Theor Appl Genet (1985) 70:309–314

Intrachromosomal mapping of crossability genes in wheat (*Triticum aestivum*)

L. A. Sitch, J. W. Snape and S. J. Firman

Plant Breeding Institute, Maris Lane, Trumpington, Cambridge CB2 2LQ, England

Received November 15, 1984; Accepted January 5, 1985
Communicated by R. Riley

Summary. Intrachromosomal mapping studies were used to locate the positions of the genes *Kr1* and *Kr2*, which control the crossability of wheat with *Hordeum bulbosum*, on chromosomes 5B and 5A, respectively. The location of *Kr1* was established using the telocentric mapping technique and found to be on the long arm of chromosome 5B, distal to the centromere with a mean recombination frequency of $44.8 \pm 3.28\%$. *Kr2* was located on the long arm of chromosome 5A by linkage with the major gene markers *Vrn1*, controlling vernalization requirement, and *q*, controlling ear morphology. *Kr2* is closely linked to *Vrn1*, with a mean recombination frequency of $4.8 \pm 4.66\%$, and is distal to *q* with a mean recombination frequency of $38.1 \pm 10.60\%$. The similar locations of *Kr1* and *Kr2* on homoeologous chromosomes suggest that these two loci are homoeoallelic. Significant correlations between *Hordeum bulbosum* and rye crossability confirmed that *Kr1* and *Kr2* control the crossability of wheat with both species.

Key words: Crossability genes – Wheat – Intrachromosomal mapping – Rye – *Hordeum bulbosum*

Introduction

Within hexaploid wheat, *Triticum aestivum*, considerable genetic variability exists for crossability with rye (*Secale cereale*).

Lein (1943) showed that this crossability was controlled by two loci, *Kr1* and *Kr2*, where the dominant alleles reduced crossability, *Kr1* being the more and *Kr2* the less potent in effect. Examination of substitution lines of individual chromosomes of the poorly crossable wheat variety 'Hope', into the highly crossable wheat variety 'Chinese Spring', showed that chromosomes 5A and 5B conferred the low crossability of 'Hope' with rye (Riley and Chapman 1967a), chromosome 5B having the greater effect. Riley and Chapman therefore concluded that the crossability genes, *Kr1* and *Kr2*, were located on chromosomes 5B and 5A, respectively. Krowlow (1970) proposed that chromosome 5D also carries *Kr3* influencing crossability with rye.

A high positive correlation exists between the crossability of wheat with rye and with *Hordeum bulbosum*. Genotypes with a high rye crossability are crossable with *H. bulbosum* and genotypes of low rye crossability are non-crossable with *H. bulbosum*. Highly significant correlation coefficients, $r = 0.79$ (Snape et al. 1979) and $r = 0.75$ (Falk and Kasha 1981), suggest that the same genetic system is involved in the control of the crossability of wheat with these two species. Indeed, Snape et al. (1979) studied the crossability of the 'Hope' into 'Chinese Spring' chromosome substitution lines with *H. bulbosum*, and showed that the two crossability genes were located on chromosomes 5B and 5A, 'Chinese Spring' ('Hope' 5B) again having the greatest effect.

Lange and Riley (1973) mapped *Kr1* on the long arm of chromosome 5B using a telocentric mapping procedure. Based on estimates of rye crossability, a mean recombination frequency of $11.45 \pm 3.0\%$ was obtained. Assuming that the crossabilities with rye and *H. bulbosum* are controlled by the same genetic system, a mapping study of *Kr1* based on estimates of *H. bulbosum* crossability woud be expected to show a similar map location.

This paper presents results of studies on the location of *Kr1* and *Kr2* on chromosomes 5B and 5A, respectively, using *H. bulbosum* crossability, and examines the relationship between rye and *H. bulbosum* crossability in recombinant wheat genotypes.

Materials and methods

Mapping of Kr1

Two mapping studies were carried out to locate *Kr1* on the long arm of chromosome 5B using the telocentric mapping technique (Sears 1962, 1966). This was identical in both studies, but was carried out by different workers in consecutive years.

