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The Effect of 2D(2R) Substitution on the Agronomical Traits of Winter Triticale in Early Generations of Two Connected Crosses

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The association between genomic constitution and agronomic traits was studied in F_2 plants and $F_{3:4}$ families of two crosses between a winter hexaploid triticale line with a 2D(2R) chromosome substitution and two hexaploid triticale cultivars carrying the complete rye genome (BBAARR). The analyses revealed that 2D(2R) substitution reduces plant height and spikelet number per spike, increases the 1,000-kernel weight, does not reduce grain shrivelling, and promotes early heading and anthesis. 2D(2R) substitution lines exhibit deeper postharvest seed dormancy, which provides resistance to preharvest sprouting. However, 2D(2R) substitution lines are not recommended for winter hexaploid triticale cultivar development purposes due to their reduced grain productivity.

Keywords: *Triticosecale*, chromosome substitution, plant height, grain shrivelling, preharvest sprouting

Abbreviations: ANOVA – analysis of variance; DNA – deoxyribonucleic acid; GE – genotype-environment (interaction); GI – germination index; GNS – grain number per spikelet; GWS – grain weight per spike; MSL – main stem length; PCR – polymerase chain reaction; QTL – quantitative trait locus; SNS – spikelet number per spike; SSR – simple sequence repeat; TBE – Tris-borate-EDTA buffer; UV – ultraviolet

Introduction

Hexaploid triticale (*Triticosecale* Wittm., BBAARR, 2n = 42) is usually grown for feed grain and as a hay or a grazing crop. However, most of the available triticale cultivars are not suitable for human consumption due to their weak gluten strength, preharvest sprouting and shrivelled grain (Mergoum et al. 2009). The incorporation of bread wheat (*Triticum aestivum* L., BBAADD) D-genome chromosomes into hexaploid triticale might improve some of these agronomical traits (Budak et al. 2004; Sodkiewicz et al. 2011). The 2D(2R) substitution is among the most widespread substitutions in spring triticale lines and cultivars (Mergoum et al. 2004; Lapin et al. 2007; Divashuk et al. 2010b; National Research Council 1989).

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Triticale lines with the 2D(2R) substitution tend to mature earlier and are shorter, day-length insensitive and resistant to preharvest sprouting (Rybka 2003; Mergoum et al. 2004; Kurkiev 2008). However, 2D(2R) substitution decreases resistance to stem rust and tolerance to the presence of aluminium ions and to high soil acidity (Royo et al. 1993; Darvey et al. 2000; Kim et al. 2001; Budzianowski and Woś 2004).

Most previous studies on the effects of 2D(2R) substitution in hexaploid triticale were performed in backcrossed lines of late generations that were subjected to selection or lines and cultivars with 2D from different sources (Reddy and Zereena 1999; Kim et al. 2001; Rybka 2003; Budak et al. 2004; Budzianowski and Woś 2004; Kurkiev 2008; Gill et al. 2010; Divashuk et al. 2010b). Thus, the study of the effect of 2D(2R) substitution on agronomic traits in early generations of crossing that have not been subjected to selection, is useful for planning breeding strategies.

The 2R chromosome (the largest chromosome in the rye genome) is eliminated frequently in crosses between hexaploid triticale and bread wheat (Gupta and Priyadarshan 1982). Studies of the meiotic behaviour of 2D and 2R in dimonosomic lines of wheat showed no pairing between them (Silkova et al. 2014). The only T2R.2DL translocations found thus far have resulted from ruptures in the centromeric region, which were followed by centric fusion; thus, these events did not involve small chromosome segments (Krasilova et al. 2012).

Due to this finding, 2D(2R) substitution can be identified in individual plants using a small number of PCR-based molecular markers that are distributed along the chromosome. Earlier, we successfully used microsatellite markers (SSRs) to identify substitutions and translocations in triticale lines and compared these techniques with traditional cytogenetic methods (Lapin et al. 2007; Divashuk et al. 2010a).

