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Inheritance of Resistance to *Zucchini Yellow Mosaic Virus* in Watermelon

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Abstract. **Sources of resistance to the *Zucchini yellow mosaic virus*-Florida strain (ZYMV-FL) have been identified within the *Citrullus* genus. Inheritance of resistance to ZYMV-FL was studied in PI 595203 (*Citrullus mucosospermus*), a resistant watermelon accession. The F_1, F_2, and BC_1 progenies derived from the cross 'Calhoun Gray' (CHG) × PI 595203 and 'New Hampshire Midget' (NHM) × PI 595203 were used to study the inheritance of resistance to ZYMV-FL. Seedlings were inoculated with a severe isolate of ZYMV-FL at the first true leaf stage and rated weekly for at least 6 weeks on a scale of 1 to 9 on the basis of severity of viral symptoms. A single recessive gene (*zym*-FL) was found to control the high level of resistance to ZYMV-FL in PI 595203.**

Watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] is a major cucurbit crop that accounts for 7.5% of the world area devoted to vegetable crop production (FAO, 2015). In the United States, watermelon is used fresh as a dessert, or in salads. Major production states in the United States. are Florida, California, Texas, Georgia, and North Carolina (USDA, 2017). Production increased from 1.2 million Mg (metric tons) in 1987 to 5.1 million Mg in 2017, with a farm value of $579 million (USDA, 2017).

Plant diseases incited by viruses are a major limiting factor in commercial watermelon production worldwide. More than 10 viruses are known to be a problem in watermelon field production (Ali et al., 2012; Wang et al., 2017). The major viruses affecting watermelon in the United States are *Zucchini yellow mosaic virus* (ZYMV), *Papaya ringspot virus*-watermelon strain (PRSV-W), and *Watermelon mosaic virus* (WMV). All three viruses are nonpersistently transmitted by several species of aphids, and mixed infections are common (Ali et al., 2012; Chen et al., 2008; Guner et al., 2018; Morata and Puigdomènech, 2017; Wehner et al., 2001). Chemical control of the vectors is not usually an efficient method of controlling the disease. Cultural controls such as treatment with mineral oil sprays and light-reflective surfaces, and cross-protection with weak ZYMV isolates showed limited effectiveness and required additional input costs. Therefore, genetic resistance remains the simplest, most effective, and most efficient means of limiting losses to these diseases (Ali et al., 2012; Levi et al., 2016a; Nagendran et al., 2017; Yu et al., 2011).

ZYMV was first described in 1981 in squash grown in northern Italy and France, where it was named *Muskmelon yellow stunt virus* (Lisa and Dellvalle, 1981; Tiwari and Rao, 2014). ZYMV infects all the agriculturally important species of Cucurbitaceae family (e.g., *C. lanatus*, *Cucumis sativus*, *Cucumis melo*, and *Cucurbita* spp.) and is considered the most destructive virus in watermelon production worldwide (Nagendran et al., 2017; Provvidenti, 1991). ZYMV is transmitted in a nonpersistent manner by several aphid species (e.g., *Aphis gossypii* Glover) and easily transmitted mechanically. In areas where cucurbit crops are not grown continuously, the virus overwinters on wild species. Natural infection appears to be limited to species of the Cucurbitaceae, but members of 11 families of dicotyledons are considered diagnostic hosts (Tiwari and Rao, 2014).

ZYMV, with flexuous particles ≈750 nm long containing a single strand of RNA, belongs to the genus *Potyvirus* in the family Potyviridae (Romay et al., 2014; Tiwari and Rao, 2014). At least 25 strains of ZYMV have been identified (Desbiez and Lecoq, 1997). Provvidenti et al. (1984) reported the occurrence of Connecticut (CT) and Florida (FL) strains of ZYMV, with the FL strain occurring more widely in the United States. In the 1990s, Provvidenti also identified a new ZYMV strain infecting cucurbit fields around Beijing, China, *Zucchini yellow mosaic virus*-China strain (ZYMV-CH). Plants infected with any of the ZYMV strains reduce their photosynthetic capacity and display stunted growth, deformed fruit, and early mortality (Guner and Wehner, 2008). Symptoms of severe ZYMV infection in cucurbit crops include yellow mosaic, stunting, blistering, and laminar reduction on leaves, and fruit remaining small, developing knobby areas, greatly malformed, and mottled (Nagendran et al., 2017).

