Theor Appl Genet (1985) 71:208–215

Induction of recombination between rye chromosome 1RL and wheat chromosomes

R. M. D. Koebner and K. W. Shepherd
Department of Agronomy, Waite Agricultural Research Institute, Glen Osmond, South Australia 5064, Australia

Accepted March 30, 1985
Communicated by R. Riley

Summary. The *ph1b* mutant in bread wheat has been used to induce homoeologous pairing and recombination between chromosome arm 1RL of cereal rye and wheat chromosome/s. A figure of 2.87% was estimated for the maximal frequency of recombination between a rye glutelin locus tightly linked to the centromere and the heterochromatic telomere on the long arm of rye chromosome 1R in the progeny of *ph1b* homozygotes. This equates to a gametic recombination frequency of 1.44%. This is the first substantiated genetic evidence for homoeologous recombination between wheat and rye chromosomes. No recombinants were confirmed in control populations heterozygous for *ph1b*. The *ph1b* mutant was also observed to generate recombination between wheat homoeologues.

Key words: Homoeologous pairing – Wheat/rye recombinants – *ph1b* mutant

Introduction

Following the demonstration of the role of the pairing control (*Ph*) gene on chromosome 5B of bread wheat in restricting meiotic pairing to homologues (Sears and Okamoto 1958; Riley and Chapman 1958), there has been much interest in removing this restriction so that desirable genes in related alien species can be transferred to wheat chromosomes. Three approaches have been used to achieve this aim – removal of chromosome 5B (Riley and Kimber 1966), suppression of the *Ph* gene effect by the genome of *Aegilops speltoides* (Riley et al. 1968), and mutation of *Ph* (Sears 1981).

Although many desirable characters are known to occur in cereal rye (*Secale cereale*), and the requisite wheat-rye hybrids and addition, substitution and translocation line derivatives have been available for many years (Driscoll 1984), there has been only one report claiming successful gene transfer from cereal rye to wheat by homoeologous recombination (Joshi and Singh 1978). In this example an amphihaploid suspected of being deficient for 5B or to possess a *Ph* mutation was backcrossed to euploid wheat and euploid progeny exhibiting both rye and wheat characters were thought to have been derived from homoeologous exchanges between wheat and rye chromosomes. Their published data do not, however, eliminate the possibility that these lines arose from whole chromosome substitutions or centric fusion translocations now known to occur commonly in triticale-wheat hybrids (Lukaszewski and Gustafson 1983; Merker 1984).

The recent application of the C-banding technique to the meiotic chromosomes of cereals has allowed direct observation of wheat-rye chromosome pairing. Wheat-rye pairing frequency in the presence of *Ph* is typically low (Lelley 1976; Mettin et al. 1976; Naranjo et al. 1979; Naranjo and Lacadena 1980; Jouve et al. 1980; Naranjo and Palla 1982), and even in its absence this frequency is not markedly increased (Dhaliwal et al. 1977).

To obtain genetic evidence for the ability of the *ph1b* mutant (Sears 1977) to induce homoeologous pairing and thereby genetic recombination between rye and wheat chromosomes, a translocation line involving rye chromosome arm 1RL and wheat chromosome arm 1DS was chosen as the experimental material. A translocation line, rather than a whole chromosome addition or substitution line, was used, based on the notion that, in a plant heterozygous for the translocation, the normal pairing of the short arm common to the translocation chromosome and the entire 1D would bring the homoeologous arms 1RL and 1DL physically together at meiotic prophase I and thereby encourage homoeologous pairing between these arms. Rye chromosome arm 1RL was suited to this wheat-rye recombination study, as it carries two well-spaced and easily scorable genetic markers, namely a storage protein gene and a prominent heterochromatic telomere.

Materials and methods

The steps involved in the recovery and verification of wheat-rye recombinants are illustrated in Fig. 1. A wheat-rye translocation line involving the substitution of 1DL by 1RL of 'Imperial' rye in wheat cv. 'Chinese Spring' (Lawrence and Shepherd 1981) was crossed to the *ph1b* mutant of Sears (1977). Endosperm halves of the resultant F2 progeny seed were analysed by SDS-PAGE (Lawrence and Shepherd 1980) to select plants containing both the Glu-D1 and Glu-R1 proteins, controlled by genes on the long arms of chromosomes 1D and 1R respectively (Lawrence and Shepherd 1980, 1981). The embryo halves of these translocation heterozygotes were grown and anthers at metaphase I of meiosis were collected and fixed in 3 ethanol : 1 glacial acetic acid. Pollen mother cells (PMCs) were analysed by the standard Feulgen procedure in an attempt to isolate *ph1bph1b* genotypes. Suspected *ph1bph1b* homozygotes were crossed with *Aegilops variabilis* (= *Triticum kotschyi*) to confirm their genotype (Sears 1977); four individuals deriving from each such cross were grown and cytologically investigated at meiosis as above. Progeny obtained by selfing of the *ph1bph1b* translocation heterozygotes, and, as a control, progeny of translocation heterozygotes containing one dose of *Ph1b*, were screened for their glutelin constitution by SDS-PAGE.