The parental lines used were the wheat variety 'Highbury' which possesses the dominant allele, *Kr1,* and is therefore non-crossable with *H. bulbosum,* and the genotype 'Chinese Spring' ditelosomic for the long arm of chromosome 5B, which carries the recessive allele and is therefore crossable with *H. bulbosum.* All crosses were made under glasshouse conditions. The parental lines were first crossed to produce the monotelodisomic hybrid and this was then used as the pollen parent in crosses to the 'Chinese Spring' monosomic 5B line. From the resulting progeny, monosomic and monotelosomic progeny were cytologically selected by examining metaphase chromosomes in root-tip preparations using the Feulgen staining technique. The selected progeny were grown and crossed with *H. bulbosum* in an unheated glasshouse during the summer.

H. bulbosum hybridizations were carried out using wheat as the female parent. Florets were emasculated 2 to 3 days prior to anthesis, and apical and basal spikelets, and all except the two outermost florets of the remaining spikelets, were removed to achieve uniform maturity throughout the ear. When receptive, stigmas were pollinated with freshly collected *H. bulbosum* pollen taken from a mixture of tetraploid *H. bulbosum* clones. The ears were sprayed with gibberellic acid (75 p.p.m.) one day after pollination. Two or three ears were pollinated on each plant.

The crossability (number of seeds set scored at 14 days after pollination) of the parental and recombinant lines was expressed as a percentage of the number of florets pollinated on an individual ear basis, and then averaged over contributing ears to give the overall crossability of a particular plant. An absence of seed on all the pollinated ears of a given plant was taken to indicate the presence of the dominant *Kr1* allele. The presence of seed indicated the recessive *kr1* genotype.

In the first mapping study *H. bulbosum* crossability was assessed on 103 progeny selected cytologically and a further 127 progeny were selected and tested in the second study.

In assessing crossability, full expression of the *Kr/kr* allele in the hemizygous state was assumed. However, a subsequent experiment was carried out to evaluate the effect of aneuploidy on *H. bulbosum* crossability. Estimates of per cent seed set were made on 8 ears each of 'Chinese Spring' euploid, 'Chinese Spring' monosomic for chromosome 5B and 'Chinese Spring' ditelosomic for the long arm of chromosome 5B, using the tetraploid *H. bulbosum* clone PB168.

To establish the relationship between *H. bulbosum* and rye crossability, 42 selected parental (*Kr1*) and recombinant (*kr1*) monosomic plants from the second mapping study were self pollinated, and monosomic progeny extracted for rye crossability assessments. The rye crosses were made under unheated glasshouse conditions using techniques identical to those for *H. bulbosum* pollinations. Three ears on each of two to five plants of each line were crossed with the rye cultivar 'Petkus Spring' as the pollen parent, and also one ear with *H. bulbosum* pollen to detect any misclassification of the previously classified non-crossable lines.

Mapping of Kr2

Kr2 was mapped on chromosome 5A relative to the two marker genes *Vrn1* (which controls vernalization requirement) and *q* (which determines ear morphology), by testing the crossability of single chromosome recombinant lines (Law 1966). The recombinant lines used in this study were developed by C.N. Law and A.J. Worland (Plant Breeding Institute, Cambridge) from the cross of 'Chinese Spring' with the single chromosome substitution line, 'Chinese Spring' (*Triticum spelta* 5A).

'Chinese Spring' (*T. spelta* 5A) possesses the dominant crossability allele, *Kr2,* donated by *T. spelta,* and 'Chinese Spring' the recessive allele, *kr2.* The genetic background, that of 'Chinese Spring', contains the crossable *kr1* allele on chromosome 5B. 'Chinese Spring' (*T. spelta* 5A) is therefore crossable but has a lower crossability with *H. bulbosum* than 'Chinese Spring'. Six lines of each parental wheat genotype, seven lines of the *Vrn1/Q* recombinant genotype and two lines of the *vrn1/q* recombinant genotype were used.

The crossing techniques were identical to those described above.

Assessments of *H. bulbosum* crossability were made on six replicate plants for each line, three ears were pollinated on each plant using the tetraploid clone PB168. The per cent seed set (number of grains set as a percentage of the total number of florets pollinated) was calculated on individual ears, averaged over each replicate plant and then over each line.

