Euphytica 32 (1983) 593–600

CROSSABILITY AND EMBRYO DEVELOPMENT IN WHEAT-RYE HYBRIDS

GITTA OETTLER

Landessaatzuchtanstalt, Universität Hohenheim, Postfach 700562, D-7000 Stuttgart 70,
Fed. Rep. Germany

Received 13 September 1982

INDEX WORDS

Triticum aestivum, bread wheat, *Triticum durum,* durum wheat, *Secale cereale,* inbred lines, intergeneric crossability, embryo development.

SUMMARY

Crossability and embryo development were studied in the crosses of one *Triticum aestivum* and three *T. durum* genotypes with nineteen rye inbred lines. Parental wheat and rye genotypes exerted a significant influence on the characters seed set, number of seeds containing embryos and viable plantlets obtained from embryo culture. It was established that the common winter wheat cultivar Götz is of intermediate crossability. The rye inbred lines varied substantially in their capacity to fertilize several wheat genotypes. Interactions between wheats of different crossability classes and their seed set with rye lines were detected. Significant correlations were obtained between seed set and viable plantlets recovered in vitro.

INTRODUCTION

The crossability between wheat and rye is known to be genetically controlled. Various investigations provide evidence that the A, B and D genome of wheat as well as the R genome of rye carry crossability gene(s) (LEIN, 1943; RILEY & CHAPMAN, 1967; KROLOW, 1970; TANNER & FALK, 1981; LELLEY, 1982; OETTLER, 1982). The level of crossability in common wheat with rye as pollinator has generally been classified by many authors (TOZU, 1966; SNAPE et al., 1979; JALANI & MOSS, 1981; THOMAS et al., 1981) as follows:

Crossability	Seed set (%)
low	0– 10
intermediate	10– 50
high	50–100

European common wheats predominantly belong to the first category. Insufficient information exists as to the degree of crossability of the rye parent. Experimental evidence from spring and winter rye materials indicates considerable differences between inbred lines in their ability to pollinate various wheat genotypes (TAIRA et al., 1978; LELLEY & TAIRA, 1979; TANNER & FALK, 1981; OETTLER, 1982).

The development of fertilized ovules in wheat-rye hybrids is strongly influenced by the ploidy level of the wheat parent. In tetraploid wheat-rye crosses embryo culture technique is a prerequisite for the production of viable hybrid plantlets (KROLOW, 1970; MOSS, 1970; MARAIS & PIENAAR, 1977), while in hexaploid wheat-rye crosses the ovules generally develop in vivo.

The present study was conducted with one hexaploid and three tetraploid winter wheats and a set of nineteen winter rye inbred lines. It provides data on the influence of parental genotypes on seed set, embryo viability and development in crosses between wheats belonging to different crossability classes and rye inbred lines tracing back to various European source populations. Embryo culture technique was used throughout.

MATERIALS AND METHODS

The following parental materials were used:

1. One cultivar of hexaploid winter wheat (*Triticum aestivum* L.): Götz.
2. Three lines of tetraploid winter wheat (*Triticum durum* L.): D 30, D 40 and D 50 from the Hohenheim durum-collection.
3. Nineteen homozygous inbred lines of winter rye (*Secale cereale* L.) from the Hohenheim rye-collection.

Of the 76 possible cross combinations 57 were produced and analyzed.

Plants were grown and crossed under controlled conditions in the glasshouse with a day/night cycle of 16/8 hours, day/night temperatures of 22°/16°C and a relative humidity of 70%. Spikes of the wheat parent were emasculated prior to anthesis and pollinated immediately as suggested by THOMAS & ANDERSON (1978), using the approach method (CURTIS & CROY, 1958). For the common wheat 25–30 heads and for the durums 15–20 were emasculated.

After pollination female plants were sprayed with a solution of gibberellic acid (7.5 mg/l) for several days to enhance seed setting and embryo development. At 18 to 20 days after pollination embryos were collected for culture on a modified medium proposed by JENSEN (1976). Culture vials were incubated in darkness at 18–20°C until root and coleoptile growth was initiated, and then transferred to a growth cabinet with a 24 hour light regime at 20–25°C. Plantlets showing good development were transplanted into pots containing a mixture of soil, vermiculite and peat moss (2:1:1).

