PLANT RESISTANCE

Expression and Suppression of Resistance to Greenbug (Homoptera: Aphididae) in Synthetic Hexaploid Wheats Derived from Triticum dicoccum × Aegilops tauschii Crosses

J. LAGE, B. SKOVMAND, and S. B. ANDERSEN


ABSTRACT Fifty-eight synthetic hexaploid wheats, developed by crossing Triticum dicoccum Schrank, and Aegilops tauschii (Coss.) Schmal., were evaluated at the seedling stage, together with their parents, for resistance to greenbug (Schizaphis graminum Rondani) under greenhouse conditions. Seedlings of different synthetic hexaploids showed large phenotypic differences for resistance. All the T. dicoccum parents were susceptible, while high levels of resistance were observed in some of the Ae. tauschii parents. Of the synthetic hexaploids derived from resistant Ae. tauschii parents, a high proportion (76%) showed levels of resistance to the greenbug biotype used that were comparable to those of the resistant parent. While there were clear indications of the presence of suppressor genes for greenbug resistance in the A and/or B genomes of T. dicoccum in some synthetics, positive epistatic interaction was also found in synthetic hexaploids with higher levels of resistance than that of either parent. Resistance from different Ae. tauschii accessions was expressed differently when crossed with the same T. dicoccum, indicating diversity among the resistance genes present in the test synthetic hexaploid wheats. Based on resistance reactions, the genes conferring greenbug resistance in these synthetic hexaploids are probably different from resistance genes previously transferred to wheat from Ae. tauschii.

KEY WORDS Schizaphis graminum, synthetic hexaploid wheat, resistance screening, genetic interaction

WHEAT (Triticum aestivum L.) is the most widely grown cereal grain in the world. It is the staple food for 35% of the world’s population and is becoming increasingly important in the developing world (CIMMYT 2002). Greenbug (Schizaphis graminum Rondani), found all over the world, is one of the most serious insect pests of wheat, but also infests other small-grain cereals and sorghum (Sorghum bicolor (L.) Moench). Effective resistance has not been found in bread wheat, but has been incorporated into the crop from various related species. The greenbug resistance gene gb1 has been transferred to bread wheat from Triticum turgidum L. variety durum (Curtis et al. 1960), Gb2 and Gb6 from Secale cereale L. (Sebesta and Wood 1978, Porter et al. 1991, Porter et al. 1994), Gb3 and Gb4 from Aegilops tauschii (Coss.) Schmal. (syns. Aegilops squarrosa and Triticum tauschii) (Joppa et al. 1980, Martin et al. 1982), and Gb5 from Aegilops speltoides Tausch (syn. Triticum spelta L.) (Tyler et al. 1985).

The appearance of 11 different greenbug biotypes in the United States from 1981 to 1992 (Porter et al. 1997, Teetes et al. 1999) has stimulated a continued search for new sources of resistance to this pest. Production of new synthetic hexaploid wheat by interspecific crosses between tetraploid Triticum spp. and Ae. tauschii has proven an efficient way of introducing disease and insect resistance into wheat from Ae. tauschii (Harvey et al. 1980, Joppa et al. 1980, Kena and Lange 1992, Mueeb-Kazi 1995, Villarel et al. 1996, Aguilar-Rincón et al. 2000). Joppa et al. (1980) obtained a greenbug-resistant synthetic hexaploid wheat by crossing resistant Ae. tauschii and susceptible durum wheat, and then transferred this resistance (Gb3) to the wheat germplasm line Largo (Joppa and Williams 1982). Harvey et al. (1980) also obtained greenbug-resistant synthetic hexaploids (Gb4) derived from resistant Ae. tauschii accessions.

However, synthetic hexaploid wheats derived from one or two parents resistant to a disease or pest are no guarantee that resistant synthetics will be obtained. Ma et al. (1995) and Kema et al. (1995) showed that only a few synthetic hexaploid wheats obtained from crosses involving a stripe rust-resistant parent expressed levels of resistance comparable to those of the parent. Similar results were obtained by Villarel et al. (1992) with leaf rust-resistant material. This phenomenon is commonly known as disease-resistance suppression and often occurs when genes from alien spe-
Table 1. Greenbug feeding damage sustained by synthetic hexaploid wheats derived from different Ae. tauschii × T. dicoccum crosses, and of their parents.

