Effect of Host Resistance on Pathogenesis of Maize Dwarf Mosaic Virus

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ABSTRACT

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The pathogenesis of maize dwarf mosaic virus (MDMV-A) in maize was characterized in locally and systemically infected tissues of susceptible and resistant maize genotypes. Resistant genotypes used in this investigation had been classified by the absence of systemic symptom expression. Because some plants of the resistant genotype occasionally expressed systemic symptoms, we refer to the presence of symptoms as the susceptible phenotype and the absence of symptoms as the resistant phenotype. MDMV capsid protein was detected 2 days after inoculation in the inoculated leaf at the site of inoculation in both susceptible and resistant genotypes. Proximal invasion from the site of inoculation also was detected in both susceptible and resistant genotypes although invasion was delayed 6 days in the resistant genotypes. The resistant genotype, PB3187, expressed both susceptible and resistant phenotypes. When a leaf was inoculated before the emergence of the next three subsequent leaves, systemic symptoms were expressed (susceptible phenotype). However, when a leaf was inoculated after the emergence of the next three subsequent leaves, the resistant phenotype was expressed. Infectious virus was found within the inoculated leaf, within stalk tissue below the inoculated leaf, and in the roots of PB3187 plants expressing either the susceptible or resistant phenotype. Infectious virus was detected only in tissue above the inoculated leaf in PB3187 plants expressing the susceptible phenotype but not in equivalent leaves of plants expressing the resistant phenotype. This phenomenon of differential phenotype expression was not affected by plant age or temperature. We propose that the resistance mechanism expressed in PB3187 acts at a specific point of systemic virus transport, thereby limiting upward virus transport from the roots to young, developing leaves.

Maize dwarf mosaic virus (MDMV) consists of virus isolates closely related to sugarcane mosaic virus (12). MDMV has caused significant losses in maize (*Zea mays* L.) production in the United States and other temperate regions of the world (3,6). Incorporation of resistance to MDMV into some maize hybrids has significantly reduced losses caused by infection with MDMV. The resistant phenotype in maize is characterized by an absence of systemic symptoms. Studies have been conducted to determine the genetic, biochemical, and physiological processes involved in resistance, yet the genetics of MDMV resistance in maize is poorly understood. Most studies have focused on determining the probable number of resistance genes and the way they interact by the expression of symptoms in plants. However, some resistant genotypes express symptoms (that is, they have a susceptible phenotype) in a small proportion of inoculated plants (8,9,11). Assuming that these inbred and hybrid genotypes are no longer segregating, the inconsistent symptom expression indicates that resistance may be influenced by developmental, physiological, and/or environmental factors. Consequently, reliance on symptom severity and disease incidence for the selection of resistance has been controversial (5) and has delayed progress in elucidating the mechanisms of resistance (10,11,15).

Possible mechanisms involved in virus resistance include virus inactivation, resistance to initial infection, reduced multiplication, resistance to cell-to-cell movement (short distance transport), and resistance to systemic movement (long-distance transport) (7,13). Tu and Ford (16) found that levels of maize dwarf mosaic virus strain A (MDMV-A) accumulation did not differ within the inoculated leaf of resistant and susceptible genotypes, indicating that virus multiplication was not inhibited. Virus was not detected in newly emerged leaves of symptomless, resistant plants but was present in symptomatic, susceptible plants, indicating that virus was localized within the inoculated leaves of resistant plants. Virus was detected only in 'resistant' genotypes exhibiting systemic symptoms. Jones and Tolin (8) observed that, in systemically infected leaves, MDMV multiplied and attained concentrations as high in the resistant genotypes as in susceptible genotypes, even though symptom expression was delayed by 5 to 6 days. The delay of symptom expression was attributed to a delay in movement rather than reduced multiplication. Symptoms in the resistant plants consisted of longitudinal bands or streaking symptoms rather than the typical mosaic pattern. Lei and Agrios (9) examined maize dwarf mosaic virus strain B (MDMV-B) movement within the inoculated leaf. Again, they observed that resistant and susceptible genotypes produced similar levels of MDMV-B in the inoculated leaf and that invasion occurred faster and developed further in the susceptible genotype. There was no symptom expression or virus detected in leaves above the inoculated leaf of resistant plants. However, infected hybrids from crosses of some resistant and susceptible inbred lines exhibited narrow bands of chlorotic tissue.

