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Vol. 14 No. 1 1986 Cereal Research Communications

AN INVESTIGATION INTO THE GENETIC RELATIONSHIP BETWEEN INTERSPECIFIC CROSSABILITY AND CHROMOSOME PAIRING IN WHEAT

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SUMMARY

In wheat, genes controlling interspecific crossability and chromosome pairing have been located on the same chromosomes suggesting a possible common genetic control. To examine this hypothesis wheat genotypes and wheat x rye hybrids segregating for allelic differences at the crossability locus, Kr1 on chromosome 5B, were examined for frequencies of meiotic chromosome pairing. In these materials no relationship between crossability and pairing could be established. The wheat x rye hybrids, however, appeared to be segregating for a factors(s) independent of the locus Kr1 affecting the level of pairing. The implications of these results are discussed.

INTRODUCTION

In wheat an association is apparent between interspecific crossability and the level of meiotic chromosome pairing. For example, loci controlling crossability of wheat with rye, with Hordeum bulbosum, and with H. vulgare, have been located on the chromosomes of homoeologous group 5 (Riley and Chapman, 1967a; Snape et al., 1979; Sitch and Snape, 1985; Krowlow, 1970; Fedak and Jui, 1982). This group of chromosomes also carries genes controlling chromosome pairing at meiosis. Thus the homoeologous pairing locus, Ph1, is located on chromosome 5B (Riley, 1960; Sears, 1985), and Feldman (1966) identified loci affecting pairing on all the group 5 chromosomes. In addition, Miller et al. (1983) demonstrated a negative correlation between crossability with H. bulbosum and pairing, determined by the homoeologous group 3 chromosomes.

It is possible, therefore, that these two functions could be pleiotropic effects of the same genes. This paper presents the results of an investigation into this relationship in a sample of wheat genotypes and in wheat x rye hybrids, in which the differences in seed setting ability were known to be controlled by allelic variation at the crossability locus, Kr1.

MATERIALS AND METHODS

Wheat genotypes and wheat x rye hybrids were derived showing allelic differences at the crossability locus, Kr1 on chromosome 5B. To develop these lines an initial cross was made between the crossable cultivar, Chinese Spring, ditelosomic for the long arm of chromosome 5B (2n = 42+2t),

and possessing the crossable allele kr1, and the cultivar Highbury, disomic for chromosome 5B (2n = 42) and possessing the non-crossable allele Kr1 reducing or preventing crossability. The monotelodisomic hybrid (2n = 41+t) was then used as the male parent in a cross with the line of Chinese Spring monosomic for chromosome 5B (2n = 41). Monosomic progeny (2n = 41) were then selected cytologically, using the Feulgen-squash technique. The crossability of each plant, and thus the Kr1/kr1 genotype, was assessed as described by Sitch et al. (1985) using crossability or non-crossability with H. bulbosum as the indicator. An absence of seed on all spikes of a given plant pollinated with H. bulbosum was taken to indicate the presence of the dominant Kr1 allele. The presence of one or more seeds indicated the presence of the recessive kr1 allele.

Four Kr1 and three kr1 monosomic plants were chosen at random, self-pollinated, and disomic plants (2n = 42) were extracted from their progenies. These plants were scored to determine the level of meiotic pairing in the alternative homozygotes.

In addition, monosomic plants (2n = 41) were extracted from the selfed progeny of five Kr1 and five kr1 plants and crossed with the spring rye cultivar, Petkus Spring, as described by Sitch et al. (1985). The resultant wheat x rye hybrid seeds were germinated and plants with the full hybrid chromosome complement (2n = 28) were identified from root-tip preparations and grown on for an examination of meiotic pairing.

All wheat and wheat x rye hybrid plants were first grown in a glasshouse. Approximately two weeks prior to meiosis, the plants were transferred to a growth cabinet, maintained at 20°C with continuous light and 90 per cent humidity.

Anthers containing pollen mother cells at first metaphase were located using aceto-carmine squashes and fixed and stained using the Feulgen technique. In preparations mounted in proprionic orcein the number of univalents, bivalents (rods and rings), trivalents and other chromosome associations were noted, where possible, in at least 30 pollen mother cells in each of three anthers of each replicate plant.

