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Fine Physical Mapping of *Ph1*, a Chromosome Pairing Regulator Gene in Polyploid Wheat

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ABSTRACT

The diploid-like chromosome pairing in polyploid wheat is controlled by the *Ph1* (pairing homoeologous) gene that is located on chromosome arm 5BL. By using a combination of cytogenetic and molecular techniques, we report the physical location of the *Ph1* gene to a submicroscopic chromosome region (*Ph1* gene region) that is flanked by the breakpoints of two deletions (5BL-1 and *ph1c*) and is marked by a DNA probe (*Xksu*S1). The *Ph1* gene region is present distal to the breakpoint of deletion 5BL-1 but proximal to the C-band 5BL2.1. Two other DNA probes (*Xpsr*128 and *Xksu*75) flank the region–*Xpsr*128 being proximal and *Xksu*75 being distal. The estimated size of the region is less than 3 Mb. The chromosome region around the *Ph1* gene is high in recombination as the genetic distance of the region between 5BL-1 breakpoint and C-band 5BL2.1 (not resolved by the microscope) is at least 9.3 cM.

IN polyploid wheat, the diploid-like chromosome pairing mechanism is principally controlled by the *Ph1* (pairing homoeologous) gene that is located on the long arm of chromosome 5B (RILEY and CHAPMAN 1958; SEARS and OKAMOTO 1958). By telocentric or polymorphic C-band analyses, the *Ph1* gene was mapped at a 1–5 cM distance from the centromere (SEARS 1977; JAMPATES and DVORÁK 1986). Two mutants for the *Ph1* gene (*ph1b* and *ph1c*) are available. In a previous paper we confirmed the two mutants to be interstitial deletions (GILL and GILL 1991). We also reported a DNA fragment mapping in the *Ph1* gene deletions of the two mutants, but the exact relationship, in terms of the physical location of the *Ph1* gene and the DNA marker, was not established.

In the present study, we have mapped the gene to a submicroscopic chromosome region (*Ph1* gene region). The region is marked by a DNA probe (*Xksu*S1), bracketed by breakpoints of two deletion lines (5BL-1 and *ph1c*) and is flanked by two other DNA probes (*Xksu*75 and *Xpsr*128). The estimated size of the *Ph1* gene region is less than 3 Mb.

MATERIALS AND METHODS

The *Ph1* gene mutant lines: The two interstitial deletion mutants of the *Ph1* gene (*ph1b* and *ph1c*), used in the study, were generated independently using X-ray irradiation (SEARS 1977; GIORGI and BARBERA 1981). The mutant *ph1b* is in hexaploid wheat (*Triticum aestivum* L. em. Thell.) cultivar Chinese Spring (CS) whereas the mutant *ph1c* is in tetraploid wheat (*Triticum turgidum* L.) cultivar Cappelli (CPP). A 'CPP' stock (dup. *Ph1*) with a duplicated interstitial region, encompassing the *Ph1* gene, is also available (DVORÁK, CHEN and GIORGI 1984). All the mutant lines were used to identify DNA fragments mapping in the *Ph1* gene deletions.

Chromosome deletion lines: The chromosome deletion lines used for the physical mapping of the *Ph1* gene and restriction fragment length polymorphism (RFLP) markers were generated using the gametocidal chromosome of *Triticum cylindricum* (ENDO 1988; T. R. ENDO and B. S. GILL, unpublished). The deletion lines were characterized by C-banding analysis (GILL and KIMBER 1974; ENDO 1988).

Chromosome 5B recombinant population: Chromosome 5B disomic substitution line of *Triticum dicoccoides* in 'CS' (produced by late E. R. SEARS) was crossed to 'CS.' The F_1 was crossed as a male to monotelosomic 5BL. Plants with 41 chromosomes (lacking telosomic 5BL) were selected and allowed to self in order to recover recombinant 5B chromosomes in disomic condition. Fifty-eight recombinant lines were isolated and used for genetic mapping of chromosome 5B-specific RFLP markers.

All the genetic and aneuploid stocks are maintained at the Wheat Genetic Resource Center (WGRC), Kansas State University, Manhattan, Kansas.