In preliminary experiments, we also observed that the resistant hybrid Pioneer Brand (PB) 3187 and inbred T232 exhibited both resistant and susceptible phenotypes. The presence of infectious virus within uninoculated areas of the inoculated leaf of resistant genotypes at levels equivalent to those found in susceptible genotypes indicates that MDMV is not inactivated, can infect and multiply in the plant, and can move cell to cell (1,8,9,16). These results favor a mechanism of action that inhibits systemic movement of MDMV and indicates that expression of the resistant phenotype depends on an environmental, developmental, or inducible factor. The specific objective of this research was to compare local and systemic virus invasion in susceptible and resistant genotypes. In addition, differential phenotype expression in PB3187 was characterized by examining the physiological and

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environmental factors such as plant age, leaf age, and temperature that might influence expression.

MATERIALS AND METHODS

Virus. MDMV-A (17) was maintained in the susceptible maize cultivar Seneca Chief. Lyophilized infected tissue served as the inoculum for plants used as the source of inoculum for experiments. Inoculum was produced by homogenizing the infected leaves of plants in 0.05 M potassium phosphate buffer, pH 7.2 (1:10, w/v). Plants were inoculated by applying sap from infected tissue with a cotton-tipped applicator to a 4-cm area in the center of leaves previously dusted with Carborundum.

Virus assays. MDMV-A was assayed by a modified double antibody sandwich enzyme-linked immunosorbent assay (ELISA) (4) or by infectivity on Seneca Chief sweet corn. Immunolon 1 plates were coated for the modified ELISA with polyclonal MDMV-A antiserum (0.5 μg/ml) at 36 C for 1 hr and then washed with PBS-Tween (0.15 M phosphate-buffered saline, pH 7.4, containing 0.05% Tween-20 and 0.2% ovalbumin). Plant extracts were prepared by grinding tissue (1:25, w/v) in PBS-Tween containing 2% polyvinylpyrrolidone. The extracts were incubated overnight in plates at 4 C, washed in PBS-Tween, and then incubated in the second antibody (monoclonal MDMV-A antiserum 0.2 μg/ml) for 2 hr at 36 C. After the standard wash, goat-antimouse alkaline phosphatase conjugate was incubated for 2 hr at 24 C. Then, after the standard wash, *p*-nitrophenyl phosphate substrate was added and incubated at 24 C for 1 hr, and the absorbance at 405 nm was measured.

Infectious virus was assayed by grinding tissue 1:10, w/v, in 0.05 M potassium phosphate buffer, pH 7.2. The sample extract was then rubbed onto five Seneca Chief corn plants (susceptible genotype). The inoculation procedure was the same as described previously. The plants were rated for symptoms 14 days after inoculation. The sample was rated positive for infectious virus if symptoms were expressed. Initial symptoms in maize can be characterized as small chlorotic spots and short streaks that develop into a mosaic pattern.

Effect of leaf age and plant age on phenotype expression. Preliminary experiments indicated that the expression of the resistant phenotype by PB3187 may have depended on the developmental stage of either the leaf or the plant at the time of inoculation. The effect of leaf age was tested by inoculating leaf 4 at a sequential series of developmental stages: at emergence of leaf 4 or upon emergence of leaves 5, 6, 7, or 8. Each treatment consisted of six plants and the experiment was repeated once. The plants were examined for systemic symptoms and assayed by ELISA and infectivity. ELISA samples were taken from the inoculated fourth leaf, sheaths of leaves 4, 5, and 6, adventitious roots, leaves 5, 6, 7, and 8, and stem pith at the nodes of leaves 4, 5, 7, and the growing point.

The effect of plant age on expression of the resistant phenotype was tested by inoculating leaves 2, 4, 6, or 8 either before the next leaf emerged from the whorl or after the emergence of leaves 5, 7, 9, or 11, respectively. Each inoculation treatment consisted of five plants. The plants were examined for symptom expression over a period of 30 days and the experiment was repeated once.

