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THE GENETICS OF VIRUS RESISTANCE IN MAIZE (*ZEA MAYS* L.)

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ABSTRACT - The identification and mapping of genes and quantitative trait loci (QTL) associated with virus resistance in maize (*Zea mays* L.) are reviewed. Genes or major QTL for resistance to *Maize dwarf mosaic virus* (MDMV), *Sugarcane mosaic virus* (SCMV), *Wheat streak mosaic virus* (WSMV), *Maize mosaic virus, Maize streak virus, High Plains virus* and *Maize chlorotic dwarf virus* have been mapped in the maize genome. Resistance to other viruses including *Maize rayado fino virus,* maize fine streak virus and maize necrotic streak virus has been identified, but not characterized genetically. Clusters of maize virus resistance genes are located on chromosomes 3, 6 and 10. The cluster on chromosome 6 (bin 6.01 near umc85) carries resistance to three members of the *Potyviridae* (MDMV, SCMV and WSMV). The clusters on chromosomes 3 (bin 3.05 near umc102) and 10 (bin 10.05 near umc44) carry resistance to phylogenetically diverse viruses as well as bacterial and fungal pathogens.

KEY WORDS: Quantitative trait loci (QTL); Maize; Virus resistance.

INTRODUCTION

On August 26, 2002, the Ohio maize community gathered for the inaugural 'Stringfield Lectures', which honored the life and work of former U.S. Dept. of Agriculture and Ohio Agriculture Experiment Station maize geneticist, Dr. Glen Stringfield. Dr. William (Bill) Findley, the recipient of the first Stringfield Award, was a pioneer in the identification and development of virus-resistant maize for Ohio and the U.S. Dr. Findley was a USDA Research Geneticist with the joint Agricultural Research Service-Ohio State University corn-breeding program that was responsible for the rapid identification of germplasm resistant to the maize viral disease complex in the 1960s. This program developed the resistant maize inbred lines Oh513, Oh514, and Oh1EP, and several synthetic populations that are resources for virus resistance. The group also studied the genetics of resistance. They used classical analysis of segregation to show that two or three genes were responsible for *Maize dwarf mosaic virus* (MDMV) resistance in Oh07 (Dollinger *et al.*, 1970), and reciprocal chromosomal translocations to identify resistance genes on chromosome six in Oh07, Mo22 and Pa405 (Findley *et al.*, 1973; Louie *et al.*, 1991). In honor of Bill Findley's outstanding contributions to corn breeding and genetics, it seemed appropriate to examine recent research advances in the genetics of maize virus resistance.

GENETIC OF VIRUS RESISTANCE

There are at least eight viruses that cause significant agronomic losses in maize world-wide: MDMV, SCMV, MSV, MCDV, MMV, MRDV, MRCV, MCMV, MStV and MRFV (Table 1). In addition, there are several maize-infecting viruses that may be emerging disease threats or that are of interest to researchers. For example, WSMV does not cause significant agricultural problems, because few maize lines are susceptible to the virus. However, genetic analysis of resistance to WSMV, a member of the family *Potyviridae*, has been used as a model for analysis of resistance to the potyviruses MDMV and SCMV (McMullen *et al.*, 1994). MNeSV and MFSV are emerging maize viruses in the families *Tombusviridae* and *Rhabdoviridae*, respectively (Louie *et al.*, 2000; Redinbaugh *et al.*, 2002). HPV is an emerging virus that remains poorly characterized.

