

# The Hopper-borne Diseases of Maize and Control by Vector Resistance

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## Abstract

*Of the more than 30 distinct viruses and 2 mycoplasma-like organisms that attack maize, a few—maize dwarf mosaic, maize chlorotic dwarf, maize rayado fino, maize streak, and the stunting mycoplasma-like organisms—have the potential to cause economic yield losses. These pathogens are disseminated efficiently by insect vectors that locate their hosts and reach their preferred feeding sites without destroying the host cells. Genetic manipulation of the host can interfere with the normal insect vector-host plant relationships. Control of the economically important hopper-borne diseases of maize by vector resistance would appear to be an effective strategy because 1) the hopper vectors are, in most cases, dependent on and prefer maize as a food source, 2) maize is the major economic crop severely affected by the diseases, 3) there is a highly specific relationship between these pathogens and the hopper vectors, and 3) these pathogens are limited to specific tissues of maize.*

More than 30 distinct viruses and 2 mycoplasma-like organisms (MLOs) attack maize *Zea mays* L. (Damsteegt 1981), and some—maize dwarf mosaic virus in the USA during the mid-1960s; maize mosaic in Hawaii and mainland USA, as well as in Central America and the Caribbean, including Mexico; maize streak in Africa south of the Sahara and adjacent islands; and the stunting diseases in Latin America—have caused significant yield losses. Maize streak and corn stunt are still considered major factors of yield instability in places where they are endemic. A few others (maize chlorotic dwarf in the USA, maize mosaic in the tropics, maize rayado fino in Latin America, and maize rough dwarf in some European countries and the Middle East) are considered potential threats to maize production in those areas (Conti 1985; Gordon et al. 1983; Harrison 1985; Rose 1978).

In nature, these pathogens are disseminated by different organisms, called vectors, most of which are arthropods. In all, 99% of the known arthropod vectors are insects and 76% of these belong to Homoptera, including the aphids (Stenorrhyncha) and the leaf- and planthoppers (Auchenorrhyncha) (Conti 1985; D'Arcy and Nault 1982; Harris 1981; Maramorosch and Harris 1979; Nault and Knoke 1981; Nault and Rodríguez 1985). These insects are pests in that they not only cause direct damage by sucking the plant sap but also, and more importantly, transmit pathogens of economically serious diseases. Except for maize dwarf mosaic, all of the maize diseases mentioned above are hopper-borne.

This paper briefly describes a few of the more economically important viruses that affect maize, emphasizing some aspects of the insect-pathogen, pathogen-maize host, and insect-host (feeding behavior) relationships, and relates these relationships to disease control by vector resistance. The term "hopper" is restricted to the leaf- and planthoppers of maize; and "virus" to virus and MLOs of maize.

## Economically Important Hopper-borne Viruses in Maize

### Maize chlorotic dwarf virus (MCDV)

Maize chlorotic dwarf virus (MCDV) induces fine chlorotic striping along the secondary and especially the tertiary veins of fully expanded leaves. Younger leaves in the whorl become chlorotic, and leaf reddening or yellowing and shortening of internodes often result. MCDV is an isometric particle, 30 nm in diameter and contains a single stranded ribonucleic acid genome (ssRNA). It is semi-persistently transmitted by three species of leafhoppers. The most efficient vector is *Graminella nigrifrons* (Forbes) (Table 1), which also has the widest distribution. Nymphs and adults are equally effective in transmitting the virus. Aside from maize, MCDV readily infects Johnson grass (*Sorghum halepense* (L.) Pers.), the main overseasoning host), grain sorghum, millet, milo, Sudan grass, crabgrass, and foxtails. MCDV is predominant in the phloem and bundle sheath of the host plants (Gordon et al. 1981; Gordon et al. 1983; Nault and Knoke 1981).

Since its discovery in 1969, MCDV has been reported only in the USA. Previously it was considered to be a "strain" of the corn stunt pathogen (CSP) (Nault and Bradfute 1979). This virus is now considered second in importance to maize dwarf mosaic virus among the virus diseases of maize in the USA (Gordon et al. 1981). Kuhn et al. (1975) estimated yield loss from this disease in a susceptible hybrid grown without insecticide protection to be 55%.

### Maize rayado fino virus (MRFV)

The first symptoms in plants infected with maize rayado fino virus (MRFV) are small chlorotic dots or short stripes along the secondary or tertiary veins near the base and around the midpoint of young to nearly fully expanded leaves. As symptoms develop, the dots and short stripes fuse longitudinally and usually form long chlorotic striping, which may extend up to the tip of the leaf and result in plants that are stunted and have narrow, short leaves (Damsteegt 1981; Gamez 1980).

