

Crossability of tetraploid and hexaploid wheats with ryes for primary triticale production

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Summary

Crossability of wheat and rye was investigated during thirteen crop cycles in two contrasting locations to 1) evaluate tetraploid and hexaploid wheat parents in crosses with rye, 2) identify genotypes with high crossability and 3) assess the impact of environment on seed development. The majority of the tetraploid wheats crossed with rye had seed set around 20%, but very low embryo viability. Several wheat genotypes with seed set above 50% were identified. The hexaploid wheats crossed with rye showed poor seed set, but plant recovery was relatively high. The majority of the hexaploid wheats with highest seed set (20–30%) were from China. The results suggest differences in crossability between the rye populations, and wheat species by rye interactions. The crossability of the tetraploid and hexaploid wheats was affected by climate in the two locations.

Introduction

Triticale (×*Triticosecale* Wittmack), as a synthetic crop, is genetically not as diverse as naturally evolved crops. Wheat-rye crosses expand the genetic base of triticale particularly by exploiting the tetraploid wheat (*Triticum durum* Desf.) and rye (*Secale cereale* L.) gene pools, which are otherwise difficult to access. Octoploid primary triticales, derived from crossing hexaploid wheat (*Triticum aestivum* L.) and rye, are used for introgressing D genome genes into triticale (Lukaszewski, 1986). Wheat-rye crosses also contribute to the improvement of bread wheat (Zeven, 1987).

Crossability between wheat and rye (seed set) is controlled by genes Kr1 and Kr2 (Lein, 1943) on wheat chromosome 5B and 5A (Riley & Chapman, 1967). When dominant these genes prevent hybrid

seed formation by active inhibition (Lange & Wojciechowska, 1976; Falk & Kasha, 1981). Kr1 has a greater effect than Kr2. An additional gene, Kr3, on chromosome 5D, was indicated to have a weak effect on crossability (Krolow, 1970; Snape et al., 1979; Fedak & Jui, 1982).

In a triticale breeding programme, the progenitors of primary triticales are chosen according to their agronomic qualities. Crossability of the parents varies and is frequently unpredictable. Crossability could be improved prior to making the intergeneric cross if lines with high crossability could be identified.

This study uses data from thirteen cycles of primary triticale production in the CIMMYT (International Maize and Wheat Improvement Center) triticale breeding programme. The objectives were to 1) evaluate tetraploid and hexaploid wheat par-

ents in crosses with rye, for assessing specific problems occurring with each type of cross, 2) evaluate crossability of wheat and rye progenitors of triticale to identify genotypes with high crossability and 3) assess the impact of environment on seed set and caryopsis development.

Materials and methods

During thirteen crop cycles (1984–1991), 1440 tetraploid wheat × rye and 550 hexaploid wheat × rye crosses were made in the field. The crosses included 374 tetraploid wheat and 200 hexaploid wheat cultivars. With some cultivars crosses were made with several sister lines. The wheat lines were mainly semi-dwarf durum and bread wheats of CIMMYT origin, but wheats of South-American, Indian and East-Asian origin were included. Open pollinated rye populations were used as pollen parents. The most frequently used ryes included populations from Canada, Europe, West Asia, China, Morocco and Brazil.

The crosses were made in winter at Cd. Obregon in northwestern Mexico (27°N 109°W 39 masl) under irrigated conditions, and during the summer cycle at El Batan in the central Mexican highlands (19°N 98°W 2249 masl) under rainfed conditions with supplementary irrigation. During the cycles studied, mean temperature during the pollination time at Cd. Obregon was about 1.5°C higher than at El Batan. Daily temperature varied more at Cd. Obregon than at El Batan. The El Batan cycles were characterized by frequent rains and less sunshine than the Cd. Obregon cycles.

About 24 florets were emasculated per spike. Pollination was done 4–6 days after emasculation. Immature caryopses were collected 18–22 days after pollination and embryos were rescued immediately into TL medium (Taira & Larter, 1978). The cultures were kept at +8°C for two weeks and then incubated in daylight at room temperature until germination. The plants were transferred into peat pots when roots and shoots had developed. Plants were treated with 0.1% colchicine supplemented with 2% dimethyl sulfoxide (DMSO) at the 2–4 tiller stage.

