Heterosis and Effect of the \textit{Rht} 3 Gene on Plant Height and Its Components in Hybrid Bread Wheat with \textit{T. timopheevi} Cytoplasm

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Summary
The heterosis of plant height and its components of hybrid bread wheat and the effect of \textit{Rht} 3 gene were investigated in this paper. The results showed that all characters of hybrids had heterosis and heterobeltiosis, but their values varied among crosses and internodes; the heterosis and heterobeltiosis of length of basal internode were larger than those of other internodes and length of spike; there were less heterosis and heterobeltiosis for all characters in the hybrids from female parents with the \textit{Rht} 3 gene than those in other hybrids. The \textit{Rht} 3 gene increased the effects of lengths of second and third internodes and their heterosis on plant height and changed the relationships among the components in F$_1$ hybrid. In the combinations from A-line with the \textit{Rht} 3 gene, the R lines were much more important to determine the plant height and its components of their hybrids than A lines, and so, it was relatively easier for breeders to control these characters of hybrid wheat. In the combination from A-line without the \textit{Rht} 3 gene, both A and R lines affected F$_1$ hybrids for the characters examined to different extent, thus, two parents should be strictly screened for those characters to make new hybrid combinations. It should be noted that the length of spike of R line was much more responsible for that of its hybrid in combinations both with and without the \textit{Rht} 3 gene, and therefore, the R line with long spike should be developed in order to obtain hybrid wheat with long spike.

Key Words: Heterosis, plant height, \textit{Rht} 3 gene, \textit{T. timopheevi} cytoplasm, hybrid wheat.

Introduction
Hybrid wheat with \textit{T. timopheevi} cytoplasm has been studied for several decades in some countries. It has reported that hybrids perform significant heterosis of yield (Liver and Heynes 1968, Pass and Smith 1983, Wilson and Driscoll 1983, Zhao et al 1990). Plant height is a very important character for heterosis of hybrid wheat. The heterosis of plant height in hybrid wheat was very high (8-10 \%) and the grain weight/spike also increased largely, but the straws were tall and lodging so that the heterosis of yield could not well perform (Zhao et al 1985). Some scientists have studied the heterosis and genetic features of plant height in hybrid wheat (Sun and Wang 1985, Zhao et al 1985, Wang et al 1985, Wang 1985), and suggested that there were relatively high levels of heterosis and heterobeltiosis of plant height. However, the values of heterobeltiosis were less but with larger differences than those of heterosis among crosses (Sun and Wang 1985, Wang 1985).

Plant height is composed of the lengths of many internodes and the spike. Singhval and Singh (1978), based on their own study and other previous reports (Allan and Vogel 1963, Konzak et al 1966, Sasaki et al 1968, Baiier et al 1974), suggested that plant height, length of spike and various internodes, and the number of internodes for the wheat plant were affected by genes on different chromosomes. Wei et al (1990) reported that the lengths of various internodes had different heterosis and heterobeltiosis in the F$_1$ generation of wheat (\textit{T. aestivum} L.); the respective internode lengths were quantitative characters, and they had their own independent genetic patterns and were influenced by different gene numbers and effects; the second internode fitted addition-dominance pattern, there were interactions of genes in other internodes. In hybrid wheat with \textit{T. timopheevi} cytoplasm, Sage (1978) suggested that the cytoplasm reduced the length of the first internode and plant height of wheat. However, it has not clearly been known how heterosis of these characters are expressed.

The \textit{Rht} 3 gene performs partial dominance and has additive effect (Fick 1974), and can reduce grain sprouting before harvest. The hybrids having the \textit{Rht} 3 gene yielded higher than their parents with the highest yield (Gale et al 1988) and conventional cultivars (Zhao et al 1990), and their plant heights could not be taller than those of their taller parents (Zhao et al 1990). As the \textit{Rht} 1, \textit{Rht} 2, \textit{Rht} 10 genes etc., the \textit{Rht} 3 gene is also effective to dwarf plant height (Gale and Law 1977, Gale and Marshall 1975, Youssefian 1983), Zhao et al (1990) reported that the lengths of internodes and their plant height were reduced by introduction of the \textit{Rht} 3 gene into tall wheat, especially the first, second and third internodes, which resulted in a 50 \% reduction in plant height. For the \textit{timopheevi} CMS line and its hybrid, the \textit{Rht} 3 gene is more useful to dwarf plant height than other dwarfing genes (Zhao et al 1990). However, it is not known how the \textit{Rht} 3 gene affects internodes in the hybrid.