Arm ratio/arm fraction length (FL) measurements: A mean of five chromosomes was used for chromosome measurements of the deletion lines and of 10 for the mutant lines. Standard errors were also calculated for the comparison of the chromosome measurements. The arm ratios were calculated by dividing the long arm measurements with that of the short arm. The FL values for the deletion breakpoints were calculated by dividing the arm ratio of the deletion chromosome with that of the normal homolog. The FL values for the C-bands were calculated from the distance of the C-band from the centromere divided by the total arm length. The FL of chromosome 5BL of the mutant lines was calculated by dividing the arm ratio of the mutant line with that of the respective wild-type counterpart ('CS' or 'CPP').

Scoring of the *Ph1* gene: The *Ph1* gene was scored for all the mutant and the deletion lines used in the study. The mutant lines, and the deletion lines either homozygous or

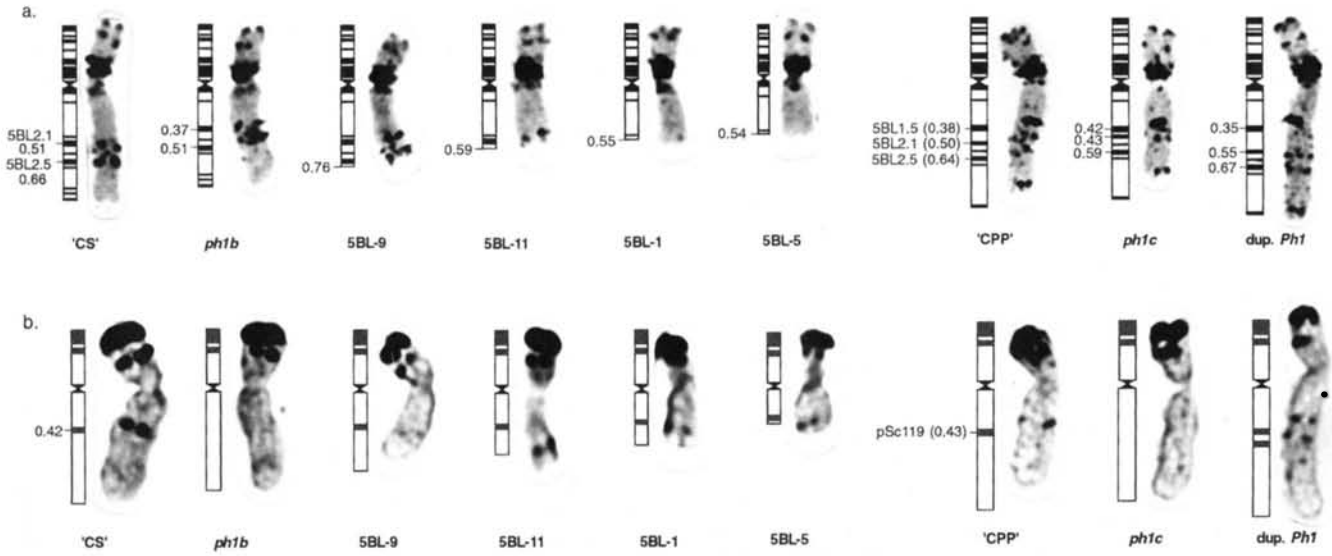

FIGURE 1.—(a) Karyotypic and idiogrammatic representation of C-banding patterns of chromosome 5B in 'CPP,' 'CS' and various mutant and chromosome 5BL deletion lines. The FL position of the C-bands and of the breakpoints is given on the left. (b) The ISH pattern of probe pSc 119 on chromosome 5BL of the mutant and the deletion lines. The ISH site at FL 0.42 (0.43 in 'CPP') is present in all the deletion lines, absent in the two mutant lines (*ph1b* and *ph1c*), and present in tandem duplication in dup. *Ph1*.

heterozygous for the deletion 5B chromosome, were crossed with *Triticum peregrinum* (syn. *Aegilops variabilis*). For the mutant lines and homozygous deletion lines, two F_1 seeds (from the cross with *T. peregrinum*) were analyzed by C-banding of mitotic metaphase chromosomes (ENDO 1988). For the heterozygous deletion lines, however, mitotic metaphase chromosomes of 10 F_1 plants were analyzed in order to identify the F_1 plants with the appropriate deletion in the 5BL chromosome. The meiotic metaphase 1 (M1) chromosome pairing was then studied on the selected F_1 plants. For each plant, chromosome pairing data of 10–20 cells were pooled. The chromosome pairing frequencies were compared with those of control F_1 ('CS' × *T. peregrinum*).