Measures of crossability included seed set (seeds per pollinated floret), seeds with embryo, plant set (plants per pollinated floret) and embryo viability (plants per rescued embryo). Average number of haploid plants per cross and doubling rate (amphidiploids per amphihaploid) were noted. Data from all crosses were included for the summary analysis. However, for estimation of the distribution of the wheat lines in different crossability classes, the highest seed set of each line, indicating the potential crossability, was used. Data from hexaploid wheat-rye crosses during El Batan cycle 1989 were omitted due to total failure of seed set. Frequency data were analysed using the χ^2 test. Correlation between climatic parameters and crossability parameters were calculated.

To evaluate the rye parent in the crosses, only ryes used in crosses with ten or more wheats were studied. The performance of each rye population, measured as seed set, was compared with that of other rye populations crossed with the same wheat genotypes. The average difference in seed set between each rye population and the other rye populations was used to evaluate the relative performance of each rye studied. To compare the rye performance between tetraploid and hexaploid wheats, the average differences were transformed into a normalised index. This was calculated by dividing the value for average difference in seed set of

Table 1. Crossability for tetraploid and hexaploid wheats in crosses with ryes

	Wheat species	
	Tetraploid	Hexaploid
Seed set ^a (%)	15.8	4.5
Seeds with embryo (%)	55.9	73.8
Embryo viability ^b (%)	11.2	46.4
Plant set ^c (%)	0.99	1.54
Crosses with plants (%)	43.8	53.6
Plants per cross	1.3	1.9
Doubling rate ^d (%)	31.9	26.8

^aSeeds per pollinated floret

^bPlants per embryo

^cPlants per pollinated floret

^dAmphidiploids per amphihaploids

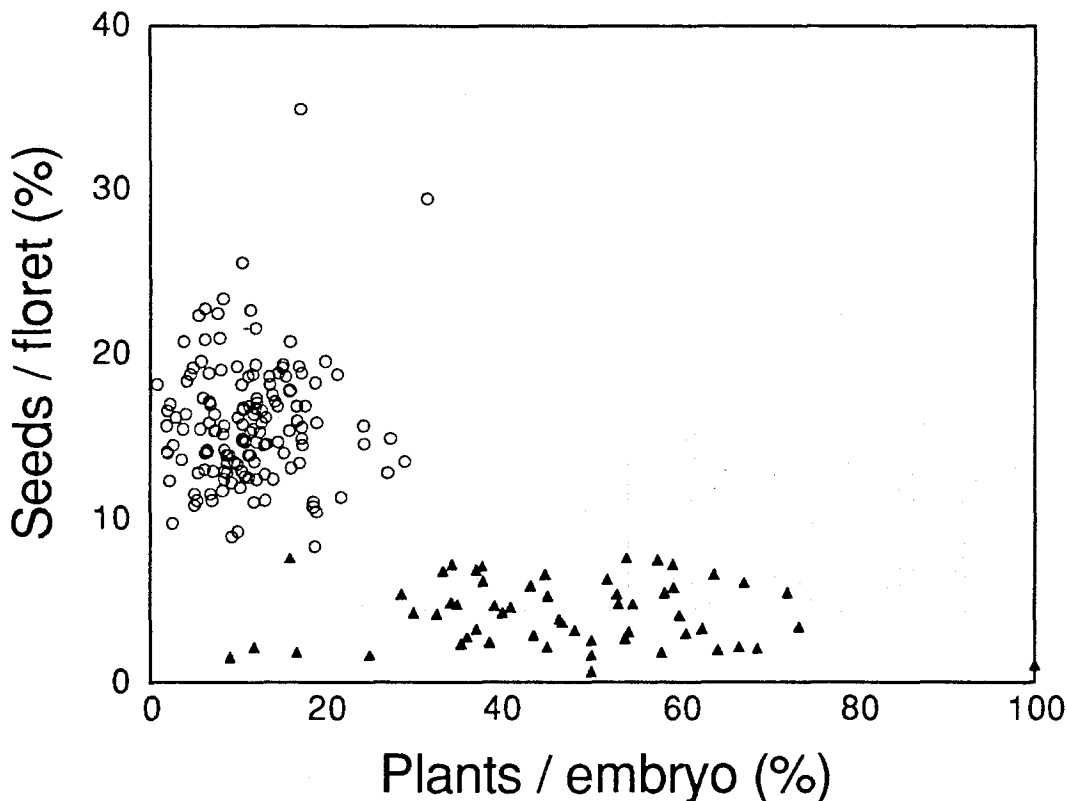


Fig. 1. Seed set (% seeds/floret) and embryo viability (% plants/embryo) for tetraploid (○) and hexaploid (▲) wheats.

each rye population by that of the rye population with the highest value.

