food security for smallholder farming communities. In light of the serious damage MLND causes on maize, this disease clearly

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needs more scientific attention. This compendium will provide effective information for smallholder farmers to help identify and control MLND, including the pathogens, geographical distribution, host range, disease symptoms, transmission, diagnostics, prevention, control, etc.

2. Pathogens causing MLND

MLND is caused by co-infection on maize with maize chlorotic mottle virus (MCMV) in the genus *Machlomovirus* of the family *Tombusviridae* and one of several cereal-infecting viruses in the *Potyviridae* family (collectively referred as potyviruses or potyvirids), such as sugarcane mosaic virus (SCMV) (genus *Potyvirus*) (Adams *et al.* 2013; Fentahun *et al.* 2017), maize dwarf mosaic virus (MDMV) (genus *Potyvirus*) (Goldberg and Brakke 1987), Johnsongrass mosaic virus (JGMV) (genus *Potyvirus*) (Stewart *et al.* 2017), and wheat streak mosaic virus (WSMV) (genus *Tritimovirus*) (Scheets 1998).

The genome of MCMV is a positive-sense single-stranded RNA of 4.4 kb that does not contain a cap or a 3′-terminal polyadenylated tail (Nutter *et al.* 1989; King *et al.* 2012; Scheets 2016). Seven open reading frames (ORFs) have been reported for the MCMV genome (Nutter *et al.* 1989; Scheets 2000, 2016) (Fig. 1). The ORF1 encoding P32 is located at the 5′-proximal end of the genome and predicted to be expressed from the genomic RNA. Mutagenesis of P32 revealed that P32 is not required for virus replication or movement. However, transcripts lacking P32 expression accumulated lower level of transcripts in protoplasts and delayed and attenuated virus infection in maize plants (Scheets 2016). ORF2 overlaps with ORF1 and leaky translational scanning allows expression of P50 and its read-through protein P111, both of which are predicted to be associated with MCMV replication (Scheets 2016). Two subgenomic RNAs (sgRNAs) (sgRNA1 of 1.47 kb and a noncoding sgRNA2 of 0.34 kb) are produced from the genome (Scheets 2000). The sgRNA1 is predicted to encode four proteins, that is, P7a, P31, P7b, and CP. P7a and its read-through protein P31 are expressed from ORF3.

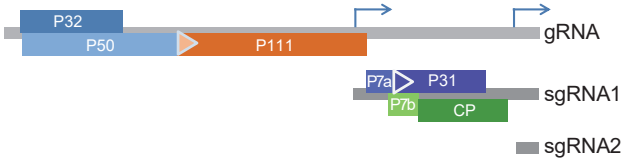

Fig. 1 Genome organization and protein products of maize chlorotic mottle virus. The open reading frames are marked as boxes on the genomic RNA (gRNA) and subgenomic RNA1 (sgRNA1) in each reading frame.

P7b is predicted to be encoded by a small ORF through an unusual CUG start codon (Scheets 2008). P7a and P7b are predicted to be associated with viral movement (Scheets 2016). P31 is a pathogenicity determinant which is important for viral accumulation and symptom development (Jiao *et al.* 2021). CP is expressed from the second start codon in sgRNA1 participating in the assembly of virions and cell-to-cell movement of MCMV (Nutter *et al.* 1989; Scheets 2016). Phylogenetic analyses of the complete sequences of known MCMV isolates showed that the sequence diversity is extremely limited with approximately 1–4% nucleotide sequence variability (Mahuku *et al.* 2015a; Redinbaugh and Stewart 2018). Moreover, the isolates from Asia and Africa share the highest similarity. MCMV virions are approximately 30 nm in diameter and exhibit icosahedral symmetry (Fig. 2) (Xie *et al.* 2011). MCMV virions are stable for up to 33 days *in vitro* and the thermal inactivation point is 80–85°C. Virions are stable at pH 6 and even lower and are stabilized by divalent cations (King *et al.* 2012).