The present experiment was conducted to investigate...
the heterosis, heterobeltiosis of plant height and its components and the effect of Rht 3 and parents on these characters in hybrid wheat.

Materials and Methods

This experiment was carried out on the farm of Sichuan Academy of Agricultural Sciences, Chengdu during 1991 and 1992. The following materials were used: 4 CMS lines – Chuan 3A, Chuan 4A (without the Rht 3 gene) and Chuan 11A and Chuan 33A (with the Rht 3 gene); 4 restorer lines – R997, R2870, R3526 and R4135; and their 15 hybrids. Each plot consisted of 2 rows of one material spaced 10 cm apart within the row and 20 cm between rows each 100 cm in length. The experiment was a random design with 1 replication. At the third leaf stage, the population was thinned to 1 plant per hill.

After florescence, the lengths of internodes, spike and plant height of 10 main stems in each plot were measured (Table 1). Heterosis (HS) and heterobeltiosis (HBS) were calculated according to the following formulae:

$$HS = \frac{F_1 - MP}{MP} \times 100\%,$$

$$HBS = \frac{F_1 - \text{High parent}}{\text{High parent}} \times 100\%$$

The correlation analysis was performed to detect the relationships among the characters, the HS and HBS of the characters, and between F1 hybrids and their parents.

Results

Heterosis and heterobeltiosis

Heterosis (HS) of PH and its components was found in 15 crosses, but the values varied with crosses (Table 1). Only one cross (Chuan 11A × R4135) had negative HS of PH (−1.7 %), and the average HS of all crosses was 7.53 % (CV: 66.46 %). However, the HS value (5.04 %) of PH of all crosses derived from female parent with the Rht 3 gene was less than the HS (10.59 %) of others without the Rht 3. Among the components, the HS (0.41 %) of LS in all crosses was the least, and its CV was 168.1 %; the LBIIs with and without the Rht 3 gene had the largest HS (11.14 and 28.64 %, respectively), but there was variation among genotypes and the LBIIs of most crosses had the largest HS among their other internodes (range from −25.4 to 43 % and −20.2 to 72.4 %). On the average, the magnitude of the HS values in all characters of crosses with the Rht 3 gene was LBI/(11.14 %) > LSI/(6.49 %) > LTI/(5.35 %) > LFI/(5.29 %) > LS/(−1.65 %); and of crosses without the Rht 3 gene was LBI/(28.64 %) > LTI/(19.28 %) > LSI/(12.06 %) > LFI/(8.26 %) > LS/(2.77 %). This result was different from that of Wei et al (1990), who obtained negative HS of LBI.