For each cross combination the following data were determined: number of florets pollinated, seed set (crossability), proportion of seeds containing culturable embryos, and viable plantlets recovered from in vitro technique. Seeds with globular shaped embryonic structures smaller than approximately 0.4 mm were not regarded as being culturable.

All percentage values were corrected, weighted and transformed to arcsin according to BARTLETT (1947) and SNEDECOR & COCHRAN (1967), and subjected to analyses of variance for unbalanced data as given by VAN BAAREN (1973) and modified by UTZ (unpubl.). The means of parental genotypes were obtained as least squares estimates, corrected for missing values. Further, correlation analyses were performed on the arcsin values and tests for homogeneity of correlation coefficients were conducted.

Table 1. Number of florets pollinated for crossing one common wheat ('Götz') and three durum wheats (D 30, D 40, D 50) with nineteen rye inbred lines as pollinators.

Rye parent (male)	Wheat parent (female)			
	Götz	D 30	D 40	D 50
L 18	654	452	434	242
L 25	842	–	–	–
L 35	734	–	–	–
L 37	718	440	446	154
L 60	812	406	416	152
L 68	688	368	462	152
L 70	590	364	444	140
L 138	623	338	384	94
L 145	740	402	462	158
L 150	690	353	438	146
L 155	698	–	–	–
L 161	671	420	396	128
L 170	692	–	–	–
L 184	608	293	358	110
L 185	–	414	442	150
L 188	562	–	–	–
L 271	772	346	390	106
L 281	652	–	–	–
L 301	784	352	438	240

RESULTS

Wheat-rye crossability. The number of florets pollinated for producing the individual cross combinations is shown in Table 1. The low number of florets for the female D 50 is a result of unfavourable plant development in the glasshouse. Only 10 heads or less were available for emasculation.

Seed set for the wheat genotypes of the present study, supplemented by data of the cultivars 'Jubilar' and 'Kormoran' from an earlier investigation (OETTLER, 1982), is presented in Table 2. The overall range lies between 0.0% and 36.6%. With regard to the female parent two distinct classes can be recognized. Combinations with 'Jubilar' and 'Kormoran' have a seed set below 10%, while for 'Götz' and the durum combinations it lies between 10% and 50%.

Mean values of seed set for each parental genotype are exhibited in Table 3. The range of variation among 'Götz' and the three durum wheats is small and does not reflect any difference due to ploidy level. The variation among rye lines is high and ranged from 0.0% to 30.7%. Significant differences for both parental genotypes were revealed by the analysis of variance (Table 4). Interactions between wheat and rye parents for seed set are indicated in Table 2.

Correlations between wheat parents for arcsin seed set are given in Table 5. The correlation coefficients range from a non-significant negative value of –0.19 to a highly significant positive value of 0.74. 'Kormoran' does not correlate with any tetraploid wheat and D 50 shows no correlation at all. 'Jubilar' and 'Götz' correlate equally well with D 30 and D 40, and all three *T. aestivum*.

Table 2. Seed set (%) of three common wheats ('Jubilar', 'Kormoran', 'Götz') and three durum wheats (D 30, D 40, D 50) pollinated with twenty rye inbred lines.

Rye parent (male)	Wheat parent (female)					
	Jubilar[1]	Kormoran[1]	Götz	D 30	D 40	D 50
L 18	–	–	3.5	10.4	2.8	5.8
L 25	1.8	3.1	22.4	–	–	–
L 35	1.3	0.3	4.4	–	–	–
L 37	1.6	1.3	36.6	31.1	15.2	18.2
L 60	0.2	0.3	9.2	20.2	7.7	15.1
L 68	4.3	6.4	29.8	26.1	19.3	26.3
L 70	1.5	0.3	16.4	24.2	26.8	4.3
L 138	0.2	0.2	2.9	19.2	2.3	31.9
L 145	0.7	0.1	27.7	16.4	18.2	12.0
L 150	0.8	1.4	35.4	29.7	31.1	13.0
L 155	0.7	1.3	30.9	–	–	–
L 161	1.6	1.4	24.4	35.2	35.6	3.1
L 170	1.0	0.6	11.6	–	–	–
L 184	0.7	0.2	14.3	9.6	4.2	3.6
L 185	0.0	0.0	–	18.4	3.6	0.7
L 188	0.1	0.0	0.2	–	–	–
L 256	2.4	2.5	–	–	–	–
L 271	0.4	0.5	4.1	19.9	13.6	21.7
L 281	1.8	1.5	12.3	–	–	–
L 301	0.5	0.3	5.7	25.2	7.8	10.0

[1] Data from Oettler (1982).