The genomes of potyviruses are also positive-sense single-stranded RNAs. In contrast to MCMV, maize-infecting potyviruses show great diversity within and between species. According to the standard of classification in the family *Potyviridae*, the species are determined by 76% nucleotide sequence identity and 82% amino acid similarity (Adams *et al.* 2005). Moreover, the biological differences (vectors and host range) vary widely. However, the genome organization is very similar (Shukla *et al.* 1994). The 5′ end of genomic RNA is covalently linked by VPg and the 3′ terminus is polyadenylated. Potyvirus contains one ORF encoding a large single polyprotein which is self-cleaved into a set of multi-functional proteins. These proteins are P1, HC-Pro, P3, 6K1, CI, 6K2, VPg, NIa-Pro, NIb, and CP in sequence. In addition, a small additional short overlapping ORF

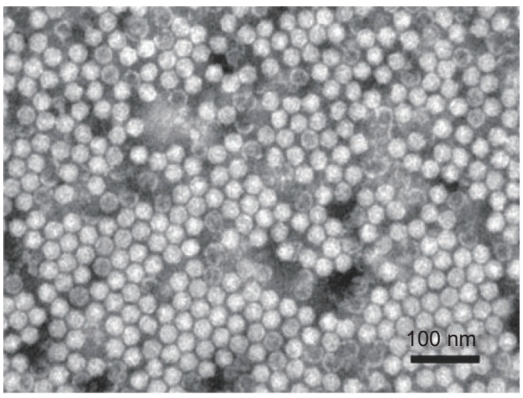

Fig. 2 Purified isometric virus particles of maize chlorotic mottle virus. The scale bar represents 100 nm.

embedded within the P3 cistron was found to encode P3N-PIPO by frameshifting transcriptional slippage (Chung *et al.* 2008; Olspert *et al.* 2015; Yang *et al.* 2021). P3N-PIPO has been identified throughout the family and proved to be essential for virus intercellular movement. Virions of potyviruses (except the genus of *Bymovirus*) are flexuous filaments, 680–900 nm in length and 11–13 nm in diameter, with helical symmetry and a pitch of about 3.4 nm (King *et al.* 2012).

3. Distribution and impact of MLND

3.1. Geographical distribution

The MLND is caused by the synergistic infection of MCMV and one of cereal-infecting potyviruses. MLND-associated viruses in the *Potyviridae* family are ubiquitous worldwide, and different species predominate in different geographical regions. SCMV is found worldwide, and MDMV is distributed widely in Europe and the United States (Mahuku *et al.* 2015a). In addition, WSMV, JGMV, and sorghum mosaic virus cause diseases on maize with limited distribution (Mahuku *et al.* 2015a). In the United States, MDMV is common and SCMV is also present (Stewart *et al.* 2014). In Africa, JGMV and MDMV are present, but SCMV is predominant (Wangai *et al.* 2012; Mahuku *et al.* 2015a; Stewart *et al.* 2017). In the 1920s and 1930s, SCMV was described in South Africa and East Africa (Storey 1924; Hansford 1935). In a survey of SCMV infecting maize in the 1980s, SCMV was observed in Tanzania and Kenya excluding the coastal and Nairobi regions (Louie 1980) where SCMV currently is present (Mahuku *et al.* 2015a), indicating some expansion of distribution.

As SCMV and MDMV have been widely distributed, the geographical distribution of MCMV is crucial for the occurrence of MLND. MCMV was first identified in Peru in 1971 (Castillo and Hebert 1974). MLND broke out in Kansas in United States causing significant losses, which was followed by outbreaks in the States of Nebraska and Hawaii (Niblett and Claflin 1978; Doupnik 1979; Jiang *et al.* 1992). In recent years, the disease has been identified in Asia and Africa. In 2009, MCMV was detected in Yunnan Province of China inducing MLND through co-infection with SCMV (Xie *et al.* 2011). In 2011, the first outbreak of MLND in Africa was reported in East Africa along the Rift Valley Regions of Kenya (Wangai *et al.* 2012) and the disease spread quickly. Now, MLND has been identified across several African countries, from Ethiopia in the north to Tanzania in the south and Kenya in the east to the Democratic Republic of the Congo (Redinbaugh and Stewart 2018). The current geographical distribution of MLND has been reported spanning over fifteen countries, which are listed in Table 1.