<table>
<thead>
<tr>
<th>Parent of SH</th>
<th>SH</th>
<th>Damage score&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aec&lt;sup&gt;a&lt;/sup&gt;</td>
<td>T.d&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Aec&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>219&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>17104&lt;sup&gt;c&lt;/sup&gt;</td>
<td>76509&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>309</td>
<td>16939</td>
<td>76415&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>17066</td>
<td>76426</td>
<td>17084</td>
</tr>
<tr>
<td>18108</td>
<td>76611</td>
<td>19133</td>
</tr>
<tr>
<td>19160</td>
<td>76600</td>
<td>372</td>
</tr>
<tr>
<td>305</td>
<td>19099</td>
<td>76436</td>
</tr>
<tr>
<td>19133</td>
<td>76608&lt;sup&gt;d&lt;/sup&gt;</td>
<td>19148</td>
</tr>
<tr>
<td>409</td>
<td>392</td>
<td>17635&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>16900</td>
<td>76333&lt;sup&gt;d&lt;/sup&gt;</td>
<td>16900</td>
</tr>
<tr>
<td>16908</td>
<td>76377&lt;sup&gt;d&lt;/sup&gt;</td>
<td>16908</td>
</tr>
<tr>
<td>19133</td>
<td>76608&lt;sup&gt;d&lt;/sup&gt;</td>
<td>19133</td>
</tr>
<tr>
<td>19148</td>
<td>76677</td>
<td>19148</td>
</tr>
<tr>
<td>454</td>
<td>16948</td>
<td>76386&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>16916</td>
<td>76390&lt;sup&gt;d&lt;/sup&gt;</td>
<td>16916</td>
</tr>
<tr>
<td>16946</td>
<td>76502&lt;sup&gt;d&lt;/sup&gt;</td>
<td>16946</td>
</tr>
<tr>
<td>17084</td>
<td>76473</td>
<td>17084</td>
</tr>
<tr>
<td>17084</td>
<td>76473</td>
<td>17084</td>
</tr>
<tr>
<td>18172</td>
<td>76566&lt;sup&gt;d&lt;/sup&gt;</td>
<td>18172</td>
</tr>
<tr>
<td>19158</td>
<td>76633&lt;sup&gt;d&lt;/sup&gt;</td>
<td>19158</td>
</tr>
<tr>
<td>16916</td>
<td>76600&lt;sup&gt;d&lt;/sup&gt;</td>
<td>16916</td>
</tr>
<tr>
<td>16900</td>
<td>76333&lt;sup&gt;d&lt;/sup&gt;</td>
<td>16900</td>
</tr>
</tbody>
</table>

<sup>a</sup>Aec = Ae. tauschii; T.d = T. dicoccum; and SH = synthetic hexaploid wheat.

<sup>b</sup>Damage score of greenbug-infested plants 15 d after infestation; 1 = no injury, 6 = plant death or near death. Scores based on average of two rows of plants.

<sup>c</sup>Ae. tauschii accession numbers.

<sup>d</sup>CIMMYT Wheat Introduction (CWI) numbers.

...cies are incorporated into cultivated wheat (Gill and Baupp 1987, Hanusova et al. 1996).

The current study reports the occurrence of a high frequency of greenbug-resistant germplasm in a set of synthetic hexaploid wheat derived from Triticum dicoccum Schrank. crossed with greenbug-resistant and greenbug-susceptible Ae. tauschii lines. Furthermore, both positive and negative (suppressors) interactions for the expression of resistance were observed between genes of the two parental species.

Materials and Methods

The greenbug population used for evaluation was derived from aphids collected in the fields around the International Maize and Wheat Improvement Center (CIMMYT) in El Batan, Mexico. The greenbugs were reared in a greenhouse maintained at 16–20°C and a relative humidity of 70% under conditions of natural daylight. Initial tests showed that the bread wheat cultivars Amigo (Gb2) and Largo (Gb3) were both susceptible to this population, whereas the rye cultivar Inyane Rye showed resistance (data not shown). This indicated that the greenbug used in the current study is either biotype G or a new Mexican biotype. The greenbug population was maintained on barley (Hordeum vulgare L.) in cages in a greenhouse at CIMMYT.

Fifty-eight different synthetic hexaploid wheats derived from interspecific crosses involving 22 accessions of the tetraploid T. dicoccum and 15 accessions of the diploid Ae. tauschii were included in the screening (Table 1). The synthetic hexaploids were produced by the Wheat Wide Crosses Program at CIMMYT, as described by Mujeeb-Kazi et al. (1996). All T. dicoccum accessions had previously been selected for their resistance to Russian wheat aphid (Diuraphis noxia [Mordvilko]) (Robinson and Skovmand 1992).