Assessments of rye crossability were made on all 21 lines, based on three replicate plants and three ears per plant using 'Petkus Spring' as the pollen parent.

Results

Location of Kr1 on chromosome 5B

Within the monotelodisomic hybrid between 'Chinese Spring' ditelocentric 5BL and 'Highbury', recombination can occur only on the long arm of chromosome 5B. By using this as the pollen parent, recombinant monosomic and monotelosomic progeny can be obtained where the hemizygous chromosome originated from the hybrid.

From the cytological classification of the progeny, the relative frequency of monosomic : monotelosomic progeny was 90 : 13 in the first mapping study and 109 : 18 in the second study. There was therefore a clear preferential transmission of complete chromosomes rather than telocentric chromosomes through the pollen, and these frequencies are in agreement with those found by Lange and Riley (1973).

An analysis of variance of differences between the 5BL recombinant lines in crossability with *H. bulbosum,* using per cent seed set data transformed to angles, showed significant ($P < 0.001$) variation between the lines, confirming the segregation of the crossability genes. A similar analysis of the crossable genotypes alone showed significant variation ($P < 0.001$) in crossability presumably due to the segregation of *Kr2* and background genes. The crossability of the monosomic and monotelosomic genotypes differed; the monosomic and monotelosomic progeny having untransformed means of 4.8% and 13.2% seed set, respectively, in the first study and 3.5% and 11.5% seed set in the second study.

From examination of karyotype and crossability, the progeny were classified into two parental and two recombinant groups. Within the parental types, monosomic ($2n = 41$) plants were non-crossable and mono-

telosomic (2n = 40 + t) plants were crossable. Recombination between the crossability locus and the centromere produced non-crossable monotelosomic and crossable monosomic progeny. Table 1 shows the number of plants possessing each of the four possible karyotype-crossability combinations, for the two mapping studies separately and for the two sets of data combined. A 2-dimensional contingency χ^2 analysis (Crawford-Sidebottom 1970) of the proportion of plants within the four groups, failed to detect any significant difference between the two mapping studies ($\chi^2_3 = 4.25$). Therefore, for subsequent analysis, the data were pooled over studies.

The frequency of monosomic (2n = 41) and monotelosomic (2n = 40 + t) genotypes and of parental and recombinant genotypes was tested for a 1 : 1 segregation using a χ^2 analysis. A highly significant difference between cytological groups ($\chi^2_1 = 122.71$, $P < 0.001$) reflected the preferential transmission of the monosomic over the monotelosomic 5B chromosome within the male gametes. However, the overall ratio of parental to recombinant genotypes did not differ significantly from a ratio of 1 : 1 ($\chi^2_1 = 2.50$). This indicates an independent segregation of *Kr1* from the centromere, with a mean recombination frequency of 44.8 ± 3.28%.

The effects of aneuploidy on crossability with H. bulbosum

The crossabilities of the euploid, monosomic and ditelosomic 'Chinese Spring' genotypes are shown in Table 2.

A 2-dimensional contingency χ^2 analysis of the variation in the relative numbers of pollinated florets with or without seed, showed significant genotypic differences in seed set ($\chi^2_2 = 29.90$, $P < 0.001$).

There is therefore a clear effect of aneuploidy on *H. bulbosum* crossability where a reduction in the dosage of the short arm of chromosome 5B is associated with an increase in crossability. Thus, in 'Chinese Spring' the short arm of chromosome 5B appears to carry a suppressor(s) of crossability, with the long arm carrying the *kr1* allele facilitating crossability. These results explain the higher crossability of the monotelosomic relative to the monosomic 5BL recombinant progeny in the mapping study. However, since monosomy increases crossability, this is unlikely to cause misclassifications of *Kr1* and *kr1* genotypes, unless there is a significant effect of allelic variation between the short arms of chromosome 5B of 'Highbury' and of 'Chinese Spring'.