The aim of this study was to examine the effect of 2D(2R) substitution on yield components, plant height and seed dormancy in early generations of winter hexaploid triticale crosses.

Materials and Methods

Plant material

The plant material used was derived from crosses between three triticale accessions, namely crosses between line 21759/97 and cultivar Fidelio and between 21759/97 and cultivar Alexander. 21759/97, a 2D(2R)-substituted line of hexaploid triticale, was used as a donor of the 2D chromosome. Fidelio and Alexander are promising triticale cultivars with complete A, B and R genomes. Seventy individual plants from each of the generated F_2 populations were randomly sampled and self-pollinated in 2010. Using the results of plant genotyping (described below), F_2 plants possessing only 2D or only 2R chromosomes were selected. F_3 plants grown from seeds obtained from self-pollinated individual plants of F_2 in 2011 and F_4 plants grown from seeds obtained from cross-pollinated sib plants of F_3 in 2012 are referred to as families. The F_2 populations and the F_3 and F_4

families derived from the crosses are designated as $F_{2(3,4)}$(21759/97×Fidelio) and $F_{2(3,4)}$(21759/97×Alexander).

Growing conditions

$F_{2(3,4)}$ plants were grown in field plots at the Russian State Agrarian University – Moscow Agricultural Academy (Moscow) in 2010, 2011 and 2012. F_2 populations were grown in 1-m^2 field plots. F_3 and F_4 families were sown on single-row plots at 20 seeds per row and at an inter-row spacing of 30 cm.

Agronomical traits

Spikelet number per spike (SNS), grain number per spikelet (GNS), and spike density were measured in the F_2 population using individual randomly sampled plants from each cross. Tilling capacity, main stem length (MSL), SNS, GNS, grain weight per spike (GWS), spike density, and 1,000-kernel weight were measured using ten randomly sampled plants from 42 families of $F_{3:4}$(21759/97×Alexander) and 53 families of $F_{3:4}$(21759/97×Fidelio) and were counted as averages for each family. Field emergence and winter survival were calculated using all available plants for each family. The durations of the development stages were recorded for each family as a whole.

Grain plumpness was estimated visually using a four-point scale (poor, satisfactory, good and excellent). Germination index (GI) was estimated for freshly harvested grains in Petri dishes using 20 grains from each F_2 plant and two 100-grain samples from the F_3 and F_4 families. The grains were germinated during 14 days in darkness at 25°C, and GI was calculated according to the formula:

$$GI = \frac{14 \times n_1 + 13 \times n_2 + \ldots + 1 \times n_{14}}{D \times N},$$

where n_1, n_2, ..., n_{14} are the number of grains that had germinated on day 1, day 2, ..., day 14, respectively; N is the total number of viable grains; and D is the total number of days. The maximum index is 1.0 if all grains germinate by day 1, and lower indices indicate higher levels of seed dormancy.

Plant genotyping

DNA was extracted from the leaves of F_2 plants according to the protocol described by Bernatzky and Tanksley (1986).

Chromosome 2D was detected using the chromosome-specific PCR-based microsatellite markers (SSRs) *Xwmc111* and *Xgwm261* for the short arm and *Xgwm539* and *Xbarc1143* for the long arm (Röder et al. 1998; Somers and Isaac 2004; Song et al. 2005). Chromosome 2R was detected using an STS marker for the Sec2 gene that is located on 2RS (Lee et al. 1994). PCR conditions were optimised in our previous work

(Lapin et al. 2007). The amplified DNA fragments were subjected to electrophoresis in 1.5 or 2% agarose gels using TBE buffer at 6 V/cm and were visualised by UV transillumination after ethidium bromide staining. The protocol published in Korzun et al. (1998) was used to determine allelic variation for the microsatellite marker *Xgwm261,* which is linked with *Rht8*. Fragments of various sizes for *Xgwm261* were detected using an ABI3130xl Genetic Analyzer (Applied BioSystems, Foster City, CA).