The most economical, environmentally-sustainable and effective means for controlling viral dis-

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TABLE 1 - *The major viruses causing disease in maize.*

Virus	Acronym	Virus Family	Disease Problems
Maize dwarf mosaic virus	MDMV	*Potyviridae*	WW[1]
Sugarcane mosaic virus-MDB	SCMV	*Potyviridae*	WW
Wheat streak mosaic virus	WSMV	*Potyviridae*	WW
Maize mosaic virus	MMV	*Rhabdoviridae*	Carribean
Maize streak virus	MSV	*Geminiviridae*	Africa
Maize chlorotic dwarf virus	MCDV	*Sesquiviridae*	U.S.
Maize chlorotic mottle virus	MCMV	*Tombusviridae*	U.S.
Maize rayado fino virus	MRFV	*Marafiviridae*	Carribean
Maize rough dwarf virus	MRDV	*Fijiviridae*	Europe/Asia/Africa
Maize Rio Cuarto virus	MRCV	*Fijiviridae*	South America
Maize stripe virus	MStV	tenuivirus	WW
Rice black streak dwarf virus	RBSDV	*Fijiviridae*	Asia
Rice tungro spherical virus	RTSV	*Sesquiviridae*	Asia
High Plains virus[2]	HPV	unknown	U.S.
Maize necrotic streak virus[2]	MNeSV	*Tombusviridae*	—
Maize fine streak virus[2]	MFSV	*Rhabdoviridae*	—

[1] WW, worldwide.
[2] emerging virus, the extent of agricultural impact is not known.

eases of maize is the deployment of resistant germplasm. Identification and development of resistant hybrids by breeders is complicated by year-to-year inconsistencies in viral disease pressure. The sporadic nature of viral disease problems is understandable, because disease establishment requires the interplay of a virus reservoir (e.g., a virus-infected perennial weed), the viral vector and virus-susceptible germplasm. Development of highly efficient inoculation techniques or identification of sites with consistent severe disease pressure may be used to overcome fluctuations in disease pressure.

Marker-assisted selection can provide a means for maintaining virus resistance alleles even in the absence of disease. To employ marker-assisted selection, virus resistance must first be identified in maize germplasm and then mapped to specific regions of the maize genome. Identification and mapping of genes or quantitative trait loci (QTL) for virus resistance also provides information on the numbers of genes or regions that must be transferred by breeding programs and aids in identification of sources for resistance. To date, genes or QTL for resistance to MMV, MSV, MCDV, HPV, and three *Potyviridae* species have been identified and mapped in maize (Table 2).

Resistance to Potyviridae

The *Potyviridae* is the largest and most destructive family of plant viruses (Shukla *et al.*, 1994). Several members of the *Potyviridae* infect maize: the aphid-transmitted potyviruses MDMV, SCMV, *Johnsongrass mosaic virus* (JGMV, also known as MDMV-O), *Sorghum mosaic virus* (SrMV), and the mite-transmitted tritimovirus WSMV (Shukla *et al.*, 1994; Stenger *et al.*, 1998). These viruses share the same overall genome organization and have significant sequence similarity (Kong *et al.*, 1998; Stenger *et al.*, 1998; Chen *et al.*, 2001). Because of their agronomic importance and ease of mechanical transmissibility, resistance to members of the *Potyviridae*, particularly MDMV, SCMV and WSMV, has been studied extensively in maize.

The short arm of chromosome 6 in or near the *nucleolar organizer region (nor)* is clearly important for resistance to the *Potyviridae*. Loci for resistance to MDMV, WSMV and SCMV have been designated *Mdm1* (McMullen and Louie, 1989; Simcox *et al.*, 1995), *Wsm1* (McMullen and Louie, 1991; McMullen *et al.*, 1994) and *Scm1* (Melchinger *et al.*, 1998; Xia *et al.*, 1999; Xu *et al.*, 1999; Dussle *et al.*, 2000; Dussle *et al.*, 2003), respectively. These loci segregate as dominant genes in the U.S. line Pa405

and several European lines. Each of these genes co-segregates with the RFLP marker(s) *umc85* and *bnl6.29*. Although attempts have been made to produce high-resolution genetic maps for virus resistance in this region (SIMCOX *et al.*, 1995; XU *et al.*, 1999; DUSSLE *et al.*, 2003; YUAN *et al.*, 2003), it has not yet been possible to separate the three resistance genes.