3.2. Host range and symptoms

MCMV can systemically infect different varieties of maize. Sugarcane (*Saccharum officinarum*) (Wang *et al.* 2014), sorghum (*Sorghum bicolor*) (Huang *et al.* 2016), coix seed (*Coix chinensis*) (Huang *et al.* 2016), and finger millet (*Eleusine coracana*) (Kusia *et al.* 2015) all appear to be natural hosts of MCMV. In the laboratory, many species including many monocot crops and other weedy grasses have been tested susceptible to MCMV by mechanical inoculation, but the primary hosts are members in the family *Gramineae* (Niblett and Claflin 1978; Bockelman *et al.* 1982; Mahuku *et al.* 2015a; Mudde *et al.* 2019a), such as barley (*Hordeum vulgare*), proso millet (*Panicum miliaceum*), foxtail millet (*Setaria italica*), wheat (*Triticum aestivum*), napier grass (*Pennisetum purpureum*), African couch grass (*Digitaria abyssinica*), purple nutsedge (*Cyperus rotundus*) and sand love grass (*Eragrostis trichodes*). There is still no conclusive experimental evidence that MCMV can be transmitted from these hosts to maize plants by vectors and what roles these alternate hosts play in disease infection cycles remain unknown. Similarly, maize-infecting potyviruses infect a range of poaceous crops, forages, and weeds.

Infection by MCMV alone or separately by one of the potyviruses cannot induce MLND and symptoms are relatively mild (Uyemoto *et al.* 1981). Maize plants infected by MCMV show symptoms of chlorotic mottling on leaves, and sometimes mild stunting in growth. Necrosis, severe stunting, shortened inflorescences, and premature plant death are sometimes reported with MCMV in natural field conditions. These more severe MLND-like symptoms could be caused by a mixed infection but that has not been determined. Environmental conditions also affect the severity of MCMV symptoms (Redinbaugh and Stewart 2018). A single infection by one of the potyviruses on maize typically causes mosaic, stunting, and mild chlorosis, very similar to the symptoms induced by MCMV infection. When MCMV co-infects with one of the members in the family *Potyviridae*, the effects are synergistic in disease progression and symptom development. MCMV titer and particle accumulation in co-infected plants becomes extremely higher as compared to MCMV-only infected plants (Scheets 1998). The concentration of MCMV is also higher in co-infected plants, but concentrations of SCMV and MDMV are not changed (Goldberg and Brakke 1987; Xia *et al.* 2016). Co-infection symptoms are very severe, even resulting in plant death on maize, which prompted the title of the

Table 1 The geographical distribution of maize lethal necrosis disease (MLND)

Location Continent/Country/Region	First reported	Potyvirus[1)]	Reference	Note[2)]
Africa				
Democratic Republic of the Congo	2014	SCMV	Lukanda *et al.* (2014)	
Ethiopia	2015	SCMV	Mahuku *et al.* (2015b)	
Kenya	2012	SCMV	Wangai *et al.* (2012)	
Mozambique	2014	NR	Redinbaugh and Stewart (2018)	MR
Rwanda	2013	SCMV	Adams *et al.* (2014)	
South Sudan	2015	NR	Mekureyaw (2017); Redinbaugh and Stewart (2018)	MR
Tanzania	2012	NR	Makumbi and Wangai (2013)	
Uganda	2013	NR	IPPC (2014)	
Asia				
China				
Sichuan	2013	NR	Wu *et al.* 2013)	
Yunnan	2009	SCMV	Xie *et al.* (2011)	
Taiwan	2014	SCMV	Deng *et al.* (2014)	
Thailand	1982	NR	Klinkong and Sutabutra (1983)	
North America				
Mexico	1989	NR	Carrera-Martinez *et al.* (1989)	
United States				
Hawaii	1992	MDMV	Jiang *et al.* (1992)	
Kansas	1976	MDMV	Niblett and Claflin (1978)	
Nebraska	1976	WSMV/MDMV	Doupnik (1979); Uyemoto (1983)	
Texas	1979	NR	Redinbaugh and Stewart (2018)	MR
South America				
Argentina	1981	NR	Teyssandier *et al.* (1982)	
Brazil	1981	NR	Redinbaugh and Stewart (2018)	MR
Ecuador	2016	NR	Quito-Avila *et al.* (2016)	
Peru	1971	NR	Castillo and Hebert (1974)	