Statistical analysis

The effect of 2D(2R) substitution was determined by processing the data using one-way and two-way ANOVA. The effects of genotype [2D(2R) substitution], environment and genotype-environment interaction (GE) were estimated using two-way ANOVA. Confidence intervals were calculated using Student's *t*-test. To reveal the association between 2D(2R) substitution and grain plumpness, Fisher's exact test (1934) was used. Statistica 6.0 software and an on-line calculator for Fisher's exact test were used (http://in-silico.net/tools/statistics/fisher_exact_test).

Results

PCR analysis

We assumed that the amplification of microsatellite markers for chromosome 2D and no amplification of the STS marker for *Sec2* indicate a triticale plant possessing 2D(2R) substitution and vice versa (Fig. 1). If the amplification of markers for both chromosomes was detected, the plant was considered heterozygous, that is, carrying both 2R and 2D chromosomes.

The markers distributed along the 2D chromosome were always detected together in the same individuals of the F_2 populations. Therefore, it was concluded that there were no large deletions and translocations involving chromosome 2D in the analyzed plant material. In F_2(21759/97 × Alexander), 28 homozygotes and 11 heterozygotes for the 2D(2R) substitution were found, and 31 plants did not carry the 2D(2R) substitution. In F_2(21759/97 × Fidelio), 17 homozygotes and 20 heterozygotes for the 2D(2R) substitution

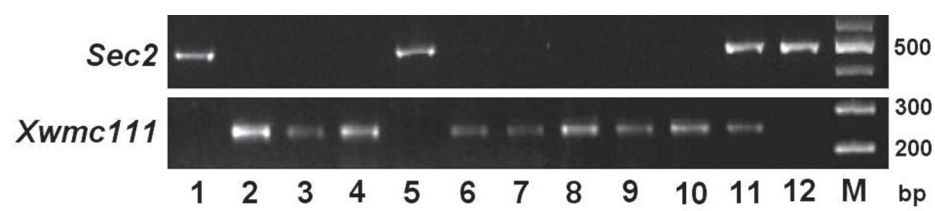

Figure 1. Agarose gel electrophoresis of PCR products of STS marker for *Sec2* gene and *Xwmc111* microsatellite marker. Lanes indicate the plants in F_2(21759/97 × Alexander): 2, 3, 4, 6 – 10 possess 2D(2R)-substitution, 1, 5, 12 do not have substitution, 11 possess both 2R and 2D chromosomes. M – 100 bp Plus DNA Ladder, Thermo Scientific

were revealed, and 33 plants did not carry the 2D(2R) substitution. The number of plants having both 2R and 2D chromosomes was smaller than expected; that might be due to their lower viability.

Fifteen families with the 2D(2R) substitution and 24 without the 2D(2R) substitution from $F_{3:4}$(21759/97 × Alexander) and 8 families with the 2D(2R) substitution and 33 families without the 2D(2R) substitution from $F_{3:4}$(21759/97 × Fidelio) were selected using PCR analysis.

Main stem length

The difference in MSL between plants with the 2D(2R) substitution and plants without the 2D(2R) substitution (ΔMSL) was significant in $F_{3:4}$(21759/97 × Alexander) families: ΔMSL was 12 cm in F_3(21759/97 × Alexander) (mean MSL was 84 cm) and 25 cm in F_4(21759/97 × Alexander) (mean MSL was 123 cm) (Table 1). The effects of genotype (2D(2R) substitution), environment and genotype-environment interaction (GE) were estimated using two-way ANOVA. Significant effects of genotype ($F = 64.5$; $p < 0.01$), environment ($F = 262.8$; $p < 0.001$) and GE ($F = 7.9$; $p = 0.06$) on plant height were observed. PCR analysis of 21759/97 revealed that this line carries the 165 bp allele of *Xgwm261*, which is not associated with the *Rht8* dwarfing allele.

