# Maize Lethal Necrosis (MLN):

## A Technical Manual for Disease Management


**Editor**

**B.M. Prasanna**



CIMMYT International Maize and Wheat Improvement Center

CGIAR Research Program on Maize

In collaboration with international and national research and development partners

# Chapter 3

# Modes of Transmission of MLN-causing Viruses

**Anne Wangai[1]*, Anani Bruce[2], Johnson Nyasani[3], Sevgan Subramanian[4], and B.M. Prasanna[2]**

## 1. Introduction

Plant viruses have devised several mechanisms for infection, transmission and spread among the hosts. Insect vectors play a key role in the survival and propagation of the plant viruses. The epidemiology of plant viruses is indeed largely dependent on the insect vector population dynamics including their long- and short-range dispersal, host selection and feeding behaviours (Eigenbrode and Bosque-Perez, 2016). In the case of transmission and spread of MLN-causing viruses, the following appear to play a prominent role:

- Insect vectors
- Seed contamination and transmission
- Transmission through soil
- Mechanical transmission

## 2. Insect Vectors of MLN-causing Viruses

Transmission of Insect vectored plant viruses can be classified into four types namely, non-persistent; semi-persistent; persistent-circulative and persistent-propagative (Ng and Falk, 2006). MLN is caused by co-infection of maize plants with *Maize chlorotic mottle virus* (MCMV) belonging to the genus *Machlomovirus* in the family *Tombusviridae*, and one of the potyviruses, especially *Sugarcane mosaic virus* (SCMV) belonging to the Family *Potyviridae*. MCMV is transmitted in a semi-persistent manner (Cabanas et al., 2013) by thrips, especially corn (maize) thrips, *Frankliniella williamsi* Hood (Nault et al., 1978, 1981; Cabanas et al., 2013), and Chrysomelid leaf beetles, belonging to the genera *Diabrotica*, *Chaetocnema*, *Systena* and *Oulema* (Nault et al., 1978). SCMV and other potyviruses are transmitted in a non-persistent manner by various aphid species infesting cereals, especially belonging to genus, *Aphis, Rhopalosiphum, Sitobion* and *Macrosiphum* (Adams et al., 2014, Brault et al., 2010; CABI, 2019).

The range of vectors for MCMV and SCMV in Africa are not fully understood. However, several insect pests belonging the families Thripidae, Chrysomelidae, Curculionidae, Nitidulidae and Aphididae that can transmit MCMV and SCMV infests maize in East Africa. Some of these insects have proven to be efficient in vectoring the two component viruses of MLN (Table 1). However, further research is needed to determine the ability of these vectors in virus transmission, their ecology, impacts and their role in the epidemiology of MLN in Africa (Mahuku et al., 2015).

### 2.1. Thrips

#### 2.1.1. Maize thrips *(Frankliniella williamsi)* [Order: Thysanoptera; Family: Thripidae]

The maize thrips, widely distributed in East Africa (Moritz et al., 2013), are very slender, cigar-shaped insect (2mm long). The insect is yellowish orange to greyish black in color, with narrow wings fringed with hairs. The nymphs are smaller, paler, and wingless. Adults and nymphs infest the underside of young leaves, within the leaf sheaths and especially in growing points, during the first four weeks in the seedling stage and during the tasseling stage. Direct damage due to their feeding on the plant sap in maize is very minimal, but as a vector of MCMV it causes significant damage to the crop. Host range of *F. williamsi* is largely restricted to cereal crops, such as maize, wheat, finger millet, sorghum, and other grasses. Maize thrips do not transmit SCMV even when exposed to plants with mixed infections (Nyasani et al., 2015). Transmission of MCMV by maize thrips is estimated at 78% (Nyasani et al., 2015).

