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Influence of wheat and rye parents on agronomic characters in primary hexaploid and octoploid triticale

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Summary. Thirty-five hexaploid and twenty octoploid primary triticales (x*Triticosecale* Wittmack) derived from homozygous wheat and rye inbred lines were used (1) to investigate the parental wheat, rye, and interaction effects and (2) to estimate quantitative genetic parameters for agronomic traits. The winter triticales were tested in four environments in a three-replicate split-plot design with drilled 1 m^2 plots. Superior performance of hexaploid triticales as compared to the octoploids was revealed. Substantial genetic variation and high heritability estimates were found for nearly all of the characters investigated. Estimates of wheat, rye, and wheat × rye interaction variance components disclosed parental main effects to be the most important source of genetic variation in primary triticales. The rye parent was dominant for all characters affecting fertility, and the wheat parent was more important for vegetative development. Character correlations were very similar for triticales of both ploidy levels. The lack of association between grain yield and tillering and the positive correlation between kernels per spike and thousand kernel weight indicated physiological disorders specific for primary triticales.

Key words: x*Triticosecale* Wittmack – *Triticum* ssp. – *Secale cereale* inbred lines – Parental effects – Genetic parameters

Introduction

In the intergeneric hybrid triticale (x*Triticosecale* Wittmack) the gene pools of both its constituent genera, *Triticum* and *Secale*, should be exploited to broaden the genetic base of this artificially synthesized crop. There is little knowledge available, however, on the amount of variation contributed by wheat, rye, and the interaction between them to the phenotypic expression and genetic variation of characters in the amphidiploid. Primary triticales synthesized from wheat and rye inbred lines are suitable material for analyzing the relative importance and exploitability of these three categories of genetic effects. The wheat and rye components in such triticales are genetically well defined since their parents are homozygous lines.

The information which exists on the importance in triticales of the parental wheat, rye, and interaction effects is scarce or inconsistent because few research studies have been done with appropriate materials (Lelley and Gimbel 1989; Oettler et al. 1988; Wandelt 1988) and the number of genotypes investigated is limited. For effective selection the breeder needs an extensive knowledge of quantitative genetic parameters, such as heritabilities or character correlations, in the crop. Considerable information is available on secondary triticales (e.g., Lapinski et al. 1988; Sandha et al. 1980), but it is scarce on primary genotypes and is based on 1 year observations only (Oettler 1986; Oettler et al. 1988). A multi-environment drilled field test with genetically defined triticales of both ploidy levels has not yet been reported.

The objectives of this study were (1) to assess the importance of wheat, rye, and wheat × rye interaction effects by estimating variance components and (2) to determine variances, heritabilities, and character associations in primary hexaploid and octoploid triticales.

Materials and methods

Primary hexaploid and octoploid triticales from the Hohenheim collection, all of winter habit, were used for this study. The

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triticales were produced by crossing five lines of *Triticum durum* L. and two cultivars of *T. aestivum* L. with a set of 12 homozygous *Secale cereale* L. inbred lines from the Hohenheim collection (Table 1). Only 35 hexaploid and 20 octoploid combinations of the theoretically possible 60 and 24 factorial crosses, respectively, were available (Table 4). The seed for the present experiment was produced by selfing the homozygous triticale lines for four or five generations.

Field tests were conducted in 1986 and 1987 at both Stuttgart-Hohenheim and Oberer Lindenhof, Schwäbische Alb. Plots of 1 m^2, drilled in rows at a seeding rate of 320 kernels per m^2, were arranged in a split-plot design with three replications and ploidy levels as main plots. The following data were recorded on a per plot basis: days from May 1st to heading, plant height (cm), productive tillers per m^2, grain yield (g/m^2), thousand kernel weight (g), and test weight (kg/hl). Spikelets per spike and kernels per spike were assessed on five randomly chosen spikes per plot. In the octoploid materials test weight could not be recorded for 20% of the plots because of a too low grain yield.