Colonization of resistant and susceptible genotypes by MDMV-A within the inoculated leaf. Colonization by MDMV-A was monitored in two susceptible genotypes: B73 and PB3368A, and five resistant genotypes: T232, Pa405, PB3187, DK689 (Dekalb-Pfeizer Genetics), and X172b (Dekalb-Pfeizer Genetics). The genotypes T232, Pa405, and B73 were inbreds, whereas genotypes PB3368A, PB3187, Dk689, and X172b were hybrids. Plants were inoculated on the fourth leaf after the seventh leaf had emerged. Colonization within the fourth leaf was determined by examining invasion of areas proximal and distal to the 4-cm inoculated region in the center of the leaf (Fig. 1). Coat protein was assayed by ELISA. Samples were collected from the inoculated center and in sections 0 to 5 cm and greater than 5 cm, both distally and proximally from the inoculated center. The plants were assayed 0, 1, 2, 4, 6, 8, 12, 16, 24, and 32 days after inoculation or until leaf senescence. In addition to the inoculated leaf, samples also were assayed from the center of leaves 6, 8, and 12 to detect systemic virus invasion. The plants were arranged in a complete randomized block design consisting of three replications. Mean ELISA absorbance values obtained from each genotype were compared by least square mean comparison.

Effect of temperature on symptom expression. The effect of temperature on symptom expression was tested using genotypes PB3187 and T232 (resistant) and PB3368A (susceptible). Corn seeds were germinated in a greenhouse at 28 C. Seven-day-old plants then were transferred to growth chambers. Plants were inoculated on the fourth leaf after the seventh leaf had emerged. Inoculated plants were incubated in temperature-controlled chambers at 22, 28, and 34 C. The plants were monitored for symptom expression for 20 days. Nine plants of each genotype were inoculated at each temperature regime. The experiment was conducted twice.

Constitutive or induced resistance. To determine if the resistance mechanism was constitutive or induced, plants were given a primary virus inoculation (when the plant was predicted to express a resistant phenotype) followed by a subsequent challenge inoculation (when the plant would express a susceptible phenotype). In these experiments, the second leaf of all experimental plants was inoculated after the emergence of leaf 6 (resistant stage) with either buffer, MDMV-A crude extract (1:10, w/v), or inactivated (crude extract heated at 80 C for 15 min) MDMV-A. The plants were then challenged by inoculating the sixth leaf (susceptible stage) with MDMV-A crude extract 6 days after the primary inoculation. Ten plants were inoculated for each treatment, and the experiment was conducted three times. The previously described inoculation procedure was modified by inoculating the entire leaf. The plants were rated for symptoms 20 days after the last inoculation. Samples from the inoculated leaves and systemically infected leaves were assayed by ELISA for MDMV-A coat protein.

RESULTS

Effect of leaf and plant age on phenotypic symptom expression. Susceptible genotypes inoculated with MDMV developed