*Corresponding author (anne_wangai@yahoo.com)
[1]Formerly at Crop Biotechnology—Kabete Center, Biotechnology Research Institute, Kenya Agricultural and Livestock Research Organization (KALRO), Nairobi, Kenya & Adjunct Scientist at CIMMYT, Nairobi, Kenya; [2]CIMMYT, ICRAF Campus, UN Avenue, Gigiri, Nairobi, Kenya; [3]Kenya Agricultural and Livestock Research Organization (KALRO), Food Crop Research Institute, Embu, Kenya; [4]International Centre of Insect Physiology and Ecology (*icipe*), P.O. Box 30772-00100, Nairobi, Kenya.

**Table 1.** Insect vectors of MLN-causing viruses in East Africa.

| Common Name | Scientific Name | Order & Family | Transmits | Photo | Reference(s) |
|---|---|---|---|---|---|
| Maize thrips | *Frankliniella williamsi* | Thysanoptera: Thripidae | MCMV |  | Nault et al. (1978, 1981); Cabanas et al. (2013); Nyasani et al. (2015); Mwando et al. (2018) |
| Onion thrips | *Thrips tabaci* | Thysanoptera: Thripidae | MCMV |  | Nyasani et al. (2015); Mwando et al. (2018) |
| Common blossom thrips – pale form | *Frankliniella schultzei* | Thysanoptera: Thripidae | MCMV |  | Nyasani et al. (2015) |
| Western Flower thrips | *Frankliniella occidentalis* | Thysanoptera: Thripidae | Reported to transmit MCMV in China, but not in Kenya. |  | Zhao et al. (2014); Nyasani et al. (2015); Kinyungu et al. (2018) |
| Flea beetle | *Chaectocnema pulicaria* | Coleoptera: Chrysomelidae | MCMV |  | Nault et al. (1978, 1981) |
| Nitidulid beetle | *Carpophilus* sp. | Coleoptera: Nitudilidae | MCMV |  | Nyasani et al. (2014) |
| Maize weevil | *Sitophilus zeamais* | Coleoptera: Curculionidae | MCMV |  | Nyasani et al. (2014) |
| Maize coccinellid leaf beetle | *Epilachna* sp. | Coleoptera: Coccinellidae | MCMV |  | Nyasani et al. (2014) |
| Green maize aphid | *Rhopalosiphum maidis* | Hemiptera: Aphididae | SCMV |  | Nyasani et al. (2014); Kinyungu et al. (2018); Klein and Smith (2020) |
| Wheat Aphid | *Sitobion avenae* | Hemiptera: Aphididae | SCMV |  | Yasmin et al. (2011) |

#### 2.1.2. Common blossom thrips (*Frankliniella schultzei*) [Order: Thysanoptera; Family: Thripidae]

Common blossom thrips have a very wide distribution and a broad host range. It is mainly found in tropical and subtropical areas throughout the world. *Frankliniella schultzei* manifests in two different colour morphs, a dark and a pale form. The two colour morphs have distinct differences in morphology, molecular profiles, and biology (Gikonyo et al., 2017; Moritz et al., 2013). Mixed colonies of both colour forms are reported in Kenya, Sudan and Uganda in Africa. Only the pale form of *F. schultzei* has been found as a vector of MCMV (Nyasani et al., 2015) with more than 70% transmission. Common blossom thrips can be differentiated from the maize thrips by characters such as placement of the third ocellar setae inside and lower in the ocellar triangle, lack of companiform sensilla in the metanotum, and differences in the metanotal markings (Moritz et al., 2013).

#### 2.1.3. Western flower thrips (*Frankliniella occidentalis*) [Order: *T*hysanoptera; Family: Thripidae]

Western flower thrips, *Frankliniella occidentalis*, have a broad host range and are normally prevalent in the mid- to high altitude regions. Adult females are very variable in colour, ranging from yellowish orange to dark brown. It is a major pest of ornamentals, French bean, tomato and other solanaceous crops. It is occasionally found on maize (Moritz et al., 2013). Female of these thrips can be differentiated from *F. williamsi* by darker body colour, absence of discal setae in the abdomen, and type of coloration of the antennal segment (Moritz et al., 2013).

