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Maize Dwarf Mosaic, the Most Important Virus Disease of Sorghum

Sorghum (*Sorghum bicolor* (L.) Moench) was probably first domesticated in eastern Africa in the regions of Ethiopia and Sudan. From there, cultivation of sorghum spread throughout Africa and Asia and finally to the Americas and Australia. Today, sorghum is one of the world's major food crops, particularly in areas of high temperature and low rainfall. Because of its ability to grow in some of the world's most austere environments, its versatility as a food and feed grain, and its high yielding capability, sorghum will continue to be one of the most precious cereal commodities for human beings. J. C. Harlan states that "sorghum is one of the really indispensable crops required for the survival of man" (10).

Sorghum can be prepared in a variety of ways for human consumption, e.g., steamed porridges and breads, syrup, and nonfermented and fermented beverages (particularly beers during good harvest periods). Some cultivars with high lysine content are used to supplement infant diets, and in many regions of Africa, sorghum is eaten as a fresh vegetable, much as we in the United States eat sweet corn or "roasting ears."

Sorghum has developed from a tentative food crop into one of the most successful commercial feed crops. Sorghum has been shown to have the highest conversion of sunlight energy to biomass, making it a high-energy crop, and provides an alternative to maize in environments unfavorable to maize culture. Forage sorghums are valuable warm-season annual crops; even wild species such as johnsongrass (*S. halepense* (L.) Pers.) make good forage and hay crops. Sorghums are grown commercially in Brazil for use in ethanol production. Brooms made from broomcorn (*S. bicolor* (L.) Moench subsp. *technicum* (Koern.) Jav.) are another commercial product (10).

The Sorghum Viruses

The first virus disease described in sorghum was sugarcane mosaic, identified in 1923 by Brandes and Klapaak (4). Since then, 15 viruses have been described as pathogens of sorghum. In 1962, Tarr (27) reviewed the viral diseases of sorghum and reported they caused surprisingly little damage. His list of viruses and viruslike agents of sorghum included sugarcane mosaic virus, maize mosaic virus, red stripe virus, Fiji disease virus, ratoon stunting (no longer classified as caused by a virus), brome mosaic virus, cucumber mosaic virus, oat psuedorosette virus, barley yellow dwarf virus, rice stripe virus, lucerne or alfalfa dwarf (no longer classified as caused by a virus), and freckled yellow stripe or maize streak virus. With the exception of sugarcane mosaic virus (SCMV) and brome mosaic virus, however, these have been shown to infect sorghum only by experimental transmission or occasionally in the field. Viruses added to the list since 1962 include maize dwarf mosaic virus, panicum mosaic virus, maize rough dwarf virus, peanut clump virus, maize chlorotic mottle virus, sugarcane chlorotic streak virus, maize stripe virus, and maize chlorotic dwarf virus (33). The most recent addition is sorghum stunt mosaic virus, reported from California in 1981 (15).

The Most Important Virus

In 1964, Dale (7) described a mechanically transmitted virus from corn that infected johnsongrass and sorghum. This virus was subsequently designated maize dwarf mosaic virus (MDMV) and is separated from SCMV and its strains by the abililty to infect both 2n and 4n johnsongrass. Shepherd (23) demonstrated the serological relationship of MDMV to SCMV and suggested MDMV be named the johnsongrass strain of SCMV, or SCMV-Jg. Most workers use the name maize dwarf mosaic virus and add strain designations, i.e., MDMV-A, MDMV-B, MDMV-C, MDMV-D, MDMV-E, MDMV-F (14), and MDMV-O (16), but some still use the designation SCMV-J or SCMV-Jg (28). Only strains A and B are known to be naturally transmitted to sorghum.

Maize dwarf mosaic is considered the most important virus disease of sorghum worldwide and occurs almost everywhere sorghum and johnsongrass grow. It has been reported from France, Bulgaria, Rumania, Yugoslavia, Italy, Australia, Thailand, the Philippines, the United States, Mexico, Colombia, Venezuela, South Africa, Israel, Peru, and Argentina. Losses range from 100% with susceptible cultivars such as New Mexico 31 and Redlan × Caprock to less than 5% with tolerant cultivars such as Martin and Wheatlan.