MRFV is an isometric particle, about 25-30 nm in diameter, containing an ssRNA genome. Rate zonal density gradient centrifugation of purified virus preparations separates the top and bottom components; the top component does not contain a nucleic acid (Gamez 1980). The virus is transmitted in a typically persistent but intermittent manner by five species of *Dalbulus*. The most efficient species, ubiquitous in the Americas, is *D. maidis* (DeLong and Wolcott) (Table 1). Nymphs and adults of both sexes can transmit the virus, which multiplies inside

the body of the vector. Only maize, the teosintes, and *Tripsacum australe* Cutter and Anderson are reported as hosts of MRFV. The virus is predominant in the phloem and associated parenchyma (Gamez and Leon 1985; Nault and Knoke 1981).

MRFV, like MCDV, was considered a "strain" of the CSP until its viral nature was established in 1969 (Gamez 1980; Nault and Bradfute 1979). The virus has been found in areas where *D. maidis* occurs; these include the southern USA, Mexico, Central America and the Caribbean, and as far south as Peru and Argentina in South America (Nault et al. 1979; Gamez 1980; Gamez and Leon 1985). Its damage to maize in Central America has been estimated at 45 to 50% and may reach 100% grain yield reduction with newly introduced cultivars (Conti 1985; Damsteegt 1981; Gamez 1980).

Reported strains of the virus include the Brazilian corn streak and Colombian maize stripe. Bermuda grass etched line virus, is a previously undescribed virus occurring in Morocco that infects Bermuda grass (*Cynodon dactylon* (L.) Pers.) and Johnson grass. It has also been shown to infect a number of cereal crops such as maize, wheat, and oats, but not barley or sugarcane; it is serologically related to MRFV (Damsteegt 1981; Gamez 1980; Lockhart et al. 1985).

#### **Maize stunting mycoplasma-like organisms (MLOs)**

There are two distinct types of leafhopper-borne MLOs that cause stunting in maize. These are the corn stunt spiroplasma (CSS), a motile, helical mycoplasma, and the maize bushy stunt mycoplasma (MBSM), a pleiomorphic MLO. There is no evidence of a possible relationship between these two MLOs (Davis and Lee 1982, 1983; Nault and Bradfute 1979). They were also previously considered "strains" of the CSP until their etiologies were unequivocally established in the early 1970s. At present, the term "corn (maize)

stunt" is reserved for the maize diseases caused by CSS (which was known in the past as Rio Grande corn stunt) (Davis and Lee 1983).

Severe stunting is usually observed on maize that is infected early by CSS. The plants show the characteristic chlorotic or yellowish green banding or striping starting from the base of the leaf and tapering off toward its tip. Plants infected before flowering may develop tassels that do not fully develop and appear sterile. It is not unusual for such plants to develop multiple ears (4 to 6), but those that develop from the lower nodes are very thin and bear small earlike structures at their tips (N. Bajet and B. Renfro, unpublished; Nault 1980). The first and second uppermost ears are larger and more fully developed than the lower ones, although only a few seeds develop. Symptoms also develop on the husks. Under greenhouse conditions, infection by MBSM results in severe stunting, excessive tillering, and intense reddish to purplish color in the leaves, accompanied by a conspicuous streaking, but without chlorotic spots. Infected maize develops tears in the margins of the leaves, which are curled and shortened. Both MLOs inhabit the phloem of host plants (Davis and Lee 1982; McCoy 1982; Nault 1980).

These two MLOs are efficiently transmitted by *D. maidis* and *D. elimatus* (Ball) (Table 1) (Nault 1980; Nault and Knoke 1981). Other species have been shown to transmit them experimentally including *Cicadulina mbila* (Naudé) for CSS (Nault 1980; Markham and Alivizatos 1983). Their transmission is persistent and they multiply in and cause pathological effects in their vectors (Nault 1985; Purcell 1982). Their distribution, as with MRFV, parallels the distribution of their vectors, mainly *D. maidis*. These two MLOs and MRFV, which are transmitted by common species, are probably involved in the stunting diseases of maize (stunt complexes) (Nault 1980; Nault and Bradfute 1979).

CSS is more prevalent in, but not necessarily restricted to, the warm humid environments of the American tropics. Maize plants with symptoms typical of MBSM infection collected from 30 to 2,600 m above sea level, and *Dalbulus* spp. collected from maize plants grown at about 2,400 m above sea level in Mexico were shown by enzyme-linked immunosorbent assay and dark field light microscopy to be infected with CSS (N. Bajet and B. Renfro, unpublished; Gordon et al. 1985). We were not able to test for the presence of MBSM. Other than maize, CSS infects both annual and perennial teosintes. Only the annual teosintes are reported as collateral hosts of MBSM (Nault 1980, 1985). Two species of dicots have been infected experimentally with CSS and the leafhopper *C. mbila* was shown to be a vector (Markham and Alivizatos 1983).

