Theor Appl Genet (1985) 70:422–426

Genetic interactions between wheat and rye genomes in triticale

1. Cytological results

C. Jung*, T. Lelley and G. Röbbelen
Institut für Pflanzenbau und Pflanzenzüchtung, Universität Göttingen, Von-Siebold-Strasse 8, D-3400 Göttingen, Federal Republic of Germany

Received December 12, 1984; Accepted February 4, 1985
Communicated by F. Mechelke

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 and the triticale derivatives were crossed in all possible combinations within each species group. Chiasma and univalent frequency of parents and hybrids were determined. The primary triticale lines had more univalents and less chiasmata per pollen mother cell than the corresponding wheat and rye parents together. The parental wheat F_1 exhibited negative heterosis for chiasma frequency whereas all rye hybrids had much higher chiasma frequencies than their inbred parents. Triticale F_1s generally showed lower chiasma frequencies and more univalents than their parents, but the degree of pairing failure was dependent upon which of the parental species within the triticale, wheat or rye, was in the heterozygous state. F_1s with heterozygous wheat genome only showed the least reduction in chiasma number (presumably caused by gene actions within the wheat genome), while F_1s with heterozygous rye genome showed high reduction in chiasma frequency and an increase in pairing failure (induced by negative interactions between the heterozygous rye and the wheat genome in triticale). A high correlation was found between the frequency of undisturbed pollen mother cells and the frequency of aneuploids in the subsequent generation. A higher number of aneuploids occurred in those populations which were heterozygous for the rye genome.

Key words: Triticale – Diallel – Chiasma frequency – Aneuploidy – Genetic interaction

Introduction

Meiotic irregularities are characteristic features of triticale (Müntzing 1979; Scoles and Kaltsikes 1974; Gupta and Priyadarshan 1982). Müntzing (1939) first reported that compared to the parental lines, F_1 hybrids of triticale show increased meiotic instability. This finding was later confirmed by several authors (Merker 1971; Sapra and Heyne 1973; Salmon et al. 1977; Pohler et al. 1978). After introducing the Giemsa technique for differential chromosome staining, it became evident that pairing failure in triticale almost exclusively occurs within the rye genome (Thomas and Kaltsikes 1974; Lelley 1975). Chromosomes of the self-pollinating tetraploid wheat and the open-pollinating cultivated rye regularly form bivalents. Following inbreeding, chiasma frequency in diploid rye decreases; obviously the extent of the reduction depends on the actual genotype (Lamm 1936; Müntzing and Akdik 1948; Rees 1955; Lelley 1978a).

In the present report two major possible causes will be investigated which may lead to pairing failure in triticale: (1) inbreeding depression of the rye genome in the predominantly self-pollinating triticale and (2) genetic interactions between the wheat and rye genomes within triticale.

The effect of inbreeding and those of interactions can only be separated if the triticale genotypes studied have been produced by using genetically defined homozygous parental wheat and rye lines (Lelley 1978b). In the last seven years a large number of pure lines of wheat and rye were used in our laboratory to create new primary triticale lines. To distinguish these from conventionally produced triticales, the designation 'thd', i.e. triticale hexaploid defined, will be used in this study. In such lines the diploid parental genotypes and the corresponding wheat and rye components of the amphidiploid triticale are genetically identical. A direct comparison of the cytological behaviour of the wheat and rye parents and their counterparts in the triticale is feasible if Giemsa staining is applied to distinguish the

---

* Present address: Institut für Angewandte Genetik, Universität Hannover, Herrenhäuser Strasse 2, D-3000 Hannover 21, Federal Republic of Germany

wheat from the rye chromosomes. The expected chiasma frequency in the triticale genotype is then the sum of that found in the two parents. Furthermore, such triticale material enables the production of hybrid combinations that are heterozygous either in their wheat or in their rye component (e.g. $W_1W_1R_1R_1 \times W_1W_1R_2R_2 = W_1W_1R_1R_2$).

The application of the Giemsa technique on this kind of F_1 combinations gave us the first indications that heterozygosity of the rye genome causes a reduction in chiasma frequency of the rye chromosomes in triticale. This result was in sharp contrast to the expectations based on the hybrid performance of the pure parental genotypes of diploid rye (Lelley 1981).

In the present study the results obtained from a triticale diallel of six thd lines, including two wheat and three rye genotypes, are described. These document that interaction between the wheat and the rye components of triticale is a major cause for reduced chiasma frequency and that a correlated increase in the number of unpaired chromosomes is closely related to the frequency of aneuploid progeny in triticale.

