Heritability of Resistance in Winter Wheat to Wheat Spindle Streak Mosaic Virus


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ABSTRACT


The heritability of resistance to wheat spindle streak mosaic virus in winter wheat was studied using a seven-parent diallel analysis. Parents and F1 progenies were evaluated for disease reaction based on virus particle counts determined by immunoabsorbent electron microscopy. Resistance was found to be a highly heritable trait controlled by a few dominant genes. A two-locus genetic model was proposed to account for the observed resistance classification of the parents and the patterns of inheritance exhibited in the F1 progenies.

MATERIALS AND METHODS

Three Michigan cultivars and four advanced experimental lines from the Michigan State University winter wheat breeding program, all showing differential reactions to WSSMV, were chosen as parents in a diallel mating design. The parental pedigrees, which originated from widely diverse genetic backgrounds, included both red and white soft winter wheat (Table 1). The seven parents were crossed in all possible combinations to produce 42 F1 progenies. Preliminary analysis revealed nonsignificant maternal effects; therefore, reciprocal crosses were not included in the diallel analysis. The remaining 21 F1 progenies and seven parents were evaluated for disease reaction based on numbers of virus particles in leaf tissue using ISEM (8).

Soil infested with the fungal vector Polymyxa graminis Led. was collected from a field in Saranac, MI, where wheat previously had shown severe WSSM symptoms. Four parts of infested soil were mixed with one part sterilized sand to increase soil aeration and drainage. Sterilized wooden flats were filled with the infested soil mixture, and seeds from the 21 F1 progenies and seven parents were planted in a randomized block design in rows with five seeds per row. Each flat represented a single replication and contained 30 entries, including 7 parental rows, 21 F1 progeny rows, and 2 control rows of a known susceptible cultivar (Ionia). Three replications were planted in November 1983. Seeds were germinated in the greenhouse, and seedlings were kept at 20 ± 3 C

<table>
<thead>
<tr>
<th>Experimental or CI No.</th>
<th>Common name</th>
<th>Origin</th>
<th>Kernel color</th>
<th>Reactiona</th>
</tr>
</thead>
<tbody>
<tr>
<td>B14469</td>
<td>Ionia</td>
<td>USA</td>
<td>White</td>
<td>S</td>
</tr>
<tr>
<td>CI 17381</td>
<td>Augusta</td>
<td>USA</td>
<td>White</td>
<td>S</td>
</tr>
<tr>
<td>CI 17287</td>
<td>Tecumseh</td>
<td>USA</td>
<td>White</td>
<td>MS</td>
</tr>
<tr>
<td>B4145</td>
<td>Experimental line</td>
<td>USA, New Zealand</td>
<td>White</td>
<td>MR</td>
</tr>
<tr>
<td>B7321</td>
<td>Experimental line</td>
<td>Russia</td>
<td>Red</td>
<td>MR</td>
</tr>
<tr>
<td>B6018</td>
<td>Experimental line</td>
<td>USA, Japan</td>
<td>White</td>
<td>R</td>
</tr>
<tr>
<td>B9028</td>
<td>Experimental line</td>
<td>Yugoslavia, Mexico</td>
<td>Red</td>
<td>R</td>
</tr>
</tbody>
</table>

* S = susceptible, MS = moderately susceptible, MR = moderately resistant, and R = resistant. Disease rating (reaction) is based on virus particle counts as described previously (8).
RESULTS AND DISCUSSION

WSSMV particle counts for parents and F1 progenies ranged from 0 to nearly 400 particles per grid square (Table 2). Plants with counts of >70 particles per grid square were considered susceptible to WSSMV, those with counts between 21 and 70 particles were rated moderately susceptible, those with 0-10 particles were rated moderately resistant, and those with 1-20 particles were rated resistant to WSSMV (8). F1 progeny resulting from crosses between susceptible parents (as in Augusta × Ionia) were also susceptible to WSSMV based on virus particle counts (Table 2), whereas crosses between resistant parents (as in B7321 × B6018) produced resistant F1 progeny with few to no virus particles. Crosses between susceptible and resistant parents (as in Augusta × B9028) produced resistant F1 progeny, whereas crosses between parents with intermediate reactions to WSSMV (as in Tecumseh × B7321) also produced resistant F1 progeny. These data indicate that genes for resistance to WSSMV are additive.

The preliminary analysis of variance of parents and F1 progenies showed highly significant differences between genotypes (data not shown). These results were expected because the parents were chosen for their differential reactions to WSSMV. Broad-sense heritability for resistance to WSSMV was very high (0.98), indicating that variation was the result of genetic rather than environmental factors. There were no significant differences between replications.

