Hybrid seed development and viability in crosses of *T. aestivum* (cv. Chinese Spring) monosomic lines with *S. cereale*

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Summary. The diploid and tetraploid wheats have a crossing barrier that inhibits development and viability of the F1 hybrid seeds which result from their pollination with rye. This barrier is ineffective in synthetic or natural hexaploid wheat x rye crosses. From the results obtained by crossing the Chinese Spring monosomic series to a diploid rye composite, it was concluded that the breakdown of this barrier in hexaploid wheats is determined by polygenes, but may also involve gene-dosage effects. While more than half of the hexaploid-wheat chromosomes may contribute to the breakdown of the barrier, chromosome 1D had the strongest effect. Its absence resulted in shrivelled and inviable hybrid kernels similar to those obtained when the *T. durum* cultivar Langdon was crossed with rye.

**Key words:** Wheat – Rye – Crossing barrier

Introduction

The *Kr* genes that regulate the frequency of kernels set in wheat x rye crosses are well documented (Lein 1943; Riley and Chapman 1967; Jalani and Moss 1980). However, little is known about a second, and apparently independent, crossing barrier which suppresses hybrid seed development in diploid and tetraploid wheat x rye crosses (Krolow 1970). Such hybrid kernels are characteristically shrivelled and inviable. The suppression of F1 hybrid seed development was only partial when certain diploid and tetraploid wheats were crossed to the more primitive species of rye, e.g., *S. sylvestre* and *S. vavilovii* (Krolow 1964, 1970; Nakajima 1955). A synthetic tetraploid wheat (Tetra Canthatch) derived from hexaploid Canthatch (Kerber and Rowland 1974) produced only shrivelled kernel when crossed with rye (Marais and Pienaar 1977). In hexaploid wheat x rye crosses (Marais and Pienaar 1977) as well as synthetic hexaploid wheat x rye crosses, i.e., AABBDD x rye (Marais and Pienaar 1977) or AAAABB x rye (Krolow 1970, 1973) development of the hybrid kernels is fairly normal. Pollination of hexaploid triticale with diploid or tetraploid rye produced well-developed kernels (Pienaar 1985). Substitutions of D genome chromosomes for individual A and B genome homoeologues of the durum variety Langdon (Joppa 1985) did not improve the development of the F1 seed obtained in crosses of these substitution lines with rye (Pienaar and Marais 1986).

Starvation of the endosperm and embryo as a secondary result of abnormal post-fertilization development may be a component of hybrid-seed failure (Brink and Cooper 1940, 1947). Aberrant endosperm and embryo growth were regular features in wheat x rye hybrids (Keyworth and Larter 1979), and the cellular- and nuclear-doubling times differed from that in normal wheat endosperm resulting from self-fertilization (Wojciekowska and Lange 1977). Hypotheses aiming to explain the causes of failure of hybrid seed development in interspecific crosses were considered by various authors, but presently none of these explanations seem to have a proven, general applicability (Brink and Cooper 1947; Nishiyama and Yabuno 1978; Johnston et al. 1980).

In this investigation, which aims to study the effects of individual wheat chromosomes on the expression of the seed developmental barrier in wheat x rye crosses, use was made of the Chinese Spring monosomic series developed by Sears (1953), because the *kr1kr1kr2kr2* genotype of this cultivar does not prevent hybrid seed set. The development of the wheat female gametophyte
is such that the egg cell and polar nuclei receive identical chromosomes (Briggs and Knowles 1967). Thus, meiosis in a monosomic plant results in the simultaneous absence or presence of the monosomic chromosome in both the egg cell and the polar nuclei. Regarding monosomic plants, Morris and Sears (1967) explained that chromosome lagging during meiosis on average produces 75% egg cells with 20-chromosomes and 25% with 21-chromosomes. The transmission rates differ for different monosomics (Tsunewaki 1963), and in Chinese spring 20-chromosome egg cells may range from approximately 57–82%, whereas 21-chromosome egg cells may range from 18–43%.

Materials and methods

Seeds of the complete Chinese Spring monosomic series (obtained from Prof. E. R. Sears, University of Missouri-Columbia, Missouri) were germinated, and the monosomic plants were identified and raised in a greenhouse. Up to eight plants per monosomic line were used in crosses with a diploid rye composite developed by the Department of Genetics, University of Stellenbosch. Euploid plants of Chinese Spring and Langdon (T. durum) were included to serve as indicators of the neutralized and fully operative effect of the seed developmental barrier, respectively. Hybrid kernels were harvested and graded visually as “filled” or “shrivelled”. The thousand-kernel mass of each group of hybrid kernels was determined. After allowing for a three to four-month post-harvest resting period, the F₁ kernels were germinated in Petri dishes at 20°C.

With respect to each monosomic line, the ratio of filled: shrivelled kernels and viable: inviable kernels expected if absence of the specific chromosome resulted in total reinstatement of the seed developmental barrier, were calculated. For this purpose the monosome transmission rate data given by Tsunewaki (1963), and the hybridization results obtained with Chinese Spring and Langdon in the present study, were used. The calculations were based on the assumption that the seed development and viability of a proportion of the wheat x rye F₁ kernels, which corresponds to the transmission rate of the monosome through the egg cell, equals that of euploid Chinese Spring. Seed development and viability of the balance of the F₁ seeds, i.e., those with 27 chromosomes, could be similar to that of the tetraploid wheats.

The seed classification and germination data were subsequently transformed to the form Arcsin √ percentage, to allow for the execution of one-way analyses of variance (with unequal numbers of observations per entry) as outlined by Snedecor and Cochran (1967). Tests of significance (t) were done to ascertain whether the results produced by a specific monosomic line differed from that obtained on normal Chinese Spring.

These results were also plotted. The effectiveness in percentage, of the seed developmental barrier, was calculated as follows for both seed quality and viability in each Chinese Spring x rye cross.

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\text{Effectiveness} = \frac{(A-B)}{(C-B)} \times 100
\]

Where, A = Observed frequency of shrivelled/inviable kernels; B = Observed frequency of shrivelled/inviable kernels in Chinese Spring x rye crosses; C = Expected frequency of shrivelled/inviable seeds with the barrier fully operative.

Results and discussion

The crossing and germination results are given in Table 1, and the degree of shrivelling of the hybrid seeds obtained in each monosomic line x rye cross, as well as their viability, are graphically illustrated in Fig. 1. The base line in these graphs represents the level of kernel development/viability observed in the cultivar Chinese Spring, while a 100% expression of the barrier is comparable to the poor F₁ seed development/viability obtained in the T. durum x rye crosses. The relatively high 1,000-kernel mass of the shrivelled hybrid seeds resulting from the Langdon x rye cross.