[1)] SCMV, sugarcane mosaic virus; MDMV, maize dwarf mosaic virus; WSMV, wheat streak mosaic virus; NR, not reported.
[2)] MR, no substantiated report mentioned in the review.

disease MLND (Fig. 3). Maize is susceptible to MLND at all growth stages specifically spanning seedling to near maturity. Infected plants develop a diverse range of symptoms depending on the maize variety, developmental stage of infection, environmental conditions, etc. In most cases, chlorotic mottle starts from the base of the young leaves in the whorl and extends toward the leaf tips, followed by leaf necrosis at the leaf margins that progress to the mid-vein resulting in whole leaf drying and premature aging (Niblett and Claflin 1978). If necrosis occurs in the young whorl leaves, the plants may show 'dead heart' symptoms. Severely infected plants form small cobs with little or no grain set. The entire crop can frequently die before tasseling (Niblett and Claflin 1978; Wangai *et al.* 2012).

Fig. 3 Maize plants with maize lethal necrosis disease.

3.3. Impact

Maize is one of the most important cereal crops, and the MLND outbreak on maize causes serious impacts to corn production. As indicated in an early report from Peru, losses in maize yield due to MLND were between 10 and 15% (Castillo and Hebert 1974). In Kansas, crop losses due to MLND were estimated to be 50–90% (Niblett and Claflin 1978; Uyemoto 1980) depending on the variety of maize and the environment. In 2011, MLND was reported inducing serious damage to maize production in Kenya

(Wangai *et al.* 2012), affecting almost all commercial maize varieties, causing estimated yield losses of 30–100% depending on the stages of disease and varieties of maize (Mahuku *et al.* 2015a). Subsequently, MLND spread rapidly in sub-Saharan of East Africa and most recently Ecuador, across an area of nearly 1.2 million km^2 (Redinbaugh and Stewart 2018). The economic impact on smallholder farmers across Ethiopia, Kenya, Rwanda, Tanzania, and Uganda was estimated to be 291–339 million USD, with somewhat greater estimated future annual losses over the next five years (Pratt *et al.* 2017). On the other hand, maize production costs are increasing as farmers use herbicides and insecticides to control weeds and insect vectors transmitting the disease. Furthermore, seed production costs also increase as seed is treated by the seed companies. Maize is widely planted by a large number of farmers, so the increased use of pesticides in the production of maize may have potentially negative impacts on the environment. The 85–95% of produced maize kernels were used as staple foods in smallholder farming systems in the region of Africa (Shiferaw *et al.* 2011), thus the extensive or complete crop losses potentially increase the risk of food security problem and may ultimately lead to serious social security issues at the national and social levels.

