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Utilization of F_1 Monosomics for Genetic Analyses Involving Awn Expression, Glume Color, Seed Setting, and Seed Abortion in Crosses of Tetraploid and Hexaploid Wheats

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Summary. F_1 plants, monosomic for chromosomes 1A to 7B, from crosses of three lines of *Triticum durum* var. Khapli with the Chinese series were investigated together with their backcrosses to normal Chinese Spring. The three Khapli lines were designated K1-A, K1-B, and K1-D. Five parameters were analyzed: awn development, glume color, degree of selfing, crossing ability, and seed abortion.

Morphological examination of F_1 monopentaploid plants revealed that, in the three lines, chromosomes 5A, 1B, 3B, 4B, 5B, and 6B had promotor genes and 2A, 6A, and 2B had inhibitor genes for awn development. Results on glume color suggested the presence of at least three inhibitor genes on 1B, 5B, and 7B, and three promotor genes on 3A, 6A, and 6B chromosomes of Chinese Spring.

The first backcross of interspecific hybrids seemed to indicate that some chromosomes (1A, 1B, and 4B) originating from the Khapli lines possessed promotor genes, others (2B and 4A) carried inhibitor genes for seed setting. Similarily, the genetic factor (s) carried by chromosome 5A increased seed abortion whereas those on 2B and 6B reduced it.

Self fertility in K1-D hybrids was probably the result of the inhibitor factor (s) on 7A and promotor genes on 3B, 4B, 5B, and 6B chromosomes coming from K1-D.

Introduction

In 1954 Sears developed a complete series of nullisomics, monosomics and tetrasomics in hexaploid wheat. Following this, numerous workers have assigned genes to particular chromosomes in common wheat by monosomic analysis, but a complete series of monosomics in tetraploid wheat is not yet available. However, Kuspira and Millis (1967) used an alternative method of analysis involving crosses between a tetraploid variety and monosomic lines 1A to 7B of a hexaploid cultivar followed by a cytogenetic analysis of the F_1 plants. Bozzini and Giorgi (1971) using this technique identified the chromosomes controlling eight polygenic characters in a tetraploid variety of wheat. By this technique it is not possible to locate dominant genes on a particular chromosome. The conventional F_2 monosomic analysis also is not successful because of the excessive sterility in most of the F_1 plants (Hynes, 1926; Thompson and Hollingshead, 1927; Waterhouse, 1933; Love, 1941; Waterhouse, 1952; Mokhtarzadeh, 1970, unpublished data). In the present investigation attempts were made to ascertain the potentialities of the testcross method for monosomic analyses involving awn expression, glume color, crossability or seed setting, and seed abortion.

Materials and Methods

Seed of *Triticum aestivum* (2n = 6x = 42, AABBDD) var. Chinese Spring (Cns) monosomics was obtained from Dr. E.R. Sears, of the U.S. Department of Agriculture, Agricultural Research Service, Columbia, Mo. Each of the 14 lines of A and B genome monosomics Cns was crossed to three lines of *T. durum* (2n = 4x = 28, AABB) var. Khapli. The three Khapli lines, designated here as K1-A, K1-B, and K1-D, were obtained from the Department of Agronomy, North Dakota State University, Fargo, N.D.

All the three lines had long awns, of 8 to 9 cm, whereas Chinese Spring was awnless. The glume color of Cns was yellowish but that of K1-D was almost black. All the parental lines derived from Khapli had high self-fertility. The fertility of Cns monosomic lines has previously been reported by Sears (1954). The somatic chromosome number of each F_1 plant was determined in the root tip of the germinating seed. Seedlings with 34 (monopentaploid) and 35 (disomic or pentaploid) chromosomes were selected and transplanted in the greenhouse.

Three days after emasculation, each F_1 female head was pollinated with fresh, mature pollen of Chinese Spring and the number of florets crossed was recorded. In order to supply enough fresh pollen, a large number of seeds from Cns were planted in pots as well as in greenhouse ground benches, at different dates. One head from each F_1 plant was covered for selfing.

At harvest the numbers of fully developed and abortive seeds were recorded. Percent seed set and seed abortion for each line were calculated according to the following formulas:

1-Percent seed set;

$$\frac{\text{total number of fully developed and abortive seeds}}{\text{total number of florets crossed}} \times 100$$

2-Percent abortive seed;

$$\frac{\text{total number of abortive seeds}}{\text{total number of fully developed and abortive seeds}} \times 100$$

Oberservations on awn types and glume color were made when plants were ready for harvest. Awn types were classified as fully-awned, short-awn, awnleted,

and awnless. Glume color was classed as dark, medium, and light.