MDMV has an unusually wide host range—over 200 species of grasses are susceptible (21)—and is transmitted both mechanically and by aphids. Shepherd and Holderman (24) reported a low incidence of seed transmission of MDMV in corn. In experiments in which seed from both naturally and artificially infected sorghum plants were sown in controlled environmental rooms and in the greenhouse, I was unable to demonstrate seed transmission of MDMV in 42,428 sorghum seedlings. All plants with unusual appearance were assayed individually for MDMV. In addition, bulk extracts were made of all plants without apparent symptoms in each trial of 250 seedlings and tested serologically and by bioassay. In all cases, there was no evidence of virus transmission through grain sorghum seed.

Symptoms of MDMV infection in the field (Fig. 1) and in the greenhouse can vary considerably according to sorghum genotype, virus strain, and temperature. Time of infection also influences symptom expression, which is greatest with infection at the two- to three-leaf stage. Susceptible sorghum lines are severely stunted by early infection. The classic symptoms include mosaic (Fig. 2A), red leaf (Fig. 2B), red stripe, necrosis (Fig. 2C), stunting, delay in flowering, and reduction in head length, number of heads, seed size (9), number of seeds per head, and grain yield. Host genotype mediates the mosaic and red stripe reactions, whereas genotype and temperature control the red leaf reaction (19,25). Red leaf develops on infected plants at ambient temperatures of 16 C or below.

MDMV Disease Cycle

Strain A of MDMV is vectored by 23 species of aphids (12). This array of vectors interacts with several ecological factors to produce MDMV epidemics in sorghum. Johnsongrass, the perennial MDMV-A inoculum reservoir, plays a central role in the disease cycle (Fig. 3) (1). The greenbug (*Schizaphis graminum* Rondai) and other aphid species commonly overwinter on small grains and winter grasses. Aphid survival and early-season population increase depend on winter severity. Aphid populations overwinter in Mexico and South Texas and increase as the vernal green-up of johnsongrass occurs and temperatures rise from south to north, followed by the sequential south-to-north planting of sorghum into the Great Plains.

Development of the winged form of aphids depends on several factors, including temperature and colony crowding. Aphids appear to be the primary agent responsible for spread of MDMV-A, although the virus is also mechanically transmissible. Even though the virus is nonpersistently transmitted by aphids, long-distance dispersal occurs in the Great Plains (26,30). The greenbug can remain infectious with MDMV-A for as long as 21 hours (3) and thus can transmit the virus to crops growing beyond the northern limits of johnsongrass. A recurring short cycle from infected sorghum back to maize, sorghum, johnsongrass, and annual grasses increases the inoculum reservoir and intensifies the epidemic.

Epidemics and Losses

In 1965, maize dwarf mosaic was found occurring naturally in Arkansas along the Red River (8). In 1966, the virus was identified from both sorghum and johnsongrass in the Brazos River Bottom and the Rio Grande Valley in Texas (34). MDMV reached epiphytotic levels in Texas and the Great Plains in 1967. We identified the virus in 1967 from diseased sorghum leaves sent to our laboratory from various locations in Texas, New Mexico, Oklahoma, and Kansas. In 1968, MDMV was again highly destructive to sorghum and was identified from material sent to us from Arizona. Major factors contributing to the epidemic were the commercial sorghum genotypes grown in the Southwest in 1967, most of which were Redlan × Caprock hybrids. Both Redlan and Caprock were later shown to be highly susceptible and associated with the red leaf symptom.

In 1967, the year of greatest sorghum losses to MDMV in Texas, the yields were reduced by over 15%. The state yield average was only 51 bu/acre, or down 8% from the 1966 average of 55 bu/acre (2). In 1968, the average loss to MDMV-A was estimated at 10%, but incidence of the virus in sorghum increased from 25 to 30% (31). Today, the MDMV incidence in sorghum is 10% and the estimated loss is only 2%. The incidence of the virus in johnsongrass, however, is near 100%. MDMV-A is currently found throughout the sorghum and johnsongrass range in the United States.