4. Transmission of the pathogens

MCMV can be transmitted by insect vectors, seeds, and soil. After MCMV emerged in the United States, some putative vectors were tested for transmission, finding that six different species of chrysomelid beetles can transmit MCMV both at larval and adult stages with no latent time, while aphids and leafhoppers could not (Nault 1978; Jensen 1985). These experimental transmissible beetles include the cereal leaf beetle (*Oulema melanopa*), corn flea beetle (*Chaetocnema pulicaria*), flea beetle (*Systena frontalis*), southern corn rootworm (*Diabrotica undecimpunctata*), northern corn rootworm (*Diabrotica longicornis*), and western corn rootworm (*Diabrotica virgifera*) (Nault 1978; Jensen 1985; Jiang *et al.* 1992). In areas where corn is planted continuously, viruses were spread from older plants to younger plants by larva and adult beetles. The adults were more efficient than larvae because the movement of larvae was restricted after hatching in the soil. Since MCMV was detected in *Diabrotica* beetles in the field, beetles were considered as the major vectors for Kansas–Nebraska MLND outbreaks (Nault 1978; Jensen 1985). While in the 1990s, MLND emerged in Hawaii, the known beetle vectors were not present, but maize thrips (*Frankliniella williamsi*) were abundant. The subsequent tests with many potential vectors, including leafhoppers, aphids and corn thrips, indicated that only corn thrips can transmit MCMV (Jiang *et al.* 1992). Later on, western flower thrips (*F. occidentalis*) were also proven to transmit MCMV in a semi-persistent manner, retaining transmissibility for up to six days after the acquisition of viruses (Cabanas *et al.* 2013; Zhao *et al.* 2014). Both larvae and adult thrips can transmit MCMV, but adults are more important in virus spread because the adults are more mobile (Cabanas *et al.* 2013). Recently, high densities of thrips in affected fields are speculated to be associated with the emergence of MLND in Africa and Asia (Riley *et al.* 2011; Mahuku *et al.* 2015a). In the practice of detection and plant quarantine, it was found that MCMV can be seed-borne. When seeds were harvested from MCMV-infected maize plants, a high rate of 45–72% were positive by RT-PCR detection in local markets in Kenya (Mahuku *et al.* 2015a). The facts show that seeds can be contaminated with MCMV from virus-infected plants, while it is not necessarily indicated that the presence of MCMV in seeds will definitely be transmitted to progeny plants. Several experiments showed that the rates of MCMV transmission to progeny plants were 0–0.33% (Bockelman *et al.* 1982; Jensen *et al.* 1991; Delgadillo Sánchez *et al.* 1994). More recently, MCMV was detected in 2 of 600 (0.33%) seedlings from imported maize seeds by Chinese researchers (Zhang *et al.* 2011). Though the transmission rate is fairly low, it is of great importance epidemiologically, as it increases risks that a new and dangerous virus may be introduced into new areas through seeds. For MCMV, preliminary experiments illustrated that a high incidence (70%) of seedlings were infected with MCMV which were planted in contaminated soil taken from MLND-infected fields, as compared with 4% of seedlings planted in sterile soil (Mahuku *et al.* 2015a). Further research needs to determine how long the length of a maize-free period is required to prevent MCMV transmission through soil.

The cereal-infecting viruses in the *Potyvirus* genus are transmitted by aphids in a non-persistent manner and are transmissible experimentally by mechanical inoculation (King *et al.* 2012). SCMV and MDMV are transmitted by *Rhopalosiphum maidis*, *Rhopalosiphum padi*, *Myzus persicae*, *Schizaphis graminum*, and other species (Brault *et al.* 2010). Aphids are distributed worldwide and are ubiquitous in maize-growing areas. Aphid populations have an obvious characteristic of periodicity based on climate changes, such as season, temperature and rainfall. In addition, SCMV can also be seed-transmitted at the rate of 0.4 to 3.9% depending on different cultivated varieties (Li *et al.* 2011). WSMV is transmitted by the eriophyid wheat curl mite (*Acer tulipae* Keifer) in a persistent manner (Slykhuis 1955).

5. Infection cycles on maize plants

Even a low rate of seed transmission, it is epidemiologically significant. It's likely that the potyviruses are already present and indigenous in maize and other monocot species. Seed contamination is likely the initial source of inoculum for MCMV, which finally sets off the MLND in the newly-emerged areas. Virus-infected maize plants may be the most important reservoirs in areas where MLND is already emerging, the infected plants of sugarcane, sorghum, barley, wheat, millet, and other crops or weed hosts are also potentially involved in viral prevalence (Redinbaugh and Stewart 2018). In the areas where maize is grown back-to-back, the continuous presence of maize plants provides sufficient virus reservoirs, which can explain the phenomenon that monocrop culture system is closely related to serious outbreak of MLND.