Table 1. Origin of durum wheat, bread wheat, and rye inbred lines used to synthesize primary triticales

Genus	Line	Origin: Country/population
Durum wheat	D 4	Mexico
	D 8	Italy
	D 9	USSR
	D 30, D 40	Rumania
Bread wheat	Jubilar, Götz	Germany[a]
Rye	L 60, L 68, L 70	Brandt's Marien
	L 271	Carsten
	L 18, L 35, L 185, L 301	Petkus
	L 145, L 150, L 155, L161	Population crosses

[a] Götz is a progeny of 'Jubilar' and has a 1B/1R translocation (Zeller and Fuchs 1983)

The statistical analyses were performed separately for hexaploid and octoploid genotypes using random models and treating experiments as macro-environments. Analyses of variance were conducted for the crosses as entries with the computer program PLABSTAT (Utz 1988) and an extension according to Henderson's (1953) Method 1. Heritabilities of entry means (averaged over four macro-environments and three replications) and phenotypic character correlations between these means were estimated within this program. The sequentially rejective Bonferroni procedure (Holm 1979) was used in testing variances and correlations. In a second step, the components of variance for the unbalanced factorial structure of the crosses were analyzed with the restricted maximum likelihood (REML) procedure (Robinson 1987). Least squares estimates were used for the average performance of rye and wheat parents in their amphiploids. The general means of the two analyses (in Table 2 and 4) are different due to the unbalanced nature of the data.

Results

Grain yield in the hexaploid triticales was more than twice that of the octoploids (Table 2). Spikelets per spike, kernels per spike, and thousand kernel weight were also higher in the hexaploids. The octoploid triticales were later heading, shorter, had more productive tillers and a higher test weight as compared to the hexaploid lines. These differences between the mean values of the two ploidy levels were significant for most traits.

Both hexaploid and octoploid triticales displayed considerable genetic variation for all traits (Table 2). Significant genotype × environment interaction variances were found at both ploidy levels for most traits. However, the interaction and error variances were relatively small as compared to the genotypic variances, resulting

Table 2. Mean values, estimates of variance components (Var. cp.), and heritabilities (h^2) in primary hexaploid and octoploid triticales tested in four environments and significance levels of the differences between the means of the two ploidy levels for several agronomic traits

Ploidy level	Parameter	*df*	Days to heading	Plant height (cm)	Grain yield (g/m^2)	Tillers per m^2	Spikelets per spike	Kernels per spike	1000-kernel weight (g)	Test weight (kg/hl)
6 ×	Mean		46.6	127.4	427.3	349.8	26.1	32.3	47.9	52.3
	Var. cp.									
	Genotype (G)	34	10.04**	202.9**	23,867**	1,081**	4.16**	55.01**	26.61**	21.35**
	G × Environment	102	0.82**	13.7**	6,009**	912**	1.08**	24.80**	5.71**	3.55**
	Error	269	0.46	38.9	2,496	2,950	1.14	22.69	7.16	2.96
	h^2		0.98	0.97	0.93	0.70	0.92	0.87	0.93	0.95
8 ×	Mean		53.8	97.5	201.6	361.6	24.3	23.6	36.7	56.6
	Var. cp.									
	Genotype (G)	19	5.95**	106.5**	6,482**	1,162**	5.79**	35.89**	26.98**	7.90**
	G × Environment	57	1.21**	13.7**	1,707**	−277	1.23**	4.02	2.53**	3.06**
	Error	148	0.45	15.4	866	4,702	1.07	34.48	3.02	1.85
	h^2		0.95	0.96	0.93	0.78	0.94	0.90	0.97	0.90
Significance level 6x vs. 8 ×	Mean		*	**	**	*		**	**	*

*,** Significant in sequentially rejective Bonferroni procedure at $P = 0.05$ and 0.01, respectively

Table 3. REML estimates of variance components and their standard errors in primary hexaploid and octoploid triticales tested in four environments and variation of parental main effects in percent of the total genotypic variation for several agronomic traits

Ploidy level	Source	*df*	Days to heading	Plant height (cm)	Grain yield ($\times 10^{-1}$)	Tillers per m^2 ($\times 10^{-1}$)	Spikelets per spike	Kernels per spike	1000-kernel weight (g)	Test weight (kg/hl)
6×	Wheat (W)	4	2.74±2.14	167±123	195±196	0±12	1.92±1.55	0.0± 2.3	11.7± 9.8	5.7±5.1
	Rye (R)	11	6.69±3.15	46± 26	2,010±963	110±60	1.76±1.13	46.0±24.0	10.2± 5.9	11.7±6.4
	W×R	19	1.26±0.46	25± 9	296±127	17±18	1.38±0.50	10.2± 4.4	6.4± 2.4	6.1±2.1
	$\frac{W+R}{W+R+W\times R}\times 100$		88	90	88	86	73	82	77	74
8×	Wheat[a]	1	2.56±3.96	27± 51	0± 61	7±18	0.00±0.56	0.0± 4.9	0.0± 5.3	0.0±0.7
	Rye	11	4.49±2.48	34± 40	364±281	99±59	3.22±2.40	10.7±15.5	0.0±13.3	7.3±4.5
	W×R	7	1.44±0.91	67± 37	322±193	8±28	2.68±1.57	26.7±15.7	34.9±17.8	3.0±1.9
	$\frac{W+R}{W+R+W\times R}\times 100$		83	47	53	93	55	29	0	71