The average HS of PH was small (0.15 %), although

<table>
<thead>
<tr>
<th>Cross</th>
<th>LFI</th>
<th>LSI</th>
<th>LTI</th>
<th>LBI</th>
<th>LS</th>
<th>PH</th>
</tr>
</thead>
<tbody>
<tr>
<td>With Rht3 gene</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chuan 11 A × R397</td>
<td>11.5</td>
<td>1.6</td>
<td>8.1</td>
<td>−4.5</td>
<td>9.9</td>
<td>2.6</td>
</tr>
<tr>
<td>Chuan 11 A × R2870</td>
<td>−0.4</td>
<td>−15.0</td>
<td>11.7</td>
<td>−13.0</td>
<td>10.1</td>
<td>−9.7</td>
</tr>
<tr>
<td>Chuan 11 A × R3526</td>
<td>11.1</td>
<td>3.2</td>
<td>1.5</td>
<td>−24.7</td>
<td>5.6</td>
<td>−20.6</td>
</tr>
<tr>
<td>Chuan 11 A × R4135</td>
<td>3.6</td>
<td>−8.2</td>
<td>4.5</td>
<td>−16.5</td>
<td>−10.8</td>
<td>−15.1</td>
</tr>
<tr>
<td>Chuan 33 A × R997</td>
<td>7.5</td>
<td>6.2</td>
<td>8.7</td>
<td>0</td>
<td>7.1</td>
<td>−1.3</td>
</tr>
<tr>
<td>Chuan 33 A × R2870</td>
<td>−1.4</td>
<td>−9.3</td>
<td>6.4</td>
<td>−14.3</td>
<td>4.2</td>
<td>−15.5</td>
</tr>
<tr>
<td>Chuan 33 A × R3526</td>
<td>12.2</td>
<td>11.1</td>
<td>14.7</td>
<td>−12.4</td>
<td>8.7</td>
<td>−19.1</td>
</tr>
<tr>
<td>Chuan 33 A × R4135</td>
<td>1.9</td>
<td>−7.1</td>
<td>5.3</td>
<td>−4.3</td>
<td>8.0</td>
<td>1.4</td>
</tr>
<tr>
<td>Average</td>
<td>5.29</td>
<td>−2.31</td>
<td>6.49</td>
<td>−11.21</td>
<td>5.35</td>
<td>−11.66</td>
</tr>
<tr>
<td>Without Rht3 gene</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Chuan 3 A × R997</td>
<td>9.5</td>
<td>3.8</td>
<td>10.5</td>
<td>−9.2</td>
<td>23.5</td>
<td>0.8</td>
</tr>
<tr>
<td>Chuan 3 A × R3526</td>
<td>6.2</td>
<td>−1.4</td>
<td>5.7</td>
<td>4.5</td>
<td>6.8</td>
<td>2.3</td>
</tr>
<tr>
<td>Chuan 3 A × R4135</td>
<td>2.9</td>
<td>2.1</td>
<td>8.0</td>
<td>−10.3</td>
<td>24.4</td>
<td>0</td>
</tr>
<tr>
<td>Chuan 4 A × R997</td>
<td>14.4</td>
<td>10.9</td>
<td>24.8</td>
<td>16.2</td>
<td>20.5</td>
<td>12.6</td>
</tr>
<tr>
<td>Chuan 4 A × R2870</td>
<td>−0.4</td>
<td>−13.3</td>
<td>14.1</td>
<td>5.2</td>
<td>37.9</td>
<td>37.9</td>
</tr>
<tr>
<td>Chuan 4 A × R3526</td>
<td>0.2</td>
<td>−1.2</td>
<td>7.8</td>
<td>−12.4</td>
<td>1.7</td>
<td>−9.2</td>
</tr>
<tr>
<td>Chuan 4 A × R4135</td>
<td>24.4</td>
<td>15.6</td>
<td>13.5</td>
<td>6.9</td>
<td>11.0</td>
<td>2.9</td>
</tr>
<tr>
<td>Average</td>
<td>8.26</td>
<td>2.36</td>
<td>12.06</td>
<td>0.13</td>
<td>19.28</td>
<td>6.76</td>
</tr>
<tr>
<td>Total average</td>
<td>6.07</td>
<td>−0.13</td>
<td>9.09</td>
<td>−5.02</td>
<td>11.85</td>
<td>−2.00</td>
</tr>
<tr>
<td>CV (%)</td>
<td>110.3</td>
<td>689.1</td>
<td>72.7</td>
<td>181.96</td>
<td>162.91</td>
<td>731.45</td>
</tr>
</tbody>
</table>

Notes: LFI=Length of first internode (cm)
LTI=Length of third internode (cm)
LS=Length of spike (cm)
LSI=Length of second internode (cm)
LBI=Length of basal internode (cm)
PH=Plant height (cm)
* The Chuan 3 A × R2870 has no data.
most of the crosses derived from the CMS lines without the \( \text{Rht} \) \text{3} \) gene had larger and positive HBS, with an average of 7.53%, while all the others had negative HBS (-5.51%). The HBS of all the components were negative, the HBS of LFI was the largest (-0.13%) and that of LBI was the least (-8.31%).

Especially almost all the characters of crosses derived from CMS lines with the \( \text{Rht} \) \text{3} \) gene were shorter than their high parents, due to the LBI of these hybrids which were not easy to exceed the LBI of their high parents. Zhao et al. (1990) reported similar results of PH in hybrids from female parents with the \( \text{Rht} \) \text{3} \) gene. Therefore, this CMS line was very useful for controlling plant height of hybrid wheat.