#### **Maize streak and other related diseases**

Early symptoms of maize streak virus (MSV) infection in maize are circular to oval whitish spots between the veins of expanding leaves. These spots may be scattered but increase in number later, become more elongate, and fuse longitudinally, forming long whitish streaks (Bock 1974; Harrison 1985; Rose 1978).

MSV is the type virus of the geminivirus group. The virus particle is geminate, about 38 x 20 nm and consists of single stranded deoxyribonucleic acid (ssDNA) genome (Bock 1974; Harrison 1985). Of the six to nine species of *Cicadulina* that transmit it persistently (Table 1), *C. mbila* is the most common and is an efficient vector. However, *C. triangula* Ruppel was reported to be the most efficient species. Both nymphs and adults can acquire the virus, retain it through molt, and transmit it. There is no evidence of multiplication of MSV in its vector (Bock 1974; Conti 1985; Dabrowski 1985; Damsteegt 1981; Harrison 1985; Nault and Knoke 1981; Rose 1978).

MSV has a relatively wide host range but is restricted to the Gramineae. Hosts include the tribes Agrostideae, Andropogoneae, Aveneae, Eragrostideae, Glyceriaceae, Hordeae, Maydeae, Oryzeae, Paniceae, Sporoboleae, and Zoysieae (Damsteegt 1981, 1983; Rose 1978). To date MSV has been reported only from Africa and the neighboring islands of Madagascar, Mauritius, and Reunion. A variant of MSV occurs in India and infects maize under controlled conditions, but has not been found to infect maize in nature. A geminivirus that was isolated from *Digitaria saguinalis* (L.) Scop. from Vanuatu (formerly New Hebrides) was shown to be serologically related to MSV (Dollet et al. 1986). In the Indian subcontinent, the strains of this disease are called bajra streak, wheat stunt, maize mottle, and Uba cane streak (Damsteegt 1981).

**Disease Control by Hopper Resistance**

There are a number of ways to control virus and MLO diseases of crops. These measures are either directed to the sources of inoculum and to the disease in the field or to the vectors (All 1983; All et al. 1981; Kuhn et al. 1975; Zitter and Simons 1980). With maize, only insecticides have been used to control insect vectors. Host plant resistance to these hopper species has not been identified.

Controlling insect-borne diseases by vector resistance is an indirect control strategy. Its primary effect is to decrease the efficiency of the vectors to acquire and/or inoculate the pathogens into the pathogen host. These insects are efficient vectors because they can nearly always locate their hosts and reach their preferred feeding sites, and the cells in these tissues are not destroyed during feeding (D'Arcy and Nault 1982; Purcell 1985). The secondary effect is on the amount of secondary spread of the pathogen (Jones 1986; Kennedy 1976; Moyer 1986). Thus, host selection or localization and feeding behavior are the events to consider in developing

host resistance to vectors. Vector resistance as a means of disease control needs understanding between any two components of the epidemic (hopper-maize, hopper-virus, maize-virus) to be successful.

**Feeding behavior of hoppers**

The plant feeding homopterans have piercing-sucking mouthparts, which enable them to feed selectively on specific tissues of the host (D'Arcy and Nault 1982; Purcell 1982, 1985). Host selection and feeding by the hoppers are complex insect behaviors, which are dependent on stimuli and how the stimuli are perceived by the insect (D'Arcy and Nault 1982; Purcell 1982, 1985). These processes are described by Backus (1985):

Assuming that all the key stimuli are adequate, the hoppers start feeding as soon as they arrive on a potential host plant. Their feeding follows a 'typical sequence

consisting of plant surface exploration, stylet probing, fluid ingestion, and probe termination. During exploration, the insect moves about and searches, orients to, and selects a location and position on the plant. Its labium repeatedly touches the plant surface and is usually accompanied by secretion of the sheath saliva at the tip of the stylet. These exploratory activities are then followed by the insertion of its stylet into the plant (probing). The first stage is test probing wherein the labium is appressed firmly while the stylets penetrate downward. A drop of sheath saliva is secreted, which adheres to the plant surface and forms a salivary flange. The mandibular stylets are inserted only a short distance into the leaf. During exploratory probing (second stage of probing), the maxillary stylets are inserted deeper into the plant, where they

