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# Detection of QTLs for crossability in wheat using a doubled-haploid population

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**Abstract** An intervarietal molecular-marker map was used for the detection of genomic regions influencing crossability between wheat (*Triticum aestivum* L. em Thell) and rye (*Secale cereale* L.). Analysis of deviance and logistic marker-regression methods were conducted on data from doubled haploid lines from a cross between "Courtot" and "Chinese Spring". A major quantitative trait locus (QTL) involved in crossability, associated with the marker *Xfba367-5B*, was detected on the short arm of chromosome 5B. An additional locus, *Xwg583-5B*, was indicated on the long arm of chromosome 5B. This minor QTL might correspond to *Kr1* which was presumed to be the major gene controlling crossability. Another locus of the genome, *Xtam51-7A* on chromosome 7A, was significantly associated with this trait. Alleles of "non-crossability" were contributed by the non-crossable cultivar "Courtot". The three-marker model explains 65% of the difference in crossability between the two parents. The present results are discussed in relation to those previously carried out to locate the *Kr* genes by using the telocentric mapping technique.

**Key word** Crossability · Wheat · Rye · Molecular markers · QTL · *Kr* genes

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## Introduction

The crossability of hexaploid wheat (*Triticum aestivum*) with rye (*Secale cereale*) was first studied by Backhouse (1916). By using the readily crossable variety "Chinese Spring" and the poorly crossable variety "Shirno", he reported that crossability between wheat and rye was determined by a recessive genetic system. Two genes in wheat were assumed to control the wheat/rye crossability. The dominant alleles of these genes, *Kr1* and *Kr2*, are responsible for the poor crossability, *Kr1* having the strongest effect (Lein 1943). The same major genetic system governed the crossability of wheat with rye and *Hordeum bulbosum* (Snape et al. 1979; Falk and Kasha 1981), while Lein (1943) established the relationships between genotypes and phenotypes for wheat used as a female in the wheat-rye crosses. These authors proposed less than 5% crossability when the two genes were dominant (*Kr1Kr1*/*Kr2Kr2*) and more than 50% when they were both recessive (*kr1kr1*/*kr2kr2*). The intermediate genotypes *Kr1Kr1*/*kr2kr2* and *kr1kr1*/*Kr2Kr2* corresponded to 10–30 and 30–50% crossability, respectively.

*Kr1* has been assigned to chromosome 5B and *Kr2* to chromosome 5A (Riley and Chapman 1967a). Using a telocentric mapping technique, Lange and Riley (1973) mapped *Kr1* on the long arm of chromosome 5B. With the same strategy, Sitch et al. (1985) located *Kr1* and *Kr2* on the homoeologous chromosome arms 5BL and 5AL, suggesting that these two loci were homoeoallelic.

Falk and Kasha (1983) showed that there may be multiple alleles for reduced crossability with rye and *H. bulbosum* on both chromosomes 5A and 5B, using lines containing the 5A, 5B, or 5D chromosomes of the non-crossable cultivars "Hope", "Atlas 66" and "Cheyenne" substituted into the cultivar "Chinese Spring". A similar study by Sitch and Snape (1986), using the non-crossable varieties "Hope" and "Capelle-Desprez", confirmed that allelic variation exists at the

*Kr1* and *Kr2* loci. Another gene, *Kr3*, was located on chromosome 5D by Krowlow (1970) but its effect seemed to be weaker than those of *Kr1* and *Kr2* (Snape et al. 1979; Falk and Kasha 1983).

More recently, a new wheat/rye crossability gene, *Kr4*, was identified on chromosome 1A using a line from landraces of the Sichuan Province, China, which is more crossable with rye than "Chinese Spring" (Zheng et al. 1992).