Materials and methods

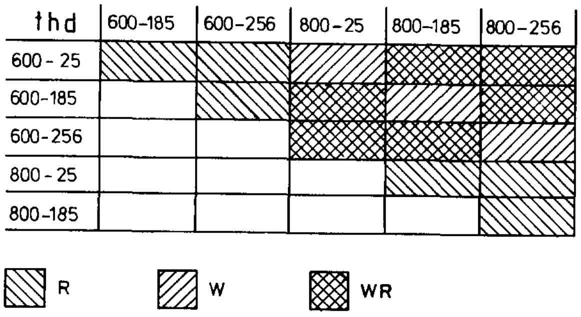
Two *T. durum* genotypes, Nos. D600 and D800, and three inbred lines of *S. cereale,* Nos. L25, L185 and L256, were used to produce six primary hexaploid triticale (thd) lines according to the method suggested by Lelley (1978). Crosses were made between these six thd lines as well as between the two wheat and the three rye parents in all possible intraspecific combinations except reciprocals. The resulting 15 different triticale hybrids could be arranged in three groups:

- hybrids designated with 'R' are heterozygous only for the rye genome,
- hybrids designated with 'W' are heterozygous only for the wheat genome,
- hybrids designated with 'WR' are heterozygous for both genomes (Fig. 1).

All triticale plants were cytologically examined by applying the conventional Feulgen technique. For the present study only euploid plants were used. After germination, the plants were kept in the greenhouse for about three weeks and then planted in the field in single rows. The parental rye genotypes were of winter type; they required six weeks of vernalization before planting.

Chiasma frequency and number of univalents per pollen mother cells were studied in metaphase I by aceto carmine squash preparations of 30–50 pollen mother cells per plant and at least three plants per genotype. The percentage of pollen mother cells without univalents, i.e. undisturbed cells, was calculated. For each thd line, the expected chiasma frequency was determined as the sum of the chiasma frequencies of their corresponding wheat and rye parents. The difference between expected and observed chiasma frequency is expressed as a percentage.

Heterosis was computed as percent difference between the mean performance of the parents and the F_1.



thd	600-185	600-256	800-25	800-185	800-256
600 - 25	▧	▧	▨	▩	▩
600-185		▧	▩	▨	▩
600-256			▩	▩	▨
800 - 25				▧	▧
800-185					▧

▧ R ▨ W ▩ WR

Fig. 1. Diallel combination of six lines of triticale indicating the presence of heterozygosity in the component rye (R), wheat (W) and both (WR) genomes

Results

Univalents were not observed in the pollen mother cells of the wheat parents. However, a considerable pairing failure occurred in the rye inbreds due to reduced chiasma frequency as a typical consequence of inbreeding in rye (Table 1). While in the wheat F_1 chiasma frequency was reduced, a highly significant increase of this trait was found in the three rye F_1s (Table 2).

Chiasma frequencies of the thd lines were in all cases lower than the expected values (Table 1). The highest reduction was found, in those triticale lines which contained inbred line L185 as the rye component. The disturbances at metaphase I expressed as univalents per pollen mother cells were also much higher in the thd lines than in the parental species (Table 1).

All triticale F_1s showed a highly significant negative heterosis with respect to chiasma frequency in com-

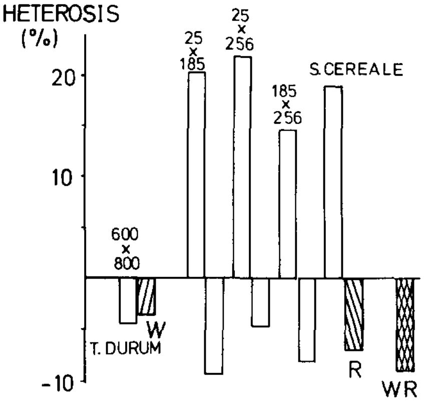


Fig. 2. Heterosis for chiasma frequency of the three groups of crosses within triticale, heterozygous for 'W', 'R', and 'WR' respectively, and of the parental F_1s within *T. durum* and *S. cereale.* The *left column* shows heterosis in the parental, the *right* heterosis in the corresponding triticale F_1

Table 1. Chiasma frequency, univalency and aneuploidy of the parental *T. durum, S. cereale* and thd lines