Fig. 1. Commercial field of grain sorghum infected with maize dwarf mosaic virus.

Fig. 2. Symptoms of maize dwarf mosaic virus infection of sorghum include (A) mosaic, (B) red leaf, and (C) necrosis.

Approaches to Control

Insecticides. Control of MDMV involves many varied and interrelated factors. MDMV is most vulnerable to control where 1) the aphid vectors carry the virus, 2) the grass species overseason the virus, and 3) sorghum hosts abound. Even under these conditions, combined control practices must be economical and practical. The systemic insecticide aldicarb (Temik) was tested in a vector control trial at Lubbock, Texas, where a heavy greenbug population and an adjacent virus source from mechanically and naturally infected sorghum existed. The insecticide was applied to seedlings of RS 626 sorghum at two rates, 0.45 and 0.90 kg/ha. Untreated control plots were paired with treated plots. Aphid control was excellent, but 4 weeks after treatment, untreated plots had 64% virus infection and treated plots had 54%. Failure to reduce infection by more than 10% even though the aphids were killed was attributed to the fact that the virus is transmitted nonpersistently and can be transmitted during a single searching probe. The aphid vector may have been killed as soon as it probed but it had already transmitted the virus to the seedling.

In the use of insecticides to control virus diseases, the pathogen-vector relationship is more important than the direct damage the insects cause to the crop. Also, crops and annual grasses may be reinfested by long-distance dissemination of viruliferous aphids. The major factors affecting this approach to control are acquisition feeding, latent period, and transmission threshold. Generally, insecticides have been most effective in controlling the transmission of viruses with semipersistent or persistent relationships; diseases caused by nonpersistent viruses such as MDMV-A are relatively unaffected (5).

Resistance. Resistance is not easily found. Approximately 1,600 lines from the World Sorghum Collection have been tested, but about 12,400 lines have not. Some may yield resistant germ plasm.

Eradication of the overseasoning host may be difficult and expensive, since several species of perennials may carry the virus. Early in the search for host resistance to MDMV, we inoculated material from the World Sorghum Collection using a small Thayer and Chandler model 4272C airbrush in the greenhouse. It became evident early that all the material inoculated developed mosaic and/or red leaf and necrosis. In order to test larger populations, we designed a two-row, three-point-hitch field inoculation rig (Fig. 4). When a spray gun is used for inoculation, differences in pressure and inoculum concentrations result in differential disease ratings among genotypes. Ten