Other factors of minor importance are involved in crossability between wheat and rye. Miller et al. (1983) found that the homoeologous group-3 chromosomes might carry factors affecting crossability between "Chinese Spring" and *H. bulbosum*. These results were confirmed by Romero and Cuadrado (1992) who observed an influence of chromosomes 3D and 3B on crossability. Snape et al. (1979) used "Chinese Spring", "Hope", and "Chinese Spring"/"Hope" substitution lines to determine which chromosomes controlled crossability with *H. bulbosum*. Eight chromosomes from "Hope" (1B, 1D, 2D, 3 A, 3D, 4A, 4B et 6D) appeared to promote crossability. Finally, Sitch et al. (1985) showed that an increase of crossability was associated with the absence of the short arm of chromosome 5B, suggesting that this arm carries a "suppressor of crossability" in "Chinese Spring".

Previous studies describing the location of the *Kr* genes used telocentric mapping procedures or substitution-line analyses. Recently, an intervarietal molecular map was developed using a doubled-haploid (DH) population obtained from a cross between the wheat cultivar "Chinese Spring", a readily crossing variety, and "Courtot", a non-crossable variety (Cadalen et al. 1997). The aim of the present study was to use this map to locate the *Kr* genes, and to find other regions of the genome involved in the control of crossability.

## Materials and methods

### Plant material and crossability evaluation

The mapping population consisted of DH lines and was produced at Clermont-Ferrand by anther culture from "Courtot" × "Chinese Spring" $F_1$-hybrids. This population was described by Felix et al. (1996) and Cadalen et al. (1997). One-hundred-and-ten DH lines were used in the present study to test for the presence of QTLs in the whole genome and 187 DH lines were employed to explore, more particularly, the effect of the homoeologous group-5 chromosomes.

All crosses with rye were carried out under greenhouse conditions, using wheat as the female parent. Apical and basal spikelets were removed to obtain similar stages of maturity throughout the ears. Twenty florets per ear were emasculated 2–3 days prior to anthesis. When receptive, stigmas were pollinated with fresh pollen collected from the rye cultivar "Dankowskie Nowe" previously tested for pollen viability. Three ears from one or two plants of each DH line were crossed with the rye cultivar. At maturity (about 50 days after pollination), the number of florets with or without seeds were determined separately for every spike included in the experiment. Hybrid seeds were checked individually by their size and shape. However, to estimate the distribution of the DH lines in the different crossability classes, data from the spike with the highest seed set, as an indicator of the potential crossability, and data from the sum of three ears were taken into account.

### Molecular markers and RFLP analysis

The probes used in this study, as well as the techniques for DNA extraction, digestion, electrophoresis, blotting and hybridization, were described by Cadalen et al. (1997). The protocol using non-radioactive probes was detailed in Lu et al. (1994) and Sourdille et al. (1996).

Some microsatellite sequences (Devos et al. 1995; Plaschke et al. 1995, 1996; Röder et al. 1995) were also mapped in this population. PCR reactions were performed in a final volume of 20 µl in a Perkin Elmer 9600 thermocycler. The reaction buffer contained 80 ng of template DNA, 0.2 mM of each deoxynucleotide, 1.5 mM $MgCl_2$, 500 nM of each primer, and 0.4 units of *Taq*-DNA-polymerase (Boehringer). Thirty cycles with 30 s at 94°C, 30 s between 50 and 65°C from case to case, and 30 s at 72°C were performed, followed by a final elongation step of 5 min at 72°C. The detection of microsatellites using a non-radioactive silver-nitrate staining method was described by Tixier et al. (1997).

### Statistical analysis

The map obtained from the DH population was constructed using Mapmaker/exp version 3.06 (Lander et al. 1987) as detailed by Cadalen et al. (1997).

A wheat-rye cross can be considered as a binary event (one category is the "success" of the cross and the other one is the "failure"). The total count of "successes" out of $N$ trials is a random variable, which is expected to follow a binomial law of parameters $N$, $p$, where $p$ is the common probability of success. Therefore, the classical assumptions of the linear model are not fullfiled.