#### 2.1.4. Onion thrips (*Thrips tabaci*) [Order: Thysanoptera; Family: Thripidae]

The onion thrips, *Thrips tabaci*, prefers to feed on plants belonging to Alliaceae (onion, garlic), Brassicaceae (cabbage, kale) and Solanaceae (tomato, potato, eggplant). It is occasionally observed on cereal crops such as maize. The adult, which is about 1mm in length, is pale yellow to brownish. It can be differentiated from thrips belonging to *Frankliniella* with seven segmented antennae, incomplete row of setae on the forewing, and presence of rows of microtrichia in the pleurotergites (Mortiz et al., 2013). Onion thrips can cause up to 70% transmission of MCMV in maize.

### 2.2. Beetles

#### 2.2.1. Flea beetle (*Chaetocnema* sp.) [Order: Coleoptera; Family: Chrysomelidae]

The adults are small to moderately sized with enlarged hind femora that allow for the springing action of these insects when disturbed. Many flea beetles are attractively coloured; dark, shiny, and often metallic colours predominate. Adult flea beetles cause the most damage by feeding on the leaves and stems. They create shallow pits and small rounded, irregular holes (usually less than 1/8th inch) in the leaves. Flea beetle, *Chaetocnema pulicaria* identified as a vector of MCMV in the US (Nault et al., 1978, 1981) is also occasionally observed on maize in East Africa. However, its ability to vector MCMV in Africa needs to be confirmed.

#### 2.2.2. Maize weevil (*Sitophilus zeamais*) [Order: Coleoptera; Family: Curculionidae]

The adults are small brownish-black weevils with elongated snout and geniculate antennae. The elytra have fine microsculpture and is shinier with four pale reddish- or orange-brown markings on elytra. However, this is largely a stored product pest, which also infests maize occasionally. Laboratory assays indicate its ability to transmit MCMV (Nyasani et al., 2014).

Apart from flea beetles and maize weevils, maize in east Africa is also infested by other occasional beetles such as *Epilachna* sp. (Coccinellidae: Coleoptera) and Nitidulid corn-sap beetle, *Carpophilus* sp. which can also transmit MCMV (Nyasani et al., 2014).

### 2.3. Aphids

Aphids are small, pear shaped, soft-bodied insects that suck the plant sap and vector some plant viruses. Aphids' development rate, lifespan, and quantity of offspring are essentially determined by temperature and host plant quality. They reproduce both parthenogenetically and sexually. Under optimal conditions, more than 40 nymphs per female and up to 50 generations per year are laid. An early infestation is often discovered when aphids are found on leaves or on the unopened tassels. Symptoms of infestation include yellow-brown spots on the leaves, leaf wilting and curling, and development of sooty molds on honey dew produced by aphids. Direct damage due to aphids is only significant with high infestation levels, while as vector of viruses such as SCMV and other potyviruses they can significantly damage maize.

#### 2.3.1. Green corn aphid (*Rhopalosiphum maidis*) [Order: Hemiptera; Family: Aphididae]

The head, antennae, legs, cornicles, tail, and transverse bands on the abdomen are blackish brown, with the rest of the body green in colour. The body has sparse short hairs. The length of the antennae is less than half the length of the body. Cornicles are not longer than the finger-like tail. In winged females, the head and thoracic section are black-brown and the cornicles are shorter than in the wingless females. The corn aphid is primarily a species of warm and humid areas and mostly reproduces parthenogenetically. A closely related species, *Rhopalosiphum padi* is also infrequently observed in maize. It can be differentiated from *R. maidis* due to a darker body colour.

#### 2.3.2. Wheat aphid (*Sitobion avenae*) [Order: Hemiptera; Family: Aphididae]

The adults are medium-sized, spindle shaped and can be observed in green and brown colour forms. The antennae are black, shorter than the body length, legs are yellow with the tips of the segments black. The cornicles are longer.