Wounds are essential for viruses to penetrate the cell walls which can be created by mechanical injury of human activities or the feeding of insect vectors (Kiruwa *et al.* 2016). The insect vectors can acquire virus particles or genome as they feed on virus-infected plants. When they feed on virus-free plants, the virus particles or genome can be deposited or injected into cells through the wounds. Once inside the host cells, viruses will replicate using host machinery, move cell-to-cell through plasmodesmata and ultimately induce systemic infection. The infected plants will be involved in secondary cycles and repeated cycles continuously with the aid of vectors, ultimately resulting in an outbreak of disease. Recent study also revealed that MCMV induces changes in host plant volatiles to elicit attraction to maize thrips, which could enhance virus transmission (Mwando *et al.* 2018).

6. Effective integrated pest management for MLND

MLND seriously threatens maize production globally. To ensure maize production, many factors must be taken into account, such as the production, profitability, inputs and environmental contamination. In these conditions, the practice of integrated pest management (IPM) was the best choice in the management of MLND (Mahuku *et al.* 2015a; Kiruwa *et al.* 2016; Mekureyaw 2017; Redinbaugh and Stewart 2018; Boddupalli *et al.* 2020). The effective IPM for MLND includes three parts according to the occurrence of MLND: strengthening detection, focusing on prevention and effective control (Fig. 4).

6.1. Strengthening detection

The first step in controlling plant diseases is the correct identification of the causal pathogen(s) (Webster *et al.* 2004). Rapid and sensitive detection of MCMV is critical for the early warning and rapid application of prevention measures to control the wide spread of MLND. Many methods can be used to diagnose the virus or the disease, including symptomatology, serological methods, nucleic acid-based methods, electron microscopy, etc. (Mekureyaw 2017). The symptom observation, serological and nucleic acids-based methods have been widely used in the practical diagnosis of MLND.

The symptoms of MLND have been detailed in the above description, while it is very difficult to make a definitive diagnosis based solely on symptoms, as the symptoms vary significantly based on maize varieties, time of infection, environment and the possibility of multi-pathogen infection (Mahuku *et al.* 2015a; Kiruwa *et al.* 2016; Mekureyaw 2017). Suspected MLND plants need further confirmatory tests by serological, nucleic acid-based methods or others.

Serological methods have been used for the detection and diagnosis of plant viruses since the early 1960s. Various immunological methods are extensively used for the rapid and specific identification of a large number of field samples (Martin *et al.* 2000; López *et al.* 2003). The serological tests are based on an antigen-antibody reaction which is associated with colorimetric properties. Many different methods and their variants are included, for example, enzyme-linked immuno-sorbent assay (ELISA), triple antibody sandwich ELISA, double antibody sandwich ELISA, direct antigen coating ELISA, dot-immunobinding assay, Western blots, immuno-capture reverse transcription-PCR (IC-RT-PCR), immuno-electron

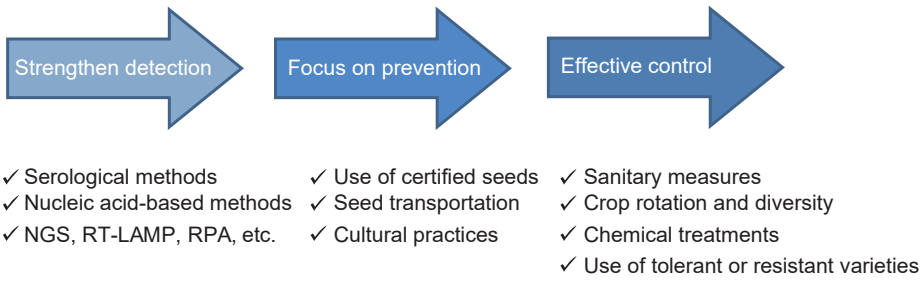

Fig. 4 Conceptual framework for integrated pest management of maize lethal necrosis disease (MLND). NGS, next-generation sequencing; RT-LAMP, one-step reverse transcription loop-mediated isothermal amplification; RPA, recombinase polymerase amplification.