DNA analysis: Chromosome 5D-specific DNA probes from the D genome RFLP map (GILL *et al.* 1991; K. S. GILL, unpublished) were used for gel blot DNA hybridization analysis of the mutant and the deletion lines. The probes, interchromosomally mapped on wheat homoeologous group 5, were also used (generously provided by MARK SORRELLS and MIKE GALE). Wheat homoeologous group 5 nullisomic-tetrasomic and ditelosomic lines of 'CS' (SEARS 1954, 1966) were used to map DNA fragments to their respective arms of group 5 chromosomes. The gel blot DNA hybridization analysis techniques were as previously described (GILL *et al.* 1991; GILL and GILL 1991).

***In situ* hybridization (ISH) analysis:** The repetitive DNA probe pSc 119 (BEDBROOK *et al.* 1980) detects an ISH band on chromosome 5BL (RAYBURN and GILL 1985). Therefore, the probe was used for ISH analysis of the deletion and mutant lines. The ISH analysis was as described previously (RAYBURN and GILL 1985; MUKAI, ENDO and GILL 1991).

RESULTS AND DISCUSSION

Deletion line characterization: The chromosome 5BL deletion lines used in the study were characterized by their arm ratio (FL) and the C-banding pattern (Figure 1a). The C-banding pattern of the long arm of chromosome 5B of wheat is very distinct. In addition to the major centromeric band, there are three major C-bands (5BL1.5, 5BL2.1 and 5BL2.5) [chromosome banding nomenclature is according to GILL, FRIEBE and ENDO (1991)]. The hexaploid wheat cultivar 'CS' and tetraploid wheat cultivar 'CPP' are polymorphic for the band 5BL1.5 that is present in 'CPP' but absent in 'CS.'

Chromosome deletions generated by the gametocidal chromosome of *T. cylindricum* arise from a single break followed by the loss of the distal chromosome region (ENDO 1990; GILL, GILL and ENDO 1992). The breakpoints of the deletions 5BL-9, 11, 1 and 5 are at FL 0.76, 0.59, 0.55 and 0.54, respectively. The breakpoint measurements of the deletion lines are independent of their position relative to the C-bands because the breakpoint FL values were calculated by dividing the arm ratio of the deletion line with that of the normal. The length of all the deletion chromosome arms is more than the expected based on the position of the breakpoint relative to the C-bands. For example, the breakpoint of the deletion 5BL-1 is just proximal to the C-band 5BL2.1 at FL 0.51 whereas the estimated FL value for the breakpoint is 0.55. Similarly, the FL value (0.59) for the deletion 5BL-11 indicates the breakpoint to be in the distal half of the chromosome region between the C-bands 5BL2.1 and 5BL2.5 (at FL 0.51 and 0.66, respectively) whereas the breakpoint actually is closer to the C-band 5BL2.1 compared to 5BL2.5 (Figure 1a). The discrepancy could not be an estimation error because the observation is consistent with deletion lines for other wheat chromosomes also (T. R. ENDO and B. S. GILL, unpublished). Two hypotheses can be proposed

to explain the increment in the length of the deletion chromosome arms. Either the chromatin of the deletion chromosome arm does not package as efficiently as the chromatin of the normal arm during mitosis, or a chromosome segment is added to the sticky end of deletion arm. The ends of the deletion chromosome arms possess telomeric sequence although there are no interstitial telomeric ISH sites in normal wheat chromosomes (WERNER *et al.* 1992). However, the discrepancy is for the position of the breakpoint relative to the C-bands rather than the total length of the arm. Therefore, the chromatin of the deletion chromosomes does not package as efficiently as it does for the normal chromosomes, and thus appears longer.

***Ph1* gene scoring:** SEARS (1977) described a reliable approach to score *Ph1* gene. The material under study is crossed to a tetraploid wild relative *T. peregrinum* (US) and chromosome pairing of the F_1's is studied. In the presence of *Ph1* gene, mostly univalents are observed at meiotic M1. In the absence of the gene, however, bivalents or higher order chromosome association are observed.