### 2.4. Management of Insect Vectors of MLN-causing Viruses

Management of cropping systems and crop habitats is critical for effective management of key insect vectors such as thrips and aphids. For instance, avoiding intercropping or mixed cropping of maize with cruciferous vegetables (cabbage, kale) and Alliaceae crops (onion, garlic) is critical to reduce infestation of thrips such as *Thrips tabaci*. Since most of the cereal aphids and corn thrips prefer graminaceous hosts, effective management of grass weeds in the maize farms can reduce early onset of thrips and aphid population. High population of thrips and aphids, especially maize thrips and green corn aphids, at the early stages of crop growth can be detrimental. Coating maize seeds with systemic insecticides can ensure early-stage protection of seedlings against thrips and aphids, and thereby MCMV and SCMV.

Both thrips and aphids can be controlled naturally by a wide array of natural enemies, such as ladybird beetles, lacewing bugs, pirate bugs, syrphid flies, braconid and eulophid parasitoids, and predatory mites. Outbreaks of thrips and aphids often occurs with extensive use of organophosphates and synthetic pyrethroids for the control of other major pests, such as stemborers and fall armyworm. These pesticides kill the natural enemies of aphids and thrips, resulting in their resurgence. Hence it is critical to effectively monitor aphids and thrips population with yellow sticky traps for timely and need-based management interventions, preferably with biorational pesticides.

Application of biopesticides based on entomopathogenic fungi, *Metarhizium anisopliae* can provide early season protection against thrips and aphids. For sustainable management of MLN, the control strategies for insect vectors should be well integrated with other MLN management efforts, such as clean seeds, resistant cultivars, closed season planting, and maize-legume crop rotation.

## 3. Seed Contamination versus Seed Transmission

“Seed contamination” refers to the presence of a pathogen within a seed or on the seed surface. “Seed transmission” refers to the passage of a pathogen from the seed to the seedling, and further to the whole plant (Sastry, 2013). Any pathogen that may be either inside or attached to the outside surface of a seed that can affect the plant germination or affect an emerging seedling causing the disease symptoms may, in broad sense, be referred to as “seed-borne”. It is well established that plant viruses are effectively introduced into new countries and continents through contaminated or infected seed.

### 3.1. Seed Transmission of MCMV

There is a serious concern about the transmission of plant pathogens through seed, including MLN-causing viruses like MCMV. Jensen et al. (1991) indicated that seed transmission rates of MCMV in maize seed from MCMV-infected plants range from 0 to 0.33%. To gain a better understanding of the mechanisms underlying MCMV transmission through seed, Bernardo et al. (2018) investigated the MCMV distribution and infectivity in infected seeds from Kenya and Hawaii. The virus was detected at high levels in the pericarp and pedicel in hand-dissected seeds using ELISA. Significantly lower levels of virus were detected in the endosperm and embryo, and no virus was detected in embryos that were washed after dissection. Subsequent immunofluorescence microscopy of seed sections indicated MCMV was localized to the pericarp and pedicel. These results indicated that MCMV virions are limited to maternal tissues in the seed, and seed treatments may reduce seed contamination and transmission of MCMV by seed.

Kimani et al. (2021) analyzed the seed contamination rates of MCMV in four commercial seed lots; the results ranged from 4.9 to 15.9%. MCMV transmission frequency for 37,617 seedlings, tested in 820 pools of varying seed amounts, by Double Antibody Sandwich-Enzyme-linked Immunosorbent Assay (DAS-ELISA), was 0.17%, whereas a transmission frequency of 0.025% was obtained from 8,322 seedlings tested in 242 pools by real-time RT-PCR (Reverse Transcription-Polymerase Chain Reaction). Seeds from plants mechanically inoculated with MCMV had an overall seed transmission rate of 0.04% in 7,846 seedlings tested in 197 pools. The study showed that even with substantial contamination of maize seed with MCMV, the transmission of the virus from the seed to seedlings was low. However, even a low rate of seed transmission could be epidemiologically significant because viruses may be introduced into new areas/countries through infected seed (Mahuku et al., 2015). In conjunction with secondary spread by insect vectors, low rates of seed transmission can translate into high numbers of infected plants, resulting in epiphytotics (Maule and Wang, 1996). Recent grow-out tests with maize seeds obtained from plants with varied levels of MLN infection, revealed high levels of MLN incidence in the seedlings in both the laboratory (55–100%) and field (10.9–36.5%). MLN transmission was not observed with certified seeds obtained from plants with no incidence of MLN (Kinyungu et al., 2021).

