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Genetic interactions between wheat and rye genomes in triticale

2. Morphological and yield characters

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Summary. Six primary triticale lines were produced from two advanced breeding lines of *Triticum durum* and three inbred genotypes of *Secale cereale*. The wheat and rye parents as well as the triticale derivatives were then crossed each within the same group of species in all possible combinations. Parents, F_1s, and F_2 populations were used to study the inheritance of a set of morphological and yield characters. The results suggest that, in general, in triticale allelic interactions within the wheat and the rye components are suppressed in favour of intergenomic interactions. Heterozygosity in the rye genome appeared to be detrimental for triticale, whereas heterozygosity in the wheat genome only resulted in positive interactions between certain characters. The retention of a high level of heterosis for kernels per spike in the F_2 generation of such hybrids indicates interactions between genes which are in the homozygous state in the rye but remain in the heterozygous state in the wheat genome. If heterozygosity in the wheat component occurs between genes in the A and B genomes (homoeoalleles), it can be fixed in true breeding lines. This condition may ultimately lead to the fixation of their benefical effect on the interaction between wheat and rye genome. Aneuploidy caused a significant decline in performance for most of the investigated characters.

Key words: Triticale – Diallel – Heterosis – Aneuploidy – Intergenomic interaction

Introduction

The mode of inheritance of quantitative characters as well as the magnitude of heterosis in triticale has so far only been studied by crossing varieties or advanced breeding lines in a diallel fashion (Kaltsikes and Lee 1973; Reddy 1976; Srivastava and Arunachalam 1977; Rao and Joshi 1979; Gill et al. 1979; Carrillo et al. 1983). In all these investigations triticale was treated as an established amphidiploid such as common wheat. No attention was paid to the role of interactions between the wheat and the rye genomes in the phenotypic expression of characters, although in addition to its possible agronomic importance, triticale as a synthetic amphidiploid allows a study of the evolutionary significance of such intergenomic interactions. For this kind of investigation the performance of a triticale line has to be compared to that of its wheat and rye parents. Such comparisons can only be made with primary triticale lines containing well defined parental genotypes (Lelley 1978). In a previous study (Jung et al. 1985), cytological data were described which were obtained from a diallel cross between six primary triticale genotypes (so-called thd lines: 'triticale hexaploid defined') and from the intraspecific hybrids of the two parental wheat and three rye genotypes. In the present study, morphological and yield characters of the parents, F_1s, and F_2s of the same triticale crosses are compared with the results received from the corresponding hybrids of the parental wheat and rye genotypes. The data strongly suggest that allelic interactions within the genomes leading to heterosis in the diploid hybrids are generally suppressed in the amphidiploid triticale in favour of interactions between the wheat and rye genomes.

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Materials and methods

Two *T. durum* genotypes Nos. D600 and D800, and three inbred lines of *S. cereale,* Nos. L25, L185 and L256, were used to produce six primary hexaploid triticale (thd) lines according to the method suggested by Lelley (1978). Crosses were made between these six thd lines as well as between the two wheat and three rye parents in all possible intraspecific combinations except reciprocals. The resulting 15 different triticale hybrids could be arranged in three groups according to which one of the parental genomes, rye ('R'), wheat ('W'), or both ('WR'), were heterozygous (see Fig. 1 in Jung et al. 1985). Parents, F_1s, and F_2 generations were cultivated as has already been described in a previous paper (Jung et al. 1985). For studying genetic interactions, only data from euploid plants were used. In order to determine the effect of aneuploidy on morphological characters and yield components, the performance of the aneuploid plants was also recorded. Because of severe leaf rust infection, the rye F_2 population could not be evaluated.

The following data were determined: days to heading, tillers per plant, plant height, spike length, spikelets per spike, kernels per spike and thousand kernel weight. Heterosis was calculated as percent difference of an F_1 or F_2 trait compared to the midparent value. Significance was ascertained by *t*-test.

For the triticale diallel, general and specific combining ability (gca and sca) were estimated using Griffing's (1956) model I, method IV (excluding parents). Specific combining ability effects (s_{ij}) were computed for each hybrid combination. The relative performance of the three triticale hybrid groups ('R', 'W', and 'WR') was expressed as the mean of the respective specific combining ability effects and was designated by $s_{ij}R$, $s_{ij}W$ and $s_{ij}WR$. In comparing those mean effects the standard error (SE) was used.