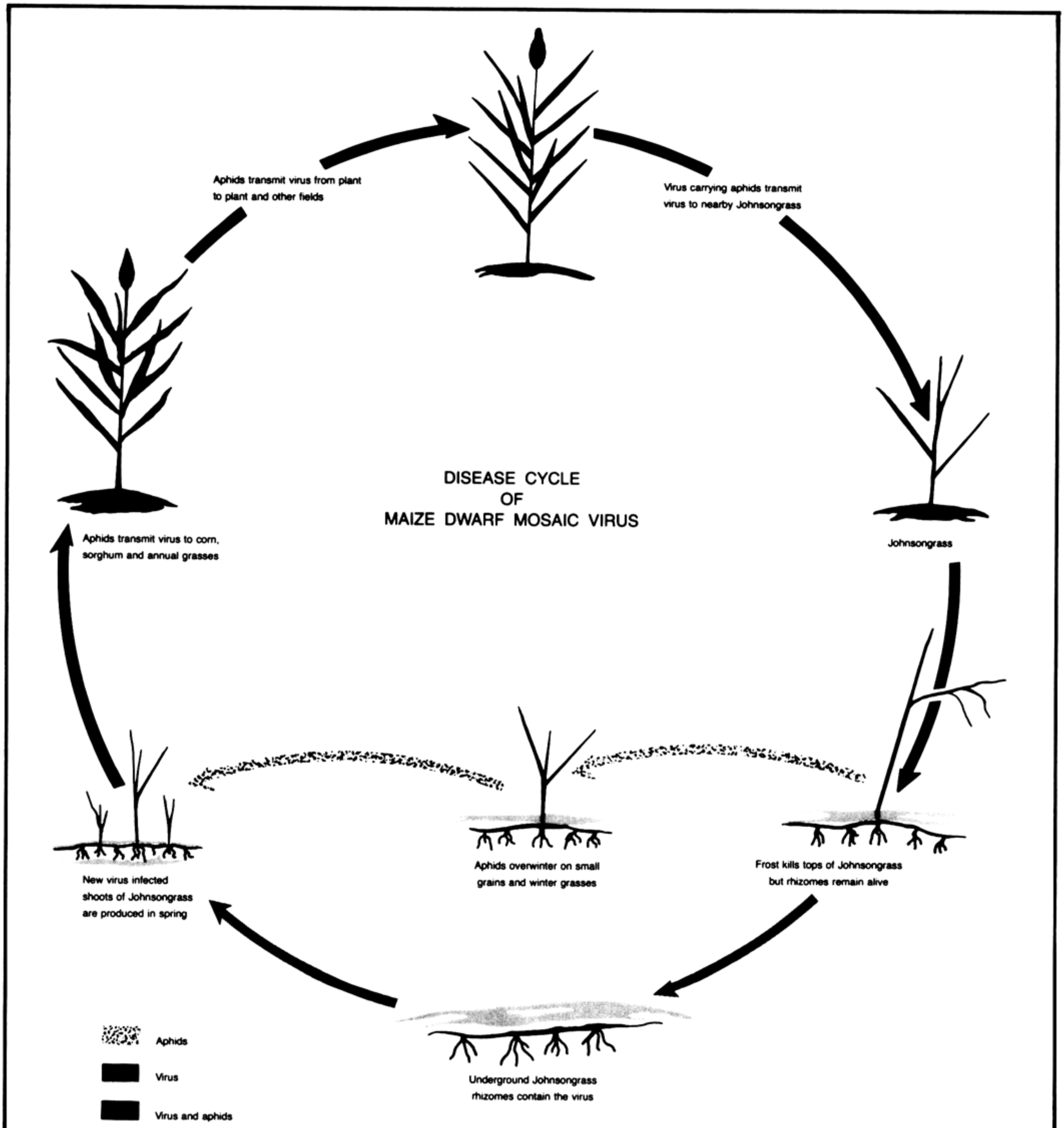

Fig. 3. Johnsongrass is the perennial reservoir for MDMV-A inoculum and thus plays a central role in the disease cycle.

sorghum inbreds of known MDMV reaction were artificially inoculated at 1:10 and 1:100 (w/v) tissue-to-buffer concentrations at pressures of 0, 1.4, 4.2, and 7.3 kg/cm^2 and rated on an individual plant basis after 21 days. The effects of pressure, concentration, and genotype on the disease severity index (DSI) were varied. Significant interactions were detected between pressure and concentration of inoculum. High pressures and greater virus concentrations increased genotypic susceptibility. Even though DSI changed under different pressure/concentration combinations, the inbred lines responded uniformly and the rankings remained unchanged. The interaction of spray gun (DeVilbiss MGB series 507 with No. 58 nozzle), pressure, and inoculum concentration was optimized at 7.3 kg/cm^2 at a 1:10 virus dilution.

Tolerance is the first type of resistance used to control MDMV in grain sorghum. Field trials using airbrush inoculations were conducted in an attempt to identify genetic material that when diseased yields as much as, or

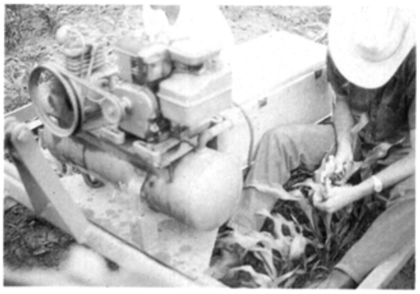

Fig. 4. Rig for two-row airbrush inoculation of plants in the field.

nearly as much as, healthy controls (22). Tolerance to MDMV-A in grain sorghum was identified in five lines. The lines and their yield reductions when diseased were: RS 621, no reduction; Tx 414, no reduction; RS 625, 3.1% reduction; Wheatland (BTx 399), 3.8% reduction; and Martin (Tx 398), 8.7% reduction. In comparison, yield reductions for three susceptible controls were 33.7% for Redlan (Tx 378), 45.5% for Caprock (RTx 7000), and 47.6% for Combine Kafir-60 (Tx 3197). Tolerant grain sorghum materials were made available to commercial hybrid seed companies in 1968, and crosses with one tolerant inbred produced commercial hybrids that were tolerant and marketed by 1970.