Crosses with the 34 chromosome F_1 were used as checks or controls and the heterogeneity chi-square test was applied to their results on seed setting and seed abortion. The significance of differences between pentaploid and monopentaploid plants of each line for crossability and seed abortion was examined using student's "t" test.

Results and Discussion

Details of crosses between monopentaploid hybrids with hexaploid Chinese Spring are presented in Table 1. Since no significant difference was ascertained for seed setting and seed abortion in the pentaploid progenies the mean of backcross F_1 was used in the comparison.

Seed setting

Seed setting data, used as a measure of crossability, indicated that all monopentaploid families in K1-A, K1-B, and K1-D had a lower seed set than the control hybrid. It may be concluded that all chromosomes from the A and B genomes of the Khapli lines influenced the seed setting of the interspecific hybrids. This agreed with the previous suggestion (Sears, 1954) that all chromosomes in the common wheat influence fertility. Analysis of the deviating monopentaploid families showed that the absence of a particular chromosome in the hybrid resulted in the significant increase or decrease of the seed set; it would appear that these chromosomes carry inhibitor or major promotor genes for the seed setting of the test-cross progeny. The presence of all chromosomes carrying the major or minor promotor genes for seed setting may collectively have a complementary epistatic effect on the suppressor genes and result in the relatively high seed set of the pentaploid hybrids.

Chromosomes 1A, 1B, and 4B in the three Khapli lines, in addition to 2A in K1-A, 7A in K1-B, and 6B in K1-D, may be considered as chromosomes with a major effect on the promotion of seed setting in the hybrids. Whenever one of the above-mentioned chromosomes was missing the seed setting of that particular hybrid was significantly reduced (Fig. 1). Similarily, chromosomes 4A and 2B in the three Khapli lines, in addition to 6A and 7A in K1-A, and 6B and 7B in K1-B, can be considered the carriers of inhibitor genes, because of the relatively high percentage of the seed set in monopentaploid lines for these chromosomes.

The reduced crossability of monopentaploid as well as pentaploid hybrids could be due to several factors, such as lack of receptivity of the stigma in various florets in a head, pollen quality, and environmental factors per se.

Disturbance in seed setting of the interspecific hybrids may be expected as a result of interactions between A and B genomes originating from different sources (Pissarev, 1966). In addition, the absence of chro-

Table 1. Percent seed set and seed abortion in backcross F_1 plants from crosses between (Chinese Spring monosomics x K1-A, K1-B, and K1-D) F_1 and normal Chinese Spring

Crosses	% Seed set			% Seed abortion		
	K1-A	K1-B	K1-D	K1-A	K1-B	K1-D
1A	11**	9**	6*	23	33	45
2A	12**	13	19	20**	40	43
3A	19	20	10	28	31*	41
4A	25	19	32	21*	32	47
5A	14	12	14	19**	28**	32**
6A	20	11	15	39	26**	34*
7A	21	7**	12	25	33	41
1B	10**	7**	3**	31	29*	39
2B	24	23	55	41	66	63
3B	16	11	14	26	36	27**
4B	7**	7**	4**	36	47	40
5B	19	18	8	28	44	34*
6B	14	21	3**	45	67	56
7B	16	24	12	12**	32	38
Disomics	32	54	42	30	40	36

* Significant at 5 % level.

** Significant at 1 % level.

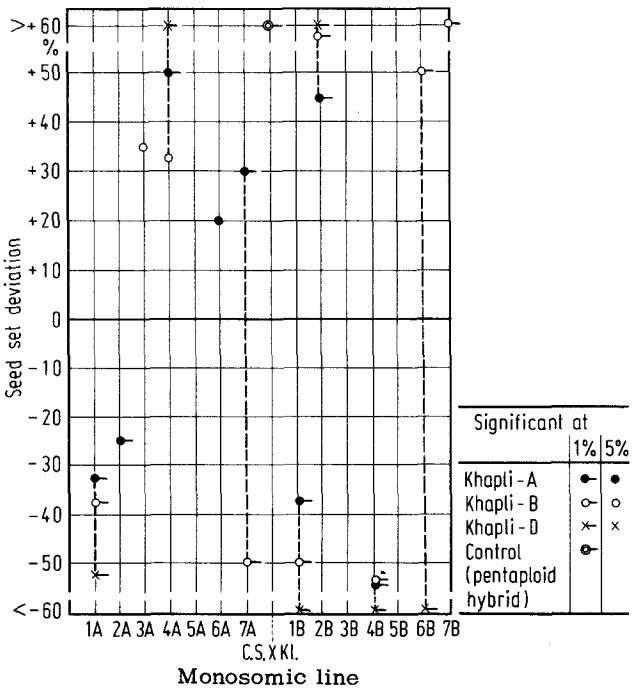

Fig. 1. Diagram showing deviation in seed setting of hybrid control and 14 monosomic lines of K1-A, K1-B, and K1-D from the mean of monosomic lines