Results

The performance of the thd lines as well as that of the parental wheat and rye genotypes is presented in Table 1.

Regarding the F_1s, the wheat hybrid showed highly significant, positive heterosis only for the yield characters, i.e. for kernel number per spike and for thousand kernel weight (Table 2). Heterosis was negative for plant height, and no heterosis was observed in the other investigated traits. The performance of the *T. durum* F_2-population was for almost all characters much lower than that of the F_1. For the rye hybrids a highly significant heterosis was obtained for all characters (Table 2). Heterosis for plant height and thousand kernel weight might have been overestimated since the inbred lines suffered more under leaf rust infection than the F_1 hybrids. The triticale F_1s also showed heterosis for all characters studied. A remarkable high heterosis remained in the F_2 for two yield characters, viz. tillers per plant and kernels per spike.

Among the triticale hybrids, in which only one of the genomes, wheat or rye, was in the heterozygous state, those F_1s which were heterozygous only for the rye genome ('R') had the highest heterosis in characters concerning vegetative vigour, i.e. plant height and tillers per plant, but they did not show heterosis for the yield characters kernels per spike and thousand kernel weight. A comparison of the data of all the characters studied with the corresponding heterosis values of the parental rye F_1 hybrids revealed that, with the exception of tillers per plant, in none of the characters the extent of heterosis approached that found in the rye hybrids. This difference was most conspicuous for the yield characters, i.e. kernels per spike and thousand kernel weight. Again with the exception of tillers per plant, the performance of the F_2 generation of the 'R' group hybrids remained much below that of the F_1.

Triticale hybrids having only the wheat genome heterozygous ('W') displayed the highest heterosis for the yield characters kernels per spike and thousand kernel weight. Heterosis remained high in the F_2 for tillers per plant and kernels per spike. Good agreement was found when comparing the performance of the 'W' F_1 hybrids with the performance of the corresponding parental wheat hybrid, with the exception of days to heading and plant height. No correspondence, however, exists when F_2 generations of parental wheat and 'W' triticales are compared.

Aneuploidy appeared with different frequencies in triticale parents and in the hybrid progenies. The highest average of aneuploid plants was found with 27% in the F_2. Generally, with increased aneuploid frequency a concomitant reduction in all investigated characters was significant being most prominent for kernels per spike. Table 3 reveals that the lowest reduction occurred in those populations which are heterozygous for the wheat genome ('W') only.

F values for the triticale diallel (without parents) were significant for all characters with the single exception of spike length (Table 4). Therefore, no estimation of sca variance was made for this character in F_1. For days to heading, plant height, and spikelets per spike, gca variance of the F_1 was higher than sca variance. On the other hand, sca variance exceeded gca variance substantially for the yield characters tillers per plant, kernels per spike, and thousand kernel weight (Table 4). In the F_2, the proportion of sca variance decreased for plant height, spike length, tillers per plant, and thousand kernel weight. It increased substantially for spikelets per spike, whereas no change could be seen for days to heading and kernels per spike.

In order to determine which kind of hybrid genotypes, 'W', 'R', or 'WR', were the best in the diallel, a comparison between the mean sca effects was made (Table 4). In F_1, hybrids heterozygous only for the rye genome ('R') behaved best for tillers per plant. 'WR' hybrids gave the best results for days to heading and spikelets per spike, whereas for kernels per spike the

Table 1. Performance of the used parental *T. durum* (D600 and D800), *S. cereale* (L25, L185 and L256) and primary triticale (thd) lines