However, it is known that the least-squares estimation in regression theory remains valid for non-Gaussian data. The normality assumption is only required to establish the sampling distribution of the test statistics, namely the $F$ test. Therefore, in this study, the marker linear-regression method (Kearsey and Hyne 1994) was used to estimate the additive effect of a QTL and the ratio of additive on phenotypic variance by:

$$\text{avp(additive variance part)} = a^2/\sigma_P^2,$$

which is the part of the additive variance explained by the QTL. The phenotypic variance $\sigma_P^2$ was estimated from the data of crossability measured on the 187 DH lines.

Alternatively, specific methods, such as logistic regression, have been developed in the framework of generalized linear models (glm) to accommodate non-Gaussian data, by explicitly taking into account the underlying distribution law (Mc Cullagh and Nelder 1983). These methods provide a suitable framework for hypothesis testing with binomial data. The application of logistic regression to QTL mapping has been described by Hackett and Weller (1995) and Rebaï (1997).

Logistic regression was first applied to each individual marker. We used the Wald statistical test $T = \beta/\sigma(\beta)$, where $\beta$ is the logistic regression coefficient. This statistic is asymptotically distributed as a chi-square with 1 *df*. However we observed that in the case of a binary regressor (marker genotype), this test was far from being a chi-square with 1 *df*, and that the default output of standard software led to many false positives. Therefore, we used the corrected Wald test, by dividing T by the estimated over-dispersion parameter, and compared it to a Student distribution (Collet 1991, pp 196–200). However, as this test is only asymptotically valid, we used a conservative $\alpha$ risk of 0.001 in order to keep the global risk of a type-I error below 0.05. Once the marker with the major effect was identified, we

systematically tested the addition of every marker in a glm procedure. In this case, the two models (one marker versus two markers) can be tested using the Fisher *F* statistics. Indeed, since the residual deviance showed over-dispersion, the deviances of the two models could be assumed to follow independent chi-square distributions.

Logistic regression was then adapted to the Kearsey and Hyne (1994) method of marker regression. For that purpose, the excess of 'successes' should be computed between each class of genotype for each marker along a linkage group, instead of the differences of means in linear regression. Then the residual deviance is computed at each position, x, of the putative QTL, and plotted against x. Similarly, logistic regression was extended to the two-QTL model of marker regression as proposed by Hyne and Kearsey (1995). In this latter case, the two models (one QTL versus two QTLs) can also be tested using the Fisher *F* statistic.

## Results

### Trait analysis

Because data from the highest seed set and those from the sum of the three spikes gave the same results, only the former were analysed in the following study. This allowed the presence of some non-genetic variation of seed numbers between the three spikes for some lines to be avoided.

The two parents of the DH population, "Courtot" and "Chinese Spring", were highly different: 95% success for crosses with "Chinese Spring" and only 10% with "Courtot". Differences in scores between "Courtot" and "Chinese Spring" were supposed to be mostly due to the presence of the *Kr1* gene and confirmed previous results (Gay and Bernard 1994). From these results the genotype of "Courtot" is presumably *Kr1Kr1/kr2kr2* while that of "Chinese Spring" is *kr1kr1/kr2kr2*.

Even if the shape of the distribution (Fig. 1) may indicate two major classes, the first one, the most important, with a mode of 0, and the second one with a mode of 0.6, there was no evidence for a particular genetic model with one or more major gene(s) segregating in the population.

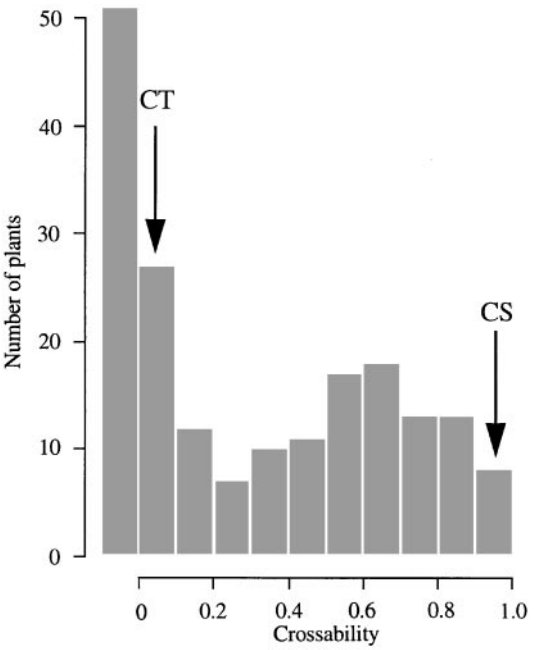


**Fig. 1** Distribution of crossability among the DH population. Crossability is measured by the ratio: number of kernels/number of pollinated florets (20) of the spike with the highest seed set. *CT* "Courtot", *CS* "Chinese Spring"