mosomes influencing fertility and crossability may reduce significantly the fertility of the monopentaploid hybrids. Loss of chromosomes carrying genes which promote or suppress fertility can be revealed by very low or very high fertility in the monopentaploid plants when compared with the average of the monosomic lines (Bozzini and Giorgi, 1971). In this experiment chromosomes 1A, 1B and 4B in the three lines can be considered the carriers of promotor genes, whereas, chromosomes 4A and 2B carry the suppressor genes for fertility in the hybrid (Fig.1). The cytoplasmic effect of the hexaploid parent in reducing the hybrid fertility has already been ruled out (Kihara, 1968; Suemoto, 1968).

Seed abortion

Data on the percentage of abortive seed (Table 1 and Fig.2), show that chromosomes 2B and 6B in the three Khapli lines, in addition to four other chromosomes (6A and 4B in K1-A, 4B in K1-B, and 4A in K1-D), were the most essential chromosomes for preventing abortive seeds. However, the absence of chromosome 5A in the three Khapli lines, plus four other chromosomes (2A and 7B in K1-A, 6A in K1-B, and 3B in K1-D), significantly lowered the percentage of abortive seeds. Therefore, at least nine chromosomes had factors which controlled seed viability in the three Khapli lines.

Failure to obtain complete or viable seeds could largely be due to abnormal chromosome relationships between embryo and endosperm (Stebbins, 1958), and the dosage of genes and genomes in the endosperm. In addition, the deleterious effect of genes located on chromosomes 2A, 5A, 6A, 3B, and 7B could probably be the prime cause of the observed zygotic lethality in the corresponding Khapli lines. The same factors might have been the cause of zygotic lethality in the interspecific hybrids reported previously (Thompson and Hollingshead, 1927; Waterhouse, 1933 and 1952).

Self fertility

Result of selfing in K1-D line was as follows: chromosome 7A produced the highest percent of selfed seeds per plant (73.3 percent). It was not possible to obtain any selfed seed in monopentaploid hybrids for chromosomes 3B, 4B, 5B, and 6B. Plants of other monopentaploid families had a range of 0.6 to 5.0 percent of selfed seeds per plant. To interpret the result it was assumed that: the expected transmission of n and n-1 gametes in monopentaploid hybrids followed that of the monosomic hexaploid species reported by Sears (1954); chromosome 7A of K1-D carried gene (s) for promotion of selfing; and genes for suppression of selfing were on chromosomes 3B, 4B, 5B and 6B.

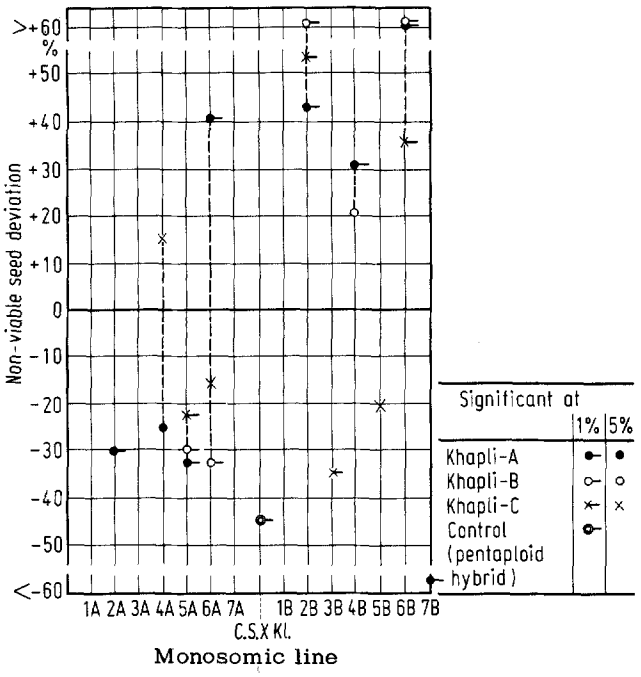

Fig.2. Diagram showing deviation in seed abortion (non-viable seed) of hybrid control and 14 monopentaploid lines of K1-A, K1-B, and K1-D from the mean of monosomic lines