Mdm1 is the only clearly identified locus for MDMV resistance in maize, although segregation analyses suggested the presence of up to five resistance loci in Pa405 (ROSENKRANZ and SCOTT, 1984; MIKEL *et al.*, 1984). MCMULLEN and LOUIE (1989) speculated that there are genetic modifiers of *Mdm1* activity. However, multiple genes have been implicated in SCMV and WSMV resistance. *Scm2*, a dominant gene for SCMV resistance, was mapped to the interval flanked by the RFLP markers *umc92* and *umc102* near the centromere of chromosome 3 in European flint lines (XIA *et al.*, 1999; DUSSLE *et al.*, 2000, 2003). Similarly, MCMULLEN and co-workers (1994) identified *Wsm2* in the same region of chromosome 3 in Pa405. A third gene for WSMV resistance (*Wsm3*) mapped to the long arm of chromosome 10 between *umc163* and *umc44*. Interestingly, a minor QTL for SCMV resistance is also located in this region (XIA *et al.*, 1999).

Potyvirus resistance apparently arose more than once, because the RFLP markers (*umc85* and *bnl6.26*) near *Scm1/Mdm1* have similar banding patterns in several different resistant European lines, whereas banding patterns for the same markers are quite different in the resistant U.S. line Pa405 (XU *et al.*, 2000). Resistance to various potyviruses has been identified in germplasm from around the world including U.S. Cornbelt and Southeastern elite lines, Caribbean lines, South American and Asian lines as well as African lines (LOUIE *et al.*, 1990; BREWBAKER *et al.*, 1991).

Resistance to geminiviruses

MSV causes significant losses for producers in Africa and on Indian Ocean islands. Although highly tolerant germplasm has been identified by several international maize breeding programs (BARROW, 1992; PERNET *et al.*, 1999a,b; WELZ *et al.*, 1998), genetic characterization of this resistance has been hampered by the obligate transmission of MSV by *Cicadulina* leafhoppers. Furthermore, biosafety concerns limit resistance screening to areas where the virus is indigenous. Nonetheless, resistance was mapped in several different populations using field inoculations in Africa, and a major QTL for MSV resistance was identified on the short arm of chromosome 1 (KYETERE *et al.*, 1999; WELZ *et al.*, 1998; PERNET *et al.*, 1999a,b). Alleles at this locus were additive (KYETERE *et al.*, 1999) or partially dominant (WELZ *et al.*, 1998, PERNET *et al.*, 1999a,b) depending on the resistance source. While the locus on chromosome 1 explained most of the resistance in all four studies, minor QTL were also found. In the Réunion Island germplasm, one of these minor QTL maps to the same region of chromosome 10 as *Wsm3* (PERNET *et al.*, 1999b).

The identification of a single major resistance locus and threat of its breakdown under field conditions have led researchers to search for other avenues for MSV resistance. The development of insect resistance to reduce MSV transmission by leafhoppers is one approach (reviewed by BOSQUE-PEREZ, 2001). Another is to incorporate MSV resistance genes from other species into maize. Boulton and co-workers investigated MSV resistance in barley (M. Boulton, John Innes Center, Norwich, personal communication). Barley, wheat and rice cultivars varied widely in susceptibility to MSV. A single dominant gene that mapped to chromosome 6H in a doubled haploid population conferred resistance in barley cv. Triumph. Current data indicate this region of the barley genome is not syntenous with the region of maize chromosome 1 carrying *Msv1*, suggesting the two genes are not orthologs.