Embryo development. Mean values of maternal genotypes for seeds with embryos (Table 3) showed little, but still significant differences. Variation among pollinators for this character was slightly higher and also significant (Table 4).

The proportion of plantlets resulting from in vitro culture given in Table 3 reveals a striking difference between hexaploid and tetraploid wheat parents. The highest value was reached with 'Götz' (50.4%). Similar and much lower proportions were obtained for D 40 and D 50 (21.3% and 24.4%, respectively). Percentages for D 30 were even smaller (9.9%). The range of variation among the rye parents is similarly wide as among the wheats. Proportions range continuously from 9.1% to 57.0%. Significant differences for both types of parents were found (Table 4).

If the mean proportion of viable plantlets is related to the number of florets pollinated, it ranges from 0.9% to 5.8% for the wheats and from 0.0% to 8.1% for the ryes (Table 3). On average these values are about one tenth smaller than those related to the number of embryos cultured. While this ratio is rather constant for the wheats, it varies substantially for the ryes. Yet both parental sources of variation are statistically significant (Table 4).

Correlation analyses of seed set to plantlets obtained in vitro, when both traits have as a common base the number of florets pollinated, gave the following results for the four wheats 'Götz', D 30, D 40 and D 50: r = 0.95, 0.46, 0.78 and 0.83, respectively.

Table 3. Mean values (least squares estimates) of crossability and embryo development data for maternal wheat and paternal rye genotypes.

	Number of cross combinations	Seed set (%)	Seeds with embryos (%)	Viable plantlets as % of	
				embryos cultured	florets pollinated
Wheat:					
Götz	18	15.8	67.3	50.4	5.8
D 30	13	21.0	70.5	9.9	0.9
D 40	13	13.5	63.3	21.3	1.6
D 50	13	11.8	69.4	24.4	2.0
Rye:					
L 18	4	5.6	78.3	29.1	1.0
L 25	1	22.2	84.5	35.2	8.0
L 35	1	4.1	66.0	57.0	0.0
L 37	4	25.3	79.2	22.0	5.2
L 60	4	13.1	67.3	30.5	2.2
L 68	4	25.4	68.0	23.2	4.4
L 70	4	17.9	67.5	39.4	3.7
L 138	4	14.1	64.8	22.7	2.1
L 145	4	18.6	72.7	24.1	3.3
L 150	4	27.3	66.0	25.3	4.8
L 155	1	30.7	75.4	24.8	8.1
L 161	4	24.6	68.7	18.0	3.5
L 170	1	11.3	69.1	21.5	0.4
L 184	4	7.9	69.4	9.1	0.9
L 185	3	7.6	79.9	20.2	1.6
L 188	1	0.0	–	–	–
L 271	4	14.8	58.9	17.4	1.0
L 281	1	12.0	70.4	33.2	1.7
L 301	4	12.2	78.1	24.8	1.7

All but the coefficient r = 0.46 for D 30 were significant at the 1% level of probability, and a test for homogeneity disclosed that it was significantly different only from r = 0.95 for 'Götz'.

DISCUSSION

Wheat-rye crossability. The results demonstrate the important role of maternal and paternal genotypes in wheat-rye hybridization, and thus are in good agreement with earlier findings (OETTLER, 1982). European common wheats are known to have generally a poor crossability with rye (KROLOW, 1970; SNAPE et al., 1979). The crossability of 'Götz', however, was found to be considerably higher than one would expect for a *T. aestivum* and was of the order obtained for *T. durum*. LELLEY (1982) demonstrated for spring wheat (cv. Kolibri) that cultivars of intermediate crossability exist, and the German winter wheat 'Götz' apparently also belongs to this category.