The embryo halves of these seeds were germinated to determine the number of rye telomeres in their root tips. After 2–3 days growth on moist filter paper, one root tip was removed from each seedling to obtain a squash preparation of meristematic cells. Three such preparations were accommodated on each slide. After removal of the coverslips, the slides were dried on a hot plate for 15–20 min. The cells were treated in 5% $Ba(OH)_2$ at 60 °C for 6 min, followed by incubation in 2×SSC at 60 °C for 15 min and staining in 0.05% Giemsa (Sigma) in phosphate buffer pH 7.0 for 10 min. No permanent mounting was necessary. The interphase nuclei stained by this method contained a number of small spots, and up to three large discrete spots (Fig. 2). Fussell (1977) has shown in *Allium cepa* that these spots correspond to the C-banded regions in mitotic chromosomes. Thus the large spots are considered to represent the rye telomeres, and the smaller ones minor regions of heterochromatin present in the chromosomes of the wheat genome (Gill and Kimber 1974). Individual progeny which possessed a different number of rye telomeres to that expected from their protein phenotype were classified as non-parental types, and were grown for progeny testing to determine whether the unusual phenotype had resulted from aneuploidy, chromosome misdivision or from a recombinational event.

Results

1 Selection of F2 plants homozygous ph1b and heterozygous for 1DS-1RL

Plants homozygous for *ph1b* would be expected to show multivalent formation at metaphase I of meiosis (Sears 1977), but this criterion alone proved to be an unreliable indicator of such genotypes. Most of the F2 plants investigated had some PMCs with multivalents – this is thought to have been the result of chromosome translocations which had been induced in earlier generations by selfing of the *ph1b* mutant parent. A better indicator of *ph1b* homozygosity was a reduction in the chiasma frequency, observed as an increase in the proportion of rods over rings among the bivalents, and a noticeably higher incidence of univalents (Driscoll et al. 1979; Yacobi and Feldman 1983; Giorgi 1983). On this basis, three plants were suspected of being homozygous *ph1b*. Mean pairing of one of the three *ph1bph1b* selections was 1.22^{I} (0–6) + 5.50^{II} (2–13) + 13.50^{III} (8–19) + 0.1^{III} (0–1) + 0.16^{IV} (0–1) from 50 PMCs (range in

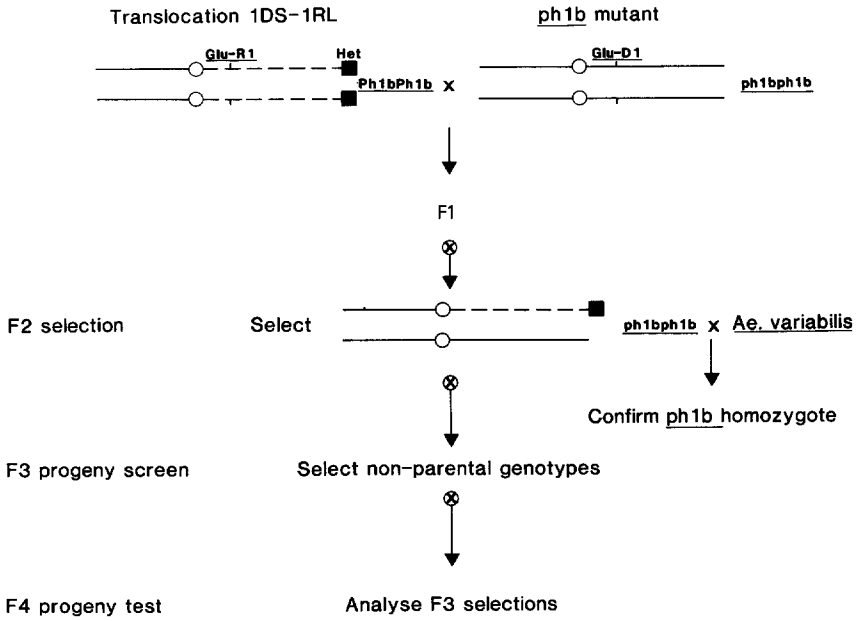

Fig. 1. Scheme for production, recovery and verification of wheat-rye recombinants