For each cell, the number of paired arms was calculated from the mean number of univalents, bivalents and trivalents per cell. The mean level of pairing in each disomic wheat plant was then described as the number of paired chromosome arms, expressed as the percentage of the possible number of paired chromosome arms per cell, i.e. 42. For analysis, the mean data for each plant were transformed to angles. To analyse the level of pairing in each wheat x rye hybrid, the number of univalents was expressed as a percentage of the total number of chromosomes, i.e. 28 for each cell and averaged over all cells for each plant.

RESULTS AND DISCUSSION

The mean number of univalents, bivalents and other chromosome associations per cell for each family, averaged over the plants scored, and

the level of pairing per cell, i.e. the percentage of paired arms, transformed to angles, are shown in Table 1. The variation in the level of pairing between and within the families was analysed using an analysis of variance, see Table 2.

There was no significant variation in the level of pairing between the seven families, between families within the groups of kr1 and Kr1 genotypes or between the overall means of the kr1 and Kr1 groups.

There does not, therefore, appear to be any relationship between the level of homologous pairing in wheat and allelic variation at the crossability locus, Kr1, in this material.

Table 3 shows the mean number of univalents and bivalents per cell, for each wheat x rye hybrid line, averaged over the plants scored and the level of pairing per cell, i.e. the percentage of univalents, transformed to angles. The limited number of plants available to be scored within the Kr1 hybrid lines reflects the presence of the allele within the original monosomic recombinant families and thus their low crossability with rye. The variation in the level of pairing between and within the wheat x rye hybrid lines was analysed, using an analysis of variance (Table 4). The error item is based on the variation between plants within the kr1 group alone, which assumes that the error variances within both crossability groups is homogeneous.

The ten wheat x rye hybrid families differed significantly in the level of pairing, the mean number of univalents per cell varying from 60.7 per cent of the chromosomes in line R119, to 83.1 per cent in line R128, Table 3. However there was no significant difference in the level of pairing between the kr1 and the Kr1 families. Thus the overall variation in the level of pairing between the ten hybrid lines was shown to reflect a significant variation in the level of pairing between the families within both the kr1 and the Kr1 groups.

The mean level of pairing of each wheat x rye hybrid line can be compared with the overall mean, using Student's t-test. Within both crossability groups, lines having a significantly lower level of pairing (R182, R249, R218 and R128) and a significantly higher level of pairing (R107, R37 and R119) were identified, see Table 3.

An absence of any relationship between crossability and pairing is shown here by the equal levels of pairing in Kr1 and kr1 wheat genotypes. However there was significant variation in the level of pairing between wheat x rye hybrids and their families appear to be segregating for a factor(s) independent of the Kr1 locus. This factor(s) may be derived from Highbury or Chinese Spring, the donors of the crossability alleles, Kr1 and kr1 respectively. If so, these two cultivars may be showing allelic variation at the Ph1 locus, or at an additional locus which influences pairing. Indeed, Nakayama and Zennyozi (1966) observed genotypic differences in the level of non-homologous pairing in hybrids derived from crosses between different wheat varieties and rye. In the present investigation, genotypic variation in the level of pairing was observed

Table 1. The mean level of chromosome pairing in kr1 and Kr1 families of wheat (ranges in parenthesis)

Family	Chromosome number	Number of plants	Meiotic chromosome associations I	II Rod	II Ring	III	% paired arms (angles)
Crossable							
W249	42	3	-	1.77 (0-5)	19.23 (16-21)	-	78.17
W218	42	2	0.50 (0-2)	0.85 (0-3)	19.70 (18-21)	-	78.25
W26	42	3	0.33 (0-4)	1.10 (0-5)	19.50 (15-21)	-	77.80
Mean			0.28 (0-4)	1.24 (0-5)	19.48 (15-21)	-	78.073
Non-crossable							
W158	42	2	0.7 (0-4)	3.25 (0-5)	17.40 (15-21)	0.05 (0-1)	72.25
W119	42	3	0.03 (0-2)	1.43 (0-4)	19.57 (17.21)	-	79.70
W128	42	3	0.20 (0-2)	1.70 (0-5)	19.17 (16-21)	-	77.53
W139	42	4	0.35 (0-2)	1.43 (0-4)	19.40 (16-21)	-	78.55
Mean			0.32 (0-4)	1.95 (0-5)	18.89 (15-21)	0.01 (0-0.1)	77.008

I, II, III = univalents, bivalents and trivalents respectively.