The *Ph1* gene was scored on the 5BL deletion lines as described above. The deletion lines 5BL-9 and 5BL-11, at M1, had an average chromosome association of 3.2 II (bivalents) + 29.8 I (univalents) and 1.5 II + 32 I, respectively, thus, possess the *Ph1* gene. The deletion lines 5BL-1 and 5BL-5, however, had an average of 0.4 IV (quadrivalents) + 1.5 III (trivalents) + 8.9 II + 14.1 I and 0.4 IV + 2.1 III + 7.9 II + 9.3 I, respectively, indicating the absence of the *Ph1* gene. Since deletion 5BL-1 is the smallest deletion where *Ph1* gene is missing and 5BL-11 is the largest deletion where it is present, the *Ph1* gene is present in the chromosome region between FL 0.55 and 0.59 [the breakpoints of deletion 5BL-1 and 5BL-11, respectively (Figure 1a)].

Comparison of FL position of the C-bands: The C-banding pattern of chromosome 5B of *ph1b* is very similar to that of wild-type 'CS' (Figure 1a). All the prominent C-bands of 'CS' are present in the mutant. Based on the visual comparison of the morphology of chromosome 5BL of *ph1b* with that of the normal 'CS,' we reported the *Ph1* gene deletion to be submicroscopic (GILL and GILL 1991). However, the C-bands 5BL2.1 and 5BL2.5 in *ph1b* are present at FL 0.37 and 0.51, respectively, compared to at FL 0.51 and 0.66 in 'CS.' The ratio of the chromosome region between centromere and the C-band 5BL2.1 by the short arm is 0.744 in *ph1b* compared to 1.000 in 'CS.' Therefore, the chromosome region between centromere and C-band 5BL2.1 possesses an interstitial deletion in *ph1b*. The total length of 5BL is 8.08 μm (GILL, FRIEBE and ENDO 1991). The size of the deletion is, therefore, 1.05 μm (the size of the region in *ph1b* is 3.07 μm compared to 4.12 μm in 'CS'). The deletion must be present just proximal to the C-band 5BL2.1 as a minor C-band at FL 0.47 in 'CS' is missing in *ph1b* (Figure 1a). The chromosome region distal to the C-band 5BL2.1 of *ph1b* is morphologically unchanged because the ratio of the region by the short arm is 0.969 and 1.004 in *ph1b* and 'CS,' respectively.

TABLE 1

DNA analysis data of the *Ph1* mutant lines and chromosome 5BL deletion lines using wheat homoeologous group 5-specific probes

	CS	5BL-11	5BL-1	*ph1b*	*ph1c*	Dup. *Ph1*
Break point (FL)		0.59	0.55			
pSc119	+	+	+	−	−	++
*Xpsr*128	+	+	+	−	−	++
*Xksu*S1	+	+	−	−	−	++
Ph1 gene	+	+	−	−	−	++
*Xksu*75	+	+	−	−	+	+
*Xksu*24	+	+	−	+	+	+

The *Ph1* gene scoring data are also given. "+" indicates the presence of the marker, whereas, "−" indicates absence.

The three interstitial C-bands of 5BL of 'CPP' are located at FL 0.38, 0.50 and 0.64 (Figure 1a). In the mutant *ph1c* the bands are present at FL 0.42, 0.43 and 0.59. The chromosome region between C-bands 5BL1.5 and 5BL2.1, and 5BL2.1 and 5BL2.5 is 0.97 μm and 1.13 μm, respectively (calculated from the FL values). The same chromosome regions in *ph1c* are 0.08 and 1.14 μm, respectively, indicating a deletion spanning 0.89 μm in the chromosome region between C-bands 5BL1.5 and 5BL2.1. The C-bands 5BL1.5, 5BL2.1 and 5BL2.5 in the dup. *Ph1* are located at FL 0.35, 0.55 and 0.67. The chromosome region between the C-band 5BL1.5 and 5BL2.1 in dup. *Ph1* is 1.8 μm compared to 0.96 μm in 'CPP.' Therefore, the size of the duplicated region is 0.84 μm. The size and the location of the duplication region suggest that chromosome region deleted in *ph1c* and duplicated in dup. *Ph1* is probably the same.

Our 'CPP' mutants characterization results confirm the findings of JAMPATES and DVORÁK (1986). They proposed the interstitial deletion of *ph1c* to be present between 5BL1.5 and 5BL2.1. They also interpreted that the duplicated region of dup. *Ph1* is the same as the deleted region of *ph1c*.