Location of Kr2 on chromosome 5A

The mean *H. bulbosum* crossabilities of the four genotypic groups for the major gene markers are shown in Table 3. The analysis of variance of these data, Table 4,

Table 1. The numbers of parental and recombinant 5BL genotypes for *H. bulbosum* crossability (C = crossable and NC = noncrossable)

	Genotype			
	Parental 41 (NC)	Recombinant 41 (C)	Parental 40 + t (C)	Recombinant 40 + t (NC)
Study 1	50	40	8	5
Study 2	53	56	16	2
Overall	103	96	24	7

Table 2. The *H. bulbosum* crossability of 'Chinese Spring' aneuploid genotypes

Genotype	No. of florets pollinated	% seed set
Euploid	217	17.9
Monosomic 5B	217	41.3
Ditelosomic 5BL	212	34.3

Table 3. The *H. bulbosum* crossability (% seed set) of the 5A recombinant genotypic groups

	vrn1	*Vrn1*
Q	27.0 (parental)	20.7 (recombinant)
q	25.2 (recombinant)	16.6 (parental)

Table 4. The analysis of variance of *H. bulbosum* crossability between the 5A recombinant groups (data of % seed set transformed to angles)

Item	df	MS	VR
Late v Early	1	2,790.14	18.610***
Square v Speltoid	1	983.93	6.563*
Late/Early v Square/Speltoid	1	0	0
Residual	17	149.93	

Significance levels: * 0.05–0.01, *** < 0.001

Table 5. The numbers of parental and recombinant 5A genotypes and the frequency of recombination between *Kr2* and the marker loci, *Q* and *Vrn1*

Marker	Parental	Recombinant	Recombination frequency
Q/q	13	8	0.381 ± 0.1060
Vrn1/vrn1	20	1	0.048 ± 0.0466

again using per cent seed set transformed to angles, shows that the differences in crossability can be accounted for by a genetic association of the crossability gene with both marker genes. *Kr2* is therefore located on the long arm of chromosome 5A. The strongest relationship is between the *Vrn1* classification of the lines and their crossability, indicating a distal location.

The individual lines could also be classified into two groups on crossability levels, either as having higher crossability and therefore a *kr2* genotype or lower crossability with a *Kr2* genotype. The number of parental and recombinant genotypes for *Kr2* and each marker locus is shown in Table 5, together with estimates of recombination frequencies.

The mean recombination frequency of $38.1 \pm 10.60\%$ between *Kr2* and *q* shows that these two loci are only loosely linked. In comparison, *Kr2* is closely linked to the *Vrn1* locus, with a mean recombination frequency of only $4.8 \pm 4.66\%$.

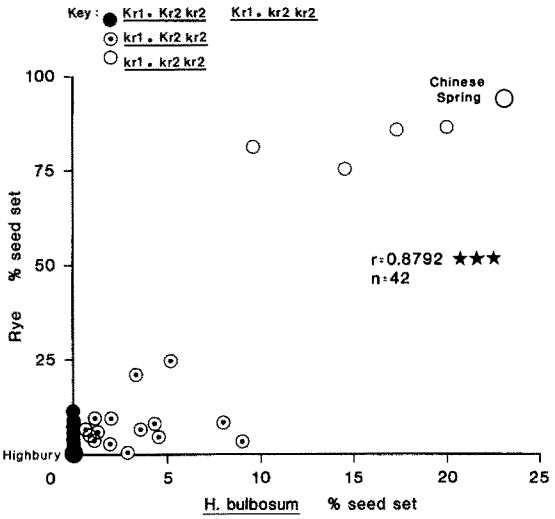

Fig. 1. The relationship between the crossabilities of the 5BL recombinant lines with *H. bulbosum* and rye

The relationship between H. bulbosum and rye crossability

A plot of the *H. bulbosum* and the rye crossability of the 5BL recombinant lines is shown in Fig. 1. Each *H. bulbosum* crossability value is based on a single ear estimate made whilst assessing rye crossability. Clearly there is a strong positive relationship and a highly significant correlation of 0.88 was obtained.

Genotypes possessing the dominant allele of the most potent gene, *Kr1,* are non-crossable with *H. bulbosum* and of low rye crossability regardless of the *Kr2* genotype. The remaining genotypes possess the recessive allele, *kr1,* and are therefore crossable with both pollen parents. Within these crossable genotypes, two clear groups are evident, presumably representing the segregation of the less potent gene, *Kr2,* in the background. The lines with an extremely low *H. bulbosum* crossability and a low rye crossability are assumed to possess the dominant *Kr2* allele, and those with a slightly higher *H. bulbosum* crossability and a high rye crossability, the recessive *kr2* allele.