The difference in MSL between plants with and without the 2D(2R) substitution was

Table 1. The effect of 2D(2R) substitution on main stem length in F_3–F_4 populations

Cross	Year	Main stem length[1]		Significance level[2] *(p)*
		with 2D(2R) substitution, cm	without substitution, cm	
21759/97 × Alexander	2011	77±5	89±5	<0.001
	2012	108±7	133±4	<0.001
21759/97 × Fidelio	2011	68±5	75±4	0.067
	2012	108±11	127±4	<0.001

[1]95% confidence intervals are given.
[2]Here and then F-Fisher's test was used for significance level determination.

slightly significant in F_3(21759/97 × Fidelio) (ΔMSL, 7 cm; mean MSL, 73 cm) and was significant in F_4(21759/97 × Fidelio) (ΔMSL, 19 cm; mean MSL, 121 cm). Two-way ANOVA showed that the effects of genotype ($F = 17.9$, $p < 0.001$) and environment ($F = 216.2$; $p < 0.001$) on plant height were significant but that the effect of GE ($F = 3.3$; $p = 0.07$) on plant height was insignificant.

Yield component analysis

On average, GWS was 2 and 1.5 times lower in $F_{3:4}$(21759/97×Alexander) and $F_{3:4}$(21759/97×Fidelio) plants with the 2D(2R) substitution than in plants without the 2D(2R) substitution (Table 2). The observed decrease in GWS is explained primarily by the decrease in SNS and secondarily by the decrease in GNS. Among the 2D(2R) substitution genotypes, SNS consistently decreased from year to year in both studied crosses. Significant decreases in GNS were observed in plants with the 2D(2R) substitution in both $F_{2:4}$(21759/97×Alexander) and F_3(21759/97×Fidelio).

The value of 1,000-kernel weight was significantly higher in $F_{3:4}$(21759/97 × Alexander) plants with the 2D(2R) substitution than in plants without the 2D(2R) substitution. In other cases, the effect of the 2D(2R) substitution on this trait was insignificant.

Tilling capacity in F_3(21759/97 × Fidelio) and winter survival in $F_{3:4}$(21759/97 × Fidelio) were slightly lower in plants possessing the 2D(2R) substitution. Field emergency was slightly lower in $F_{3:4}$(21759/97 × Alexander) plants possessing the 2D(2R) substitution.

Two-way ANOVA demonstrated that the effects of GE on yield components were insignificant in the studied families, with the exception of GNS in (21759/97 × Fidelio) ($F = 5.8$; $p = 0.004$).

Germination index

Estimation of GI in parental plants showed that Fidelio exhibited weak seed dormancy, whereas Alexander and 21759/97 exhibited pronounced after-harvest seed dormancy in 2009–2012. This is consistent with the results of a moist chamber test of preharvest sprouting resistance that was conducted in 2010 (data not shown). The GI of seeds collected from $F_{2:4}$ plants were estimated. GI was 1.04–1.80 times (significantly) lower for seeds from $F_{2:3}$(21759/97 × Fidelio) plants with the 2D(2R) substitution than for seeds from $F_{2:3}$(21759/97 × Fidelio) plants without the 2D(2R) substitution. No significant association was found between 2D(2R) substitution and the GI of seeds from F_4(21759/97× Fidelio) and $F_{2:4}$(21759/97 × Alexander) plants. Two-way ANOVA demonstrated a significant effect of environment on GI in both crosses ($p < 0.001$) and a significant effect of GE on GI only in (21759/97 × Fidelio) ($F = 5.0$; $p = 0.008$).

Spike density

Spike morphology was studied in F_2 individual plants and in $F_{3:4}$ families. Spike density was significantly lower in plants with the 2D(2R) substitution than in plants without the 2D(2R) substitution: $F_{2:4}$(21759/97 × Fidelio) ($p < 0.001$) and F_4(21759/97 × Alexander) ($p = 0.005$). Environment had a significant effect on spike density in both crosses, as shown using two-way ANOVA ($p < 0.001$): maximum spike density (29 spikelets per 10 cm of ear axis) was observed in F_2, and 23–25 spikelets per 10 cm were found in $F_{3:4}$. The 2D(2R) substitution resulted in lower spike density in (21759/97 × Alexander) on average (from 26.5 to 25 spikelets per 10 cm), and in (21759/97 × Fidelio), spike density was decreased from 27 to 24 spikelets per 10 cm of ear axis. No significant effect of GE on spike density was observed.