**Table 1. Some economically important hopper-borne diseases of maize**

Disease	Pathogen	Vectors
Chlorotic dwarf	maize chlorotic dwarf virus (MCDV)	<i>Graminella nigrifrons</i> * <i>G. sonora</i> <i>Exitianus exitiosus</i>
Rayado fino	maize rayado fino virus (MRFV)	<i>Dalbulus maidis</i> * <i>D. elimatus</i> , <i>G. nigrifrons</i> <i>Baldulus tripsaci</i> <i>Stirellus bicolor</i>
Maize streak	maize streak virus (MSV)	<i>Cicadulina mbila</i> * <i>C. storeyi</i> , <i>C. latens</i> <i>C. parazeae</i> , <i>C. similis</i> <i>C. triangula</i> *, <i>C. arachidis</i>
Corn stunt	corn stunt spiröplasma (CSS)	<i>D. maidis</i> *, <i>D. elimatus</i> <i>D. quevari</i> , <i>G. nigrifrons</i> <i>E. exitiosus</i> , <i>S. bicolor</i> <i>Euscelidius variegatus</i>
Bushy stunt	maize bushy stunt mycoplasma (MBSM)	<i>D. maidis</i> *, <i>D. elimatus</i> <i>G. nigrifrons</i> , <i>B. tripsaci</i>

Source: Nault and Knoke (1981).

\* Most efficient vector species.

search for and locate the preferred feeding tissue. Depending on the species, the hoppers exploit the phloem, xylem, mesophyll, or all three tissues. Probing is usually intracellular and the stylet is usually inserted into the interclinal junction between epidermal cells. Later the maxillary stylets penetrate through cells in their path.

Having located the suitable and preferred tissues, the insect starts ingesting fluid. The length of time the insect spends ingesting depends on the sensory stimuli perceived, which in turn may relate to nutrition and other physiological factors such as age. During ingestion, a watery saliva is continuously secreted to help digest the fluid and keep the stylet open until termination of the probe.

A more detailed discussion of this subject is presented in Backus (1985) and Maramorosch and Harris (1979).

#### **Transmission process**

There are three closely interrelated phases in the transmission of viruses by the hoppers—acquisition, latent period, and inoculation. Acquisition is the process whereby the hoppers become viruliferous through feeding on infected plants (source). They can also become viruliferous through the eggs of females infected with propagative pathogens (transovarial transmission) and by artificial means, such as feeding on suspensions of virus through artificial membranes or by microinjection. Acquisition access period (AAP) is the minimum time for a nonviruliferous hopper to become viruliferous when exposed to an infected source plant. Latent period is the time necessary for viruliferous hoppers to become infective (=inoculative). This is usually the time it takes for the pathogen to reach the salivary glands either after circulating or multiplying inside the body of the insect. Inoculation is the

introduction of the virus into specific sites of the plant during feeding. Inoculation access period (IAP) is the minimum time for an infective vector to inoculate a susceptible host plant (Conti 1985; D'Arcy and Nault 1982).

#### **Patterns of transmission**

The viruses and MLOs mentioned above are transmitted by the hoppers either semi-persistently or persistently. So far, a pathogen transmitted non-persistently by hoppers has not been discovered. The persistently transmitted pathogens are either propagative (they multiply in their vectors) like MRFV, CSS, and MBSM (Gamez 1980; Gamez and Leon 1985; Nault 1985) or non-propagative like MSV (Bock 1974; Nault and Knoke 1981). Semi-persistent transmission is characterized by a short acquisition and no latent period (i.e., MCDV). MCDV is acquired from host tissues by *G. nigrifrons* after 2 hours AAP and can be inoculated immediately. The vectors can be rendered inoculative for longer periods by allowing them longer AAP. The infectivity of the vector is lost after a molt or after several hours of IAP (Conti 1985; D'Arcy and Nault 1982; Nault and Knoke 1981; Purcell 1982).

On the other hand, the persistently transmitted viruses and MLOs can be acquired only after several hours to days of AAP and considerable latent period, usually a week or more. *D. maidis* requires about 6 hours of AAP for MRFV and less than 4 days for MBSM. About 15% of a *D. maidis* population can acquire CSS after 15 min of AAP and 100% after 7 days on a source. Only about 15 sec AAP is necessary for *C. mbila* to acquire MSV. The IAPs for these pathogens are 8 hours for MRFV, less than 7 days for MBSM, and 1 hour for CSS by *D. maidis*; *C. mbila* can inoculate MSV after only 5 min IAP. The vectors are infective for life without further access to a source (Bock 1974; Conti 1985; D'Arcy and Nault 1982; Gamez 1980; Nault and Knoke 1981; Purcell 1982).