Figure 2 shows the relationship between the crossability of the 5A recombinant lines with *H. bulbosum* and rye. Again a strong relationship is evident between the *H. bulbosum* and the rye crossability to give a significant correlation of 0.755. Further, there is a clear association between crossability and the *Vrn1* classification. Lines possessing the 'Chinese Spring' allele, *vrn1,* have a high crossability with both species and genotypes possessing the 'Chinese Spring' (*T. spelta* 5A) allele, *Vrn1,* have a low crossability. A single recombinant between the *Vrn1* and *Kr2* loci was found which had a high crossability with both species.

The positive correlation shown in Figs. 1 and 2 between *H. bulbosum* and rye crossability indicates that

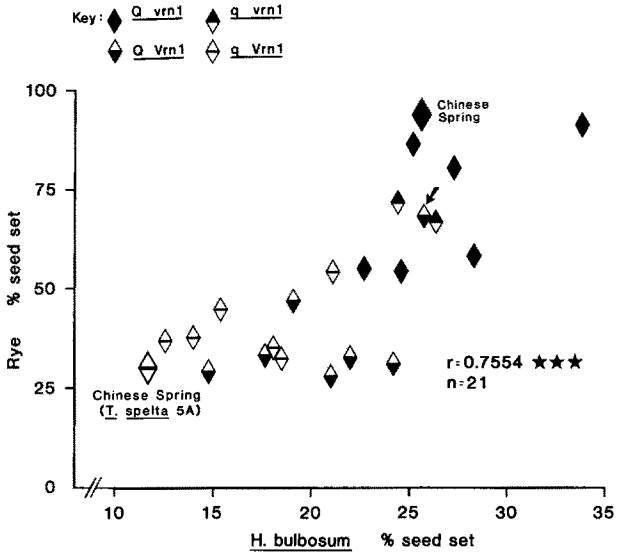

Fig. 2. The relationship between the crossabilities of the 5A recombinant lines with *H. bulbosum* and rye. (*Arrow* indicates the single *Kr2/Vrn1* recombinant)

the same genetic system, controlled by the *Kr* genes, regulates the crossability of wheat. The presence of *Kr1* and *Kr2* reduces the crossability with both pollen parents. The extent to which crossability is reduced, however, is greater for rye than for *H. bulbosum.*

Discussion

The effects of aneuploidy on H. bulbosum crossability

Clearly there is an effect of aneuploidy of chromosome 5B of 'Chinese Spring' on crossability with *H. bulbosum.*

The enhancement of crossability associated with the absence of the short arm telocentric implies the presence of a crossability suppressor on the short arm of chromosome 5B. A more detailed study of the effects of the dosage of the short arm of chromosome 5B on crossability is necessary to establish whether this is only a dosage effect or if there is allelic variation at an additional locus for crossability. If allelic variation exists, then alleles giving decreased suppression i.e. increased crossability, may be identified and combined to improve crossability further.

The genetic control of crossability appears to involve active inhibition. The removal of a single dose of the short arm of chromosome 5B improves crossability, implying that it is responsible for active suppression. The *Kr* alleles also inhibit crossability; an increase in the dose of the recessive *krl* allele did not promote crossability (Riley and Chapman 1967a).

Riley and Chapman (1967a) suggested that crossability genes arose by mutation in crossable wheats, growing in areas where rye was a native species, as a way of preventing wheat-rye intercrossing. However, it is not known why genes capable of reducing the level of crossability, such as those on the short arm of chromosome 5B, should have evolved in crossable genotypes; since in 'Chinese Spring', these genes do not appear to be capable of preventing interspecific hybridization.

Locations and homoeology of Krl and Kr2

The locations of *Krl* and *Kr2* on chromosomes 5B and 5A, respectively, are shown in Fig. 3. Both are located distally on the long arms of the homoeologous chromosomes.