ISH analysis: The ISH site for the probe pSc 119 on chromosome 5BL is present at FL 0.42 in 'CS' and at FL 0.43 in 'CPP' (Figure 1b). The ISH band that is present in all the deletion lines, however, is missing in the mutants *ph1b* and *ph1c*. The ISH site is present in the duplicated region of the dup. *Ph1* (Figure 1b). These results agree with the results of C-banding characterization of the deletion and the mutant lines. The breakpoint FL of all the deletion lines is more than 0.42, and, thus possess the ISH site. The estimated size of the chromosome region between the ISH site and 5BL2.1 is 0.72 μm (0.09 FL of 8.08 μm).

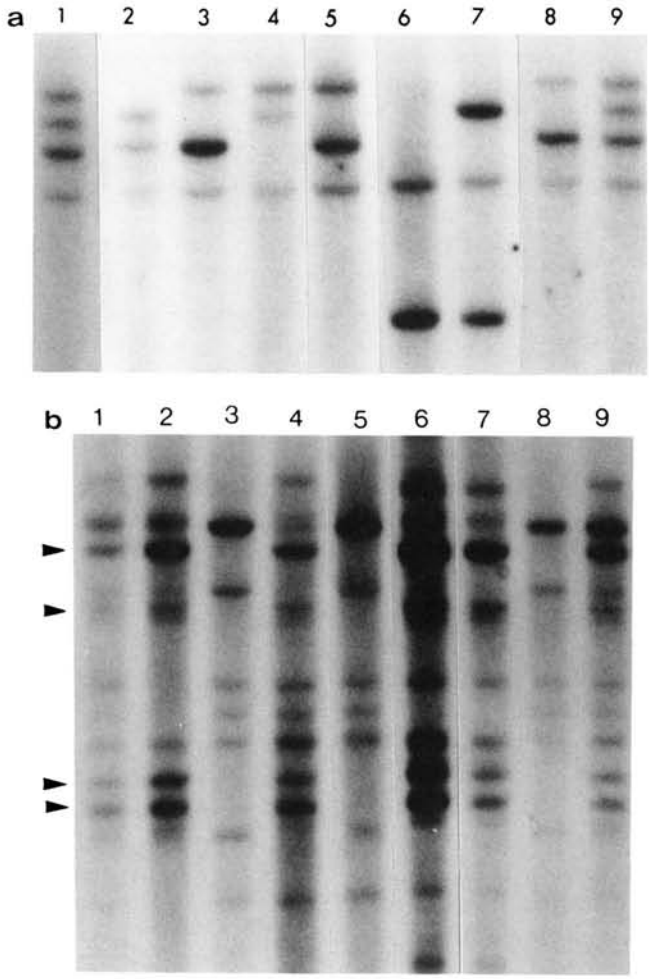

FIGURE 2.—Fifteen micrograms of *Hin*dIII digested genomic DNA were separated on 0.8% agarose gel and transferred to MSI membrane. The hybridization was performed in 50% formamide, 6 × SSPE, and 0.5% SDS at 42°. Lanes: 1, 'CS'; 2, NT5A(5B); 3, NT5B(5D); 4, NT5D(5A); 5, *ph1b*; 6, *ph1c*; 7, dup. *Ph1*; 8, 5BL-1 and 9, 5BL-11. (a) Hybridization with *Xksu*S1 and (b) with *Xksu*75.