**Table 1** The marker significantly associated with wheat-rye crossability at a significant threshold of $\alpha = 0.001$. Only the most significant locus of the chromosome arm (chr) concerned is indicated. Avp, additive variance part; *df*, degree of freedom; TT, value of corrected Wald test; *P*(T), Student test probability; -Allele, origin of allele of "non-crossability"

| Marker | Chr | Avp (%) | *df* | TT | *P*(T) | -Allele | Additive effect |
|---|---|---|---|---|---|---|---|
| *Xfba367* | 5BS | 16.8 | 177 | 5.72 | 0.0000 | CT | 13.6 |

### Analysis of deviance

From an analysis of deviance the locus *Xfba367-5B* on the 5BS chromosome arm was the most strongly associated with the trait, with the allele from "Courtot" decreasing the crossability (Table 1). This was consistent with the presence of alleles for "non-crossability" in the cultivar "Courtot". However, the most surprising was the position of the marker *Xfba367-5B* on the short arm of the chromosome (Fig. 2) instead of the long arm where the location of the gene *Kr1* was expected (Sitch et al. 1985).

We did not find any marker significantly associated with crossability on chromosomes 5A and 5D. Only one locus, *Xtam51-7A* on chromosome 7A (Fig. 2), had a significant additive effect when included in a glm procedure with *Xfba367-5B* (Table 2).

### Logistic marker regression

Marker logistic regression and analysis of deviance detected the same QTLs. The minimum residual deviance with the marker logistic-regression method occurred at the most-significant marker detected by the analysis of deviance for both chromosomes 5B and 7A (Fig. 3).

The estimated additive values were 7.7 units of crossability for the QTL associated with the locus *Xtam51-7A* and 13.4 units of crossability for the QTL associated with the locus *Xfba367-5B* (Fig. 3). Because the logistic-regression method takes into account information from all the markers of a linkage group, the additive values of the QTLs computed by the model are more