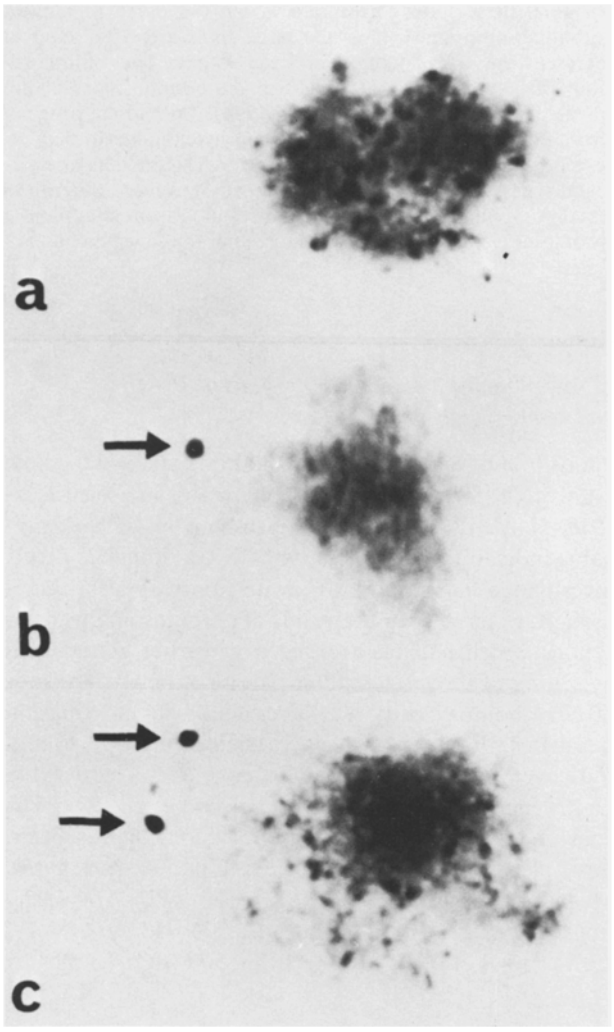

Fig. 2a–c. C-banded root tip interphase cells. **a** 0 rye telomere; **b** 1 rye telomere; **c** 2 rye telomeres. *Arrows* indicate position of rye telomeres

brackets) which contrasts with the pairing measured in eight sib plants presumed to be *Ph1b* –, namely 0.35^{I} (0–4) + 2.47^{II} (0–7) + $18.00^{(II)}$ (13–20) + 0.03^{III} (0–1) + 0.16^{IV} (0–1) from 234 PMCs. Since the identification of *ph1b* homozygotes on the basis of meiotic pairing behaviour alone was uncertain, all three selections were crossed as female to *Ae. variabilis*. The effect of the mutant allele on pairing at metaphase I of meiosis in these hybrids is similar to that in equivalent hybrids lacking chromosome 5B (Driscoll 1968). Four hybrids from each of the three selections were checked by this method and in all cases they showed a high degree of homoeologous pairing. Sears (1977) has estimated the relative transmission rate of *ph1b* through the male gamete from a heterozygote to be 0.386. Assuming that the transmission through the female gamete lies between this value and 0.5, then the probability of each selection having been *Ph1bph1b* rather than *ph1bph1b* lies between the limits of 0.022 (i.e. 0.386^4) and 0.062 (0.5^4).

2 F3 progeny: glutelin phenotype and root tip telomere number

The three confirmed homozygous *ph1b* F2 selections gave a total of 731 F3 seeds. As a control, 541 seeds were obtained by selfing of two *Ph1bph1b* translocation heterozygotes (where homoeologous pairing is presumably suppressed). The scoring of the glutelin phenotype presented no difficulties and a typical SDS-PAGE gel showing segregation for Glu-D1 and Glu-R1 is shown in Fig. 3. The data from the 3 *ph1bph1b* derived families were homogeneous for both the frequency of the glutelin phenotypes ($\chi^2_4 = 0.05$, $9.05 < P < 0.1$) and for rye telomere number ($\chi^2_4 = 9.96$, $0.02 < P < 0.05$) and were therefore pooled as shown in Table 1; similar tests on the data from the 2 *Ph1bph1b* families ($\chi^2_2 = 4.09$ and 4.03, $0.1 < P < 0.2$) also allowed pooling (Table 1).