Genotype	Chiasma frequency			Univalents per pollen mother cells	Undisturbed pollen mother cells (%)	Aneuploidy (%)
	Observed	Expected	% difference between observed and expected			
D600	27.1	–	–	0.0	100	–
D800	27.1	–	–	0.0	100	–
L25	10.8	–	–	0.2	90.2	–
L185	12.1	–	–	0.07	96.3	–
L256	11.8	–	–	0.2	92.2	–
600-25	36.7	37.9	– 3.1	0.5	78.8	11.0
600-185	34.2	39.2	–12.8	1.7	44.2	15.6
600-256	36.1	38.9	– 7.1	0.7	71.6	9.9
800-25	37.2	37.8	– 1.6	0.6	74.6	6.7
800-185	35.7	39.1	– 8.7	0.8	68.5	13.4
800-256	35.7	38.8	– 8.0	0.7	75.1	4.9
thd $\bar{x}$	35.9	38.6	– 6.9	0.8		10.3

Table 2. Chiasma frequency, univalency and aneuploidy of the *T. durum, S. cereale* and thd hybrids

Genotype	Chiasma frequency	Univalents per pollen mother cells	Undisturbed pollen mother cells (%)	Heterosis in F_1	Aneuploidy (%) in F_2
D600×D800	26.0	0.00	100	–4.1**	
L25 ×L185	13.7	0.00	100	20.3**	
L25 ×L256	13.8	0.03	98.7	22.1**	
L185 ×L256	13.6	0.04	97.8	14.4**	
600-25 ×600-185	32.0	5.4	1.9	– 9.8**	44.7
600-25 ×600-256	34.8	2.1	37.7	– 4.6**	35.1
600-25 ×800-25	35.1	1.6	46.7	– 5.0**	20.7
600-25 ×800-185	31.8	3.8	18.2	–12.2**	37.5
600-25 ×800-256	33.1	3.5	21.1	– 8.5**	8.6
600-185×600-256	32.7	3.9	7.3	– 7.2**	41.4
600-185×800-25	32.7	3.2	16.4	– 8.3**	37.5
600-185×800-185	33.9	1.6	52.0	– 2.9**	10.5
600-185×800-256	31.0	4.8	6.6	–11.2**	39.3
600-256×800-25	34.7	1.6	41.9	– 5.3**	20.0
600-256×800-125	32.4	3.1	18.7	– 9.8**	24.6
600-256×800-256	35.0	1.3	55.1	– 2.5**	6.7
800-25 ×800-185	33.4	3.1	16.2	– 8.4**	39.7
800-25 ×800-256	35.0	1.4	48.2	– 3.9**	7.1
800-185×800-256	33.0	3.3	13.0	– 7.6**	29.8
R	32.8	3.2	20.7	– 6.9**	33.6
W	35.4	1.5	51.3	– 3.5**	12.6
WR	32.8	3.6	20.5	– 9.2**	27.7

** 1%

parison to the mid parent value (Table 2). The least reduction occurred in those genotypes which were homozygous for the rye and heterozygous for the wheat genomes ('W', Fig. 2). The 'W' genotypes also had the lowest number of univalents and the lowest aneuploid frequency in their progeny. The highest reduction of chiasma frequency and the highest increase of pairing failure was found in the 'R' and 'WR' genotypes the difference between these two groups being negligible. The F_1 hybrids of the corresponding parental rye inbreds showed high positive heterosis (Fig. 2).

The relationship between meiotic disturbances and the frequency of aneuploids in the cross progeny of the thd lines was also studied. Generally aneuploid fre-

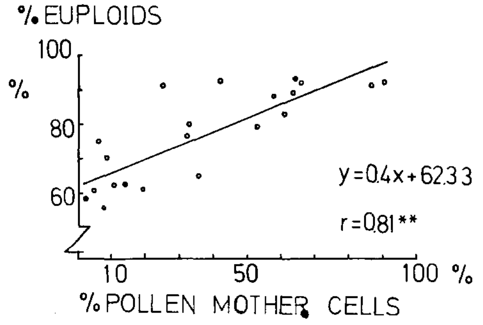


Fig. 3. Regression curve between percent undisturbed pollen mother cells of the thd lines and F_1s and percent euploids in the subsequent generation

quency was lowest in the parents (10.3%) and increased to 26.9% in the F_2 (Table 2). A high positive correlation was found ($r=0.81^{**}$) between percent pollen mother cells without univalents of the F_1s and percent euploid plants in the progeny (Fig. 3).