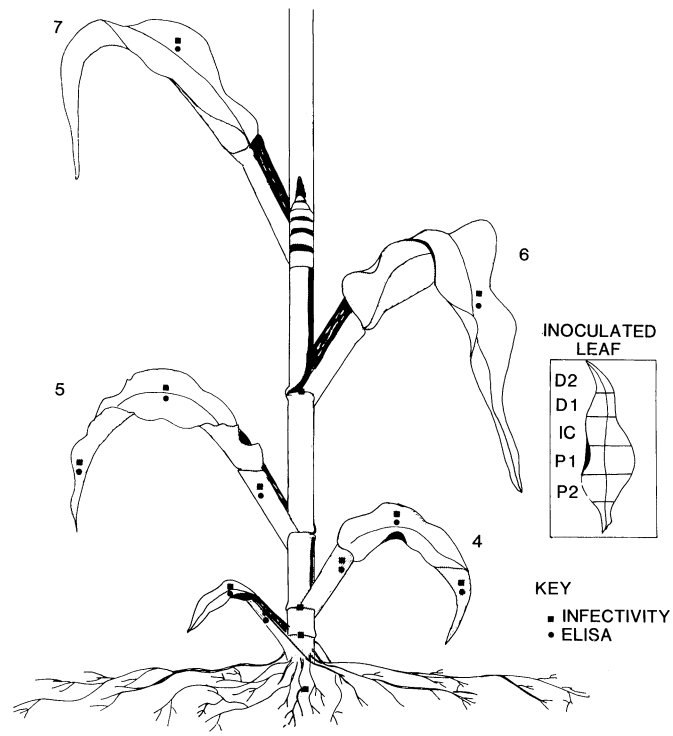

Fig. 1. Sites of the maize plants sampled for enzyme-linked immunosorbent assays (ELISA) and infectious virus assays. Samples were taken from the roots, stem, leaf sheath, and the leaf. Insert shows the five sampling sites for the inoculated leaf.

systemic symptoms and became systemically infected with the virus. Resistant genotypes, however, expressed either a susceptible or resistant phenotype, depending on the age of the leaf at inoculation. Systemic symptom expression was observed on plants that had been inoculated on the fourth leaf before the emergence of the third subsequent leaf (leaf 7); this reaction was termed the susceptible phenotype. If, however, the fourth leaf was inoculated after emergence of the third subsequent leaf, few if any plants expressed systemic symptoms; this reaction was termed the resistant phenotype.

To determine if this phenomenon was associated with leaf age or the age of the plant, successive leaves of plants of increasing age were inoculated when either the susceptible or resistant phenotype would be expected to be expressed (Table 1). For example, leaves two through eight were inoculated either before the next three succeeding leaves emerged (susceptible phenotype) or after three succeeding leaves emerged (resistant phenotype). When leaves of the resistant genotype PB3187 were inoculated before three subsequent leaves emerged, the susceptible phenotype was expressed, regardless of plant age and leaf position chosen for inoculation. Symptom expression occurred in 90–100% of the PB3187 plants in 6–24 days. As plants became older, symptom expression was delayed. In contrast, when PB3187 leaves were inoculated after the emergence of three subsequent leaves, the resistant phenotype was expressed. Symptom expression occurred in less than 20% of the plants and was delayed until 17–26 days after inoculation. In general, symptom expression in the resistant genotype expressing the susceptible phenotype was delayed when compared to susceptible genotypes. The susceptible genotype PB3368A expressed symptoms 5–10 days after inoculation in leaves 2 to 4 nodes above the inoculated leaf when leaves 2, 4, 6, or 8 were inoculated immediately after emergence. When leaves 2, 4, 6, or 8 of PB3368A were inoculated after the emergence of leaves 5, 7, 9, or 11, respectively, symptoms appeared 8–10 days after inoculation.

Infectious MDMV-A was detected in the inoculated leaf (blade, sheath, and node) and in the roots of the susceptible genotype PB3368A (data not shown) and in the susceptible and resistant phenotypes of PB3187 (Fig. 2A), regardless of the age of the leaf at the time of inoculation. However, the proportion of plants exhibiting symptoms in leaf 8 and having detectable virus in the sheaths of leaves 5 and 6 decreased as the age of the inoculated leaf increased (Fig. 2B). Infectious virus was not detected in sheath 5 and 6 or leaf 8 in the plants expressing the resistant phenotype.

TABLE 1. Effect of plant age on symptom expression in maize plants inoculated with maize dwarf mosaic virus

	Treatment		Number of plants with symptoms	Latent period[c] (days)
	Leaf inoculated[a]	Time of inoculation[b]		
Susceptible genotype PB3368A	2	S	10/10	5
	4	S	10/10	4
	6	S	10/10	6
	8	S	10/10	10
	2	R	10/10	8
	4	R	10/10	10
	6	R	10/10	10
	8	R	10/10	10
Resistant genotype PB3187	2	S	10/10	6
	4	S	10/10	8
	6	S	9/10	15
	8	S	9/10	24
	2	R	2/10	20
	4	R	1/10	26
	6	R	0/10	...
	8	R	1/10	17

[a] Leaf inoculated listed in the order of emergence.
[b] Leaves were inoculated either just after their emergence (S = susceptible) or after emergence of three subsequent leaves (R = resistant).
[c] Number of days from inoculation until symptom expression.