Genotype	Days to heading	Plant height (cm)	Spike lenght (cm)	Spilelets per spike	Tillers per plant	Kernels per spike	Thousand kernel weight (g)
D600	76.5	61.6	7.5	33.6	5.1	46.4	49.7
D800	74.7	44.6	7.6	35.2	5.1	54.6	40.4
L25	76.9	88.1	10.3	70.2	5.3	42.7	14.3
L185	81.6	55.4	7.2	62.8	3.2	28.7	6.3
L256	77.6	56.4	6.9	59.9	4.8	24.6	8.5
600-25	75.5	73.8	10.1	46.8	2.2	32.3	52.5
600-185	76.7	66.5	11.9	47.4	5.0	36.1	55.2
600-256	75.4	81.9	11.8	51.4	3.9	45.1	48.3
800-25	90.1	43.9	11.5	54.2	5.2	34.2	46.5
800-185	84.1	48.8	12.2	48.2	5.3	30.1	53.3
800-256	81.7	55.8	11.9	50.7	4.2	29.0	42.5

Table 2. Heterosis of *S. cereale* F_1 and of *T. durum* and triticale F_1 and F_2 generations calculated as percent difference to the midparent value

Genotypes	Days to heading	Plant height (cm)	Spike lenght (cm)	Spikelets per spike	Tillers per plant	Kernels per spike	Thousand kernel weight (g)
	F_1-generation						
T. durum	0.1	–4.8*	0.9	0.9	9.6	16.5**	7.6**
S. cereale	4.4*	60.0**	30.0**	16.5**	37.3**	96.5**	185.9**
triticale	1.6**	4.9**	3.9**	4.2**	25.9**	6.2*	7.6**
R	1.3**	6.3**	3.5**	4.1**	32.6**	–0.4	–2.4
W	1.4*	2.1	2.0	1.8	20.6*	17.6**	13.2**
WR	2.1**	5.1**	5.5**	5.4**	22.1**	7.2*	14.8**
	F_2-generation						
T. durum	2.5**	–4.9	–8.6**	–8.4**	–23.5**	0.5	2.8
triticale	–0.2	–1.2	1.9*	1.0	21.4**	8.1**	–1.2
R	0.21	–1.4	0.2	–0.2	16.4**	3.9	–4.5*
W	–0.54	–1.7	1.1	0.4	20.8**	14.6**	1.1
WR	–0.51	–0.9	3.9*	2.5**	26.8**	9.1**	1.0

* =5%; ** =1%

Table 3. Effect of aneuploidy on the phenotypic expression of the investigated characters in the triticale F_2

	% difference between euploid and all (including aneuploid) plants			
	R	W	WR	Total
Days to heading	0.9	0.8	1.1	0.8*
Plant height	–2.5	–1.8	–3.9	–3.0*
Spike lenght	–1.9	–1.6	–3.0	–2.1*
Spikelets per spike	–2.0	–0.9	–2.3	–1.9*
Kernels per spike	–15.9	–5.9	–12.9	–12.7*
Thousand kernel weight	–3.4	–1.5	–5.5	–3.9*
Seed quality[a]	–6.7	–8.9	–7.5	–6.9*

[a] Notes 1–9: 1 = shrivelled and 9 = plump seed

* =5%

Table 4. Combining ability of the triticale diallel

Source	Days to heading	Plant height	Spike length	Spikelets per spike	Tillers per plant	Kernels per spike	Thousand kernel weight
	F_1-generation						
gca	18.82**	291.27**	7.59	1.47**	1.23*	31.73**	5.77**
sca	1.0*	11.56**	7.60	0.38	1.34**	35.90**	39.85**
error	0.46	3.89	7.55	0.22	0.51	5.50	0.89
^{2}gca/^{2}sca	4.59/0.53	71.80/7.67	–	0.31/0.16	0.18/1.43	6.56/30.39	1.39/39.63
s_{ij}R	–0.25	0.77	–	0.01	0.29	–2.29	–0.29
s_{ij}W	–0.19	–1.75	–	–0.59	–0.24	3.91	0.15
s_{ij}WR	0.34	0.10	–	0.30	–0.17	0.33	0.22
S.E. R-W, WR-W	0.34	0.99	–	0.23	0.36	1.17	0.89
R-WR	0.28	0.81	–	0.19	0.29	0.96	0.71
	F_2-generation						
gca	34.32**	341.75**	12.71**	1.81**	1.30**	10.65**	23.54**
sca	1.15**	4.69	15.00**	0.88**	0.17	12.04**	9.57**
error	0.27	2.85	3.83	0.09	0.18	3.47	2.67
^{2}gca/^{2}sca	8.51/0.88	84.73/1.84	2.22/0.2	0.43/0.79	0.28/0	1.75/8.57	5.22/6.90
s_{ij}R	0.35	–0.09	–1.90	–0.50	–0.19	–1.44	–0.16
s_{ij}W	–0.25	–0.27	–0.33	–0.36	–0.05	2.24	0.11
s_{ij}WR	–0.23	0.23	2.37	0.67	0.21	0.32	0.11
S.E. R-W, WR-W	0.26	0.84	0.98	0.15	0.21	0.93	0.82
R-WR	0.21	0.69	0.80	0.12	0.17	0.76	0.67