Such wheat genotypes of intermediate crossability will facilitate hybridization with rye considerably. And they allow a better differentiation for variation of crossability

Table 4. Mean squares of crossability and embryo development data for wheat-rye crosses. Percentages were transformed to arcsin.

Source	Seed set (%)		Seeds with embryos (%)		Viable plants as % of			
					embryos cultured		florets pollinated	
	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS
Wheat	3	416.1^{++}	3	403.6^{++}	3	367.0^{++}	3	249.8^{++}
Rye	18	92.1^{++}	18	86.8^{++}	17	21.4^{+}	18	24.2^{++}
Remainder	35	25.1	35	20.0	35	10.5	35	8.6

$^{+}$, $^{++}$ Significant at the 5% and 1% levels of probability, respectively.

Table 5. Correlations between six wheat parents for their seed set in crosses with various rye inbred lines as pollinators. The number of rye lines common to the correlated wheats is given in brackets.

Wheat parent	Kormoran	Götz	D 30	D 40	D 50
Jubilar	0.50^{+} (17)	0.71^{++} (17)	0.50 (11)	0.73^{+} (11)	0.21 (11)
Kormoran		0.46 (17)	–0.19 (11)	–0.01 (11)	0.11 (11)
Götz			0.59^{++} (12)	0.74^{++} (12)	0.04 (12)
D 30				0.71^{++} (13)	0.16 (13)
D 40					0.02 (13)

$^{+}$, $^{++}$ Significant at the 5% and 1% levels of probability, respectively.

within the rye parents than low crossable wheats. This is well demonstrated by the data of Table 2 and agrees with statements by THOMAS & ANDERSON (1978).

For individual cross combinations seed set values were obtained (Table 2) which differed considerably from the average performance of their parents (Table 3). This suggests the presence of interactions between wheats and rye lines, each possessing specific crossabilities. Correlations between wheat parents for their crossability with rye (Table 5) support this assumption. 'Jubilar' and 'Götz', belonging to different crossability classes, correlate well with both common and durum wheats, while 'Kormoran' does not correlate with any of the durums. The deviating behaviour of D 50, however, may be a result of the poor plant development in the glasshouse. Hence, the interactions between wheat and rye with regard to their crossability do not depend on the crossability level of the wheat parent, as was indicated by TANNER & FALK (1981). But further investigations are necessary to validate these findings.

Embryo development. Mean values for the character seeds with embryos obtained for durum-rye hybrids (Table 3) are lower than is known from investigations by TAIRA et al. (1978) with a limited number of defined spring rye lines, but higher than findings by PIENAAR (1974) with rye populations as pollinators The range of variation for embryo differentiation, represented by the proportion of seeds with embryos at the time of dissection, which is caused by the wheat and rye parents is remarkably small, as compared to the other characters investigated. And no difference between ploidy levels of the wheats can be recognized. Whether such small differences among and between wheat and rye genotypes are a general feature or are mainly due to particular techniques, remains open.

The results for the character plantlets recovered in vitro indicate a superiority of the crosses with hexaploid wheats as compared to the tetraploids and are similar to values given by LARTER (1975). Hybrid embryo differentiation and development in hexaploid wheat-rye crosses at time of dissection are considerably further advanced than in tetraploid wheat-rye crosses.

To get additional information on the aspect of embryo development an attempt was made to visually classify the dissected embryos as large, medium and small, based on their size and morphological appearance. It was found that the number of large and well differentiated embryos was high in 'Götz'-hybrids as compared to the durums. The percentage of small and poorly differentiated embryos was high in all durum-crosses and highest in D 30. This may explain the large difference between 'Götz'- and D 30-hybrids of 50.4% and 9.9%, respectively (Table 3). Obviously, the maternal influence on embryo development is stronger than that of the male parent.

From a practical point of view a possibility of predicting the number of amphihaploid plants to be expected from a particular cross combination would be highly desirable. The close correlation between seed set and proportion of viable plantlets observed in the 'Götz'-, D 30- and D 40-crosses may be considered a good basis for such predictions. The structure of the data did not allow to perform correlation analyses between all characters investigated, which would have been equally interesting. But further relevant studies are in progress at present.

ACKNOWLEDGEMENTS

I am indebted to Prof. Dr H. H. Geiger for helpful discussions and critically reading the manuscript. The skilful technical assistance of Ms E. Schwarz and Mr H. Häge is appreciated.