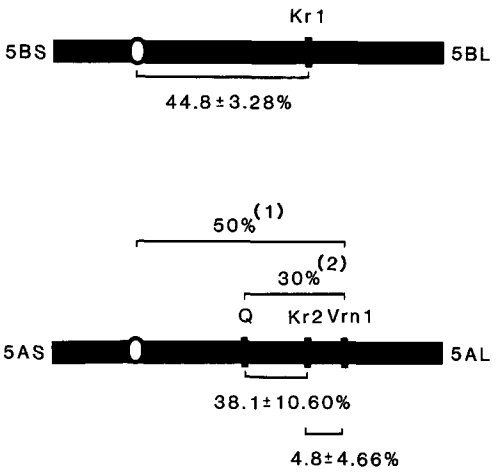

Fig. 3. The genetic location of *Krl* and *Kr2* on chromosomes 5B and 5A, respectively. The linkage estimates represent mean recombination frequency values with standard errors

The mean recombination frequency between *Krl* and the centromere (44.8±3.28%) indicates an independent segregation. The relative frequency of genotypes at the *q* and *Vrnl* loci in the sample of 5A recombinant lines suggests that *Kr2* is located between these markers and therefore proximal to *Vrnl* on the long arm of chromosome 5A. Independent segregation of *Kr2* from the centromere is implied since *Kr2* is closely associated with *Vrnl,* and *Vrnl* is known to segregate independently from the centromere (Law et al. 1976).

The similarity of the locations of *Krl* and *Kr2* on homoeologous chromosomes suggests that the genes are homoeoallelic.

The location of Kr3

In this respect it would be interesting to locate *Kr3* on chromosome 5D. However, *Kr3* only causes a minimal reduction in crossability. Indeed Riley and Chapman (1967a) were unable to detect any significant reduction in rye crossability in 'Chinese Spring' ('Hope' 5D) compared with 'Chinese Spring', although a small effect was apparent. Snape et al. (1979) showed that the reduction in *H. bulbosum* crossability caused by 'Chinese Spring' ('Hope' 5D) was equivalent to 'Chinese Spring' ('Hope' 5A), indicating that *Kr3* from 'Hope' does reduce *H. bulbosum* crossability relative to its 'Chinese Spring' allele.

Using the 'Chinese Spring' ('Hope') substitution lines, Fedak and Jui (1982) showed that all the homoeologous group 5 chromosomes of 'Hope' rendered 'Chinese Spring' non-crossable when pollinated with the barley cultivar, 'Betzes'. The location of *Kr3* on chromosome 5D could thus be achieved using cultivated barley as the pollinator.

The relationship between H. bulbosum and rye crossability

From the comparison of the *H. bulbosum* and the rye crossability of both sets of recombinant lines, it is clear that *Krl* and *Kr2* are responsible for the control of both *H. bulbosum* and rye crossability.

The relationship between *H. bulbosum* and rye crossability has previously been observed in wheat varietal comparisons (Snape et al. 1979; Falk and Kasha 1981) and substitution lines of individual chromosomes of the non-crossable varieties 'Hope', 'Atlas 66' and 'Cheyenne' in the crossable background of 'Chinese Spring' (Falk and Kasha 1983).

The mapping study carried out by Lange and Riley (1973) based on rye crossability showed that *Krl* was located near to the centromere with a mean recombination frequency of 11.45±3.0%. This result implies that the gene for rye crossability is distinct from the gene for *H. bulbosum* crossability, since in this paper this has been shown to be independently located from the centromere. If this is the case, the comparison between the *H. bulbosum* and rye crossabilities described in this paper should have revealed recombinants between the two crossability genes. No recombinant lines were identified. Rye crossability is greatly influenced by the environment and it is possible that this may have led to the misclassification of the *Krl* genotype by Lange and Riley (1973), resulting in an underestimation of the mean recombination frequency. Alternatively, the difference could have arisen from the dif-

ferent wheat varieties used in these separate studies, having different 5B chromosomes or different alleles modifying crossability in the genetic background.

The relationship between crossability and homoeologous pairing

Miller et al. (1983) demonstrated a negative correlation between *H. bulbosum* crossability and pairing determined by the homoeologous group 3 chromosomes of wheat.