### 3.2. Seed Transmission of SCMV

SCMV has not been reported to be transmitted by seed in sugarcane. However, seed cane (stalk pieces or setts), used to propagate sugarcane vegetatively commonly transmits SCMV and other viruses from one crop to the next. In the case of maize, SCMV-MB (Maize dwarf mosaic virus strain B) has been detected in the pericarp, but rarely in the endosperm or embryo of seeds 21 days after pollination. In mature seeds, it was occasionally detected in the pericarp and endosperm, but not in the embryo (Mikel et al., 1984). Experimental studies by Li et al. (2011) reported seed transmission rate of SCMV between 2.3% and 3.9% in two groups of maize seed tested. SCMV was reported to be mechanically and seed transmitted but not pollen transmitted (Brunt et al., 1996).

## 4. Transmission through Soil

By definition, a virus is soil-borne if it holds the capacity to survive in the soil debris or other living organisms and infect the plants growing in that soil. To be soil-borne, a virus should have an existence in soil outside of its natural host (Hiruki and Teakle, 1987). The majority of plant viruses are transmitted into the aerial plant parts by a variety of arthropods, mainly sap-sucking insects, such as thrips, aphids and whiteflies, while some soil-inhabiting zoosporic organisms and root-feeding nematodes can transmit a number of plant viruses into roots (Hull, 2013). Several plant viruses with single-stranded RNA (ssRNA), belonging to at least 17 genera in eight virus families, were reported to be transmitted by soil-inhabiting organisms (Andika et al., 2016).

So far, there are no published reports with conclusive evidence on the specific mode(s) of soil transmission of MLN-causing viruses like MCMV. However, soil-based vectors that have been associated with transmission of viruses in the family *Tombusviridae* (to which MCMV belongs) are fungi in the genus *Olpidium,* and at least five genera of nematodes (*Longidorus* spp., *Paralongidorus maximus*, *Xiphinema* spp., *Trichodorus* spp., and *Paratrichodorus* spp. (Andika et al., 2016).

## 5. Mechanical Transmission

All members of the virus family *Tombusviridae* (to which MCMV belongs) are readily transmitted by mechanical means. Experimentally, tombusviruses are readily sap transmissible and infected leaf extracts may retain infectivity after freezing for several years (Rochon, 1999). Thus, farm tools and machineries used in the maize fields infected with MCMV/MLN can serve as a source of inoculum. Hence, vehicles, and farm machinery/equipment entering the farmers' maize fields or seed production fields should be properly cleaned using disinfectants both before and after use.

The maize plant is also an important source of fodder for animals in the smallholders' agri-food systems. When MLN outbreak occurred in eastern Africa, farmers in some countries were advised to scout and rogue out plants showing MLN symptoms at the early stages of crop growth, and feed the rogued maize plants (with stalk, leaves and husks) to animals. The dung of the farm animals is often used as an organic manure in the fields, either alone or in combination with inorganic fertilizers. It is, thus, conceivable that animals including cattle grazing on the MLN-infected plants or fed with MLN-infected plants could potentially transmit the MLN-causing viruses to either mechanically or through organic manure. There is no evidence, however, that MLN-causing viruses can transmit to maize plants through this specific mode. However, as a precautionary measure, it is advised not to feed the farm animals with MLN-infected maize plants or other plants infected by MLN-causing viruses.