The products of the main statistics and their corresponding multipliers (9) were used to calculate the components of variation and their standard errors (Table 3). Both additive variance (D) and overall dominance variance (HI) contributed significantly to the overall genetic variance as indicated by estimates approaching a value of 1.0. In addition, D - HI was not significantly different from zero, indicating nearly complete dominance. The negative F value for WSSMV resistance indicated that a greater frequency of recessive alleles was found among the parental arrays. Also, the mean degree of dominance was \( \sqrt{H_I/D} = 1.0266 \), indicating nearly complete dominance (a value of 1.0 represents complete dominance).

Based on the regression of covariance on variance for the parental arrays (Fig. 1), the pattern of inheritance of resistance to WSSMV was one of complete dominance. An order of dominance among the parental arrays was apparent: those parents nearest the origin of the line (B6018, B9028, and B4145) contained a greater proportion of dominant alleles for resistance to WSSMV, whereas

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**TABLE 2.** Virus particle counts for parents and F1 progeny in diallel analysis of resistance to wheat spindle streak mosaic virus

<table>
<thead>
<tr>
<th>Parental number and name</th>
<th>1 Augusta</th>
<th>2 Ionia</th>
<th>3 B4145</th>
<th>4 Tecumseh</th>
<th>5 B6018</th>
<th>6 B7321</th>
<th>7 B9028</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>99</td>
<td>183</td>
<td>6</td>
<td>145</td>
<td>4</td>
<td>62</td>
<td>1</td>
</tr>
</tbody>
</table>

*Particle counts are means per grid square obtained by examining 60 grid squares for each parent and F1 progeny.

**TABLE 3.** Components of variation and their standard errors for diallel analysis of resistance to wheat spindle streak mosaic virus

<table>
<thead>
<tr>
<th>Notation</th>
<th>Estimate</th>
<th>Standard error</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>D</td>
<td>0.7681</td>
<td>±0.0439</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>F</td>
<td>-0.2351</td>
<td>±0.1054</td>
<td>.05-01</td>
</tr>
<tr>
<td>H1</td>
<td>0.8095</td>
<td>±0.1058</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>( \sqrt{H_I/D} )</td>
<td>1.0266</td>
<td>±0.0918</td>
<td>&gt;.10</td>
</tr>
</tbody>
</table>

*Data represents variance (\( V_r \)) and covariance (\( W_r \)) for resistance to wheat spindle streak mosaic virus.

**Fig. 1.** Regression of parental array covariances (\( W_r \)) on variances (\( V_r \)). Three parents clustered nearest origin are similar in reaction to wheat spindle streak mosaic virus, whereas four farthest from origin also show similar reactions to virus. Slope is significant at P < 0.01.
parents farthest from the origin (B7321, Tecumseh, Augusta, and Ionia) contained a greater proportion of recessive alleles and were more susceptible to WSSMV. The coefficient of determination ($r^2$) was 0.61, indicating that genes for resistance to WSSMV were mostly dominant.

The seven parents used in the diallel fell into six distinct classes based on virus particle counts. A two-locus genetic model is proposed to account for this classification of parents and the patterns of inheritance exhibited in the F1 progenies based on the virus particle count data (Table 4). The model has three alleles ($A_1$, $A_2$, and $A_3$) at the A locus and two alleles ($B_1$ and $B_2$) at the B locus. The $A_1$ allele is completely dominant to $A_2$ and $A_3$ and codes for resistance to WSSMV. Thus, parents with this allele (such as B6018 and B9028) show virus resistance. The $A_2$ and $A_3$ alleles show additive gene action, so that parents with the $A_3$ allele (such as Ionia) are more susceptible than parents containing the $A_2$ allele (such as B7321). The B locus also exhibits additive gene action, so that parents with homozygous $B_1$ alleles (such as Ionia and Augusta) are more susceptible to WSSMV than parents with homozygous $B_2$ alleles. The heterozygote $B_1B_2$ lies nearly midway between homozygous parents, expressing additivity. In addition, there is an additive by additive epistatic interaction between locus A and B in the absence of the $A_1$ allele.

Resistance to WSSMV appears to be a highly heritable trait controlled by a few dominant genes with some additive effect. Based on the proposed model, cultivars with $A_1$ or $B_1$ alleles show some resistance to WSSMV. This model is currently being tested by analyzing the segregating $F_2$ and $F_3$ generations. Genes for resistance to WSSMV are presently being incorporated into commercial wheat cultivars through our wheat breeding program.

**LITERATURE CITED**