Researchers have screened the germplasm resources of several cucurbit species for resistance to ZYMV, and the inheritance of the resistance has been reported in cucumber (*C. sativus*), melon (*C. melo*), and squash (*Cucurbita* spp.). ZYMV resistance is controlled by a single recessive gene in cucumber (Cardoso et al., 2010; Kabelka and Grumet, 1997), a single dominant gene in melon (Park et al., 2004; Pitrat and Lecoq, 1984), and a single dominant gene in squash (Paris and Brown, 2005).

The watermelon germplasm collection has been screened for resistance to ZYMV, and several resistant PI accessions have been identified (Boyhan et al., 1992; Guner, 2004; Provvidenti, 1991). Provvidenti (1991) reported ZYMV resistance in four PI accessions of watermelon from Zimbabwe (PI 482322, PI 482299, PI 482261, and PI 482308). The ZYMV resistance in the four resistant watermelon PI accessions appeared to be specific to the Florida strain (ZYMV-FL). Some accessions of egusi watermelon (*C. mucosospermus*) originating in Nigeria (PI 494528 and PI 494532) were reported resistant to ZYMV, and the resistance was not specific to the virus strain. However, the resistance was temperature dependent and was expressed best in warm or hot climates (Provvidenti, 1986). Provvidenti (1991) reported that resistance in PI 482261 (*Citrullus amarus*) was conferred by a single recessive gene, which he named *zym*. Boyhan et al. (1992) reported additional sources of resistance to ZYMV in PI 386026, PI 386025 (both *Citrullus colocynthis*), and the egusi PI 595203 (*C. mucosospermus*). They also confirmed ZYMV resistance in PI 482261 and PI 494528.

Guner (2004) screened 1613 PI accessions along with 41 watermelon cultivars for resistance to ZYMV. A high level of resistance to ZYMV was found in several PI accessions. These new resistant PI accessions were PI 386019, PI 490377, PI 596662, PI 485580, PI 560016, PI 494528, PI 386016, PI 482276, and PI 595201. The study also confirmed the resistance of PI 595203 (egusi), PI 386025, PI 386026, and PI 494528. However, the resistance of PI 482322, PI 482299, PI 482261, and PI 482308 as reported by Provvidenti (1991) was not confirmed. Those PI accessions had only moderate resistance to the Florida strain (ZYMV-FL) used in the study of Guner (2004).

Although it was reported that the inheritance of the resistance to ZYMV-CH in PI 595203 is controlled by a single recessive gene (Xu et al., 2004), there is not a formal report on the inheritance of the resistance to ZYMV-FL in PI 595203. Whether the ZYMV-FL and ZYMV-CH strains are the same has not been determined (Harris et al., 2009; Levi and Ling, 2017; Levi et al., 2016b; Ling et al., 2009). Therefore, the

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objective of this study was to determine the inheritance of ZYMV-FL resistance in PI 595203 (*C. mucosospermus*), an egusi watermelon type that was also identified as the source of resistance to ZYMV-CH strain, a geographically distant isolate.

Materials and Methods

Plant material. The parental lines used in this study were CHG and NHM, highly susceptible to ZYMV, and an egusi accession (PI 595203), our best source of resistance. Two families were developed by crossing PI 595203 with CHG and NHM. All crosses were made using hand-pollination in the greenhouse. Six generations (susceptible parent, resistant parent, F_1, F_2, backcross to the susceptible parent, and backcross to the resistant parent) were developed for the study of inheritance of resistance. For each of the two crosses, 180 plants were tested: 5 P_s, 5 P_r, 30 BC_1P_s, 30 BC_1P_r, 10 F_1, and 100 F_2 plants were used to test the inheritance from each cross.