Results and discussion

Parameters for the tetraploid and hexaploid wheat parents are shown in Table 1. The tetraploid wheats had a higher seed set but a lower embryo viability than the hexaploid wheats (Fig. 1). The hexaploid wheats had a higher proportion of seeds with viable embryos. Oettler (1982, 1984) showed similar results for seed set when testing lines of hexaploid and tetraploid wheats, but did not find distinct differences in plant recovery due to wheat species. The ploidy level of the maternal parent affected chromosome doubling rate, so that production of octoploid amphidiploids was less successful ($P < 0.01$), as reported by Oettler (1982).

Although it was suggested that hexaploid wheats cross more readily with rye than tetraploid wheats

(Kaltsikes, 1974), our data show that the seed set in hexaploid wheat-rye crosses was generally so low that only about half of these crosses were successful in terms of recovery of amphihaploid plants. Embryo viability varied greatly. In the crossing procedure of hexaploid wheat and rye, special attention has to be paid to the pollination, including timing of pollination and post-pollination treatment as suggested by Sitch & Snape (1987a, 1987b). Tetraploid wheat-rye crosses usually show severe endosperm failure and poor embryo differentiation (Keyworth & Larter, 1979), leading to low embryo viability. Our results corroborated this. With both tetraploid wheat-rye and hexaploid wheat-rye crosses it may be possible to enhance plant recovery by using callus culture (Shao & Taira, 1990; Immonen & Varghese, 1991).

The distribution of the wheat lines according to crossability in terms of seed set is shown in Fig. 2. The pattern for the hexaploid wheats is similar to that reported by Lange & Wojciechowska (1976)