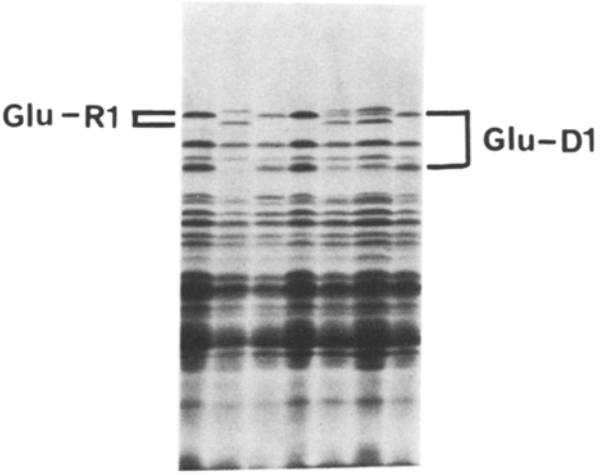

Fig. 3. SDS-PAGE patterns of F3 progeny. Note segregation of Glu-D1 and Glu-R1

Table 1. Individual segregation of glutelin phenotype and rye telomere number in two types of F3 progeny

		Glutelin phenotype			
Parental genotype	Glu-D1	+	+	–	–
	Glu-R1	–	+	+	–
ph1bph1b		264	364	102	1
Ph1bph1b		170	290	81	0
		Telomere no.			
		0	1	2	3
ph1bph1b		264	356	109	2
Ph1bph1b		171	283	87	0

If the translocation chromosome and the normal 1D segregated independently, a 1 : 2 : 1 ratio of homozygous 1D : translocation heterozygote : translocation homozygote would be expected in the F2. Inferring the chromosomal constitution of the progeny from their glutelin phenotype gives observed segregation ratios of 2.6 : 3.6 : 1 for the *ph1bph1b* genotypes and 2.1 : 3.6 : 1 for the *Ph1bph1b* genotypes. The segregation is thus distorted in favour of the gamete carrying normal 1D in both types of family. It is likely that gametes possessing translocation chromosome 1DS-1RL have a competitive disadvantage in fertilization relative to those carrying normal 1D.

The number of 1RL telomeres in the interphase nuclei of root tips normally varied from 0–2 (Fig. 2a–c) and rarely 3 (not shown). The association of the rye telomere number and the glutelin phenotype is shown in Table 2. The major difference between the *ph1bph1b* and the *Ph1bph1b* families lies in the greater diversity of non-parental classes recovered and the greater relative frequency of individuals within each class in the former families. All non-parental F3 plants were subjected to F4 progeny testing (where sufficient seed was obtained), because some of these plants (Glu-D1$^+$ Glu-R1$^+$, 2 rye telomeres; Glu-D1$^-$ Glu-R1$^+$, 1 rye telomere) could have come from aneuploidy or chromosome misdivision instead of from recombination.

3 F4 Progeny tests of non-parental F3 plants

It was not possible to progeny test all non-parental F3 plants, as some produced too few seed and others were completely sterile. This sterility seemed to be genetic in origin, since there was variation between sib plants grown in the same pot. It is likely that the chromosomal content of these sterile plants had been sufficiently disturbed during the two generations of self-fertilization in the homozygous *ph1b* condition to prevent or reduce the production of viable gametes. Sears (1977) has noted that the original isolation of the mutant was characterized by short spikes and reduced fertility.

Table 2. Joint segregation of glutelin phenotype and rye telomere number in two types of F3 progeny

		Classification of phenotype									
		Parental			Non-parental						
	Glu-D1	+	+	–	+	+	+	–	+	–	–
Parental	Glu-R1	–	+	+	–	+	+	+	+	+	–
genotype	Tel. no.	0	1	2	1	0	2	1	3	3	0
ph1bph1b		258	337	88	6	5	21	13	1[a]	1[b]	1
Ph1bph1b		170	282	80	0	1	7	1	0	0	0

[a] iso-1RL + 1DS-1RL
[b] Plant died before maturity

3.1 Glu-D1$^+$ Glu-R1$^-$, 1 rye telomere phenotype. Individuals lacking the *Glu-R1* locus should also lack the rye telomere, unless recombination has occurred. Six plants were isolated from *ph1bph1b* parents which lacked Glu-R1 and had 1 rye telomere (Table 2). Five of these gave sufficient F4 seed to confirm their identity. These progeny were uniform in their glutelin phenotype (Glu-D1$^+$ Glu-R1$^-$), but segregated for telomere number, ranging from 0–2. In these plants the linkage between the two rye characters has been broken, and they therefore must be true recombinants between rye and wheat. Further work is in progress to determine which wheat chromosomes carry the rye telomere in these recombinant lines.