\textbf{Effects of the \( \text{Rht} \) \text{3} \) gene on relationships among the PH and its component in \( \text{F}_1 \) hybrids}

Table 2 showed that, in the \( \text{F}_1 \) hybrids derived from the A-line without the \( \text{Rht} \) \text{3} \) gene, only the relationships of the LFI with LBI (\( r=0.7934^* \)) and LSI (\( r=0.8187^* \)), and between LSI and LTI (\( r=0.7588^* \)) were significant; there were no close relationships between PH and its components. However, in the \( \text{F}_1 \) hybrids derived from A-line with the \( \text{Rht} \) \text{3} \) gene, the LFI was not significantly correlated to all other characters, the LSI was not only significantly associated with the LTI (\( r=0.9416^* \)), but also with LSI (\( r=-0.8508^* \)) and PH (\( r=0.8531^* \)); and the LTI was also closely correlated to LBI (\( r=0.7151^* \)), LSI (\( r=-0.8210^* \)) and PH (\( r=0.9106^* \)). These results implied that the \( \text{Rht} \) \text{3} \) gene increased the effects of LSI and LTI on PH and changed the relationships among the above components to some extent.

\textbf{Effects of the \( \text{Rht} \) \text{3} \) gene on relationships among HS and HBS of the characters.}

As for the HS, there were significant correlations between LSI and LTI (\( r=0.8294^* \)), LTI and PH (\( r=0.7528^* \)), when their female parent (A-line) had the \( \text{Rht} \) \text{3} \) gene (Table 3). However, there were no significant relationships among HS of characters in those hybrids from the A lines without the \( \text{Rht} \) \text{3} \) gene (Table 3).

For the HBS, only the relation between LSI and LTI (\( r=0.8781^* \)) was significant in the \( \text{F}_1 \) hybrids with the \( \text{Rht} \) \text{3} \) gene; and the LSI was correlated to PH (\( r=0.8174^* \)), the relationships among the HBS of other characters were not significant in the \( \text{F}_1 \) hybrids without the \( \text{Rht} \) \text{3} \) gene (Table 3).

\textbf{Relationship between parents and their \( \text{F}_1 \) hybrids}

For PH and its components, the correlation coefficients

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|c|c|c|}
\hline
Character & LFI & LSI & LTI & LBI & LS & PH \\
\hline
LFI & 1 & -0.3738 & -0.5693 & -0.7394* & 0.4186* & 0.0271 \\
LSI & 0.4288 & 1 & 0.7588* & 0.3684 & -0.4386 & 0.6229 \\
LTI & 0.2300 & 0.9416* & 1 & 0.6274 & -0.7249 & 0.5900 \\
LBI & -0.2203 & 0.4953 & 0.7151* & 1 & -0.6275 & 0.3313 \\
LS & 0.0125 & -0.8506* & -0.8210* & -0.4594 & 1 & 0.0384 \\
PH & 0.4294 & 0.8531* & 0.9106* & 0.7480 & -0.5556 & 1 \\
\hline
\end{tabular}
\caption{Effects of the \( \text{Rht} \) \text{3} \) gene on relationships among plant height and its components*}
\end{table}

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|c|c|c|}
\hline
Character & LFI & LSI & LTI & LBI & LS & PH \\
\hline
LFI & 1 & 0.1510 & 0.1576 & -0.1055 & 0.3266 & 0.6570 \\
LSI & 0.1502 & 1 & 0.8294* & 0.2744 & 0.5108 & 0.5532 \\
LTI & 0.2274 & 1 & 0.5648 & 0.4311 & -0.7386 & 0.4111 \\
LBI & 0.1890 & 0.8781** & 1 & 0.6107 & -0.5707 & 0.7238* \\
LS & 0.3484 & 0.8878** & 1 & 0.5658 & -0.1174 & 1 \\
PH & -0.3374 & 0.8174* & 0.5265 & 0.2750 & -0.2986 & 1 \\
\hline
\end{tabular}
\caption{Effects of the \( \text{Rht} \) \text{3} \) gene on relationships among HS and HBS of the PH and its components*}
\end{table}

Note: *: Significant at \( p=0.05 \) and 0.01, respectively.