All 58 synthetic hexaploid wheats and their T. dicoccum and Ae. tauschii parents were tested for greenbug resistance in a mesh-covered cage (1 × 1 × 2.4 m) in a greenhouse with a temperature of 20°C and a photoperiod of 18.6 (L:D) h. Four seeds per genotype were sown in rows randomly arranged in square trays (7 × 24 × 30 cm), 10 rows per tray. The susceptible cultivar Seri MS2 was included as susceptible check. Two complete blocks, each with nine trays, were sown in the same cage. Newly emerged seedlings were infested by placing two to five barley leaves infested with greenbugs between the rows of test plants. Because of seed shortage and longer germination time,
Ae. tauschii parents were tested in separate trays and cages using two seeds per row in two blocks, each with two trays, as described previously. Plants were scored for damage on a 1-6 scale, as described by Starks and Burton (1977), with one equal to no symptoms and six indicating plant death or near death. Damage scores were recorded when susceptible controls reached level 5-6 on this scale, =15 d after infestation.

Greenbug feeding damage data were analyzed using SAS PROC GLM (SAS Institute 1985), considering blocks as random effects. Because many combinations between Ae. tauschii and T. dicoccon were missing among the synthetic hexaploids, the use of traditional partitioning of hybrid sums of square as a North Carolina Design 2 (Hill et al. 1998) was judged inappropriate. Instead, additive effects among synthetics were removed through regression of their damage scores against scores from the Ae. tauschii parents in an offspring-parent regression approach. Remaining differences between synthetics not explained by the regression were then thought to be a result of interactions between gene loci, because these synthetics are all homozygous.

**Results and Discussion**

Initial analysis of damage scores of synthetic hexaploids and their T. dicoccon parents showed highly significant differences in the reactions of the 80 genotypes to attack by the greenbug (Table 2). The genetic component of variance for differences among all genotypes from expectation of the mean square in the experiment was 1.45 compared with 0.31, the error component. Thus, 82.3% of total variation in this experiment could be explained by differences among genotypes.

Partitioning the sums of squares for genotypes into differences between the T. dicoccon parents, differences between synthetic hexaploids, and the average difference between the two groups showed no genetic variation for resistance to greenbug among the 22 T. dicoccon parents. Differences in resistance among the synthetic hexaploids and the average differences between synthetics and their T. dicoccon parents were highly significant (Table 2). All of the T. dicoccon parents were relatively susceptible to greenbug feeding, with average damage scores ranging from 4.9 to 6.0 (Table 1). In contrast, average scores from the 58 synthetic hexaploids ranged from quite resistant (2.3-3) to susceptible (6.0) (Table 1).

Variation for resistance to greenbug was further studied by regressing the damage score of the synthetic hexaploids on the damage scores of each Ae. tauschii parent. While this regression explained a highly significant portion (14.4%) of the among-synthetics variation for the trait (Table 2), a highly significant part of variation among synthetics remained unexplained (lack of fit, Table 2). This indicated the presence of genetic interactions between the T. dicoccon and Ae. tauschii parents used in the experiment.

Synthetic hexaploid wheats are commonly produced by crossing a tetraploid wheat (A and B genomes) with a diploid (D genome) grass to produce a haploid plant. The chromosome number is doubled to obtain 42 chromosomes either through colchicine treatment or spontaneous doubling. In theory, any trait expressed in either of the parents would also be expressed in the synthetic hexaploid, if the genetic effects were entirely additive. Because of homeology among the three genomes combined in such synthetic hexaploids, genes affecting similar traits can be expected to exist in several of the genomes. When they do, this occurrence, plus additive effects, may lead to epistatic interactions between loci.

When the regression data for the greenbug damage scores of synthetic hexaploids and their Ae. tauschii parents are viewed graphically (Fig. 1), four groups of synthetic hexaploids can be identified. Synthetics in group 1, characterized by low greenbug damage scores ranging from 2.3 to 3.5, are derived from Ae. tauschii parents that also had low damage scores (2.0-3.0). Synthetics in group 2 received high damage scores (4.3-5.5) and were derived from Ae. tauschii parents with relatively high scores (4.0-5.0). Reactions of these two groups of synthetics to feeding attack by the greenbug are in close agreement with what would be expected if additive effects of the genes for the trait are assumed.

The two remaining groups in Fig. 1 (groups 3 and 4) showed resistance reactions to greenbug attack that deviated from a simple additive genetic model. Synthetics in group 3, all derived from Ae. tauschii parents with low damage scores (2.0-3.0), showed considerably higher damage (4.3-6.0), while synthetics in group 4, derived from Ae. tauschii parents with high damage scores (4.0-5.0), showed much less damage (2.3-3.4) than expected from a simple additive model of gene action. Results with these synthetics clearly indicate interactions among genes for greenbug resistance in the two parental species.