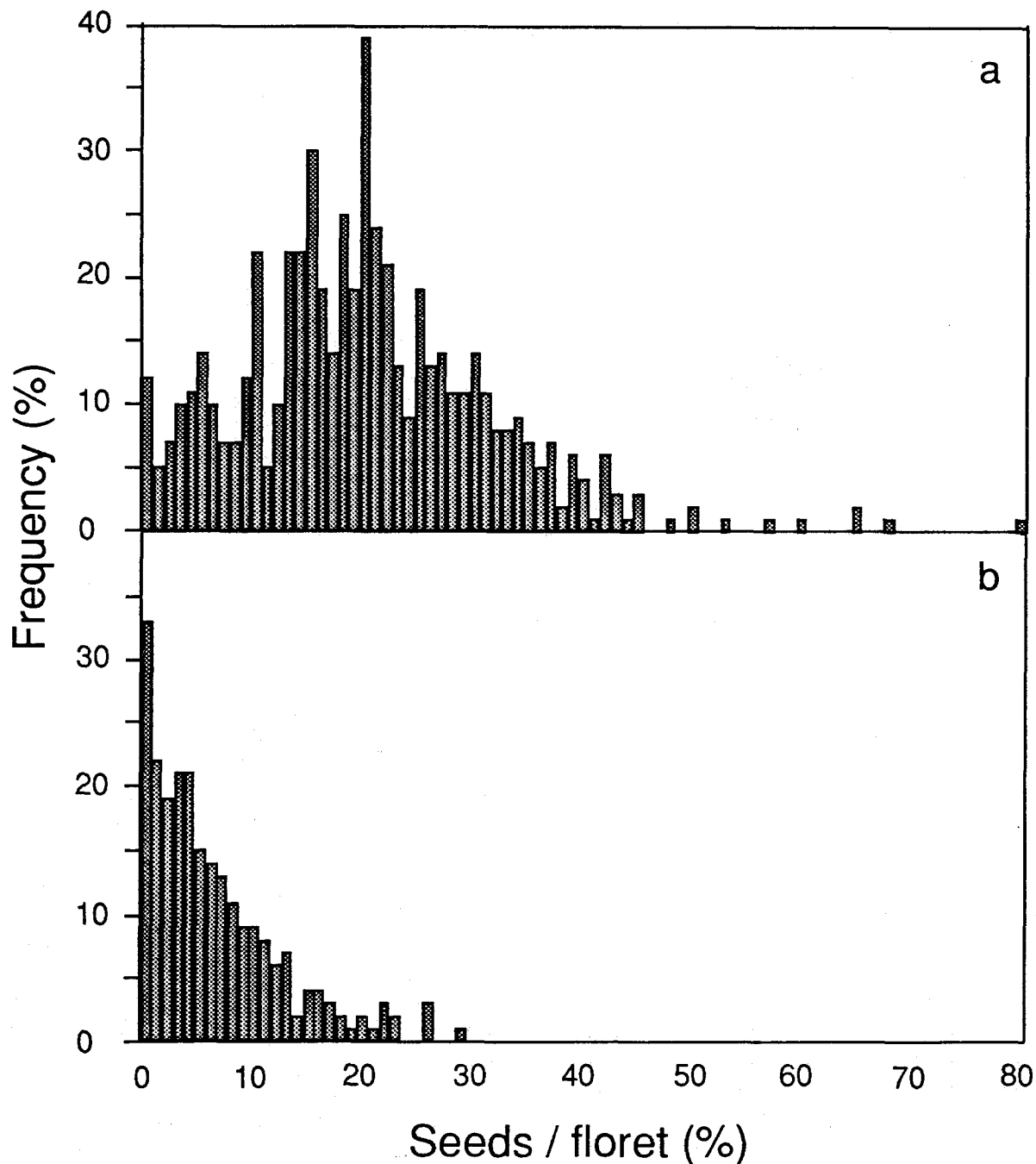


Fig. 2. Distribution of tetraploid (a) and hexaploid (b) wheats according to crossability (seeds/floret).

and Falk & Kasha (1981), but there were no lines with seed set above 30%. About 80% of the hexaploid wheat lines had crossability of 0–10%. The crossabilities were not distinctly grouped, which may reflect environmental influences or differences

in the background genotype of the wheats (Falk & Kasha, 1981). Lein (1943) suggested the following percentage classes indicating the expression of Kr chromosomes: 1–10% Kr1Kr1 Kr2Kr2, 10–30% Kr1Kr1 kr2kr2, 30–50% kr1kr1 Kr2Kr2, >50%

Table 2. Tetraploid and hexaploid wheats with the highest crossability with rye

	No. ^a	F ^b	S/F ^c max.	S/F mean	E/S ^d mean	P/E ^e mean
Tetraploid wheats						
MELTEQUE/ALOPOCHEN//FOJA	6	720	79.2	44.6	50.2	6.8
CMH73.A.494/3*MEXICALI75	2	700	67.9	58.9	18.1	52.0
HUTTLE/TUBENO	6	720	65.0	32.2	50.9	13.6
CMH.84.810	6	720	64.2	32.4	49.8	27.6
HUTTLE/YAVAROS	6	720	60.0	39.6	35.1	15.0
CMH73.A.497/3*MEXICALI75	8	960	56.7	35.0	54.2	23.1
WULF	15	1680	52.5	17.8	65.9	7.6
ALTAR84	14	1630	50.0	16.8	57.7	15.2
MEDIUM/KINGFISHER//						
SANDPIPER	3	320	50.0	34.4	30.9	2.9
NUMENIUS	3	380	47.5	39.2	20.1	20.0
AUK/OSTRERO	2	468	45.0	31.4	68.0	4.0
84TK155-001-03	1	120	45.0	0.0	37.0	0.0
BUC CANDISUR	4	514	45.0	30.7	48.7	14.3
TRINGA	7	770	43.3	17.5	43.7	11.9
ALGA	3	320	42.5	21.6	60.9	0.0
COCORIT71	10	1200	42.5	25.6	66.8	12.7
ARGANA	4	440	42.5	30.5	46.3	21.0
CALIDRIS	9	980	42.0	24.7	44.6	10.2
YAVAROS/FOJA	3	300	42.0	35.3	54.7	3.5
AROMO	11	1296	41.7	21.3	67.4	5.4
BUCEPHALA	11	1520	41.7	25.3	41.0	17.3
SACABA81 mutation	12	1484	41.7	14.8	42.7	17.0
SULA	24	2740	41.7	13.7	61.8	13.0
STERNA	27	2900	41.0	20.8	64.2	9.5
GAVIA	13	1452	40.0	26.9	41.2	7.5
MEMO/GOOSE	3	300	40.0	29.0	56.3	14.3
ROKEL	8	900	40.0	24.2	45.9	7.0
Hexaploid wheats						
BACANORA	6	720	28.3	4.9	71.4	64.0
DWL5023/SUNBIRD//SUNBIRD	4	480	25.0	20.8	89.0	68.5
TAL2697	5	600	25.0	10.7	79.7	84.3
LONG83-6515-19	1	240	24.2	24.2	82.8	31.3
LONG83-3147	1	240	22.9	22.9	85.5	27.7
SUZHOE #10	2	240	22.5	14.6	74.3	65.4
RABE	1	220	21.8	21.8	75.0	30.6
ALUBUC	4	480	21.7	8.3	62.5	12.0
LONGMAI #10	3	480	21.7	18.8	78.9	64.8
STAR	4	480	20.8	7.1	64.7	36.4
SUZHOE #9	2	240	20.0	12.5	90.0	70.4