## 6. Conclusions

One of the major challenges regarding MLN management is the existence of multiple modes of transmission. The theory behind the diversity and evolution of plant virus transmission patterns observed in nature were explained by Hamelin et al. (2016). Although there is a lot still to understand about the pathways of transmissions of MLN-causing viruses, especially from the perspective of seed and soil, the existing knowledge can aid in devising and implementing appropriate management practices that can mitigate the threat.

## 7. References


Adams IP, Harju VA, Hodges T, Hany U, Skelton A, Rai S (2014) First report of maize lethal necrosis disease in Rwanda. New Disease Report 29: 22. https://doi.org/10.5197/j.2044-0588.2014.029.022

Andika IB, Kondo H, Sun L (2016) Interplays between soil-borne plant viruses and RNA silencing-mediated antiviral defense in roots. Frontiers in Microbiology 7: 1458. https://doi.org/10.3389/fmicb.2016.01458

Bernardo P, Redinbaugh MG, Barriball K (2018) Understanding *Maize chlorotic mottle virus* transmission through seed: localization and infectivity. Presented in ICPP: Plant Health in a Global Economy (July 28-August 3, 2018), Boston, USA. https://apsnet.confex.com/apsnet/ICPP2018/meetingapp.cgi/Paper/8496

Brault V, Uzest M, Monsion B, Jacquot E, Blanc S (2010) Aphids as transport devices for plant viruses. Comptes Rendus Biologies 333: 524–538.

Brunt A, Crabtree K, Dallwitz M, Gibbs A, Watson L (1996) Sugarcane mosaic potyvirus. In: Viruses of Plants. Descriptions and Lists from VIDE Database. CAB International, University Press, Cambridge.

Cabanas DW, Higashi CHVS, Bressan A (2013) Dissecting the mode of Maize Chlorotic Mottle Virus transmission (Tombusviridae: Machlomovirus) by *Frankliniella williamsi* (Thysanoptera: Thripidae). Journal of Economic Entomology 106: 16-24.

CABI (2019) https://www.cabi.org/isc/datasheet/49801#tovectorsAndIntermediateHosts

Eigenbrode SD, Bosque-Pérez NA (2016) Chemical ecology of aphid-vectored plant viruses. In: JK Brown (ed), Vector-mediated Transmission of Plant Pathogens. American Phytopathological Society Press, pp. 3-20.

Gikonyo MW, Niassy S, Moritz GB, Khamis FM, Magiri E, Subramanian S (2017) Resolving the taxonomic status of *Frankliniella schultzei* (Thysanoptera: Thripidae) colour forms in Kenya – a morphological-, biological-, molecular- and ecological-based approach. International Journal of Tropical Insect Science 37: 57–70.

Hamelin FM, Allen LJS, Prendeville HR, Hajimorad MR, Jeger MJ (2016) The evolution of plant virus transmission pathways. Journal of Theoretical Biology 396: 75-89.

Hiruki C, Teakle DS (1987) Soil-borne viruses of plants. In: Current Topics in Vector Research. Springer, New York, pp. 177-215.

Hull R (2013) Plant Virology, 5th Edition. Academic Press, Amsterdam.

Jensen SG,Wysong DS, Ball EM, Higley PM (1991) Seed transmission of maize chlorotic mottle virus. Plant Disease 75: 497–498.

Kimani EN, Kiarie SM, Micheni C, Muriki LG, Miano DW, Macharia I, Munkvold GP, Muiru WM, Prasanna BM, Wangai A (2021) Maize seed contamination and seed transmission of Maize Chlorotic Mottle Virus in Kenya. Plant Health Progress https://doi.org/10.1094/PHP-02-21-0018-RS

Kinyungu TN, Muthomi JW, Subramanian S, Miano D, Olubayo FM, Kariuki JW (2018) Efficiency of aphid and thrips vectors in transmission of maize lethal necrosis viruses. World Journal of Agricultural Research 6(4): 144-152.