Resistance to waikaviruses

The waikavirus MCDV causes significant problems in the southeastern U.S. in the region where its overwintering host (*Sorghum halpense*) and leafhopper vector (*Graminella nigrifrons*) overlap (GORDON *et al.*, 1981). Significant efforts to identify and characterize MCDV resistance in maize were made (GUTHRIE *et al.*, 1982; ROSENKRANZ and SCOTT, 1986, 1987; LOUIE *et al.*, 1990). However, problems with incomplete virus transmission under field conditions and the presence of MDMV-infected plants limited selection for disease resistance and genetic studies. Improved methods for virus transmission (LOUIE and ANDERSON, 1993; PRATT *et al.*, 1994), the identification of highly resistant Caribbean germplasm, and the development of the MCDV resistant inbred Oh1VI (LOUIE *et al.*, 2002) have improved the outlook for mapping resistance to MCDV. Two QTLs were mapped in Oh1VI x Va35 F2 plants (JONES *et al.*, in press). These loci co-segregated with markers on chromosome 3 near *umc102* and chromosome 10 near *umc44*.

Resistance to rhabdoviruses

MMV is a maize-infecting, planthopper-transmitted (*Perigrinus maidis*) nucleorhabodvirus that causes disease in many tropical and sub-tropical areas worldwide (BREWBAKER, 1981). MMV resistance was identified in Caribbean flint germplasm, and a major QTL for MMV resistance was identified near the centromere on chromosome 3 between *umc102* and *php20508* (MING *et al.*, 1997). Recently, MFSV, a leafhopper-transmitted (*G. nigrifrons*) nucleorhabodovirus was characterized (REDINBAUGH *et al.*, 2002). Although resistance loci to this virus have not been mapped in maize, the MMV-resistant lines Hi31 and Hi34 are resistant to the virus, as is the MCDV-resistant inbred Oh1VI.

Resistance to High Plains Virus

HPV is an emerging viral pathogen that infects a number of monocots, including maize and wheat (JENSEN *et al.*, 1996). The disease is transmitted by the wheat curl mite (*Aceria tosichella* Keifer) which also transmits WSMV. Because it has not been possible to keep laboratory mite colonies free of WSMV, HPV has been transmitted in a mixed infection with WSMV. Although all of the lines tested apparently supported HPV replication in inoculated leaves, systemic spread of the virus was limited to a few lines (MARÇON *et al.*, 1997a). Resistance to double infection by HPV and WSMV co-segregated with *umc85* and *Wsm1* on the short arm of chromosome 6 (MARÇON *et al.*, 1997b, 1999). An additional locus was identified near *umc102* and *Wsm2* on chromosome 3 (MARÇON *et al.*, 1999). Unfortunately, the co-transmission of WSMV and HPV and coincidence of HPV resistance with *Wsm1* and *Wsm2* complicates interpretation of the results. Recombinants were found in the region near *umc85* that were HPV susceptible and WSMV resistant. However, because other loci were segregating for WSMV in the population, the HPV resistance QTL identified in that study may be specific to the WSMV/HPV infection complex rather than HPV alone.

Resistance to other maize-infecting viruses

For a number of other viruses that infect maize (Table 1), no resistance loci or genes have been identified. One of these, MRFV, is an agronomically important virus in Central America. Two highly tolerant inbred lines were identified from locally adapted landraces (BUSTAMANTE *et al.*, 1998), but information on the genetic basis of this resistance is not yet available. MNeSV is a newly discovered maize virus that does not currently cause agronomically important disease (LOUIE *et al.*, 2000). Nonetheless, several maize lines are highly resistant to this virus including the MCDV resistant Oh1VI (LOUIE *et al.*, 2000) and Mo17 (REDINBAUGH *et al.*, unpublished results).