^aNumber of times crossed^bPollinated florets^cSeed set^dSeeds with embryos^eEmbryo viability

kr1kr1 kr2kr2. Falk & Kasha (1981) proposed lower limits for crossability classes. Table 2 lists the wheat lines which showed highest crossability, including those with seed set of 20% and above. Seed set and embryo viability, averaged over all crosses made with these lines, indicate overall performance. These wheat lines are likely to have the Kr2 gene or possibly Kr1 in recessive form.

Five from eleven of the lines with best crossability were from China: the Longmai lines from Heilongjiang province in northeastern China and the Suzhoe lines from the Yangtze river area. Among the lines with seed set ≥ 10 , 59% were from China. Recorded seed sets were, however, not as high as reported for Chinese Spring (Zeven, 1987). The Chinese lines also included lines with consistently poor crossability; the Nangjing lines from Yangtze river area averaged 0.2% seed set. Line DWL5023/SUNBIRD//SUNBIRD, which showed consistent high crossability, has a durum wheat in its ancestry. Generally, the CIMMYT bread wheat lines with highest crossability and lowest crossability have many parents in common in their ancestry. Lines with lowest crossability (seed set $\leq 1\%$) included several lines from Brazil.

Distribution of crossability for the tetraploid wheats was different from that of the hexaploid wheats. Tetraploid wheats peaked around 20% seed set; 63% of the lines had crossability between 10 and 30%. Crossability $\geq 40\%$ was shown by 4.3% of the lines. These lines, listed in Table 2, include several with high crossability but very low embryo viability. The lines CMH73.A.494/3*MEXICALI75 and CMH73.A.497/3*MEXICALI75, which both had high seed set and relatively high plant set, have bread wheat and a Nepalese durum wheat in the ancestry. Otherwise highly crossable tetraploid wheat lines had similar ancestry to the lines with low crossability, as observed with hexaploid wheats.

Breeding for improved crossability in wheat using intermediately crossable lines might not be easy due to dominance for low crossability. Furthermore, the effect of crossability genes on embryo and endosperm development is not known (Lange & Wojciechowska, 1976).

With several wheat lines, crossability varied considerably from cross to cross. There were differences

between and within sister lines. Some hexaploid wheat lines showed high and low crossability even within the same crossing cycle. For example, the cultivar 'Bacanora 88', which had the highest seed set among the hexaploid wheats, did not set seed when crossed with three other equally crossable ryes in the same cycle. Crossability under field conditions seems to be highly influenced by factors other than genetical ones, possibly also interaction between the wheat line and the rye, although this has not been confirmed in other studies (Scoles, 1983; Tanner & Falk, 1981). The sensitivity of bread wheat crossability to external effects was also demonstrated by a total crossing failure during one cycle, when the durum wheat \times rye crosses gave a seed set close to the mean from the thirteen cycles.

Considering all crosses, seed set was significantly higher at Cd. Obregon than at El Batan (tetraploid wheats 16.8% and 15.3%, respectively, hexaploid wheats 5.8% and 3.4%, respectively, $P < 0.001$). With hexaploid wheats there was no difference between the locations in frequency of seeds with embryo or embryo viability. However, with the tetraploid wheats frequency of seeds with embryo were significantly higher at El Batan than at Cd. Obregon (percentage seeds with embryo 58.9% and 50.0%, respectively, $P < 0.001$). With tetraploid wheats environment seemed to have a different effect on seed set and on embryo development in the seed.

With the bread wheat \times rye crosses, a low but significant positive correlation ($R^2 = 0.142$, $df = 1, 33$, $F = 5.46$, $P < 0.026$) was found between the seed set and the maximum temperature during the day following pollination. Inagaki (1986) reported a positive correlation between seed set and temperature one day after pollination. The minimum temperature had no effect on seed set. With durum wheat the temperature after pollination was not correlated with seed set. It seems that the effect of factors other than genetical ones on fertilization and embryo development is different for tetraploid wheat-rye and hexaploid wheat-rye crosses.