[a] Data based on two related cultivars only

Table 4. Mean grain yields (g/m^2, tested in four environments) of primary hexaploid and octoploid triticales and means over their respective wheat and rye parents

Rye inbred line	Hexaploid triticales						Octoploid triticales		
	Durum wheat line					Mean	Bread wheat cv		Mean
	D4	D8	D9	D30	D40		Jubilar	Götz	
L 18	–	323	403	–	361	341	–	125	125
L 35	403	–	–	–	–	486	292	286	289
L 60	115	–	–	199	–	189	68	149	108
L 68	–	182	129	–	220	155	150	121	136
L 70	437	–	–	580	602	545	130	165	147
L145	338	467	373	494	–	430	318	–	318
L150	436	–	–	596	678	576	282	192	237
L155	211	–	–	–	–	294	190	58	124
L161	198	–	–	411	391	339	271	285	278
L185	519	–	–	428	402	455	167	–	167
L271	450	463	584	487	–	508	–	287	287
L301	499	449	612	608	711	616	182	315	248
Mean	328	418	421	429	459	411	205	206	205

in very high heritability estimates (around 0.9) for all traits, with the exception of tillers per m^2.

Partitioning the genotypic variance into the parental wheat and rye components and their interaction provided estimates of variance components with very high standard errors (Table 3). A high contribution of the rye parents to the genetic variation of hexaploid and octoploid triticales was observed for most traits. The wheat parent was the more important source of variation only for plant height in the hexaploids, whereas spikelets per spike and thousand kernel weight were equally affected by both parental genera.

The two zero REML estimates in the parental wheat lines of the hexaploid triticales (Table 3) were in fact close to zero. In some cases negative values or zero (e.g., thousand kernel weight) for wheat lines in octoploid triticales had to be expected for such a low number of degrees of freedom and were included for completeness only.

The hexaploid triticales had 70%–90% of the genotypic variation explained by variation of the main effects of the parental lines (Table 3). In the octoploid materials, however, parental interaction effects were large relative to the main effects for plant height, grain yield, spikelets per spike, kernels per spike, and thousand kernel weight. The amount of interaction variance for these five characters appeared to be higher in the octoploid than in the hexaploid triticales. The variation of the parental main effects in the octoploids constituted a considerably lower fraction of the total genotypic variation and covered a wider range (0–90%) than in the hexaploid triticales.

Examination of the triticale mean grain yields averaged over their respective parents (Table 4) confirmed the

Table 5. Estimated coefficients of phenotypic correlation between agronomic traits in primary hexaploid and octoploid triticales (35 and 20 entries, respectively) tested in four environments

Trait	Ploidy level	Plant height	Grain yield	Tillers per m^2	Spikelets per spike	Kernels per spike	1000-kernel weight	Test weight[a]
Days to heading	6 ×	−0.31	−0.26	0.22	−0.03	−0.47	0.10	0.16
	8 ×	−0.54	−0.51	0.18	−0.29	−0.29	−0.58	−0.10
Plant height	6 ×		0.20	−0.41	0.40	0.53*	0.34	−0.13
	8 ×		0.68*	−0.21	0.48	0.49	0.70*	0.03
Grain yield	6 ×			0.03	0.40	0.85**	0.73**	0.71**
	8 ×			−0.11	0.59	0.80**	0.66*	0.42
Tillers per m^2	6 ×				−0.05	−0.23	−0.27	−0.38
	8 ×				−0.51	−0.32	−0.34	−0.05
Spikelets per spike	6 ×					0.47	0.27	0.15
	8 ×					0.68*	0.26	0.11
Kernels per spike	6 ×						0.61**	0.38
	8 ×						0.35	0.24
1000-kernel weight	6 ×							0.57**
	8 ×							0.46

[a] 20% missing values in the octoploid triticales

*,** Significant in sequentially rejective Bonferroni procedure at $P = 0.05$ and 0.01, respectively

previous observation that the rye parents contributed greatly to determining yield. The coefficient of phenotypic correlation between the hexaploid and octoploid triticales having the same rye parent was only moderate ($r = 0.55$ ns).