Planting and management. All experiments were performed in the greenhouse of the Department of Plant Pathology at North Carolina State University in Raleigh, NC. Greenhouse temperatures ranged from 23 to 43 °C (day) and from 12 to 24 °C (night). We seeded directly in plastic pots (100 × 100 mm size, 600-mL volume) filled with a soilless mix (Canadian sphagnum moss, perlite, vermiculite, and processed pine bark). We planted two seeds per pot and thinned to one to ensure a uniform experiment (Gusmini et al., 2017).

Inoculum preparation. The virus isolate was obtained from E. Hiebert, University of Florida, Gainesville. The Florida strain of ZYMV was used to study the inheritance of resistance. Isolate 2088, a severe isolate of ZYMV-FL, was described by Wisler et al. (1995). The ZYMV isolate used for our research was a subculture of isolate 2088, maintained on 'Gray Zucchini' squash (*Cucurbita pepo* L.) from Seminis Vegetable Seeds (Woodland, CA). The inoculum was prepared by grinding infected 'Gray Zucchini' leaves using a mortar and pestle in 0.02 M phosphate buffer (Fig. 1), pH 7.0. The leaf to buffer ratio was 1:5 (1 g infected leaf to 5 mL buffer).

To maintain the ZYMV-FL isolate and increase the inoculum, we used the rub method (Guner et al., 2002). Squash plants were inoculated by dusting one leaf on each 3-week-old plant with 800-mesh carborundum and then applying the inoculum to the leaf with a pestle, which was rotated in a circular motion eight to 10 times as if painting the leaf with inoculum. After inoculation, carborundum was rinsed off the leaves to improve light interception, and the plants were maintained in aphid-proof cages. All 'Gray Zucchini' plants were seeded in Metro-Mix 200 (Scotts-Sierra Horticultural Products Company, Marysville, OH) in 160 mm diameter (1550 mL volume) clay pots. Plants were fertilized weekly with 150 mg·kg^{-1} Peters Professional 20–20–20 N–P–K (Scotts-Sierra Horticultural Products Company).

Inoculation and data collection. The previously described inoculation procedure to maintain the ZYMV-FL isolate and increase inoculum in squash plants was also used for the inheritance study (Guner et al., 2002). Plants were inoculated at the first true leaf stage and rated weekly at least six times, starting 2 weeks after inoculation. Plants were rated using a scale of 0 to 9, where 0 = none, 1 = trace of symptoms, 2 = tendrils absent, 3 = tendrils absent, slightly stunted growth, 4 = mosaic patches, necrotic spots on

Table 1. Single locus goodness-of-fit test ($P < 0.05$) for resistance to *Zucchini yellow mosaic virus*-Florida strain in two crosses of watermelon.

Parent/Progeny	No. susceptible	No. resistant	Expected ratio[z]	χ^2	*P* value
'Calhoun Gray' (susceptible) × PI 595203 (resistant)					
P_s[y]	5	0			
P_r[x]	0	5			
F_1	10	0			
BC_1P_s	30	0			
BC_1P_r	16	14	1:1	0.13	0.72
F_2	70	26	3:1	0.22	0.64
'New Hampshire Midget' (susceptible) × PI 595203 (resistant)					
P_s[y]	5	0			
P_r[x]	0	5			
F_1	10	0			
BC_1P_s	30	0			
BC_1P_r	15	15	1:1	0.00	1.00
F_2	76	21	3:1	0.05	0.82
Susceptible × resistant crosses, pooled					
P_s[y]	10	0			
P_r[x]	0	10			
F_1	20	0			
BC_1P_s	60	0			
BC_1P_r	31	29	1:1	0.07	0.80
F_2	146	50	3:1	0.03	0.87

[z]Expected was the hypothesized segregation ratio for single-gene inheritance.
[y]P_s was the susceptible parent.
[x]P_r was the resistant parent.

Fig. 1. Infected 'Gray Zucchini' leaves used to maintain and increase inoculum for the inheritance study.