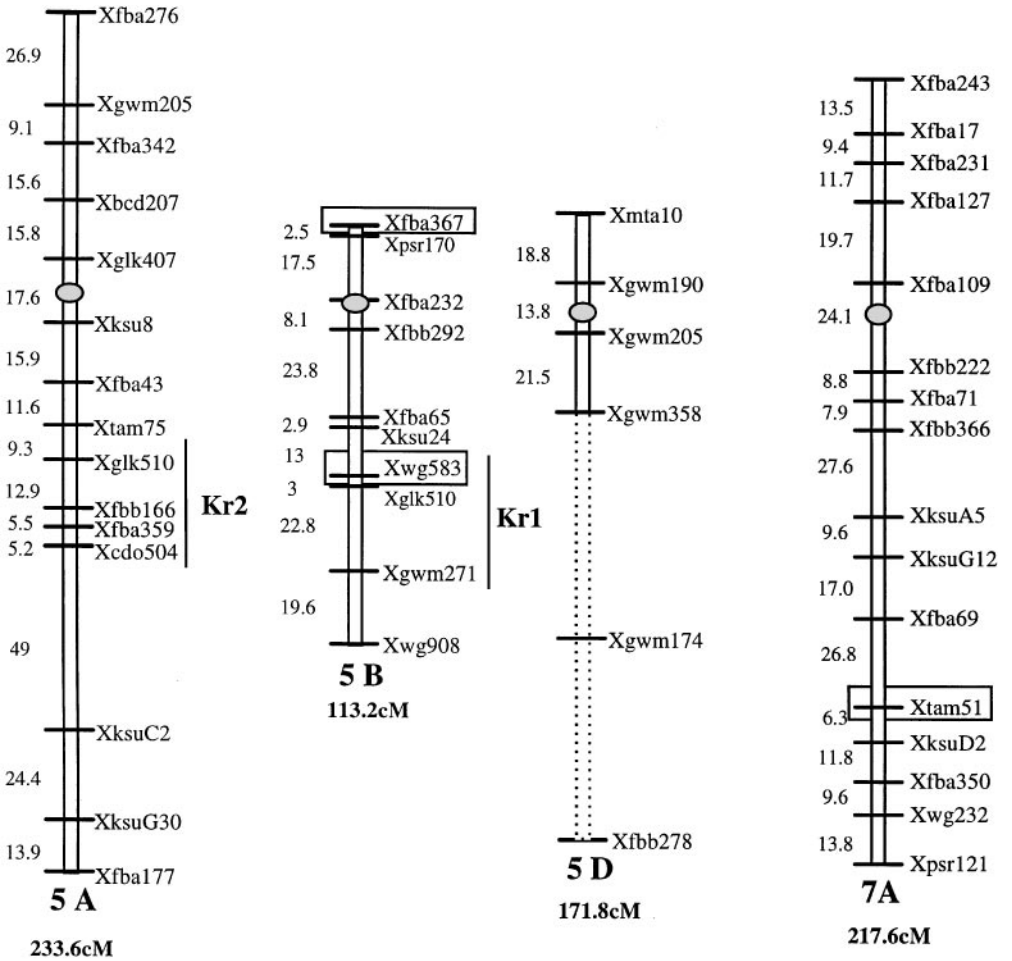


**Fig. 2** Molecular marker map of chromosomes of group 5 and of chromosome 7A of wheat. Distances on the left of the chromosomes are in centiMorgans (cM). *Dotted lines* represent genetic distances greater than 50 cM. Approximate position of the centromere is indicated by a *grey circle*. The markers involved in crossability in our study are in *boxes*

**Table 2** The marker associated with crossability at a significant threshold of $\alpha = 0.01$ when included in a model with *Xfba367-5B*. *P*(*F*), *F* probability. Other abbreviations as in Table 1

| Marker | Chr | Avp (%) | *df* | *F* value | *P*(*F*) | Allele | Additive effect |
|---|---|---|---|---|---|---|---|
| *Xtam51* | 7AL | 5.9 | 97 | 6.732 | 0.010 | CT | 8.1 |

accurate than those estimated at each marker (Tables 1 and 2). The alleles for "non-crossability" came from "Courtot", which was consistent with the fact that "Chinese Spring" is the crossable genotype.

Although the marker *Xfba367-5B* was the most significant in both methods, we could not locate this major QTL more precisely because we did not find a more distal marker on chromosome arm 5BS. This QTL had an avp value of only 16.8%.

Figure 3A shows that the one-QTL model does not fit exactly the additive value of each marker (especially near the marker *Xwg583-5B*). To study this result more thoroughly, a logistic regression marker method involving a model with two QTLs on the same chromosome was used. When this model was applied (Fig. 4), the residual deviance was significantly reduced from 55.5 to 14.9 (*F* probability = 0.014), indicating that this model was better than the one-QTL model. The additive value estimated for this minor QTL associated with *Xwg583-5B* was 6.1 units of crossability. The avp value computed for this QTL was 3.3%. This second QTL on the long arm of chromosome 5B may correspond to the *Kr1* locus which was supposed to be located at a similar position (Sitch et al. 1985).

Assuming that the three QTLs detected in our analyses are independant, the avp value explained by the model was 26%. This model contributed to 55 out of the 85 units of the difference (65%) in crossability between the two parents.