Table 2. The effect of 2D(2R) substitution on yield components and germination index in F3–F4 populations

Yield component	Year	In plants with 2D(2R) substitution	In plants without substitution
21759/97 × Alexander			
Grain weight per spike, g	2011	1.0±0.2	1.8±0.2***
	2012	1.7±0.1	2.7±0.2***
Spikelet number per spike	2010	22±1	29±1***
	2011	19±1	25±1***
	2012	22±1	28±1***
Grain number per spikelet	2010	1.2±0.2	1.5±0.2**
	2011	0.9±0.2	1.4±0.2**
	2012	1.2±0.1	1.4±0.1***
1000-kernel weight, g	2011	56±4	50±3*
	2012	66±2	66±2ns
Germination index	2010	0.42±0.07	0.45±0.06ns
	2011	0.76±0.02	0.76±0.03ns
	2012	0.80±0.02	0.78±0.01ns
21759/97 × Fidelio			
Grain weight per spike, g	2011	0.7±0.3	1.8±0.3***
	2012	1.9±0.2	2.6±0.2***
Number of spikelets per spike	2010	20±1	28±1***
	2011	18±1	25±1***
	2012	22±2	27±0.5***
Number of grains per spikelet	2010	1.3±0.3	1.5±0.1ns
	2011	0.9±0.4	1.4±0.2**
	2012	1.4±0.1	1.5±0.1ns
1000-kernel weight, g	2011	46±7	48±2ns
	2012	62±4	64±1ns
Germination index	2010	0.19±0.07	0.35±0.07**
	2011	0.74±0.05	0.77±0.01*
	2012	0.76±0.06	0.79±0.01ns

Notes: *The difference between the means of plants with 2D(2R) substitution and without is significant at 5% level ($p<0.05$); **The difference between the means of plants with 2D(2R) substitution and without is significant at 1% level ($p<0.01$); ***The difference between the means of plants with 2D(2R) substitution and without is significant at 0.1% level ($p<0.001$); ns: the difference is non-significant ($p>0.05$).

Grain plumpness

21759/97 and Fidelio produced well-filled grain with smooth surfaces, whereas Alexander produced well-filled grain with rough surfaces. The 2D(2R) substitution significantly reduced grain plumpness in $F_{3:4}$(21759/97 × Alexander) and in F_4(21759/97 × Fidelio) ($p < 0.01$). Plants with complete rye genomes possessed well-filled or excellently filled grain, whereas grain from 2D(2R) substitution plants was satisfactorily or poorly filled.

Duration of development stages

2D(2R) substitution did not significantly influence the duration of booting and the wax ripeness of the grain in both crosses; however, 2D(2R) substitution significantly accelerated heading by 2–5 days ($p < 0.05$) and significantly accelerated anthesis by 2–4 days ($p < 0.001$). Thus, 2D(2R) substitution tended to shorten the period from booting to heading.

Discussion

Our studies demonstrated a significant effect of 2D(2R) chromosomal substitution on plant height in hexaploid triticale. Our results are consistent with a number of similar works, in which 2D(2R) substitution reduced plant height in the absence of the *Rht8* gene dwarfing allele on the 2D chromosome (Budak et al. 2004; Kurkiev 2008). Tight linkage between *Rht8* and the 192-bp allele at the microsatellite locus *Xgwm261* has been reported, and this allele has been suggested as being diagnostic for *Rht8* (Korzun et al. 1998). In our study, the 165-bp allele was detected, which is one of the most widespread alleles in wheat collections (Worland et al. 1998; Korzun et al. 1998). In our case, the reduction in plant height that resulted from the 2D(2R) substitution might be due to genes other than *Rht8*, which affect plant height and are located on the 2D and 2R chromosomes.