3.2 Glu-D1$^+$ Glu-R1$^+$, 0 rye telomere phenotype. In the presence of the *Glu-R1* locus, at least one rye telomere should be present unless recombination or some other event has occurred. Six plants possessing both glutelin loci, but lacking a rye telomere were isolated in the F3 progeny, 5 deriving from *ph1bph1b* and 1 from *Ph1bph1b* parents (Table 2). All gave sufficient seed for progeny testing. This phenotype could have arisen from three types of event: recombination between 1RL and a wheat chromosome, spontaneous loss of terminal heterochromatin as observed by Merker (1975) in triticale and Singh and Röbbelen (1976) in wheat-rye addition lines, or mosaicism for the rye chromosome arm in the endosperm and the zygote. All F4 progeny tested lacked the 1RL telomere but segregated for the Glu-D1 and Glu-R1 proteins – thus precluding mosaicism. This phenotype is thought therefore to have originated from either wheat-rye recombination or from spontaneous loss of telomeric heterochromatin. In the absence of other genetic markers on 1RL, these events are indistinguishable.

3.3 Glu-D1$^+$ Glu-R1$^+$, 2 rye telomere phenotype. These plants differ from normal translocation heterozygotes in having an extra rye telomere. Twenty-one such plants were isolated in the *ph1bph1b* families (10 progeny tested in F4) and 7 in the *Ph1bph1b* families (5 progeny tested in F4) (Table 3). Possible origins of this non-parental phenotype include wheat-rye recombination, hyperploidy or the formation of an isochromosome involving 1RL. Recombinant plants can be distinguished from hyperploids by checking the rye telomere content of the F4 progeny lacking Glu-R1: recombinant types will have 1 or 2 telomeres, hyperploids none. Furthermore the frequency of progeny plants lacking Glu-R1 from hyperploid parents (i.e. having 2 doses of 1DS-1RL and one of 1D) will be much lower compared to the frequency from recombinant parents. From one of the non-parental F3 selections, 33 F4 seed were scored for glutelin constitution and telomere number, and the 3 progeny lacking Glu-R1 each had 1 rye telomere. Thus,

this F3 plant was classified as a wheat-rye recombinant. Altogether, three of the F3 selections from *ph1bph1b* behaved in this way, allowing them to be classified as recombinants (Table 3). Eleven of the remaining F3 selections in this phenotypic class (7 from *ph1bph1b,* 4 from *Ph1bph1b*) did not give any Glu-R1$^-$ progeny among a minimum of 30 progeny tested, and were thus classified as hyperploids (Table 3). The remaining F3 selection from *Ph1bph1b* tested in the F4 gave progeny which carried Glu-R1 but lacked both Glu-D1 as well as the *Gli-D1* locus located on 1DS, readily scorable on SDS-PAGE gels (Singh and Shepherd 1984). Furthermore, the telomeres in the root tips of these progeny fused occasionally into one large spot in the interphase nucleus, so that the telomere number varied in one preparation from 1 very large one to 2 normal-sized ones. These observations led to the conclusion that this F3 selection contained an isochromosome for 1RL (Table 3).

3.4 Glu-D1$^-$ Glu-R1$^+$, 1 rye telomere phenotype. F3 plants having Glu-R1 but lacking Glu-D1 will normally be translocation homozygotes, and thus plants with this glutelin phenotype are expected to have 2 rye telomeres. However, 13 progeny from *ph1bph1b* (10 progeny tested) and 1 from *Ph1bph1b* (not progeny tested) had this glutelin constitution, but possessed only 1 telomere. Such plants could have been derived from hypoploidy (one dose of 1DS-1RL, zero of 1D), wheat-rye recombination or spontaneous heterochromatic loss. The F4 progeny test was able to distinguish hypoploidy from the other two possible origins. The F4 progeny from the 3 plants classified as hypoploid (Table 4) segregated in a pattern typical of monosomics – for example, among 22 F4 progeny seeds from one F3 selection, 21 possessed Glu-R1 but not Glu-D1 and 1 had neither protein; among the Glu-R1$^+$ individuals, 13 had 1 rye telomere (translocation monosome) and 8 had 2 telomeres (translocation disome); the plant lacking both Glu-D1 and Glu-R1 also lacked any rye telomere (translocation nullisome). Three other F3 plants were classified as wheat-rye recombinants (or spontaneous loss of heterochromatin) (Table 4), because, whereas all progeny tested possessed the *Glu-R1* locus, some had no rye telomere present. F4 progeny of the remaining 3 non-parental F3 plants all lacked Glu-D1, but as many as a third also lacked Glu-R1. Unlike the rare Glu-D1$^-$ Glu-R1$^-$ F4 progeny from F3 plants classified as hypoploid, these null-glutelin progeny possessed the short arm of 1D, as evidenced by the presence of Gli-D1. The possibility that the F3 parent carried 1DS and 1RL as two independent telosomes can be discounted as the progeny did not segregate for 1DS. These 3 plants were thus the product of exchange between 1D and another wheat chromosome (Table 4). The single non-parental phenotype from *Ph1bph1b* was not progeny tested; however it is likely to have been hypoploid as were 3 out of the 10 analysed plants from *ph1bph1b.* The results of all the progeny tests in this class are shown in Table 4.