microscopy and tissue blot immuno-assays (Kumar *et al.* 2004; Lima *et al.* 2012). The characteristics that are most desirable for virus detection are high sensitivity, rapidity, simplicity, low costs and easy automation, making the serological methods extensively used in the identification of viral diseases. They have been successfully used in the identification of MCMV (Xie *et al.* 2011; Wu *et al.* 2013; Adams *et al.* 2014; Lukanda *et al.* 2014; Mahuku *et al.* 2015b), SCMV (Mahuku *et al.* 2015b), WSMV (Montana 1996; Ilbağı *et al.* 2005) and MDMV (Giolitti *et al.* 2005).

Nucleic acid-based methods detect the presence of the virus genome and are widely used in the detection of many viral diseases because of their specificity, sensitivity, rapidity, especially in the cases that antibodies of viruses are not available (Martin *et al.* 2000; López *et al.* 2003). PCR and its different variants are among the most-used nucleic acid based methods, including reverse transcription-PCR (RT-PCR), real-time PCR, multiplex PCR, nested PCR, IC-RT-PCR and fluorescence RT-PCR, etc. Many researchers are dedicated to optimize the sensitivity and specificity of the detection. The real-time PCR detection has been successfully used in MCMV detection in maize seeds and leaves (Zhang *et al.* 2011; Adams *et al.* 2014). RT-PCR has been routinely used to detect MCMV or other potyviruses in crops, weed plants and vectors (Adams *et al.* 2014; Zhao *et al.* 2014; Mudde *et al.* 2019b). Apart from the detection of viruses, PCR products can be sequenced to provide detailed genome information for the identification of virus isolates, phylogenetic analyses, etc.

Recently, next-generation sequencing (NGS) has been applied to the diagnoses of new unidentified viral diseases, which are not restricted by the availability of antibodies, knowledge of genome sequences and other information. This method involves the generation of a nucleic acid library in a non-specific manner, high-throughput sequencing and bioinformatic analysis (Adams and Fox 2016). The identification of virus is based on similarity searching against a virus genome sequence database. NGS has been successfully used to identify and characterize new and existing viruses in many plant species (Wu *et al.* 2015). The MLND break-out in Kenya is one of these cases, which was confirmed as a co-infection of MCMV and SCMV (Adams *et al.* 2013). With further technological development and cost reductions, NGS has been increasingly used in plant viral diagnostics.

Finally, other sensitive detection methods are being developed, such as one-step reverse transcription loop-mediated isothermal amplification (RT-LAMP) assay (Chen *et al.* 2017) and recombinase polymerase amplification (RPA) detection (Jiao *et al.* 2019; Gao *et al.* 2021), which could also be used as routine screen for MCMV infection in the future.

6.2. Focus on prevention

The probability of seed transmission gives the potential of MCMV to have long-distance spread. If the seeds were totally from the MCMV-infected maize plants, the probability of the presence of MCMV on seeds was very high (Mahuku *et al.* 2015a; Redinbaugh and Stewart 2018). The seed transmission rate of up to 0.33% has been reported in Hawaii and China (Bockelman *et al.* 1982; Jensen *et al.* 1991; Zhang *et al.* 2011). Though there was no determined relationship between the presence of MCMV and infectivity, the risk remains of long-distance transmission. Governments around the world should strengthen the inspection and quarantine of imported maize seeds, not limited to seeds used for planting or breeding. In those countries where MLND occurs, transportation of seeds or other maize products should be prevented from the disease-affected areas to disease-free areas (Mekureyaw 2017). In addition, the public should be informed and educated about the information of the disease through news media, posters, radio, and so on, which will help famers to practice correctly.

6.3. Effective control

The control of MCMV encompasses sanitary measures, cultural means, chemical control and use of disease-resistant varieties.