According to these assumptions, monopentaploid plants for the 7A chromosome should produce 97 % viable seed which possess at least one 7A chromosome of K1-D. Deviation from the expected seed set might be due to differential transmission of n and n-1 gametes from either the male or female side and factors causing zygotic lethality. Similarily, monopentaploid plants of chromosomes 3B or 4B or 5B or 6B should have 97 percent sterility rather than the observed 100 percent. The 3 percent of the remaining zygotes which are in the nullisomic condition might have yielded additional non-viable seeds.

The collective action of genes located on the above chromosomes may have caused the partial or complete sterility of the F_1 generation from crosses between *Triticum vulgare* and Khapli emmer wheats, reported previously (Hynes, 1926; Waterhouse, 1933; Love, 1941).

Awn expression

Observations on awning in the pentaploid and monopentaploid F_1 are presented in Table 2. Six chromosome lines (5A, 1B, 3B, 4B, 5B, and 6B) had longer awns (see

Table 2. Awn expression in F_1 plants from crosses of Chinese Spring monosomics and three Khapli lines (K1-A, K1-B, and K1-D)

Awnless		Awnleted		Short Awn		Fully awned	
plant no.	chromosome	plant no.	chromosome	plant no.	chromosome	plant no.	chromosome
26	2A	26	1A	23	5A	30	3B
19	6A	21	3A	24	1B	33	4B
10	2B	11	4A			25	5B
		24	7A			32	6B
		21	7B				
		201	disomics				

also Fig.3), and three lines (2A, 6A, and 2B) had shorter awns, in comparison with the disomic plants. The difference in awning seemed to be controlled by factors located on at least nine chromosomes. The present knowledge of factors affecting awn development in interspecific pentaploid F_1 has been summarized by Bozzini and Giorgi (1971). According to them, chromosomes 2A, 1B, 2B, 3B, 4B, and 6B in the tetraploid variety of Capeiti carried the awn-influencing genes, A1, A10, A8, a6, hd, and b2, respectively. Our observations on the three Khapli lines agree with Bozzini and Giorgi's results and add to the picture three other factors (b1, A11, and a12) located on chromosomes 5A, 6A, and 5B. Thus, full awning requires the presence of at least four recessive genes. The presence of one or more awns inhibiting allele (s) determines awnleted and other partially awned hybrids.

Chromosome 5A of the Khapli lines also had the recessive allele for the speltoidy condition, as illustrated in Fig.3.

Fig.3. Awn expression of parents and F_1 hybrids from crosses between three Khapli lines and Chinese Spring monosomics involving chromosomes 5A, 1B, 3B, 5B, and 6B
C = normal Chinese Spring; K-D = normal K1-D; dk-A = disomic K1-A; mk-A, mk-B, and mk-D = monopentaploid lines of K1-A, K1-B, and K1-D, respectively

Glume color

There was no apparent difference in the glume color of the monopentaploid F_1 of K1-D involving chromosomes 1A, 2A, 4A, 5A, 7A, 2B, 3B, and 4B, in comparison with their corresponding disomics (Table 3). However, monopentaploid lines of 3A, 6A, and 6B had lighter glume color, whereas 1B, 5B, and in particular 7B had darker glume color than their corresponding disomics. This indicates that Chinese Spring possesses glume color-inhibiting factors on three chromosomes (1B, 5B, and 7B) and promotor factors on another three sets (3A, 6A, and 6B). Previous reports (Unrau, 1950; Aslam, 1958) had indicated that the gene for glume color in some varieties of wheat was located on chromosome 1B. Chromosome 3A had also been reported to carry the inhibitor gene (s) in the hexaploid variety of Cadet (Bhowal and Jha, 1969). Chromosomes 1B and 3A of Chinese Spring may possess the alleles which inhibit and promote glume color development, respectively.

Table 3. Glume color development in F_1 plants from crosses of Chinese Spring monosomics and K1-D

Light		Medium		Dark	
Plant no.	chromosome	plant no.	chromosome	plant no.	chromosome
8	3A	4	1A	8	1B
5	6A	8	2A	10	5B
8	6B	3	4A	8	7B
		11	5A		
		8	7A		
		4	2B		
		9	3B		
		9	4B		
		47	disomics		

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