4 Recombination frequency between 1RL and wheat chromosome/s

Having established that the *ph1b* mutant can effect recombination between 1RL and wheat chromosome/s, it is of interest to estimate the frequency of this allo-

Table 3. F4 Progeny tests of Glu-D1$^+$ Glu-R1$^+$, 2 rye telomere phenotype

Parental genotype	No. of F3 selections	F3 selections tested in F4	Classification of F3 plant		
			Recombinant	Hyperploid	Isochromosome
ph1bph1b	21	10	3	7	0
Ph1bph1b	7	5	0	4	1

Table 4. F4 Progeny tests of Glu-D1$^-$ Glu-R1$^+$, 1 rye telomere phenotype

Parental genotype	No. of F3 selections	F3 selections tested in F4	Classification of F3 plant		
			Wheat-wheat recombinant	Wheat-rye recombinant	Hypoploid
ph1bph1b	13	10	4	3	3
Ph1bph1b	1	0			

syndetic recombination. Plants having one rye telomere in the absence of rye glutelin (Section *3.1*) can only have derived from crossing-over along the rye arm. Those plants with rye glutelin but without a rye telomere (Section *3.2*) could have arisen from recombination or from spontaneous heterochromatic loss. The latter mechanism could explain the single isolate from a *Ph1bph1b* parent; however unless this loss of heterochromatin is promoted by the *ph1bph1b* condition, the frequency of its occurrence in the control population (0.18%) is too low to account for the isolation of 5 such plants in 731 *ph1bph1b* progeny (0.68%). To derive a maximal estimate of the number of wheat-rye recombinants in this phenotypic class, it was assumed that all 5 arose from recombination. Three wheat-rye recombinants were identified among the 10 non-parental plants with an extra rye telomere progeny tested in the F4 (Section *3.3*). Extrapolating this proportion of recombinants to aneuploids to the 11 unanalysed non-parental F3 selections gives a likely further three recombinants of this type. Those plants with rye glutelin only, but having only 1 rye telomere (Section *3.4*), included three wheat-rye recombinants (Table 4) among the 10 analysed *ph1bph1b* derived progeny. Once again, extrapolating this proportion to the unanalysed three non-parental F3 selections gives a likely one additional recombinant of this type. The overall estimate for the maximum number of wheat-rye recombinant individuals produced in this study is thus 6, 5, 6 and 4 from each non-parental class respectively, giving a total of 21 in 731 progeny analysed, or 2.87%. This represents a gametic recombination frequency of 1.44%.

Discussion

Many workers (e.g. Lelley 1976) have observed that pairing between rye and wheat chromosomes does occur in the absence of *Ph1b,* albeit at a low frequency. However, until this study, no genetic evidence has been presented to show that this pairing can produce recombinants between wheat and rye. The 6 recombinant plants which possessed a distal marker (rye telomere) on the rye arm but no longer carried a proximal one (*Glu-R1*) were all recovered from homozygous *ph1b* parents, whereas *Ph1b* – parents produced very few non-parental types, all but one of which (of those analysed) were shown to be aneuploid rather than recombinant. Translocations of rye telomeres on to wheat chromosomes have been reported in triticale (Sapra and Stewart 1980) and in derivatives of triticale × wheat hybrids (Lukaszewski and Gustafson 1983); however their conclusions were based solely on C-banded karyotypes, and are not supported by any genetic evidence that the translocations observed are not further examples of whole arm exchanges, commonly seen in these genomic mixtures.

Of all the rye chromosomes, Naranjo (1982) has observed that 1R, and in particular its long arm (1RL) has the greatest pairing affinity with its wheat genome homoeologues. Thus the estimate of 1.44% for the gametic recombination frequency of 1RL with wheat chromosomes would be expected to represent the upper limit for recombination between a rye arm and wheat. Singh and Shepherd (1984) have mapped *Glu-R1* at 4.6 ± 1.0 cM from the centromere, while the telomere is physically at the distal end of the chromosome arm. Thus crossing-over could have occurred almost at any point along the arm.