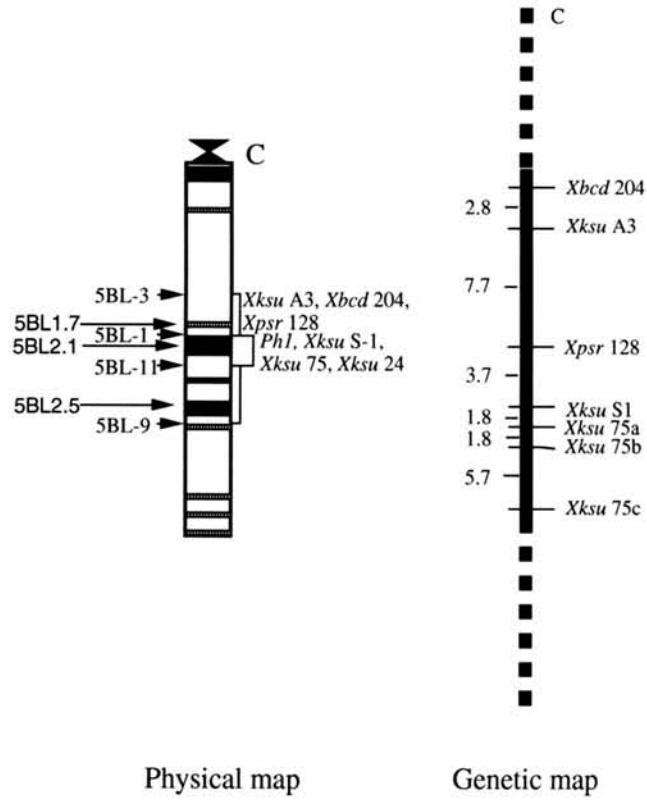

FIGURE 3.—Physical and genetic map of chromosome 5BL region around the *Ph1* gene. The deletion breakpoints are marked on the left of the physical map and the probe positions are indicated on the right. On the genetic map, the distance (in cM) between the markers is given on the left.

The deletions of the mutants *ph1b* and *ph1c* are 1.05 and 0.89 μm, present proximal to 5BL2.1. Therefore, the ISH site is missing in both the mutant lines.

Gel blot DNA analysis: We analyzed the mutant and the deletion lines by gel blot DNA hybridization analysis, using chromosome group 5 long arm specific probes, and the results are summarized in Table 1 and Figure 3. We identified 3 (out of 20) probes (*Xksu*S1, *Xpsr*128 and *Xksu*75) that mapped in the *Ph1* gene deletion of *ph1b* as each probe detected missing chromosome 5BL fragment(s) in *ph1b* (Figure 2, a and b). By deletion mapping the probes *Xksu*75 and *Xksu*S1 mapped in the chromosome region between the breakpoints of deletions 5BL-1 and 5BL-11, the same chromosome region where the *Ph1* gene mapped. The probe *Xpsr*128, however, mapped proximal to the breakpoint of the deletion 5BL-1.

The probes *Xksu*S1 and *Xpsr*128 detected missing 5BL fragments in *ph1c* also, whereas *Xksu*75 detected normal 5BL fragment bands (Figure 2b). In the dup. *Ph1*, the probes *Xksu*S1 and *Xpsr*128 detected the 5BL fragment band in twice the intensity of the normal 'CPP,' therefore, are present in the duplicated chromosome region (Figure 2a). The molecular data confirmed the cytological evidence of duplication.

The probe *Xksu*24 also mapped in the same chromosome region where *Ph1* gene mapped (in the chromosome region between the breakpoints of deletions 5BL-1 and 5BL-11). In the *Ph1* gene mutants (*ph1b*, *ph1c* and the dup. *Ph1*), however, the probe *Xksu*24 detected normal 5BL fragment bands.

The RFLP probes present around the *Ph1* gene were genetically ordered using 5B recombinant population (see MATERIALS AND METHODS) and data were analyzed using computer software "MAPMAKER." Figure 3 shows a partial physical and genetic linkage maps of chromosome 5BL of wheat. The order of the loci in the physical map agrees to that of the genetic map. On the genetic map the probe *Xpsr*128 is present proximal to *Xksu*S1 and *Xksu*75 maps distal. The probe *Xksu*75 detects three loci clustered in chromosome region spanning 7.5 cM. The chromosome region around the *Ph1* gene is high in recombination as the genetic length of the submicroscopic region (see next section) spanning *Xksu*75 and *Xksu*S1 is at least 9.3 cM.