Discussion

Data on the meiotic behaviour of intervarietal hybrids of the autogamous tetraploid wheat are not readily available from the literature. For interspecific hybrids of tetraploid wheats Thompson and Robertson (1930) reported a slight increase of meiotic irregularities, but in most cases the authors doubted "whether it was great enough to be significant". In the present work the hybrid of the two *T. durum* lines showed on the average a 4% decrease of chiasma frequency which, however, did not lead to the occurrence of univalents, i.e. to disturbed gametes (Table 2).

On the other hand, the disruption of the normal outbreeding habit of *S. cereale* has often been reported to have a negative effect on the chiasma frequency (Lamm 1936, for further discussion, see Riley and Law 1965). Similarly in this work the inbred lines of rye showed significantly lower chiasma numbers and more univalents than their F_1 hybrids (Tables 1 and 2).

In both wheat and rye, dominance and nonallelic gene effects have been suggested to be involved in the control of chromosome pairing (Rees and Thompson 1956; Watanabe 1962). Triticale F_1s often had lower chiasma frequencies than their parents (e.g. Müntzing 1939; Merker 1971; Pohler et al. 1978). But even after several generations of inbreeding and selection, Tsuchiya and Larter (1969) reported an average of 11.6% aneuploids in bulk seeds.

Based on the above description of the meiotic behaviour of hybrids of the parental species, one might expect the wheat genome to be responsible for a lowered chiasma frequency and for univalency in triticale F_1s. Pairing failure in triticale, however, was in most cases found to be restricted to the rye genome (Lelley 1975; Pohler et al. 1978). Triticale genotypes which were heterozygous only for the rye genome also had significantly lower chiasma frequencies than the parental lines with both genomes wheat and rye homozygous (Lelley 1981).

Chromosome pairing of the thd lines, as shown in this study, is generally more disturbed and chiasma frequencies are lower than would be expected from the performance of the parental genotypes. The reasons for this disorder may either be intergenomic gene interactions or interactions between genome and plasmon of the two different wheat genotypes involved. Our present data cannot rule out the possibility of such plasmon/genom interactions. But the very different behaviour of the 'W', 'R' and 'WR' genotypes with a similar tendency in both cytoplasms strongly suggests that interactions between the wheat and the rye genomes, rather than differences in the wheat cytoplasms, are responsible for the unexpected negative heterosis in the 'R' and 'WR' genotypes.

In the 'W' genotypes with heterozygosity restricted to the wheat genome, pairing is only slightly reduced compared to the parental thd lines. The relative performance of the F_1s is almost the same in the parental wheat and in the 'W' hybrids, viz. –4.1% and –3.5%, respectively. Apparently in this case the same gene action which regulates chiasma frequency in the parental wheat hybrid is responsible for the expression of the trait in triticale without any interference with the rye genome.

A totally different picture arises from the behaviour of the triticale F_1s with heterozygous rye genome, 'R' and 'WR', as compared with their parental rye F_1s. The data suggest a strong negative intergenomic interaction between the heterozygous rye genome and the wheat genome in triticale, no matter whether the latter is in homozygous or heterozygous condition. These genotypes showed the lowest average chiasma frequency of 32.8 in both 'R' and 'WR', and the lowest percentage of undisturbed pollen mother cells of 20.7 and 20.5, respectively. The fact that reduction in chiasma number is the same in the 'R' and 'WR' combinations indicates that heterozygosity in the wheat genome does not have any further effect on the behaviour of the rye chromosomes. Consequently, in 'W' hybrids pairing reduction and aneuploidy occurs in the heterozygous wheat genome.

It is to be expected that a reduction of chiasma frequency below a certain level, i.e. when univalents occur regularly, will have some consequences on the frequency of aneuploid progeny. Accordingly, in the present material plants with the lowest aneuploid frequency of 10.3 and 12.6% were obtained in the parental thd lines and in the 'W' F_1s, respectively (Tables 1 and 2). Several authors have claimed that in triticale no correlation exists between chiasma frequency and seed set (Merker 1971; Hsam and Larter 1974; Pohler et al.

1978). It is striking that in spite of having much reduced chromosome pairing, the F_1s of the present experiment showed a positive heterosis for the number of kernels per ear (Jung and Lelley 1985). In this sense our data are in good agreement with those previously reported. However, the cytological study revealed that among the seeds set on the above mentioned F_1 plants, the frequency of aneuploids was greatly increased (Table 2). A close correlation was found between percent pollen mother cells with only bivalents and percent euploid progeny (Fig. 3). Plants of the next generation developing from aneuploid seeds had on the average significantly less kernels per ear, a lower thousand kernel weight and a reduced seed quality if compared to the euploid plants (Jung and Lelley 1985). Thus the adverse effect of the reduced chromosome pairing in the F_1 hybrids is realized on the expression of morphological and yield characters one generation later.