Clustering of virus resistance in maize

Clustering of disease resistance genes in maize and other plants is notable (MCMULLEN and SIMCOX, 1995; COLLINS *et al.*, 1998). To date, most of the major QTL and genes conferring virus resistance in maize fall into three major clusters (Table 2). The *Msv1* locus on chromosome 1 is near a QTL for resistance to the *Erwinia stewartii*, the bacterium that causes Stewart's wilt (MING *et al.*, 1999). The cluster on the short arm of chromosome 6 confers resistance to viruses in the family *Potyviridae*, HPV and the southern corn leaf blight fungus, *Cochliobolus heterostrophus* Dresch. It is not currently known whether resistance to MDMV, SCMV, WSMV and HPV/WSMV is conferred by a single gene, or whether these are closely linked genes for *Potyviridae* resistance. If resistance to the *Potyviridae* is conferred by a single gene that encodes an R- or 'R-like' protein, then it is likely resistance involves the three dimensional structure of a viral protein that is conserved among MDMV, SCMV and WSMV. Some portions of the viral genomes are highly conserved. Notably, the NIb or replicase protein shares more than 65% sequence similarity among the three *Potyviridae*. However, differential responses of maize germplasm to the three viruses support the hypothesis that resistance to the three viruses is encoded by closely linked genes. Definitive evidence for either of the models will require cloning and characterizing one or more of the genes or separating the loci genetically.

Perhaps more interesting are the clusters of genes for resistance to phylogenetically unrelated viruses on chromosomes 3 and 10. These regions of chromosomes 3 and 10 also carry genes encoding proteins with the nucleotide binding site-leucine-rich repeat (NBS-LRR) motifs characteristic of R genes and loci for rust resistance (COLLINS *et al.* 1998, 1999). The complex *Rp3* locus for rust resistance on chromosome 3 carries a family of NBS-LRR genes that hybridize with the PIC13 probe (WEBB *et al.*, 2003). The presence of some members of the gene family has been associated with rust resistance. It is tempting to speculate that virus resistance in these regions is also associated with a fami-

TABLE 2 - *Clustering of virus resistance genes and QTL in the maize genome.*

Chr	Bin[1]	Marker(s)	Virus	Gene	Gene action	Comments	Reference
1	1.05	*umc57*	MSV	*Msv1*	Additive	major QTL	WELZ *et al.*, 1998; KYETERE *et al.* 1999; PERNET *et al.* 1999a, b
3	3.05	*umc102*	WSMV	*Wsm2*	Dominant	Gene	MCMULLEN *et al.* 1994
			SCMV	*Scm2*	Dominant	major QTL	XIA *et al.*, 1999; XU *et al.*, 1999
			MMV	*Mv1*	Co-dominant	major QTL	MING *et al.* 1997
			MCDV	*Mcd1*	Additive	major QTL	JONES *et al.*, unpublished
			HPV/WSMV	—	—	major QTL	MARÇON *et al.* 1997b, 1999
6	6.01	*umc85*	MDMV	*Mdm1*	Dominant	Gene	MCMULLEN & LOUIE, 1989
		bnl6.26	SCMV	*Scm1*	Dominant	major QTL	XIA *et al.*, 1999; XU *et al.*, 1999
			WSMV	*Wsm1*	Dominant	Gene	MCMULLEN *et al.* 1994
			HPV/WSMV	—	—		MARÇON *et al.* 1997b, 1999
10	10.05	*umc44*	WSMV	*Wsm3*	Dominant	Gene	MCMULLEN *et al.* 1994
			MCDV	*Mcd2*	Additive	major QTL	JONES *et al.*, unpublished
			MSV	—	Overdominant	moderate QTL	PERNET *et al.*, 1999a, b

[1] A bin is the statistically defined interval between two fixed core markers.

ly of NBS-LRR genes. Interestingly, Oh1VI, which carries QTL for MCDV resistance on chromosomes 3 and 10, is also resistant to a number of other maize-infecting viruses including the three members of the *Potyviridae*, the rhabdovirus MFSV, the tombusvirus MNeSV and HPV (REDINBAUGH *et al.*, unpublished results).