Riley and Kimber (1966) observed homoeologous pairing in a nulli-5B amphiploid of wheat and *Aegilops longissima,* but concluded that full homologues paired preferentially, so that the level of allosyndetic crossing-over was low. As wheat-wheat homoeologous recombination in the presence of homologous partners was observed in our study (Table 4), and in other studies involving the induction of wheat-rye recombination between rye arm 1RS and wheat 1DS (Koebner, unpublished data), it may be that allosyndesis, at least between wheat homoeologues, is more common than was supposed. Unless individual chromosomes can be distinguished at meiosis by techniques such as C- and N-banding or in situ hybridisation with radioactive probes, cytological observation of metaphase I pairing may not show up the occurrence of homoeologous associations. The high proportion of rod bivalents to ring bivalents and the high frequency of univalents observed in *ph1b* homozygotes (Results, section *1*) is probably a reflection of homoeologous pairing, leaving homologues unpaired as univalents. The loss in fertility typical of the stock (Sears 1977) could then be due to a combination of unbalanced gametes and the accumulated chromosomal translocations mentioned earlier.

It has long been known that F2 data are much more efficient than backcross data in the estimation of linkage where complete classification of families is possible (Mather 1938). For this reason, and out of practical considerations, selfed populations rather than the more conventional test-cross populations were employed in our study. The genetic markers used are located at opposite ends of the rye chromosome arm to be recombined, so that they would be expected to show little or no linkage within rye itself. In the wheat background, by contrast, due to the absence of homologous chromatin, the loci become very tightly linked in coupling, with an estimated recombination percentage of 1.44%. Thus, in attempting to introgress alien chromatin into wheat, it is possible to use large, easily-generated F2 populations to compensate for the expected low level of recombination. The screening of these large populations requires efficient methods for the selection of rare, desirable recombinants and as demonstrated in the present study, biochemical markers are suited for this purpose. The wheat genome remains rather poorly characterised by such genetic markers and so there is a need to

develop new biochemical and molecular markers for wheat.

The cereal rye genome offers a wide, largely untapped source of genetic variation which could be of benefit to wheat improvement, and unlike the other alien relatives of wheat which are considered as potential sources of useful genetic material, rye has the advantage of itself being a domesticated crop plant with many generations of selection for agronomic characters. Tolerance to low copper environments (Graham 1984) and the reported yield advantage and disease resistances associated with the Veery 1BL-1RS translocation (Rajaram et al. 1983) are two examples of such variation. However the replacement of large segments of wheat chromatin by that of rye, as occurs in substitution and centric fusion or radiation-induced translocations often leads to problems of yield depression (Kaltsikes and Roupakias 1975) and/or quality defects (Shepherd, personal communication). It is important therefore to reduce the amount of alien chromatin introduced to the minimum consonant with the expression of the target alien gene/s. The results of this study, and the induction of wheat-rye recombination involving 1RS (Koebner, unpublished data) show that the early conclusions – based on cytological rather than genetic evidence – that rye chromosomes will not synapse with those of wheat (Riley and Kimber 1966) were unduly pessimistic. Other alien chromatin segments are presently being studied in this laboratory to produce further examples of wheat-alien recombination.

Acknowledgement. The senior author wishes to acknowledge the financial support of a University of Adelaide Scholarship for Postgraduate Research.

References

Dhaliwal HS, Gill BS, Waines JG (1977) Analysis of induced homoeologous pairing in a *Ph* mutant wheat × rye hybrid. J Hered 68:206–209

Driscoll CJ (1968) Alien transfer by irradiation and meiotic control. In: Finlay KW, Shepherd KW (eds) Proc 3rd Int Wheat Genet Symp. Plenum Press, New York, pp 196–203

Driscoll CJ (1984) Third compendium of wheat-alien chromosome lines. Suppl 6th Int Wheat Genet Symp, Kyoto

Driscoll CJ, Bielig LM, Darvey NL (1979) An analysis of frequencies of chromosome configurations in wheat and wheat hybrids. Genetics 91:755–767

Fussell CP (1977) Telomere associations in interphase nuclei of *Allium cepa* demonstrated by C-banding. Exp Cell Res 110:111–117

Gill BS, Kimber G (1974) Giemsa C-banding and the evolution of wheat. Proc Natl Acad Sci USA 71:4086–90