The two positive samples detected when leaf 4 was inoculated after emergence of leaf 7 were in plants expressing a susceptible phenotype.

Colonization of resistant and susceptible genotypes by MDMV-A within the inoculated leaf. The temporal colonization of the inoculated leaf by MDMV-A was compared in resistant and susceptible genotypes (Table 2). MDMV-A was detected in the inoculated region of the leaf on some plants as soon as 2 days after inoculation in both susceptible and resistant genotypes. The inoculation efficiencies (number of plants infected per number of plants inoculated), as determined by ELISA, were similar for both susceptible and resistant genotypes. Invasion proximal to the inoculated area was first detected 6 and 8 days after inoculation in the susceptible genotypes PB3368A and B73, respectively. However, there was a 4–6 day delay in proximal virus detection in the resistant genotypes. Proximal invasion of the inoculated leaf by MDMV occurred in all inoculated leaves of susceptible and resistant genotypes that were positive for virus coat protein in the inoculated center. Distal invasion from the inoculated center was detected in both susceptible and resistant genotypes 12 days after inoculation (data not shown). The same plants used to assay virus invasion in the inoculated leaf also were examined for systemic virus invasion of leaves 6 and 8. MDMV-A was detected only in the symptomatic leaves of the susceptible genotypes. No symptoms were observed and no viral coat protein was detected in the uninoculated leaves of the resistant genotypes.

Effect of temperature on symptom expression. Three temperature regimes were used to determine if changes in temperature would affect systemic virus movement. Systemic symptom expression occurred in the susceptible genotype PB3368A at 22, 28, and 34 C. The resistant genotypes, T232 and PB3187, inoculated to express the resistant phenotype, did not express systemic symptoms at any of the temperature regimes tested.

Constitutive or induced resistance. PB3187 plants were

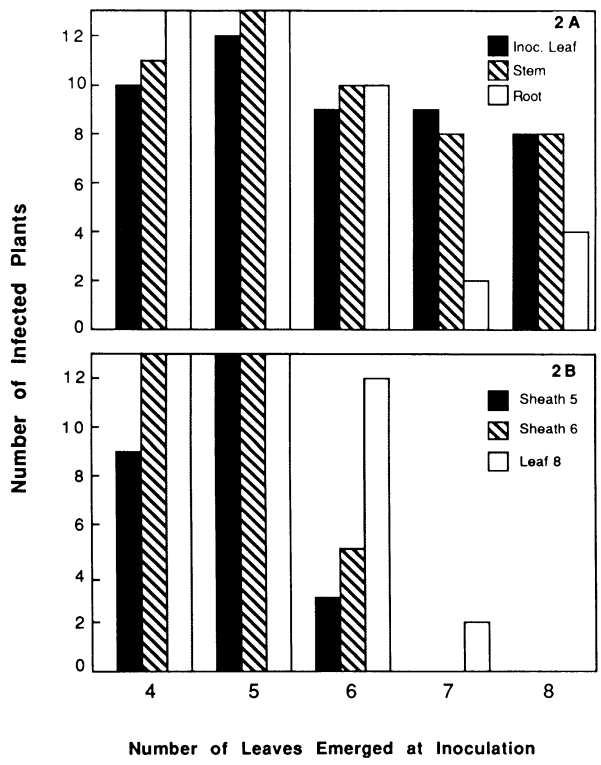

Fig. 2. Number of maize plants of the resistant genotype PB3187 expressing symptoms after inoculation of the fourth leaf at increasing stages of development with maize dwarf mosaic virus. Plants were inoculated at emergence of the fourth leaf or after emergence of leaves 5, 6, 7, or 8. **A,** Samples taken from the inoculated leaf, stem pith below the inoculated leaf, and the roots. **B,** Samples taken from leaves 5, 6, and 8.