#### **Future developments and problems**

Moyer (1986) stated that there are three instances when vector resistance as a control strategy could be successful: 1) when the vector is dependent on the virus-host as a food source, 2) when the relationship between the vector and the pathogen is very specific, and 3) when there is only one virus host (= economic crop) in the immediate area. Faster gains are obtained by genetically manipulating a single crop host species of an insect vector transmitting a pathogen that causes a serious disease; to search for, develop or incorporate a single form of resistance specific to a single vector species is simpler and more feasible. Maize is undoubtedly the preferred feeding host of leafhoppers; in fact, *D. maidis* is considered a maize specialist (Nault 1985; Gamez and Leon 1985). Thus, at least for *D. maidis* and the maize stunting pathogens it transmits, maize is the only economically important crop affected. In addition, a highly specific relationship between the hoppers and these pathogens exists, and these pathogens are localized in the phloem of maize (Bock 1974; Davis and Lee 1982; Harrison 1985; Nault 1980, 1985; Gamez 1980; Gamez and Leon 1985; McCoy 1982). It is apparent, then, that resistance to maize-pathogen vectors may be a feasible method of control.

Many problems need to be solved before a host plant resistance strategy can be directed toward leaf- and planthoppers. Methods to identify and evaluate maize germplasm for the traits of interest have not yet been developed. The hoppers are very small, highly mobile, and they do not leave easily visible feeding marks. Nevertheless, there are host plant properties that can be exploited to interfere with the normal plant-insect vector relationships. Jones (1986) broadly classified these properties as those that interfere with 1) host finding and localization 2) initial settling, and 3) the sustained feeding behavior of the vector, as well as 4) specific interference with vector

transmission of the pathogen. These mechanisms have contributed to a decrease in incidence of similar diseases in other crops and could be exploited against the maize hoppers as well.

Plant characters have been identified that specifically affect the ability of the vector to locate the host. These include leaf color and crop canopy architecture. Changes of these traits in other crops have resulted in either decreased virus severity or decreased incidence in some virus-host combinations.

The structural or morphological features that can interfere with the initial settling of the vectors include the cuticle and waxes, volatile compounds, and pubescence (Jones 1986; Tingey 1985). Changes of these traits would affect the vector during settling; searching, orienting to, and selecting a location; and assuming a proper position to feed. Should the host plant have a strong resistance that prevents probing altogether, or inhibits the vector from proceeding to the ingestion stage after brief probes, transmission may not occur and secondary spread would decrease or be minimized.

Crops, including maize, have been shown to have antibiotic effects on insect pests even though they feed, remain, and sometimes colonize the plants. However, survival rates and fecundity of the insects are lowered and thus insect pest activity and population decrease (Ortega et al. 1980). This phenomenon has never been examined in maize for these important hopper vectors. If it exists and could be used in maize, the secondary spread of the diseases would be diminished (Jones 1986; Kennedy 1976; Moyer 1986). An expression of resistance (antibiosis) that is applicable for the persistently and semi-persistently transmitted pathogens is the interference or prevention (by the host plant) of vector contact with or location of its

specific, preferred feeding site. For example, if the vectors are forced to feed in the xylem rather than in the phloem, where most of the pathogens are localized, transmission of the pathogens would likely be affected. This has been shown recently to be one of the mechanisms of resistance of *Agropyron* spp. to barley yellow dwarf virus, which is persistently transmitted by aphids (Shukle et al. 1987).

New techniques are now available for exploiting, developing, evaluating, and deploying vector resistance to control these important diseases of maize. Biochemical techniques and dyes have been successfully used to detect host plant metabolites that are closely correlated to resistance to these insect vectors (Auclair and Baldos 1982; Auclair et al. 1982). Electronic monitoring of feeding has also been used to locate the specific and preferred feeding sites of some of hoppers on different rice accessions. (Khan and Saxena 1984, 1985). In the one study where electronic recording was used with *G. nigrifrons* on maize, the procedure detected differences in the feeding patterns of the leafhopper on the maize host and other, nonhost species (Triplehorn and Nault 1984). The use of molecular markers to identify and locate linkage maps for a locus (or loci) on chromosomes that condition resistance to these important hopper species in maize or its relatives should also be very appropriate.

Exploiting and deploying vector resistance as a means to control virus and MLO diseases of maize dispersed by hoppers could be an effective strategy. This disease control tactic, which is safe to use and complements other control tactics, may be especially valuable in areas where effective insecticides are unavailable or prohibitively expensive.

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