Table 2. The analysis of variance of the level of pairing (% paired arms, angles) within kr1 and Kr1 wheat families

Item	df	MS	VR
Between families	6	12.605	1.077 NS
- kr1 v Kr1	1	1.280	0.052 NS
- between kr1 families	2	0.155	0.013 NS
- between Kr1 families	3	24.283	2.109 NS
Between plants within families	13	11.705	

Significance level: NS = not significant.

Table 3. The mean level of chromosome pairing in wheat x rye hybrid lines containing the Kr1 or kr1 alleles (ranges in parenthesis)

Family	Chromosome number	Number of plants	Meiotic chromosome associations I	Meiotic chromosome associations II (Rods)	% paired arms (angles)
Crossable					
R182	28	6	27.40 (22-28)	0.28 (0-3)	81.92 **
R249	28	6	27.40 (22-28)	0.35 (0-3)	81.42 **
R218	28	7	27.40 (20-28)	0.30 (0-4)	82.16 **
R26	28	2	27.05 (22-28)	0.50 (0-3)	79.45 NS
R107	28	2	22.10 (16-28)	2.95 (0-7)	62.70 ***
Non-crossable					
R128	28	1	27.60 (24-28)	0.20 (0-2)	83.10 *
R37	28	1	24.00 (8-28)	1.90 (0-9)	67.80 *
R240	28	1	26.70 (24-28)	0.70 (0-2)	77.60 NS
R158	28	1	27.10 (24-28)	0.50 (0-2)	79.70 NS
R119	28	1	21.30 (16-24)	3.80 (2-6)	60.70 ***
Overall Mean					75.655

Significance of difference between the mean level of pairing of each line with the overall mean:
Significance levels: NS = not significant, * p = 0.05-0.01,
** p = 0.01-0.001, *** p < 0.001.

Table 4. The analysis of variance of the level of chromosome pairing (% univalents, angles) within wheat x rye hybrid lines containing the Kr1 or kr1 alleles

Item	df	MS	VR
Between lines	9	129.638	16.132 ***
- Kr1 v kr1	1	157.570	0.947 NS
- between kr1 families	4	166.455	20.714 ***
- between Kr1 families	4	85.838	10.682 ***
Within lines	18	8.036	

Significance levels: NS = not significant, *** p < 0.01

within the wheat x rye hybrids only; not within the disomic wheat genotypes. This variation in response depending on the genetic background may represent either a dosage effect, the factor being effective only when present in a single dose, as in the wheat x rye hybrids, and ineffective when present in two doses, as within the disomic wheat genotypes. Alternatively, this difference may reflect an interaction with the rye genome and a consequent modification of the function.

It is interesting to note that the wheat genotype, W119 and its derived wheat x rye hybrid, R119, showed the highest level of pairing. Although there was no significant overall correlation between the level of pairing in the wheat genotypes and the wheat x rye hybrids ($\chi^2 = 0.38$, p 0.2), a slight negative relationship is apparent. This reflects the fact that the level of pairing in the wheat genotypes is expressed as the percentage of paired arms and that in the wheat x rye hybrids as the percentage of univalents. This suggests that the factor(s) for which these lines appear to be segregating may control pairing in both genetic backgrounds.

In the present study, no relationship was found between the level of pairing and crossability. This implies that pairing cannot be a pleiotropic effect of the Kr1 locus, unless pairing is controlled by an interaction between the Kr1 gene and a second gene for which these genotypes were not segregating. This investigation and the inconsistencies in the direction of the relationship between crossability and pairing in other studies (Miller et al., 1983) suggest that these two characters are under separate genetic control. This latter hypothesis is further supported by the proximal location of the Ph1 locus on the long arm of chromosome 5B (Sears, 1985) and the recent distal location of the Kr1 locus on the same arm of chromosome 5B (Sitch et al., 1985). Nevertheless, it is an intriguing possibility that these characters may be functionally related, as both characters allow the conservation of the integrity of a specific genotype.

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ACKNOWLEDGEMENTS

The senior author would like to thank the Agricultural and Food Research Council for supporting this research. The help of Mr. T.E. Miller in analysing the results is gratefully acknowledged.

Received 18th November 1985