Tanner & Falk (1981) reported significant differences between rye lines in crossability with wheat. Our data indicate that there are large differences between ryes in their crossability with both tetra-

Rye population

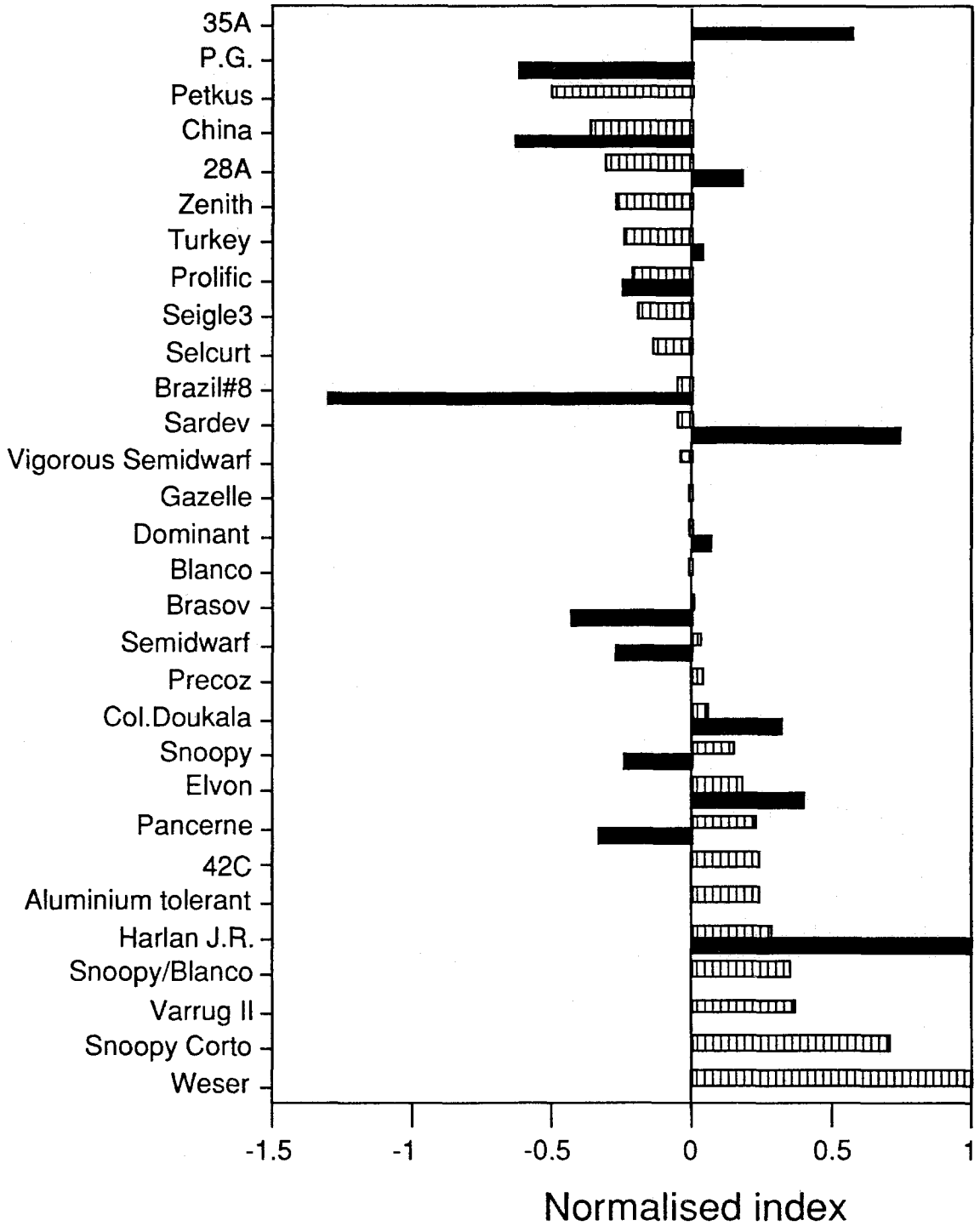


Fig. 3. Comparison of crossabilities of rye populations with tetraploid (□) and hexaploid (■) wheats.

ploid and hexaploid wheats, and also that some ryes perform noticeably better with one of the two wheat species. Average differences between the rye population studied in comparison with all other rye populations crossed with the same wheat genotypes are presented in Fig. 3. The data are not sufficient for exact estimation of the crossability of the ryes but suggest clear differences exist. The best rye populations can be identified for use in the crossing programme, and for transferring crossability to useful but poorly crossable rye germplasm.

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