REFERENCES

BAAREN, A. VAN, 1973. A computer program for least-squares analysis of non-orthogonal designs. EDV in Medizin und Biologie 4: 16–27.

BARTLETT, M. S., 1947. The use of transformations. Biometrics 3: 39–52.

CURTIS, B. C. & L. J. CROY, 1958. The approach method of making crosses in small grains. Agron. J. 50: 49–51.

JALANI, B. C. & J. P. MOSS, 1981. The effects of species, polyploidy and embryo transplantation on the crossability between *Triticum* and *Secale*. Z. Pflanzenzüchtg 86: 286–297.

JENSEN, C. J., 1976. Barley monoploids and doubled monoploids: Techniques and Experience. In: GAUL, H. (Ed.), 1976. Barley Genetics III. Proc. 3rd Internat. Genetics Symp. Garching, 7–12 July, 1975. Verlag Karl Thiemig, München, 316–345.

KROLOW, K.-D., 1970. Untersuchungen über die Kreuzbarkeit zwischen Weizen und Roggen. Z. Pflanzenzüchtg 64: 44–72.

LARTER, E., 1975. The breeding and basic research on triticale. In: Tritikale. Studies and Breeding. Internat. Symp. Eucarpia, Sect. Cereals, 3–7 July, 1973, Leningrad, UDSSR, 31–37.

LEIN, A., 1943. Die genetische Grundlage der Kreuzbarkeit zwischen Weizen und Roggen. Z. ind. Abst.-, Vererbungslehre 81: 28–61.

LELLEY, T., 1982. The inheritance in rye of crossability with common wheat. Tag.-Ber. Akad. Landwirtsch.-Wiss. DDR, Berlin 198: 191–198.

LELLEY, T. & T. TAIRA, 1979. Effect of genotype on response to colchicine treatment in wheat-rye hybrids. Z. Pflanzenzüchtg 82: 87–89.

MARAIS, C. F. & R. DE V. PIENAAR, 1977. Hybridization between wheat and rye. II. Variations in the germinability of the hybrid kernels with special reference to the effect of the D-genome. Agroplantae 9: 143–148.

MOSS, J. P., 1970. Endosperm failure and incompatibility in crosses between *Triticum* and *Secale*. Chromosomes Today 3: 124–132.

OETTLER, G., 1982. Effect of parental genotype on crossability and response to colchicine treatment in wheat-rye hybrids. Z. Pflanzenzüchtg 88: 322–330.

PIENAAR, R. DE V., 1974. Methods to improve the gene flow from rye and wheat to triticale. Proc. 4th Internat. Wheat Genetics Symp. Missouri Agr. Exp. Sta., Columbia, Mo. 1973, 253–258.

RILEY, R. & V. CHAPMAN, 1967. The inheritance in wheat of crossability with rye. Genet. Res. 9: 259–267.

SNAPE, J. W., V. CHAPMAN, J. MOSS, C. E. BLANCHARD & T. E. MILLER, 1979. The crossabilities of wheat varieties with *Hordeum bulbosum*. Heredity 42: 291–298.

SNEDECOR, G. W. & W. G. COCHRAN, 1967. Statistical Methods. The Iowa State University Press, Ames, Iowa.

TAIRA, T., T. LELLEY & E. N. LARTER, 1978. Influence of parental rye on the development of embryos and endosperm of wheat-rye hybrids. Can. J. Bot. 56: 386–390.

TANNER, D. G. & D. E. FALK, 1981. The interaction of genetically controlled crossability in wheat and rye. Can. J. Genet. Cytol. 23: 27–32.

THOMAS, J. B. & R. G. ANDERSON, 1978. Cross-incompatibility of common wheat with rye: effect of varying the day of pollination on seed set and development. Can. J. Bot. 56: 3000–3007.

THOMAS, J. B., P. J. KALTSIKES & R. G. ANDERSON, 1981. Relation between wheat-rye crossability and seed set of common wheat after pollination with other species in the *Hordeae*. Euphytica 30: 121–127.

TOZU, T., 1966. Crossability between wheat and rye. Seiken Zihô 18: 33–38.