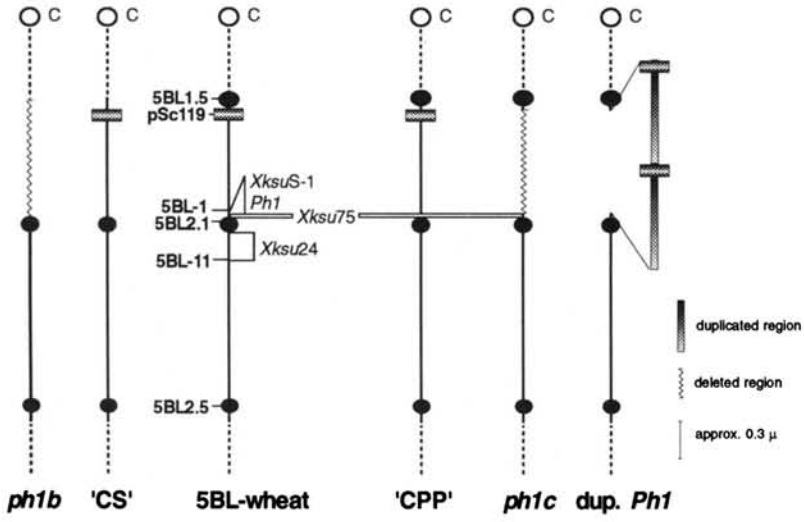

FIGURE 4.—Diagram shows the location of the *Ph1* gene with respect to the DNA and cytological markers. The chromosome regions deleted in the mutants *ph1b* and *ph1c* and the region duplicated in the duplication line are also shown.

Physical location of the *Ph1* gene: The deletion mapping located the *Ph1* gene in the chromosome region between the breakpoints of deletion 5BL-1 (FL 0.55) and 5BL-11 (FL 0.59). The breakpoint of deletion 5BL-1 is proximal to the C-band 5BL2.1. The breakpoint is probably on the proximal end of 5BL2.1 because: (i) the FL of deletion arm is 0.55 compared to FL 0.51 of the C-band 5BL2.1 and (ii) a minor C-band at FL 0.47 and the chromosome region between the minor band and 5BL2.1 is present in deletion 5BL-1 (Figure 1a). The *Ph1* gene deletions of *ph1b* and *ph1c*, however, are present proximal to 5BL2.1. Therefore, the *Ph1* gene is present proximal to the C-band 5BL2.1 but distal to the breakpoint of deletion 5BL-1. This chromosome region cannot be resolved by the microscope.

On the genetic map, the probe *Xksu*S1 is present proximal to the centromere and *Xksu*75 being distal (Figure 3). The probe order and their relative distances are the same in *T. tauschii* also (GILL *et al.* 1991; K. S. GILL, unpublished). For the mutant *ph1c*, only the probe *Xksu*S1 maps in the *Ph1* gene deletion whereas the probe *Xksu*75 detects normal DNA fragment bands. Therefore, the distal breakpoint of the *Ph1* gene deletion of *ph1c* mutant is in the chromosome region between *Xksu*S1 and *Xksu*75. The breakpoint of *Ph1* gene deletion of *ph1b* is present distal to the breakpoints of 5BL-1 and *ph1c*. The probe *Xksu*75 is flanked by the distal breakpoint of *ph1c* and the C-band 5BL2.1. The *Ph1* gene along with the probe *Xksu*S1 is, therefore, present in the chromosome region between the breakpoints of deletion 5BL-1 and *ph1c* (*Ph1* gene region).

The probe *Xksu*24 maps in the same chromosome region where the *Ph1* gene maps, however, in the region that is not deleted or duplicated in the mutant lines. Since the chromosome region deleted or duplicated in the mutant lines maps proximal to the C-band 5BL2.1, the probe *Xksu*24 maps either in or distal to the C-band. Because of lack of polymorphism (after testing with 20 restriction enzymes) we were unable to genetically map the probe in wheat. Probably because of fewer markers, the probe *Xksu*24 seemed to map on the short arm of 5D in *T. tauschii* (GILL *et al.* 1991). However, on our current *T. tauschii* map, the probe maps 14 cM distal to *Xksu*75 (K. S. GILL, unpublished).

The resolution of the light microscope is 0.2 μm which for wheat chromosomes translates to about 14 Mb of DNA. The genetic distance of the chromosome region spanned by *Xksu*S1 and *Xksu*75 is at least 9.3 cM. Since the probes *Xksu*S1 and *Xksu*75 are 1.8 cM apart, the *Ph1* gene region is smaller than the rest of the submicroscopic region distal to it. The estimated size of the *Ph1* gene region is, therefore, less than 3 Mb.