* =5%; ** =1%

hybrids heterozygous only for the wheat genome ('W') were superior. In F_2, the 'R' hybrids gave best results for days to heading, while for spike length, spikelets per spike, and tillers per plant, the 'WR' hybrids exceeded the two others. For kernels per spike again 'W' genotypes were the best.

Discussion

Studies by various authors on heterosis in triticale F_1 hybrids have produced different results with respect to morphological characters. However, for yield characters, e.g. kernels per spike or fertility, most authors have found negative heterosis (Müntzing 1939; Gill et al. 1979; Srivastava and Arunachalam 1977; Oettler 1982; Carrillo et al. 1983). Variances for general and specific combining abilities were significant, gca being in most cases higher than sca (Kaltsikes and Lee 1973; Reddy 1976; Gill et al. 1979; Carrillo et al. 1983).

The present study differs from the previous ones in three respects: (1) Only primary triticale lines (thd) were used. Primary or unselected triticale lines are considered by several authors as being meiotically more unstable relative to advanced breeding material (for review see Scole and Kaltsikes 1974). For high yielding triticale lines the frequency of aneuploids have been estimated by some authors to average between 4 and 10%. In the present material the aneuploid frequency of the different thd lines varied between 4.9 to 15.6%, with an average of 10.3%. Between meiotic disturbances, expressed as percent pollen mother cells without univalents, and the frequency of euploid progeny, a close correlation was found (Jung et al. 1985). This indicates that for the degree of meiotic stability and number of aneuploid progenies genotypic differences are decisive, which becomes most obvious if thd lines are studied.

(2) All plants used for the experiment were cytologically controlled before planting in the field, allowing an evaluation of the data with and without aneuploid plants.

(3) Due to the genomic constitution of the parents, hybrids could be subdivided into three groups, with heterozygosity either in the wheat, or in the rye, or in both genomes.

Results of this work differ from results received by other authors in that relatively high heterosis and sca values were obtained for yield characters, i.e. kernels per spike and thousand kernel weight. This discrepancy is most probably due to the use of euploid plants only to compute the data. For example, the average number of kernels per spike decreased by more than 12% if aneuploid plants were included (Table 3). A correlation coefficient of $r=0.82^{**}$ was calculated between frequency of aneuploids and decrease in fertility.

Another reason for differences in the results from those found in the literature may depend on the chromosomal constitution of the triticale material. Due to crosses between triticale and hexaploid wheat in the course of breeding work, an increased number of triticale varieties have been developed which have D genome substitutions of rye chromosomes (Pilch 1981 a, b; Lukaszewski and Apolinarska 1981). Crossing triticale lines which are different only in one pair of chromosomes leads to a consistent univalency in the hybrid and a reduced fertility of the F_1. In a diallel analysis, the presence of such a line results in an increased gca variance because all hybrids with this particular line will show a decreased performance, especially for yield characters. This explanation could apply to the findings of Srivastava and Arunachalam (1977) according to which heterosis decreased when triticale lines with higher genetic divergence were crossed. The reason for such genetic divergence could be due to differences in the chromosomal constitution of the investigated lines. No attempt was made in that experiment to identify the chromosomal constitution of the material used. In the present investigation all triticale lines contained 14 rye chromosomes.