\textbf{Relationship between parents and their \( \text{F}_1 \) hybrids}

For PH and its components, the correlation coefficients
between all F₁ hybrids and A or R lines, F₁ hybrids and A or R lines in 2 groups, with and without the Rht 3 gene, were calculated and the results were showed in Table 4.

When the Rht 3 gene was taken no account, the relationship between A-line and F₁ hybrid were significant for all traits, with the exception of LS; but the R-line was closely correlated to the F₁ hybrid only for two characters, i.e., LSI (r=0.5181**) and LS (r=0.8388**) (Table 4). Especially, the LS of R-line to that of F₁ hybrid was highly significant.

When the A-line had the Rht 3 gene, the relationships between A lines and their hybrids were nonsignificant for nearly all the characters examined except the LFI (r=0.8308***). Compared with the above correlations, the relations of R-line to F₁ hybrid for LSI, LTI, LS and PH were much more closer, and their correlation coefficients were 0.9161**, 0.9558**, 0.9496** and 0.8132*, respectively (Table 4). In the case with the Rht 3 gene, the plant height and its components of F₁ hybrid were mainly determined by the corresponding characters of R-line.

When the A lines and their hybrids had not the Rht 3 gene, there existed significant relationships both between A- and R-line with F₁ hybrid for only one trait - LSI, their coefficients were 0.9904** and 0.9308**, respectively (Table 4). Though other characters of both the A- and R-line were not significantly correlated to those of their hybrids, LTI, LS and PH of F₁ hybrid were largely affected by those of R-line, the LFI and LBI was mainly influenced by A-line other than R-line, based on the correlation coefficients.

Discussion

As to the conventional cultivars of wheat, the ideal PH is semidwarf in production (Wei et al 1990). In present study, the average PH of A lines with and without the Rht 3 gene and R lines were 53.7, 70.3 and 70.7 cm, respectively. Their hybrids with the Rht 3 gene were about 65–75 cm in height and shorter than the leading conventional varieties in Sichuan province and had strong resistance to lodging. However, the PHs of the hybrids without the Rht 3 gene were about 75–85 cm, and even 90–100 cm under dense population in other years, and taller than the conventional varieties; they easily lodge when encountered strong wind. Therefore, the Rht 3 gene should be used to dwarf the PHs of A-line and hybrid in order to improve the lodging resistance of hybrid wheat.

The Rht 3 gene is a major gene concerning of plant height and partially dominant (Dick 1974). In this paper, the result showed that the HS and HBS of all hybrids with the Rht 3 gene were less than those of hybrids without the Rht 3 gene, and the PHs of the former hybrids were shorter than their tall parents (Table 1), which implied that the Rht 3 gene was significantly effective to dwarf the plant height of hybrids. This result coincides with those in the previous reports (Gale and Law 1977, Zhao et al 1990).

The Rht 3 gene changed the relationships among plant height and its components of F₁, and especially increased the significance of correlations of LSI with LTI, LS and PH, and of LTI with LBI, LS and PH (Table 2). The correlations of HS of LTI to those of LSI and PH, and of HBS of LTI to HBS of LBI were significant (Table 3). The Rht 3 gene in A-line weakened the relations of PH and its components of A-line with those of this F₁ hybrid, and the R-line was very important to determine the PH and its components of F₁ hybrid. In this kind of combinations, it was relatively easier for breeders to control plant height of hybrid wheat. In addition, the determination coefficient for LS of R-line on the LS of hybrid (r² = 0.9017) was much larger than that for LS of A-line (r² = 0.0027) (Table 4). Therefore, the R-line with long spike should be developed in order to obtain hybrid with long spike.

In the combinations without the Rht 3 gene, plant height and its components of F₁ hybrid were influenced by the corresponding characters of A- or R-line, but the effects were not significant (except the LSI) (Table 4). The HS and HBS of these traits in this crosses were larger than those in crosses with the Rht 3 gene. So, it was difficult to determine plant height according to one
Effect of *Rht* 3 gene on plant height

parent; and both A and R lines should be strictly selected for plant height and its components when new hybrid combinations were made.

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Literature Cited