Character correlations were very similar in hexaploid and octoploid triticales except for the correlations of days to heading with kernel weight, which were significantly different in the sequential Bonferroni test (Table 5). Grain yield exhibited moderate to strong associations with all yield-related traits except tillers per m^2. Yield was also positively associated with plant height and negatively with days to heading. Productive tillers per m^2 was not related to yield and negatively associated with plant height, spikelets per spike, kernels per spike, and thousand kernel weight.

Discussion

The generally superior performance of the hexaploid triticales as compared to the octoploids agrees with previous observations (Oettler 1986). Tillering ability and fertility (number of kernels per spike) were relatively low at both ploidy levels and appear to be the main factors limiting yield in primary triticales.

The substantial genetic variation at the hexaploid and octoploid level for all of the characters investigated offers sufficient scope for selection. In addition, the moderate positive correlation for yield and test weight facilitates selection of high-yielding lines with improved grain filling. The high heritability estimates for all traits except tillering indicate that selection should be effective. High variability in triticales as compared to other cereals has also been observed in secondary forms for characters such as fertility, spike length, and number of tillers (Salmon and Larter 1978).

The estimated wheat, rye and, wheat × rye interaction variance components, although possessing high standard errors, indicate that parental main effects are the dominating source of genetic variation in primary triticales for most traits. Oettler (1986) and Lelley and Gimbel (1989) found the wheat parent to be the main source of genetic variation in primary triticales. In their analyses, however, the data were pooled over ploidy levels or over different wheat species (*T. durum* and *T. turgidum*) within the hexaploid triticales. The resulting variance estimates, therefore, were overestimated in comparison to variance parameters computed separately for the triticales produced from *T. durum* and *T. aestivum* as in the present investigation. In our materials the highest amount of variation was caused by the rye parents for nearly all traits. In the octoploid lines this may be due to the close genetic relatedness of the two wheats, 'Jubilar' and 'Götz'. But even in the hexaploid triticales the rye inbred lines explained more of the variation than the wheats except for plant height, an observation previously made by Oettler (1986), for spikelets per spike, and thousand kernel weight. These findings agree well with observations of Wandelt (1988). This author crossed durum and bread wheats with a large number of random gametes from rye populations according to a hierarchical design and calculated wheat and rye 'substitution effects'. He concluded that characters connected with fertility were mainly influenced by the rye genotype, whereas in characters of plant morphology the wheat parent was predominant. However, the variation caused by the rye parents was confounded with parental interaction effects in that hierarchical approach.

For characters of plant growth and development the higher number of chromosomes and the cytoplasm contributed by the wheat parent seem to dominate the manifestation of the characters in the amphidiploid, as has been suggested previously (Oettler 1986). On the other hand, fertility traits in triticales appear to suffer from general or specific incompatibility of some rye genomes with the genome and/or cytoplasm of wheat.

Lelley and Gimbel (1989) found interaction effects between the rye and wheat parents to be very important for the expression of tillering, fertility, and thousand kernel weight in space-planted materials. However, our data on hexaploid materials shows that interaction effects caused only about 20% of the genetic variation.

The observed trait correlations were generally in good accordance with earlier results (Oettler 1986). From the breeder's point of view associations were favorable except for some relationships with tillering ability. In secondary breeding materials tillering was not correlated with kernels per spike and thousand kernel weight, but was positively associated with yield (Sawant and Rawat 1979; Sandha et al. 1980) in the same way as in well-established crops. The association of grain yield with earliness, plant height, and test weight indicates the importance of vigor on yielding ability in primary triticales.

The positive correlation between kernels per spike and thousand kernel weight is a specific phenomenon of primary triticales (Oettler et al. 1988). Inadequate seed set, low grain weight, and poor grain filling of some primary triticales, therefore, seem to be affected by the same general genetic disorder. For secondary triticales a loose, non-existent, or even negative relationship between kernels per spike and thousand kernel weight has been observed (Carrillo et al. 1983; Sandha et al. 1980; Sawant and Rawat 1979, respectively). This indicates that favorable effects can be accumulated by selection, resulting in a normal compensating relationship between these yield components.

In conclusion, since parental main effects were the most important source of genetic variation, the gene pools of wheat and rye can profitably be exploited for the production of primary hexaploid and octoploid triticales. The dominating effect and the high amount of variation directly attributable to the rye parent on characters connected with fertility offers possibilities to synthesize high performing triticales by using pre-selected rye inbred lines that have shown high performance in previous crosses. High heritabilities and the absence of detrimental character correlations will facilitate the selection of superior primary triticales. It remains to be investigated to what extent such genotypes will enable the development of improved secondary forms.

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