challenge inoculated with MDMV-A to determine if the resistance was constitutively expressed or induced. Systemic symptoms were expressed in plants when they were challenged with MDMV-A, regardless of the primary inoculation (Table 3). The second leaf to emerge was inoculated at a stage of development when the resistant phenotype would be expected. The resistance in these plants was challenged by inoculating the sixth leaf to emerge at a stage of development when the susceptible phenotype would be expected, which occurred 5–6 days after the initial inoculation of leaf 2. When leaf 2 was inoculated at a resistant stage and leaf 6 was inoculated with buffer, only 3% of the plants expressed symptoms. When leaf 6 was challenge inoculated with MDMV after a primary inoculation of leaf 2 (either no inoculation, inoculation with buffer, or thermally inactivated MDMV), 63, 48, and 67% of the plants expressed symptoms, respectively. When both leaves were inoculated with MDMV, 70% of plants expressed the susceptible phenotype. The lack of symptoms in plants inoculated only on leaf 2 in the resistant phenotype indicates that the resistance is effective against the primary inoculation. The primary inoculation of leaf 2 with either buffer, thermally inactivated virus, or infectious virus did not prevent symptom expression in the challenge-inoculated plants.

TABLE 2. Maize dwarf mosaic virus colonization of the inoculated leaf in susceptible and resistant maize genotypes

Incubation period (days after inoc.)	Maize genotype	Phenotype[a]	Proximal 2[b] (5–10 cm)	Proximal 1 (0–5 cm)	Inoculated center[c]
2	PB3368A	S[b]	0	0	2 (0.13)
	B73	S	0	0	1 (0.05)
	PB3187	R	0	0	0
	DK689	R	0	0	0
	DKXI72b	R	0	0	2 (0.06)
	Pa405	R	0	0	5 (0.12)
	T232	R	0	0	5 (0.13)
					LSD = 0.29
4	PB3368A	S	0	0	5 (0.29)
	B73	S	0	0	2 (0.07)
	PB3187	R	0	0	3 (0.28)
	DK689	R	0	0	6 (0.10)
	DKXI72b	R	0	0	3 (0.18)
	Pa405	R	0	0	5 (0.20)
	T232	R	0	0	6 (0.31)
					LSD = 0.23
6	PB3368A	S	7 (0.07)	7 (0.22)	7 (0.55)
	B73	S	0	0	6 (0.44)
	PB3187	R	0	0	4 (0.30)
	DK689	R	0	0	5 (0.34)
	DKXI72b	R	0	0	4 (0.43)
	Pa405	R	0	0	5 (0.53)
	T232	R	0	0	5 (0.56)
					LSD = 0.44
8	PB3368A	S	7 (0.32)	7 (0.29)	7 (0.55)
	B73	S	5 (0.05)	5 (0.12)	5 (0.33)
	PB3187	R	0	0	5 (0.45)
	DK689	R	0	0	8 (0.42)
	DKXI72b	R	0	0	7 (0.31)
	Pa405	R	0	0	5 (0.64)
	T232	R	0	0	9 (0.44)
			LSD = 0.18	LSD = 0.13	LSD = 0.38
12	PB3368A	S	6 (0.51)	6 (0.62)	6 (0.66)
	B73	S	0	4 (0.12)	4 (0.50)
	PB3187	R	4 (0.21)	4 (0.40)	4 (0.54)
	DK689	R	5 (0.28)	5 (0.46)	5 (0.61)
	DKXI72b	R	5 (0.26)	5 (0.44)	5 (0.70)
	Pa405	R	0	7 (0.08)	7 (0.96)
	T232	R	0	8 (0.09)	8 (0.77)
			LSD = 0.30	LSD = 0.36	LSD = 0.48
16	PB3368A	S	9 (0.87)	9 (0.84)	9 (1.04)
	B73	S	2 (0.24)	2 (0.69)	2 (0.65)
	PB3187	R	2 (0.41)	2 (0.46)	2 (0.40)
	DK689	R	6 (0.45)	6 (0.58)	6 (0.66)
	DKXI72b	R	6 (0.50)	6 (0.57)	6 (0.71)
	Pa405	R	4 (0.04)	4 (0.27)	4 (0.79)
	T232	R	0	8 (0.24)	8 (0.88)
			LSD = 0.49	LSD = 0.54	LSD = 0.50

[a] Expression of phenotype (susceptible or resistant) based on expression of symptoms in uninoculated leaves.
[b] Number of plants positive for virus coat protein. Samples were rated positive for virus infection if mean enzyme-linked immunosorbent assay (ELISA) value was greater than 0.03 (three standard deviations above mean absorbance of healthy samples).
[c] Mean ELISA Abs_{405}.