The results demonstrate that the 2D(2R) chromosomal substitution caused a substantial decrease in the SNS, which is apparently characteristic of all 2D(2R) substitution triticales (Kurkiev 2008). In some cases, 2D(2R) substitution plants exhibited lower GNS. Apparently, the effect of the 2D(2R) substitution on GNS is associated with both the background genotype and weather conditions. The large 1,000-kernel weight observed for F_3(21759/97 × Alexander) can be explained by the low value of GNS. A similar effect of 2D(2R) substitution has been reported previously. In a similar study, the Presto 2D(2R) substitution line exhibited larger grain size and 1,000-kernel weight than complete Presto (Budak et al. 2004). In other cases, 2D(2R) substitution did not affect 1,000-kernel weight. Thus, we can assume that under given climatic conditions, winter triticale lines with the 2D(2R) substitution will exhibit lower yields than hexaploid triticale with a complete rye genome; however, the former plants might yield coarser grain.

GI was significantly decreased by the 2D(2R) substitution in $F_{2:3}$(21759/97 × Fidelio). This finding is consistent with the results obtained in previous experiments (Rybka 2003).

The association between GI and 2D(2R) substitution was not found in plants derived from the (21759/97 × Alexander) cross. It should be noted that the 2D chromosome was transmitted to triticale from the same donor (21759/97) in both crosses. This result is expected because triticale and rye varieties are polymorphic regarding the genes responsible for seed dormancy and resistance to preharvest sprouting, which are located on the 2R chromosome (Masojć et al. 2007). Furthermore, genes located on the 2R and 2D chromosomes can interact with genes from other chromosomes.

In both crosses, the grains formed in plants containing the 2D(2R) substitution were less plump and more shrivelled than those formed in plants without the substitution. However, the maternal line 21759/97 with the 2D(2R) substitution produced well-filled grain with smooth surfaces. The negative impact of the 2D(2R) substitution on grain performance was demonstrated in previous studies (Reddy and Zereena 1999). At the same time, the Presto 2D(2R) substitution line does not differ substantially from Presto according to the grain test weight, a trait that indirectly reflects grain plumpness and smoothness (Budak et al. 2004). Therefore, the adverse effect of the 2D(2R) substitution can be compensated by certain gene systems that are formed by selection for grain quality. Most likely, in our experiments, the compensation system in 21759/97 was disassembled in the progeny, leading to the shrivelled grain observed in plants containing the 2D(2R) substitution.

2D(2R) substitution shortens the growing season of triticale somewhat and unequally influences the duration of various development stages. Previously, it was observed that the 2D(2R) substitution reduces the period before flowering, albeit weakly (Budak et al. 2004).

The studied traits are quantitative; that is, they are determined not by major genes but by a set of genes that have minor effects. An effective breeding strategy is to search for quantitative trait loci (QTLs). Several QTLs conferring grain yield (QGyld.agt-2D), GNS (QGnu.ipk-2D, QGne.nfcri-2D.2), test weight (QTwt.crc-2D), kernel weight (QGwe.ipk-2D.1, QGwe.ipk-2D.4), grain-filling (SWSCF), plant height (QHt.crc-2D) and heading date (QEet.ipk-2D) were mapped to the 2D chromosome (http://ccg.murdoch.edu.au/cmap/ccg-live). Recently, the draft assembly of 2D chromosome sequence reads was developed and aligned with the consensus QTL map (Jia et al. 2013). Thus, further investigation of the obtained 2D(2R) substation triticale lines might be useful for the development of molecular markers for agronomical traits that are determined by QTLs that are located on the 2D chromosome.

Thus, we can conclude that the 2D(2R) substitution reduces plant height, thereby contributing to greater resistance to lodging, reduces the SNS, either does not influence the 1,000-kernel weight or increases it, does not improve the physical properties of the grain (plumpness and smoothness), and promotes early flowering and heading in hexaploid winter triticale plants. In some years, 2D(2R) substitution can reduce GNS. In addition, 2D(2R) substitution in hexaploid triticale can increase preharvest sprouting resistance by increasing seed dormancy at harvest. However, 2D(2R) substitution lines are not recommended for cultivar-development purposes due to the observed decrease in grain productivity.

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