Comprehensive field sanitary measures should be carried out to reduce initial inoculum (Kiruwa *et al.* 2016). Maize plants were the most significant source of viruses in the areas where MLND occurs. The infected maize plants and weeds should be removed from the field to reduce pathogen and vector populations. In the meantime, the use and replanting of recycled seeds must be avoided, and only certified MCMV-free seeds can be planted by the farmers (Kiruwa *et al.* 2016). The continuous back-to-back growing of maize from season to season will provide a virus reservoir with infected plants and vectors (Redinbaugh and Stewart 2018). Farmers are advised to practice crop rotation and crop diversity to create a break in maize planting seasons with alternative non-cereal crops, such as potatoes, sweet potatoes, cassava, and beans (Uyemoto 1983; Redinbaugh and Stewart 2018). Regular herbicide and insecticide treatments by foliar sprays can be used to control weeds and vectors, which will help reduce the population of vectors, the rate of infection and disease severity. The maize production in Hawaii achieved a good result in controlling MCMV with maize-free periods of 60 days each year, as well

as regular insecticide treatments for vector control (Jiang *et al.* 1992). Research on the model of MLND development showed that the combinations of crop rotation with the above practices can provide substantial disease management (Hilker *et al.* 2017).

Use of virus-tolerant or virus-resistant varieties is the most effective measures to control MLND. Previous studies have identified the resistance loci on maize chr.3, chr.6 and chr.10 conferring resistance to all tested potyviruses. *Scmv1* and *scmv2* are two major resistance genes on chr.6 and chr.3, respectively (Leng *et al.* 2017; Liu *et al.* 2017). Some studies suggested that some inbred lines with potyvirus resistance loci provide tolerance to MLN under controlled conditions (Balducchi *et al.* 1996; Redinbaugh and Stewart 2018). Recently, many pre-commercial, commercial maize and inbred lines have been screened by many researchers and organizations in Hawaii, Kenya, Tanzania, etc. (Ritte *et al.* 2017; Karanja *et al.* 2018). Some tropical lines were screened with moderate tolerance to MLN by inoculation of MCMV and SCMV (Gowda *et al.* 2011, 2015; Semagn *et al.* 2014). Ritte *et al.* (2017) identified that five maize landraces were tolerant candidates against MLND, which were screened from 152 maize landraces and 33 inbreed lines of Tanzanian maize germplasms and would be subjected to further testing to explore their use in breeding for MLND resistance. The 65 maize genotypes obtained from the Kenya Agricultural and Livestock Research Organization, International Maize and Wheat Improvement Center, etc. were selected to test the reaction to MLND, which validated the presence of MLND tolerance in MLN013 (CKDHL120312) and MLN001 (CKDHL120918) (Karanja *et al.* 2018). The genetic marker associated with symptom development was identified and the quantitative trait loci were transferred into susceptible maize populations to validate the resistance (Gowda *et al.* 2015; Gowda *et al.* 2018; Awata *et al.* 2021) and the maize F_1 plants derived from crosses indicated the ability to improve MNLD tolerance (Beyene *et al.* 2017). Complete immunity, however, has not been observed (Nelson *et al.* 2011). To date, good progress has been made in the development of MNLD-tolerant maize hybrids, while the development of MLND-resistant maize hybrids needs the largest research efforts in the near future for long-term control of MLND.

7. Conclusion

Over the past few years, MLND has emerged as a devastating threat to maize production and has caused huge economic losses especially for smallholder farmers. Significant progress has been made in understanding the pathogens, transmission vectors, and infection cycle of MLND. Different IPM measures such as early detection, quarantine, and sanitary measures have been developed to mitigate economic losses and epidemics caused by MLND. Like the control of other plant viruses, using resistant maize varieties are crucial and ecofriendly to control MLND. Although good progress has been made in the development of MNLD-tolerant maize hybrids, great efforts are required to develop MLND-resistant maize hybrids for long-term control of MLND. If strong naturally occurring MCMV resistance is absent in maize germplasm, additional efforts focused on understanding the interactions between the viral pathogens and maize will be useful in identification of essential host factors that could be further developed to enhance maize resistance.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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