The experiment also demonstrates that clear genetic differences exist between rye genotypes concerning their ability to combine with wheat in triticale. Inbred line L185 showed the strongest negative interactions with respect to chiasma frequency not only in the two thd lines but also in F_1s containing this particular rye genotype. Excluding such genotypes before starting crossing programmes might improve the chances to select cytologically more stable triticale lines (Lelley 1983).

Acknowledgements. The authors wish to thank Prof. Dr. H. H. Geiger and Prof. Dr. H. Hänsel for providing the rye and wheat strains.

References

Gupta PK, Priyadarshan PM (1982) Triticale: present status and future prospects. Adv Genet 21:255–334

Hsam SLK, Larter EN (1974) Effects of inbreeding on triticale selected for two levels of fertility and chiasma frequency. Crop Sci 14:213–215

Jung C, Lelley T (1985) Genetic interactions between wheat and rye genomes in triticale. 2. Morphological and yield characters. Theor Appl Genet 70:427–432

Lamm R (1936) Cytological studies on inbred rye. Hereditas 22:217–240

Lelley T (1975) Identification of univalents and rod bivalents in triticale with Giemsa. Z Pflanzenzücht 75:252–256

Lelley T (1978a) Genetic control of chiasma frequency and distribution in rye *Secale cereale.* Can J Genet Cytol 20: 471–474

Lelley T (1978b) Specific interaction for meiotic regulation of wheat and rye in triticale, consequences for triticale breeding. In: Ramanujam S (ed) Proc 5th Int Wheat Genet Symp. Indian Soc Genet Plant Breed, New Delhi, pp 1213–1217

Lelley T (1981) Meiotic behaviour of the rye genome in triticale. In: Induced variability in plant breeding. EUCARPIA Wageningen, Holland, pp 101–105

Lelley T (1983) Increased selection efficiency of triticale through restriction of recombination to one parental genome. In: Proc 6th Int Wheat Genet Symp, Kyoto, pp 919–924

Merker A (1971) Cytogenetic investigations in hexaploid triticale. 1. meiosis, aneuploidy and fertility. Hereditas 68:281–290

Müntzing A (1939) Studies on the properties and the way of production of rye-wheat amphidiploids. Hereditas 25: 387–430

Müntzing A (1979) Triticale results and problems. Adv Plant Breed Suppl, Z Pflanzenzücht 10, 103 pp

Müntzing A, Akdik S (1948) Cytological disturbances in the first inbred generation of rye. Hereditas 34:485–509

Pohler W, Kistner G, Kison HU, Szigat G (1978) Meioseuntersuchungen an Triticale. 5. Meioseverhalten, Pollenvitalität und Fertilität von Triticale-F_1-Bastarden und deren Eltern. Biol Zentralbl 97:453–470

Rees H (1955) Heterosis in chromosome behaviour. Proc R Soc London, Ser B 144:150–159

Rees H, Thompson JB (1956) Genotypic control of chromosome behaviour in rye. 3. Chiasma frequency in homozygotes and heterozygotes. Heredity 10:409–424

Riley R, Law CN (1965) Genetic variation in chromosome pairing. Adv Genet 13:57–114

Salmon DF, Larter EN, Gustafson JP (1977) F_1 evaluation of yield potential in hexaploid triticale. Crop Sci 17:933–934

Sapra VT, Heyne EG (1973) Meiosis and pollen viability in hexaploid triticale. Crop Sci 13:301–302

Scoles GJ, Kaltsikes PJ (1974) The cytology and cytogenetics of triticale. Z Pflanzenzücht 73:13–43

Thomas JB, Kaltsikes PJ (1974) A possible effect of heterochromatin on chromosome pairing. Proc Natl Acad Sci USA 71:2787–2790

Thompson W, Robertson HT (1930) Cytological irregularities between species of wheat with the same chromosome number. Cytologia 1:252–262

Tsuchiya T, Larter EN (1969) Chromosome stability in some hexaploid strains of triticale. Crop Sci 9:235–236

Watanabe Y (1962) Meiotic irregularities in intervarietal hybrids of common wheat. Wheat Inf Serv 14:5–7