DISCUSSION

Our study and that of Lei and Agrios (9) show that MDMV infects and accumulates to similar levels in inoculated tissue of both susceptible and resistant maize genotypes, indicating that MDMV replication is not affected. The significant difference that we observed between susceptible and resistant genotypes was in systemic virus transport. Virus was transported upward to younger leaves in the susceptible genotype, whereas in a typical resistant reaction, virus was not detected above the inoculated leaf. Genotypes classified as resistant to MDMV may in certain cases express a susceptible phenotype (8,16). We found phenotype expression to be associated with the physiological development of the leaf at the time of inoculation. Inoculation of leaves after they reached a specific developmental stage resulted in a resistant phenotype; inoculation of leaves at earlier stages resulted in the expression of a susceptible phenotype. Symptom expression and virus were detected in young leaves of the resistant genotype PB3187 only when the susceptible phenotype was expressed. The resistance mechanism was not affected by high temperature (34 C) nor was it inducible. Plant age did not influence phenotype expression, but symptoms were delayed in older plants.

The ability to manipulate the resistant genotype PB3187 to express a susceptible or resistant phenotype provided a model to examine sites in plants of the resistant phenotype where systemic virus movement might be affected. Infectious virus was detected throughout PB3368A and PB3187 plants expressing the susceptible phenotype (in roots, stem pith, and subsequently developing leaves). Thus, systemic transport and distribution of MDMV in maize is similar to that reported for TMV in tobacco (14). Plants expressing the resistant phenotype accumulated infectious virus within the inoculated leaf (blade, sheath, and node), stem pith below the inoculated leaf, and the roots. No infectious virus was detected in leaves younger than the inoculated leaf.

PB3187 plants expressing either susceptible or resistant phenotypes were capable of supporting cell-to-cell movement as evidenced by the movement of virus within the inoculated leaf. Furthermore, the presence of infectious virus in the roots indicates that the virus is transported out of the inoculated leaf in both susceptible and resistant phenotypes. The presence of virus in the young leaves of resistant plants expressing the susceptible phenotype is evidence that the virus is transported to the young leaves from the inoculated leaf. This upward movement of virus does not appear to occur in plants expressing the resistant phenotype. These characteristics support the hypothesis that the resistant phenotype of PB3187 is due to uncoupling of virus transport. The uncoupling of virus transport might occur in the inoculated leaf where separate mechanisms of loading for upward and downward transport exist or in the roots where virus is loaded for upward transport.

Atabekov and Dorokhov (2) proposed that systemic virus

TABLE 3. Effect of a primary inoculation of maize on systemic maize dwarf mosaic virus (MDMV) infection[a]

Primary inoculation of leaf 2 (resistant stage)	Challenge inoculation of leaf 6 (susceptible stage)	Percent plants expressing symptoms[b]
MDMV	Buffer	3
Uninoculated	MDMV	63
Buffer	MDMV	48
Attenuated MDMV	MDMV	67
MDMV	MDMV	70

[a] The challenge inoculation was performed 6 days after the primary inoculation.
[b] Percent expressing symptoms 20 days after inoculation.

movement is with the flow of assimilates in the phloem. In plants of the age used in this study, we would expect assimilates to move from the leaves toward the roots and that the flow would follow a continuous negative sucrose concentration gradient from the leaf (source) to the roots (sink). Cell-to-cell transport of assimilates is through the plasmodesmata, whereas long-distance transport is through the phloem. The transition between these two types of movement occurs at phloem loading or unloading. Thus, systemic virus movement could be prevented by inhibition of either the loading of virions, ribonucleoprotein (2), or RNA into the phloem or unloading from the phloem in either the leaves or the roots.

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