From these results, it is clear that the expression of greenbug resistance in synthetic hexaploid wheats derived from T. dicoccon × Ae. tauschii crosses depends on interactions between genes present in the two parents. Previous studies on the expression of stripe rust in the same type of synthetic hexaploids (AABBDD) have indicated the existence of suppressor genes in the A or B genomes of T. turgidum (Kema et al. 1995, Ma et al. 1995). The existence of such...
suppressors would also explain the low greenbug resistance in a synthetic hexaploid derived from a highly resistant *Ae. tauschii* and a susceptible *T. dicoccum*, as was observed in the current study (group 3, Fig. 1). Nonetheless, it is clear that epistatic interactions may also be positive, because synthetics derived from susceptible *Ae. tauschii* and *T. dicoccum* parents sometimes show low greenbug damage scores (group 4, Fig. 1).

The expression of greenbug resistance in synthetic hexaploid wheats varies according to the synthetic and the pest. Of the 33 synthetic hexaploids derived from *Ae. tauschii* accessions with damage scores of 3.0 or below (accessions 219, 372, 409, 458, 518, 879, 895, 897, and 1027), 25 showed good resistance (group 1, Fig. 1) and eight showed poor resistance (group 3, Fig. 1). In this group of germplasm, therefore, 76% of the synthetic hexaploids derived from greenbug-resistant *Ae. tauschii* parents showed levels of greenbug resistance comparable to those of their *Ae. tauschii* parent. In contrast, studies on the expression and suppression of stripe rust resistance in synthetic hexaploid wheats have reported only 16% (Kema et al. 1995) and 20% (Ma et al. 1995) of the synthetic hexaploids express levels of stripe rust resistance comparable to those of their resistant parent.

The presence of suppressor genes for greenbug resistance in the A and/or B genomes of the *T. dicoccum* parents suggests that careful selection of parents could lead to improved results during production of synthetic hexaploids. However, as a result of the relatively few synthetic hexaploids derived from each *T. dicoccum* parent, it was not possible in this study to identify specific *T. dicoccum* accessions that generally suppress or enhance resistance significantly more than others. Because of epistatic interactions, resistance derived from two different *Ae. tauschii* accessions may be expressed or suppressed when crossed with the same *T. dicoccum*. A close study of the expression/suppression of greenbug damage scores in synthetics derived from crosses involving *Ae. tauschii* accessions 409, 458, and 518 and *T. dicoccum* accessions 16900, 16908, and 17146 reveals that the resistance genes present in these *Ae. tauschii* accessions are likely to be different (Table 1). Furthermore, it remains to be seen whether the resistance levels observed in these synthetic hexaploids are maintained during introgression into the cultivated bread wheat gene pool, or whether resistance levels will be suppressed.

Of the six greenbug resistance genes assigned by Tyler et al. (1987) and Porter et al. (1994), only *Gb3* and *Gb4* are derived from *Ae. tauschii*. Thus, the resistance genes found in our study will presumably be different from *gb1, Gb2, Gb5*, and *Gb6*. Furthermore, because the cultivar Largo with *Gb3* resistance was susceptible to the greenbug biotype used in this study, *Ae. tauschii* genes conferring resistance in these new synthetics are also likely to be different from *Gb3*. A genetic analysis of the synthetic hexaploids used in this study, CI 17959 (*Gb4*), and the resistant line 97-85-3, derived from crossing a resistant *Ae. tauschii* directly with a hexaploid wheat (Flinn et al. 2001), may further determine to what extent these synthetics carry resistance genes not previously described.

It should be noted that the *T. dicoccum* accessions used for producing these synthetic hexaploids were selected for their resistance to Russian wheat aphid by Robinson and Skovmand (1992), but showed complete susceptibility to greenbug in this study. This indicates there is no correlation between resistance to these two aphid species in accordance with previous results reported by Robinson (1992) and Webster and Porter (2000).

In conclusion, various *T. dicoccum* × *Ae. tauschii*-derived synthetic hexaploid wheats were found to be resistant to a Mexican greenbug biotype used in this experiment. The resistance derived from the *Ae. tauschii* parents was in some cases suppressed, presumably by suppressor genes in the A and/or B genomes, but not as frequently as reported for stripe rust resistance in previous studies. In a few cases, there were positive epistatic interactions resulting in synthetics showing higher levels of resistance than either of the parents. Furthermore, results indicate variation among the
greenbug resistance genes present in the synthetic hexaploids. This increases the potential value of this germplasm in breeding for greenbug resistance in cultivated bread wheats.

Acknowledgments

We thank the Danish International Development Assistance (DANIDA) and the Council of Development Research (RUF), Denmark, for their financial support. We also thank A. McNab for reviewing this manuscript.

References Cited


Received for publication 17 April 2002; accepted 5 September 2002.