The fine physical mapping data of *Ph1* gene are summarized in Figure 4. In summary, the *Ph1* gene, along with the DNA marker *Xksu*S1, is present in a submicroscopic chromosome region (*Ph1* gene region) between the breakpoints of deletion 5BL-1 and *ph1c*. The breakpoint of *ph1b* is present distal to *Ph1* gene region but proximal to 5BL2.1–the region that is also submicroscopic and possesses *Xksu*75. The probe *Xpsr*128 is present proximal to the *Ph1* gene region. The chromosome region around the *Ph1* gene is high in recombination, as the genetic distance of the region spanned by *Xksu*S1 and *Xksu*75 is at least 9.3 cM. The chromosome region is also prone to breaks, as the breakpoints of the mutants *ph1b*, *ph1c* and dup. *Ph1* also map in the region.

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LITERATURE CITED

BEDBROOK, J. R., J. JONES, M. O'DELL, R. J. THOMPSON and R. B. FLAVELL, 1980 A molecular description of telomeric hetero-

chromatin in Secale species. Cell **19:** 545–560.

DVORÁK, J., K.-C. CHEN and B. GIORGI, 1984 The C-banding pattern of a *Ph*-mutant of durum wheat. Can. J. Genet. **26:** 360–363.

ENDO, T. R., 1988 Induction of chromosomal structural changes by a chromosome of *Aegilops cylindrica* L. in common wheat. J. Hered. **79:** 366–370.

ENDO, T. R., 1990 Gametocidal chromosomes and their induction of chromosome mutations in wheat. Jpn. J. Genet. **65:** 135–152.

GILL, B. S., and G. KIMBER, 1974 Giemsa C-banding and the evolution of wheat. Proc. Natl. Acad. Sci. USA **74:** 4086–4090.

GILL, B. S., B. FRIEBE and T. R. ENDO, 1991 Standard karyotype and nomenclature system for description of chromosome bands and structural aberrations in wheat (*Triticum aestivum*). Genome **34:** 830–839.

GILL, K. S., and B. S. GILL, 1991 A DNA fragment mapped within the submicroscopic deletion of *Ph1:* a chromosome pairing regulator gene in polyploid wheat. Genetics **129:** 257–259.

GILL, K. S., and B. S. GILL and T. R. ENDO, 1992 A chromosome region-specific mapping strategy reveals gene-rich telomeric ends in wheat. Chromosoma (in press).

GILL, K. S., E. L. LUBBERS, B. S. GILL, W. J. RAUPP and T. S. COX, 1991 A genetic linkage map of *Triticum tauschii* (DD) and its relationship to the D genome of bread wheat (AABBDD). Genome **34:** 362–374.

GIORGI, B., and F. BARBERA, 1981 Increase of homoeologous pairing in hybrids between a *ph* mutant of *T. turgidum* L. var. *durum* and two tetraploid species of *Aegilops*: *Aegilops kotschyi* and *Ae. cylindrica*. Cereal Res. Commun. **9:** 205–211.

JAMPATES, R., and J. DVORÁK, 1986 Location of the *Ph1* locus in the metaphase chromosome map and linkage map of the 5Bq arm of wheat. Can. J. Genet. Cytol. **28:** 511–519.

MUKAI, Y., T. R. ENDO and B. S. GILL, 1991 Physical mapping of the 18S-26S rRNA multigene family in common wheat: identification of a new locus. Chromosoma **100:** 71–78.

RAYBURN, A. L., and B. S. GILL, 1985 Use of biotin-labeled probes to map specific DNA sequences on wheat chromosomes. J. Hered. **76:** 78–81.

RILEY, R., and V. CHAPMAN, 1958 Genetic control of the cytologically diploid behavior of hexaploid wheat. Nature **182:** 713–715.

SEARS, E. R., 1954 The aneuploids of common wheat. Mo. Agric. Exp. Stn. Res. Bull. **572:** 19.

SEARS, E. R., 1966 Nullisomic-tetrasomic combinations in hexaploid wheat, pp. 370–381 in *Chromosome Manipulations and Plant Genetics*, edited by R. RILEY and K. R. LEWIS. Oliver & Boyd, London.

SEARS, E. R., 1977 An induced mutant with homoeologous pairing in common wheat. Can. J. Genet. Cytol. **19:** 585–593.

SEARS, E. R., and M. OKAMOTO, 1958 Intergenomic chromosome relationship in hexaploid wheat. Proc. Tenth Int. Congr. Genet. **2:** 258–259.

WERNER J., R. S. KOTA, B. S. GILL and T. R. ENDO, 1992 Distribution of telomeric repeats and their role in the healing of broken chromosome ends in wheat. Genome **35:** 844–848.

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