Immunity is a second type of resistance. Krish sorghum, a tall, grassy, photoperiod-sensitive cultivar, was derived from the cross *Sorghum* sp. × *S. bicolor* group Roxburghii (*S. halepense* 2n = 20 × *S. roxburghii*) (13). Krish sorghum was the first genotype observed to be resistant to SCMV-Jg, a discovery made in Australia by Teakle and Pritchard (29). It is probable that only one of the original parents, the Indian *Sorghum* sp. (= *S. halepense* 2n = 20 = Q12117), was resistant (6). Krish resistance depends on a single gene, K, with resistance dominant over susceptibility. It is effective against all four Australian strains of SCMV and is immune to the U.S. isolate of MDMV-A. In 1977, I (32) reported immunity in SC-0120-14E 73-C9-31-32. The Krish genes were transferred to 16 breeding lines (QL1-17) during 1972–1977 by Henzell et al (11). In 1979, Miller and I (17), using a backcross program to QL3, described and released two immune germ plasms, TAM-B51 and TAM-B52.

Table 1. Grain sorghum accessions with low levels of infection under mechanical and natural inoculation with maize dwarf mosaic virus

Source (unpublished)	Entry	Infection (%)
D. M. Persley et al, 1976	Q-7539(IS7596)-3Aex 80G w/h-74	5.0
J. D. Smith and R. W. Toler, 1976	NM-31(M_3)76-380-13	7.4
	NM-3(M_3)76-392-2	6.0
R. W. Toler and F. R. Miller, 1976	SC-0534(IS7596)PR	10.0
	SC-0097-14E 73-CS-271,72	5.0

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Field resistance is a third type. In 1975, Rosenow et al (*unpublished*) observed field resistance to MDMV-A in six grain sorghum lines: IS-2549C (SC-228), IS-2816C (SC-120), IS-12612C (SC-112), IS-12666C (SC-175), Rio, and TAM-2566. All lines were infected when mechanically inoculated but remained healthy under heavy infestations of viruliferous aphids in the field. Another source of field resistance was found in the Australian sorghum Q-7539, a tall, photoperiod-sensitive sorghum from Nigeria (20). Q-7539 resistance is probably multigenic and quantitative. Mechanical inoculation produces a high proportion of infected plants, but the incidence of infection in the field is low.

Resistance to infection is a fourth type and is evident when infection levels are low under both mechanical and natural inoculation. Acceptable infection levels range from 5 to 10% of plants. Five genotypes have been observed with this type of resistance (Table 1). In 1984, Miller and I (18) described a single genotype with resistance to more than one virus. The line, SC-0097-14E, has resistance to MDMV-A (less than 3% infection) and immunity to MDMV-B and SCMV-H and was released as Tx 2786.

Work still to be done includes: 1)

determining the inheritance of the different types of resistance, 2) evaluating more thoroughly the effects of the virus on plant growth and development, 3) analyzing the effects of MDVM-B and SCMV strains on growth, development, and resistance in sorghum, 4) studying the relatedness of MDMV strains D, E, F, and O and their effects on sorghum, and 5) continuing the search for resistance, particularly multiple resistance to viruses and/or strains. An international sorghum virus nursery and antiserum bank have been developed at Texas A&M University through support provided by USAID Title XII to help identify sorghum viruses and strains.

Commercial companies are continuously testing for MDMV-A resistance. The utilization of known sources of resistance in the production of new hybrids has greatly reduced MDMV-A losses in grain sorghum. MDMV-A reservoirs still exist in many sorghum-growing areas, however, and aphids persist from year to year, underscoring the potential for another epiphytotic in sorghum hybrids.

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