## Discussion

Although we detected the involvement of chromosome 5B in the control of crossability, the most-significant QTL was located on the short arm of this chromosome (at the location of the marker *Xfba367-5B*). The predominance of this marker confirmed a previous study

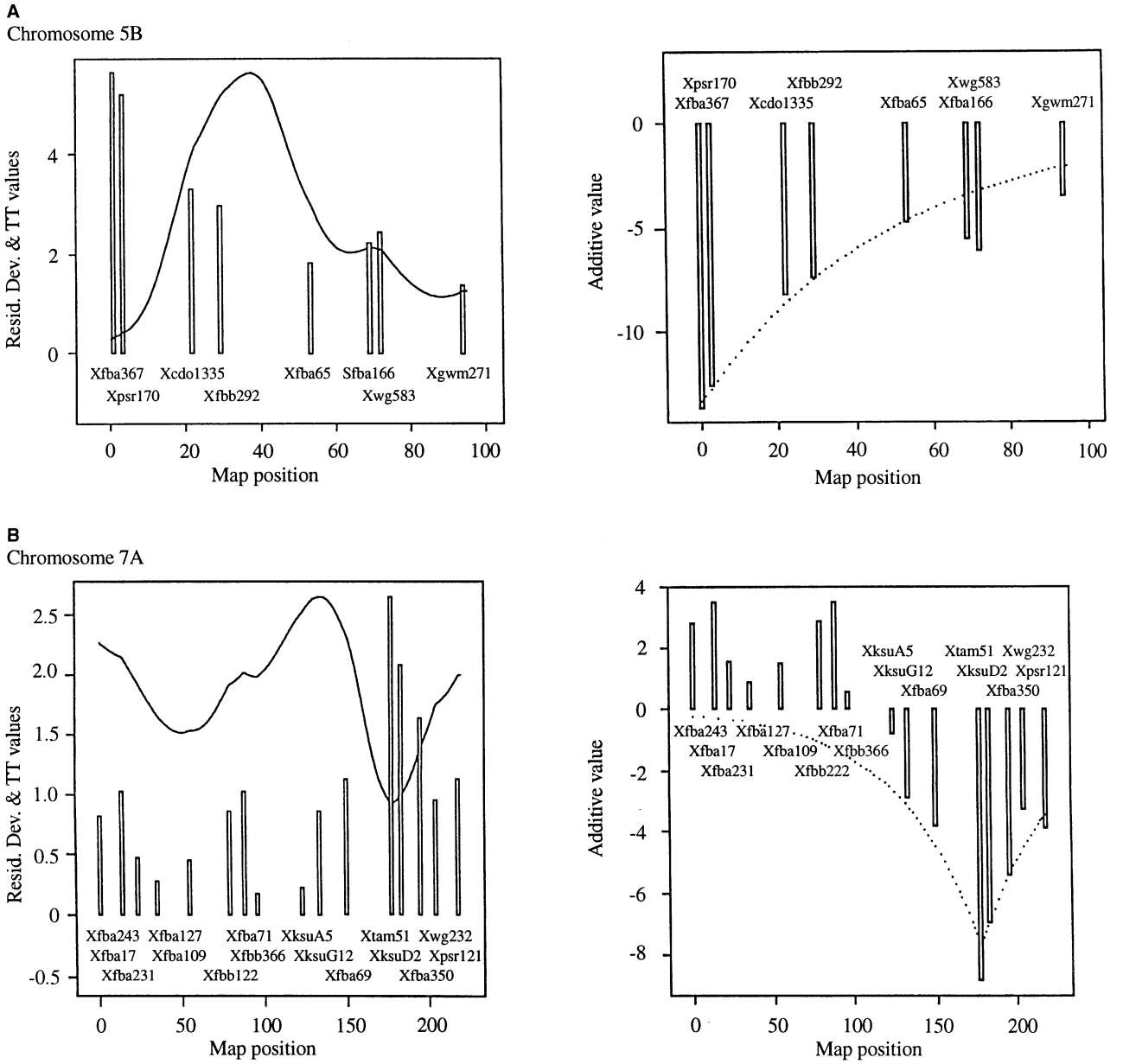


**Fig. 3A, B** Detection of loci associated with crossability in the DH population. Positions of the anchor markers are given along the abscissia in cM. The short arm of each chromosome is toward the left of each figure. The origin (*0*) indicates the first marker of the short arm. The graphs on the left represent the TT values of the corrected Wald test for each marker (*vertical bars*). The *curves* indicate the changes in residual deviances for various putative QTL positions as described in Material and methods. The *graphs* on the right represent the half-differences between the means of the two genotypics classes for each marker locus [$\frac{1}{2}(m_{Courtot} - m_{Chinese\ Spring})$: vertical bars]. The curves in *dotted lines* correspond to the additive value predicted by the model and indicate whether the allele of "non-crossability" comes from Courtot (negative values) or Chinese Spring (positive values)

performed in 1992 in our laboratory using a subset of 38 DH lines of the same population (data not shown). This result was not consistent with those of Lange and Riley (1973) and Sitch et al. (1985) who mapped the locus *Kr1* on the long arm of the chromosome 5B. Therefore, the marker *Xfba367-5B* detected a new locus controlling crossability. In the previous studies, all mapping procedures were made with the "Chinese Spring" di-telosomic 5BL line which has the recessive alleles *kr1* and *kr2* and which is crossable with rye and *H. bulbosum*. In these studies, recombination could occur only on the long arm of chromosome 5B. Thus, no effect was explored on the short arm of chromosome 5B.