Giorgi B (1983) Origin, behaviour and utilization of a *Ph1* mutant of *durum* wheat, *Triticum turgidum* (L.) var. 'Durum'. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Kyoto, pp 1033–1040

Graham RD (1984) Breeding for nutritional characteristics in cereals. In: Tinker PB, Läuchli AL (eds) Advances in plant nutrition, vol 1. Praeger, New York, pp 57–102

Joshi BC, Singh D (1978) Introduction of alien variation into bread wheat. In: Ramanujam S (ed) Proc 5th Int Wheat Genet Symp. Indian Soc Genet Plant Breed, New Delhi, pp 342–348

Jouve N, Diez N, Rodriguez M (1980) C-banding in 6× triticale × *Secale cereale* L. hybrid cytogenetics. Theor Appl Genet 57:75–79

Kaltsikes PJ, Roupakias DG (1975) Endosperm abnormalities in *Triticum-Secale* combinations. 2. Addition and substitution lines. Can J Bot 53:2068–2076

Lawrence GJ, Shepherd KW (1980) Variation in glutenin subunits of wheat. Aust J Biol Sci 33:221–233

Lawrence GJ, Shepherd KW (1981) Chromosomal location of genes controlling seed proteins in species related to wheat. Theor Appl Genet 59:25–31

Lelley T (1976) Effect of nulli/tetrasomic combinations of wheat chromosomes on the pairing of rye chromosomes in triticale. Z Pflanzenzücht 77:89–99

Lukaszewski AJ, Gustafson JP (1983) Translocations and modifications of chromosomes in Triticale × wheat hybrids. Theor Appl Genet 64:239–248

Mather K (1938) The measurement of linkage in heredity. Methuen, London

Merker A (1975) Chromosome composition of hexaploid triticale. Hereditas 80:41–52

Merker A (1984) The rye genome in wheat breeding. Hereditas 100:183–191

Mettin VD, Schlegel R, Blüthner WD, Weinreich M (1976) Giemsa-bandung von MI-Chromosomen bei Weizen-Roggen-Bastarden. Biol Zentralbl 95:35–41

Naranjo T (1982) Preferential occurrence of wheat-rye meiotic pairing between chromosomes of homoeologous Group 1. Theor Appl Genet 63:219–225

Naranjo T, Lacadena JR (1980) Interaction between wheat chromosomes and rye telomeric chromatin on meiotic pairing of chromosome pair 1R of rye in wheat-rye derivatives. Chromosoma 81:249–261

Naranjo T, Palla O (1982) Genetic control of meiotic pairing in rye. Heredity 48:57–62

Naranjo T, Lacadena JR, Giraldez R (1979) Interaction between wheat and rye genomes on homologous and homoeologous pairing. Z Pflanzenzücht 82:289–305

Rajaram S, Mann ChE, Oritz-Ferrara G, Mujeeb-Kazi A (1983) Adaptation, stability and high yield potential of certain 1B/1R CIMMYT wheats. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Kyoto, pp 613–621

Riley R, Chapman V (1958) Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature 182:713–715

Riley R, Kimber G (1966) The transfer of alien genetic variation to wheat. Rep Plant Breed Inst 1964–65:6–36

Riley R, Chapman V, Johnson R (1968) Introduction of yellow rust resistance of *Aegilops comosa* into wheat by genetically induced homoeologous recombination. Nature 217:383–384

Sapra V, Stewart MD (1980) Staining of heterochromatin bands and the determination of rye chromosomes in triticale (wheat × rye hybrids). Euphytica 29:497–509

Sears ER (1977) An induced mutant with homoeologous pairing in common wheat. Can J Genet Cytol 19:585–593

Sears ER (1981) Transfer of alien genetic material to wheat. In: Evans LT, Peacock WJ (eds) Wheat science – today and tomorrow. Cambridge University Press, Cambridge, pp 75–89

Sears ER, Okamoto M (1958) Intergenomic chromosome relationships in hexaploid wheat. In: Proc 10th Int Congr Genet, Montreal, vol 2, pp 258–259

Singh NK, Shepherd KW (1984) Mapping of the genes controlling high-molecular-weight glutelin subunits of rye on the long arm of chromosome 1R. Genet Res Cam 44:117–123

Singh RJ, Röbbelen G (1976) Giemsa banding technique reveals deletions within rye chromosomes in addition lines. Z Pflanzenzücht 76:11–18

Yacobi YZ, Feldman M (1983) The control of the regularity and pattern of chromosome pairing in common wheat by the *Ph1* gene. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Kyoto, pp 1113–1118