Roles of minor genes

Minor QTL accounting for small amounts of the genetic variation for virus resistance and modifier genes were identified in several studies (MARÇON *et al.*, 1999; PERNET *et al.*, 1999a,b; XIA *et al.*, 1999). For example, minor QTLs on chromosomes 4, 5 and 6 accounted for ~25% of the variation in HPV resistance among B73 x Mo17 RIL (MARÇON *et al.*, 1999). These loci control resistance to local infection, and were hypothesized to be associated with insect resistance. In addition, while *Mdm1* is required for the initial resistance response and acts in a dominant manner, the appearance of delayed symptoms in heterozygous plants led MCMULLEN and LOUIE (1989) to propose the presence of 'modifier' genes. In addition, minor genes for MDMV resistance were identified (ROSENKRANZ and SCOTT, 1984; MIKEL *et al.*, 1984). Inconsistencies in observing minor QTL across populations and locations may be related to environmental effects on their expression. An example is the effect of temperature on MDMV resistance (TU and FORD, 1969; SCOTT and LOUIE, 1996).

Mechanisms of resistance

Two studies of mechanisms associated with virus resistance in maize focused on investigation of MDMV infection in resistant and susceptible inbred lines (LEI and AGRIOS, 1986; LAW *et al.*, 1989). In the highly resistant line Pa405, MDMV could replicate in inoculated leaves and move from cell to cell, but systemic movement of the virus was not be detected. Although no virus resistance gene has been cloned from maize, such genes have been cloned from tobacco (WHITHAM *et al.* 1994), potato (RUFFEL *et al.*, 2002), tomato (SPASSOVA *et al.*, 2001) and *Arabidopsis* (WHITHAM *et al.*, 2000; CHISHOLM *et al.*, 2000). Interestingly, the two dominant genes for resistance to *Turnip crinkle potyvirus* in *Arabidopsis* do not encode the typical NBS-LRR containing proteins encoded by the other virus resistance genes.

Future prospects

It is likely that virus resistant maize germplasm will eventually be identified for all of the agronomically important maize-infecting viruses, and that resistance will be associated with specific genetic

markers. The search for high degrees of virus resistance in agronomically useful germplasm continues. In most cases, virus resistance is associated with one or two major resistance loci, which facilitates marker-assisted selection. It might be useful to incorporate resistance to multiple viruses from a single inbred into more agronomically adapted lines. This approach might be particularly useful for the clustered virus resistance genes and QTL. Although genetic loci associated with resistance to viruses other than MCDV have not yet been mapped in Oh1VI, transfer of specific chromosomal segments associated with multiple virus resistance from this Caribbean line to germplasm more useful to plant breeders in more temperate regions may be possible. Maps with sufficient resolution to allow identification of clones encoding resistance genes might be possible using an association mapping approach (THORNSBERRY *et al.*, 2001), or it may be possible to isolate the genes by transposon-tagging and map-based cloning approaches.

Pathogen-derived virus resistance has been used to develop highly virus resistant varieties in a number of crops (DASGUPTA *et al.*, 2003). There has been some interest in this area, and maize transformed with genes encoding the coat proteins of MDMV and MCDV have been developed. However, these have not yet been field-tested.

Although a number of genes or loci conferring virus resistance have been identified in maize, little is known about the mechanisms associated with resistance or the biochemical/molecular nature of the resistance response in maize. Systemic movement of the virus is restricted in the MDMV-resistant line Pa405. Little is known about the responses of maize lines resistant maize other viruses. Genomic approaches to defining the response of susceptible plants to virus inoculation are beginning to be used for *Arabidopsis* (WHITHAM *et al.*, 2003), but such work remains to be done in maize or other monocots. A unique opportunity to study the response to virus infection is available in maize, because resistant and susceptible germplasm is available for most viruses, and in many cases near isogenic lines carrying the resistance loci in a susceptible background are available. Further, the ability to mechanically inoculate maize with all known maize viruses using vascular puncture inoculation (LOUIE, 1995), will allow us to separate the response of maize to the virus and its vector.

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