An association between these two characters also exists on the group 5 chromosomes. On the long arm of chromosome 5B, the suppression of homoeologous pairing (Riley 1960), due to the *Ph* locus (Wall et al. 1971), and suppression of crossability occurs. On the short arm of chromosome 5B, there is an association between the apparent suppression of crossability and a pairing promoter (Riley and Chapman 1967b). Chromosome 5A also carries a pairing promoter (Feldman 1966) and the crossability gene, *Kr2*. Chromosome 5D carries a pairing promoter (Feldman 1966) and the crossability gene, *Kr3*.

It is interesting that these two homoeologous groups of chromosomes carry genes which control intergenomic chromosome pairing and crossability. Both these characters allow the conservation of the integrity of a specific genotype and could be interpreted as being pleiotropic effects of the same genes.

Although an association between pairing and crossability exists, the direction of the effects is not consistent, suggesting perhaps separate loci. This latter hypothesis is supported by the proximal location of the *Ph* locus on the long arm of chromosome 5B (Sears 1984). Nevertheless, it is an intriguing possibility that these two characters may be functionally related and this requires further investigation.

Acknowledgement. The senior author is grateful to the Agriculture and Food Research Council for a Research studentship.

References

Crawford-Sidebottom TJ (1970) Differential susceptibility of species of slugs to metaldehyde bran and to methiocarb baits. Oecologia 5:303–324

Falk DE, Kasha KJ (1981) Comparison of the crossability of rye (*Secale cereale*) and *Hordeum bulbosum* onto wheat (*Triticum aestivum*). Can J Genet Cytol 23:81–88

Falk DE, Kasha KJ (1983) Genetic studies of the crossability of hexaploid wheat with rye and *Hordeum bulbosum*. Theor Appl Genet 64:303–307

Fedak G, Jui PY (1982) Chromosomes of 'Chinese Spring' wheat carrying genes for crossability with 'Betzes' barley. Can J Genet Cytol 24:227–233

Feldman M (1966) The effect of chromosomes 5B, 5D and 5A on chromosomal pairing in *Triticum aestivum*. Proc Natl Acad Sci USA 55:1447–1453

Krowlow KD (1970) Untersuchungen über die Kreuzbarkeit zwischen Weizen und Roggen. Z Pflanzenzücht 64:44–72

Lange W, Riley R (1973) The position on chromosome 5B of wheat of the locus determining crossability with rye. Genet Res 22:143–153

Law CN (1966) The location of genetic factors affecting a quantitative character in wheat. Genetics 53:487–498

Law CN, Worland AJ, Giorgi B (1976) The genetic control of ear-emergence time by chromosomes 5A and 5D of wheat. Heredity 36:49–58

Lein A (1943) Die genetische Grundlage der Kreuzbarkeit zwischen Weizen und Roggen. Z Indukt Abstamm Vererbungsl 81:28–61

Miller TE, Reader SM, Gale MD (1983) The effect of homoeologous group 3 chromosomes on chromosome pairing and crossability in *Triticum aestivum*. Can J Genet Cytol 25: 634–641

Riley R (1960) The diploidisation of polyploid wheat. Heredity 15:407–429

Riley R, Chapman V (1967a) The inheritance in wheat of crossability with rye. Genet Res 9:259–267

Riley R, Chapman V (1967b) Effects of $5B^S$ in suppressing the expression of altered dosage of $5B^L$ on meiotic chromosome pairing in *Triticum aestivum*. Nature 216:60–62

Sears ER (1952) The behaviour of isochromosomes and telocentrics in wheat. Chromosoma 4:551–562

Sears ER (1962) The use of telocentric chromosomes in linkage mapping. Genetics 47:983

Sears ER (1966) Chromosome mapping with the aid of telocentrics. In: MacKey J (ed) Proc 2nd Int Wheat Genet Symp, Hereditas Suppl 2, pp 370–381

Sears ER (1984) Mutations in wheat that raise the level of meiotic chromosome pairing. In: Gustafson TP (ed) Gene manipulation in plant improvement. 16th Stadler Symp. Plenum Press, New York

Snape JW, Chapman V, Moss J, Blanchard CE, Miller TE (1979) The crossability of wheat varieties with *Hordeum bulbosum*. Heredity 42:291–298

Wall AM, Riley R, Gale MD (1971) The position of a locus on chromosome 5B of *Triticum aestivum* affecting homoeologous meiotic pairing. Genet Res 18:329–339