On the other hand, Sitch et al. (1985), using monosomic and monotelosomic progenies derived from a cross between "Highbury" and "Chinese Spring" ditelosomic 5BL, suggested that in "Chinese Spring" the short arm of chromosome 5B carried a "suppressor of crossability" while the long arm carried the *kr* allele. This suppressor may correspond to the locus detected

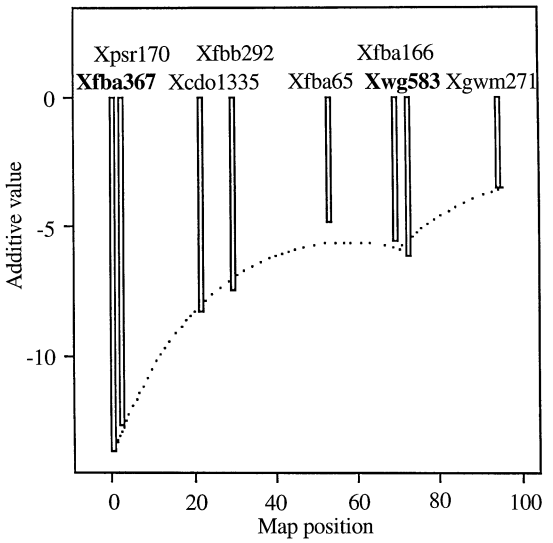


**Fig. 4** The two-QTL model. The graph represents the half-differences between the means of the two genotypic classes for each marker locus [$\frac{1}{2}(m_{Courtot} - m_{Chinese\ Spring})$: vertical bars]. The *dotted line* curve corresponds to the additive value predicted by the model and indicates whether the allele of "non-crossability" comes from Courtot (negative values) or Chinese Spring (positive values)

in the present study. Our results show that allelic variation exists for this locus on chromosome arm 5BS between "Chinese Spring" and "Courtot". This gene suppressing crossability, hereafter denoted *Skr*, appeared in the crossable genotype "Chinese Spring". The allele of "Chinese Spring" seemed to have a weaker effect than that of cv "Courtot" and thus was not able to prevent interspecific hybridization. This allele might have no effect in crosses between "Chinese Spring" and rye but might reduce crossability when "Chinese Spring" is crossed with *H. bulbosum*. To confirm these results it would be interesting to compare cv "Courtot" and "Chinese Spring", with their 5BL and 5BS ditelosomic versions, for their crossability with rye and *H. bulbosum*.

The QTL associated with the locus *Xfba367-5B* had an avp value of only 16.8%. This low value might be explained either by a large phenotypic variance, mostly due to environmental effects, or by the fact that *Xfba367-5B*, although the most distal marker on chromosome 5B, might not be very close to the *SKr* gene. If we detected a more distal marker on the chromosome we could probably locate this QTL more precisely and explain a more important part of the additive variance. Moreover, we need to determine if this locus is a "*Kr*-like" gene or if it is of a different nature.