Triticale F_1s with only the rye genome in the heterozygous state ('R') showed no heterosis for the yield components kernels per spike and thousand kernel weight, although in the corresponding parental rye hybrids heterosis was high. For all other characters heterosis was significant but remained much below the expected level (Table 2). Heterosis in the F_2 of the 'R' hybrids was much lower than in the F_1 suggesting that allelic gene action, i.e. dominance, within the rye genome is responsible for the heterosis in F_1. This situation is similar to that in rye, where F_1 heterosis is mainly attributed to dominant gene action (Wricke 1973). The large difference between the expected and observed heterosis in the 'R' hybrids can be best explained by negative interactions between the heterozygous rye and the wheat genome. The expression of allelic gene actions for kernels per spike and thousand kernel weight within the rye genome is completely suppressed by the wheat component.

In contrast to the results obtained for the 'R' hybrids, in the 'W' hybrids the estimated heterosis values corresponded well with those found in the parental wheat hybrid for all characters. Obviously, contrary to the situation in the 'R' hybrids, the rye component in the 'W' hybrids does not impair full gene expression within the heterozygous wheat genome. However, this correspondence disappears if F_2 heterosis of the 'W' hybrids and of the parental wheat hybrid is compared. In the wheat hybrid, except for days to heading, the performance of the F_2 was well below that of the F_1, which indicates dominant gene action being responsible for the F_1 heterosis. But the generally low level of this heterosis and its complete absence for some characters suggests that additive gene action is probably more important in tetraploid wheat, as was indeed found by Widner and Lebsock (1973). The F_2s of the 'W' hybrids also showed a reduced heterosis for days to heading and thousand kernel weight in comparison to the F_1; but for tillers per plant and kernels per spike heterosis remained high, suggesting that in triticale for these characters a different kind of gene action should be assumed, i.e. interactions between the wheat and the rye components (Table 2).

Analyzing combining ability a preponderance of gca variance was determined for days to heading, plant height, and spikelets per spike, which is in agreement with results of other authors (Kaltsikes and Lee 1973; Reddy 1976; Gill et al. 1979). The high sca variance for the yield characters kernels per spike and thousand kernel weight shows that there is a considerable amount of nonadditive gene action in triticale, which can be due to dominance or epistasis. The high specific effect of the 'W' genotypes for kernels per spike (Table 4) suggests that most of this sca variance is caused by heterozygosity of the wheat genome of triticale. In F_2, sca variance was still much higher than gca indicating that dominant gene action is less important. Epistasis within the wheat genome can also be excluded, if the heterosis of the parental wheat F_2 is considered. Consequently, the high sca variance for kernels per spike must come from intergenomic interactions between the wheat and rye genomes of triticale. It is, however, only positive when the wheat genome of triticale is heterozygous. The situation is different for thousand kernel weight. Here, the high sca in F_1 is due to intragenomic interactions within the wheat component, as the comparison with the data of the parental wheat hybrid discloses. In F_2, the ratio between sca and gca approaches unity. Parallel to that the heterosis of the 'W' F_2s remained far below that of the F_1s.

Genotypes with both components wheat and rye heterozygous ('WR') as in a conventional triticale hybrid also showed positive heterosis in F_2 for some characters. Their hybrid performance was generally between that of the 'W' and 'R' genotypes. For F_2, heterosis in kernels per spike the data indicate intergenomic interaction similar to that found in the 'W' hybrids.

The results of the present study lead to the conclusion that in the amphidiploid triticale, allelic gene actions within the parental wheat and rye genomes are generally suppressed in favour of interactions between these two components. These interactions have a clear negative effect on cytological characters, i.e. chiasma frequency or number of univalents (Jung et al. 1985). However, they can also be positive as in the case of kernels per spike. The study reveals that the two parental components contribute differently to these interactions. Heterozygosity in the rye genome appeared to be detrimental for triticale, whereas heterozygosity in the wheat genome resulted in positive interactions. Heterozygosity in the wheat component, as the data suggest, may occur between homoeoallels in the A and B genomes. Since between these two genomes recombination does not take place, the heterozygous condition between the homoeoalleles can be fixed. This condition may ultimately lead to the fixation of their beneficial effect on the interactions between the wheat and the rye genomes. Special breeding techniques which take into account this particular genetic situation in triticale are being developed (Lelley 1983).

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