Kinyungu TN, Muthomi JW, Subramanian S, Miano DW, Olubayo FM (2021) Transmission of viruses causing maize lethal necrosis disease through seed in commercial hybrids and effect on growth in the subsequent crop. Archives of Phytopathology and Plant Protection 54(3-4): 191-207.

Klein P, Smith CM (2020) Host plant selection and virus transmission by *Rhopalosiphum maidis* are conditioned by potyvirus infection in *Sorghum bicolor*. Arthropod-Plant Interactions 14: 811–823. https://doi.org/10.1007/s11829-020-09783-4

Li L, Wang XF, Zhou GH (2011) Effects of seed quality on the proportion of seed transmission for sugarcane mosaic virus in maize. Cereal Research Communications 39: 257-266.

Mahuku G, Lockhart BE, Wanjala B, Jones MW, Kimunye JN, Stewart LR, Cassone BJ, Sevgan S, Johnson N, Kusia E, Lava Kumar P, Niblett CL, Wangai A, Kiggundu A, Asea G, Pappu H, Prasanna BM, Redinbaugh MG (2015) Maize lethal necrosis (MLN), an emerging threat to maize-based food security in sub-Saharan Africa. Phytopathology 105: 956-965. https://doi.org/10.1094/phyto-12-14-0367-fi

Maule AJ, Wang D (1996) Seed transmission of plant viruses: a lesson in biological complexity. Trends in Microbiology 4: 153-158.

Mikel MA, D'Arcy CJ, Ford RE (1984) Seed Transmission of Maize Dwarf Mosaic Virus in Sweet Corn. Journal of Phytopathology https://doi.org/10.1111/j.1439-0434.1984.tb00746.x

Moritz G, Brandt S, Triapitsyn S, Subramanian S (2013) Identification and information tools for pest thrips in East Africa. QAAFI Biological Information Technology (QBIT), The University of Queensland, Brisbane, Australia. http://thripsnet.zoologie.uni-halle.de/key-server-neu/

Mwando NL, Tamiru A, Nyasani JO, Obonyo MA, Caulfield JC, Bruce TJ, Subramanian S (2018) Maize chlorotic mottle virus induces changes in host plant volatiles that attract vector thrips species. Journal of Chemical Ecology, 44(7): 681-689.

Nault LR, Negi LS, Niblett CL, Gordon DT, Styer WE, Coffey ME (1978) Transmission of maize chlorotic mottle virus by chrysomelid beetles. Phytopathology 68: 1071-1074.

Nault LR, Gordon DT, Loayza JC (1981) Maize virus and mycoplasma diseases in Peru. International Journal of Pest Management 27: 363-369.

Ng JC, Falk BW (2006) Virus-vector interactions mediating nonpersistent and semipersistent transmission of plant viruses. Annual Review of Phytopathology 44: 183-212

Nyasani J, Kusia E, Subramanian S (2014) Role of vectors and their host plants in the epidemiology of maize lethal necrosis in eastern Africa. In: Entomological Society of America Annual meeting, Portland, November 16–19, 2014. https://esa.confex.com/esa/2014/webprogram/Paper88365.html

Nyasani J, Kusia E, Subramanian S (2015) Thrips as pests and vectors of Maize chlorotic mottle virus in maize. In Proc. Xth International Symposium on Thysanoptera and Tospoviruses, Asilomar conference grounds, May 16–20, 2015.

Rochon D (1999) Tombusviruses. In: Granoff A, Webster RG (eds), Encyclopedia of Virology, 2nd Edition, Academic Press.

Sastry KS (2013) Seed-borne Plant Virus Diseases. Springer, India.

Yasmin T, Iqbal S, Farooq A, Zubair M, Riaz A (2011) Prevalence, distribution and incidence of major sugarcane infecting viruses in NWFP and Punjab. Pakistan Journal of Phytopathology 23: 24-30.

Zhao M, Ho H, Wu Y, He Y, Li M (2014) Western flower thrips *(Frankliniella occidentalis)* transmits Maize chlorotic mottle virus. Journal of Phytopathology 162: 532-536.