Our results confirmed the presence of a locus controlling crossability, but with a minor effect, on the long arm of chromosome 5B. Even if homoeology relationships suggested the presence of *Kr1* closer to *Xgwm271-5B* (Sitch et al. 1985; Nelson et al. 1995) (Fig. 2), we cannot exclude the possibility that the effect associated with the marker *Xwg583-5B* was due to *Kr1*. Nevertheless, this locus on chromosome arm 5BL may also result from the presence of a new gene.

A correlation between genes affecting chromosome pairing and crossability has been reported on the homoeologous group-3 chromosomes (Miller et al. 1983). On group-5 chromosomes a similar association between these two characters was also shown. Chromosome arm 5BL carries the suppressor of homoeologous pairing, *Ph1* (Riley 1960), as well as the *Kr1* locus (Riley and Chapman 1967a). Our results confirmed that a suppressor of crossability is located on the short arm of chromosome 5B which also possesses a pairing promoter (Riley and Chapman 1967b). Chromosome 5A and 5D also carry pairing promoters (Feldman 1966) and genes affecting crossability (*Kr2* and *Kr3*). These results are interesting because both characters allow the integrity of species to be conserved. The reasons why these two characters are associated on the same homoeologous group-3 and -5 chromosomes are not known. Two hypotheses may explain such linkage: (1) both genes belong to chromosome segments involved in species integrity through reproductive isolation and the control of chromosome pairing; (2) they derive by duplication from a unique ancestral gene, each copy of which has acquired a specialization in the two different functions.

*Kr2* on the long arm of chromosome 5A was not detected in the present study. According to Lein (1943), although his classification has been questioned (Falk and Kasha 1981), the genotype *Kr1Kr1/kr2kr2* corresponded to a 10–30% range for crossability. It seems that the percentage of crossability of "Courtot" with rye (10% of success of crosses), is close to the limit, for crossability of cultivars carrying the two major genes *Kr1* and *Kr2*. Our result seems consistant with those of Gay and Bernard (1994) who showed that in "Courtot" the substitution of chromosome 5A from "Courtot" by the corresponding chromosome of the highly crossable genotypes "Norin 29" or "Fukuhokomugi" had no effect, at least in the presence of *Kr1*. Consequently, the genotype of "Courtot" at these two loci must be *Kr1* and *kr2*.

No significant effect was detected on chromosome 5D where the *Kr3* gene is located. This result may be explained by the small number of markers which were assigned to this chromosome. It is more difficult to find markers on the D-genome chromosomes because of its lack of polymorphism compared to the A and B genomes (Chao et al. 1989; Cadalen et al. 1997). Alternatively, the parental alleles of *Kr3* were perhaps identical in the "Courtot" × "Chinese Spring" cross. Anyway, the effect of the *Kr3* gene on chromosome 5D seems to be very weak (Riley and Chapman 1967a; Snape et al. 1979; Falk and Kasha 1983; Zheng et al. 1992).

Another region of the genome was involved in crossability, and the effect of the locus *Xtam51-7A* of

chromosome 7A was the more consistent. No effect of this chromosome was previously described for the control of crossability with rye or *H. bulbosum* in the literature. But it remained significant when it was included in a model with *Xfba 367-5B*. It is interesting to note that the allele for "non-crossability" is carried by "Courtot". This allele might compensate for the presence of *kr2*. Further work is needed to confirm this QTL within the same cross and other mapping populations, in order to verifiy its stability.

Thus, our study demonstrates that the main crossability effects were not obviously associated with the 5L regions thought to contain the *Kr* loci. The non-crossability of "Courtot" is mainly due to the presence of a non-crossability allele at the *Skr* locus on the short arm of chromosome 5B and is complemented by the effects of non-crossability alleles at the loci on chromosome arms 5BL (*Kr1*) and 7AL.

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