Fig. 2. F_2 population segregating three susceptible: one resistant ratio for resistance to *Zucchini yellow mosaic virus*.

leaves, or both, 5 = leaves near apical meristem deformed, meristem yellow, and reduced in size, 6 = apical meristem withered and brown, 7 = apical meristem dead with more basal leaves dying, 8 = most leaves dead, main stem green/yellow, 9 = plant dead (Guner et al., 2002). After the last rating, plants were tested by enzyme-linked immunosorbent assay (ELISA) (Agdia Incorporated, Elkhart, IN) to determine the presence of the virus in the leaf tissue. Leaf tissue used for testing was sampled from the top five leaves of the plant. Plants were classified as resistant or susceptible based on their rank relative to the estimated mean value of the disease severity scale (5.0) and ELISA test results. Plants that did not have the virus in their system and had an average rating <5.0 were considered resistant, and plants with the virus in their system and an average rating >5.0 were considered susceptible (Strange et al., 2002).

Statistical analysis. The chi square tests for goodness of fit ($P < 0.05$) and homogeneity were used to examine segregation ratios (susceptible:resistant) for each F_2 and BC_1P_r progeny with the SAS statistical package (SAS Institute, Cary, NC) and the SASGene 1.2 program (Liu et al., 1997).

Yates' correction was used for those chi square tests where counts were ≤5 for any class in the ratio. However, the correction made no difference to our conclusions, so we presented the data uncorrected for ease of understanding and to avoid the tendency of Yates' method to overcorrect (Haviland, 1990).

Results and Discussion

Zucchini yellow mosaic virus (ZYMV) is one of the most destructive nonpersistently aphid-borne potyvirus infecting watermelon fields in the United States (Desbiez et al., 2003). There are nongenetic control methods, such as the use of insecticides to eliminate virus vectors, herbicides to remove alternate host (weeds) for the virus, removing old crop plants quickly, and avoiding overlapping or side-by-side plantings. In this study, we focused on the genetic approach to minimize losses caused by ZYMV (Coutts et al., 2011; Guner and Wehner, 2008) using resistance to ZYMV-FL in PI 595203.

Segregation ratios for resistance to the Florida strain ZYMV in the F_1, F_2, and BC_1 populations developed from crossing one susceptible and one resistant parent were similar to the previously published results by Provvidenti (1991) who also reported a single recessive gene for resistance to the Florida strain of ZYMV using a different accession, PI 482261. Guner et al. (2004) also tested PI 482261 for resistance to ZYMV using the same isolate (FL) as in this study and found no resistance in that accession. Probably, the isolate of ZYMV-FL used in our study was more virulent than the one used by Provvidenti (1991). In 2004, Xu et al. studied the inheritance of ZYMV-CH in PI 595203. They reported that resistance to ZYMV-CH was conferred by a single recessive gene, for which the symbol *zym-CH* was suggested. The PI 595203 is also resistant to PRSV-W and WMV. Thus, PI 595203 is an important source of resistance for those developing cultivars of watermelon with resistance to multiple viruses (Guner and Wehner, 2008; Strange et al., 2002; Xu et al., 2004).

In the F_1 progenies, all plants developed severe systemic symptoms of ZYMV, indicating that resistance in PI 595203 was inherited in a recessive manner (Table 1). This condition was confirmed by the reaction in the F_2 progenies as shown in Fig. 2, which segregated in a ratio of three susceptible to one resistant ($\chi^2 = 0.22$; P value = 0.64; $\chi^2 = 0.05$; P value = 0.82). A segregation of one susceptible to one resistant was obtained in plants of the backcross progenies to the resistant parents ($\chi^2 = 0.13$; P value = 0.72; $\chi^2 = 0.00$; P value = 1.00). Progenies of the backcross to the susceptible parents were all susceptible (Table 1). When data from both crosses (CHG × PI 595203 and NHM × PI 595203) were pooled, the F_2 progeny segregated to 146 susceptible and to 50 resistant ($\chi^2 = 0.03$; P value = 0.87), and the BC_1P_r progeny segregated to 31 susceptible to 29 resistant ($\chi^2 = 0.07$; P value = 0.80). Our results suggest that the high level of resistance to ZYMV-FL observed in PI 595203 is controlled by a single recessive gene, *zym*-FL (Guner, 2004; Wehner, 2012).

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