Molecular Mapping of Wheat: Major Genes and Rearrangements in Homoeologous Groups 4, 5, and 7

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ABSTRACT

A molecular-marker linkage map of hexaploid wheat (*Triticum aestivum* L. em. Thell) provides a framework for integration with the classical genetic map and a record of the chromosomal rearrangements involved in the evolution of this crop species. We have constructed restriction fragment length polymorphism (RFLP) maps of the A-, B-, and D-genome chromosomes of homoeologous groups 4, 5, and 7 of wheat using 114 F_7 lines from a synthetic × cultivated wheat cross and clones from 10 DNA libraries. Chromosomal breakpoints for known ancestral reciprocal translocations involving these chromosomes and for a known pericentric inversion on chromosome 4A were localized by linkage and aneuploid analysis. Known genes mapped include the major vernalization genes *Vrn1* and *Vrn3* on chromosome arms 5AL and 5DL, the red-coleoptile gene *Rc1* on 7AS, and presumptively the leaf-rust (*Puccinia recondita* f.sp. *tritici*) resistance gene *Lr34* on 7DS and the kernel-hardness gene *Ha* on 5DS. RFLP markers previously obtained for powdery-mildew (*Blumeria graminis* f.sp. *tritici*) resistance genes *Pm2* and *Pm1* were localized on chromosome arms 5DS and 7AL.

MUCH effort is presently directed at the production of genetic maps in the grass species that constitute the staple crops of humankind. Recent work in this area includes maps of barley, *Hordeum vulgare* L. (HEUN *et al.* 1991; GRANER *et al.* 1991, 1994; KLEINHOFS *et al.* 1993), rice, *Oryza* spp. (MCCOUCH *et al.* 1988; SAITO *et al.* 1991; CAUSSE *et al.* 1994; KURATA *et al.* 1994b), diploid and hexaploid oat (O'DONOUGHUE *et al.* 1992, 1995) and the diploid D-genome progenitor of cultivated wheat, *Triticum tauschii* (Coss.) Schmal. (GILL *et al.* 1991; GILL *et al.* 1993). Hexaploid wheat has also received attention (CHAO *et al.* 1989; LIU and TSUNEWAKI 1991; DEVOS *et al.* 1992, 1993b; XIE *et al.* 1993; NELSON *et al.* 1995a,b; VAN DEYNZE *et al.* 1995). Of present interest to geneticists and breeders are the comparative mapping of wheat with the various grass species (LIU *et al.* 1992; DEVOS *et al.* 1993a,b; AHN *et al.* 1993; KURATA *et al.* 1994a; VAN DEYNZE *et al.* 1995), and the work of bringing the classical wheat map (HART *et al.* 1993) into correspondence with the molecular map (CHAO *et al.* 1989; MA *et al.* 1993, 1994; EASTWOOD *et al.* 1994; VAN DEYNZE *et al.* 1995; NELSON *et al.* 1995a,b).

Hexaploid wheat contains three genomes, A, B, and D, combined in this crop species by ancestral hybridization events involving diploid and tetraploid descendants of a hypothesized diploid ancestor of all the Triticeae including wheat, rye, barley, and numerous wild relatives. It is well established that DNA probes commonly identify, in unrearranged homoeologous chromosomes, sets of orthologous loci that lie at approximately the same positions relative to each other and to the centromeres. Consensus maps of several chromosomes uniting loci from homoeologous wheat genomes and the corresponding chromosomes of barley, *T. tauschii*, *T. monococcum*, and rice have been presented by VAN DEYNZE *et al.* (1995) and NELSON *et al.* (1995a,b). Dense genetic maps of related crop species provide breeders with multiple choices of markers for tagging desired genes. Moreover, comparison of the chromosomal assignments and orders of marker loci common to several genomic maps may shed light on ancestral chromosomal rearrangements and on evolutionary relationships between different chromosomes. Wheat is especially well adapted to such studies because of the readily available nullitetrasomic and ditelosomic chromosomal stocks isolated in this species (SEARS 1966). The group-4 chromosomes have long held special interest for wheat geneticists (GILL 1974; DVORAK 1983; RAYBURN and GILL 1985; NARANJO *et al.* 1987) because of peculiarities in their cytology and pairing behavior.

The purpose of this work was to produce RFLP maps of wheat homoeologous groups 4, 5, and 7 and to locate on these maps major genes segregating in the mapping population.

MATERIALS AND METHODS

Plant material and DNA manipulations: A synthetic hexaploid wheat was generated via a cross of *T. tauschii* (DD)

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accession (219) CIGM86.940 with the durum (AABB) wheat Altar 84, by Dr. A. MUJEEB-KAZI at CIMMYT (International Maize and Wheat Improvement Center), Mexico. The synthetic was crossed with the hexaploid spring wheat cultivar "Opata 85" and the F_2 progeny advanced by single-seed descent to F_7 or F_8. RFLP mapping was carried out at Cornell with radiolabeled probes on a set of 114 of the resulting inbred lines as described in NELSON *et al.* (1995a) and at INRA with alkali-labile DIG-11-dUTP labeling (Boehringer Mannheim) on a subset of 56 lines as described in LU *et al.* (1994).

Libraries: Clone libraries used at Cornell were: BCD, barley cDNA; CDO, oat cDNA; and WG, wheat genomic libraries obtained as described in HEUN *et al.* (1991); KSU, *T. tauschii* genomic clones from B. S. GILL, Manhattan, KS; MWG, barley genomics and cMWG, barley cDNAs from A. GRANER, Grünbach, Germany; TAM, wheat genomics from G. E. HART, College Station, TX; and RZ, rice cDNAs from S. R. MCCOUCH, Ithaca, NY. Clone CSU25 (UMC317) was a maize genomic clone obtained from E. COE, Columbia, MO. Clones were maintained as plasmid inserts and amplified as needed by polymerase chain reaction (PCR). Clone libraries used at INRA were FBA and FBB wheat genomic libraries derived respectively from the cultivars "Courtot" and "Chinese Spring" and obtained from F. QUETIER, Paris, France.

RFLP data analysis and linkage mapping: Scoring of autoradiograms, linkage analysis, and assignment of markers and their associated linkage groups to chromosomes and chromosome arms by hybridization of probes to Chinese Spring (CS) nullitetra- and ditelosomic blots were as described in NELSON *et al.* (1995a). Markers whose order was established at a log-likelihood ratio (LOD) of 3.0 with the computer program Mapmaker v2.0 (LANDER *et al.* 1987) were assigned exact positions on the chromosome maps and the remainder were placed in the intervals in which they were best fit by Mapmaker's "try" command.

Gene localization: The mapping lines were planted at Ithaca in the field in early May in single 1-m rows in 1993 and in double 1-m rows in three locations in 1994. For assessing vernalization requirement, the lines were grown in duplicate pots in the greenhouse in winter 1993/94 under 16-hr artificial lighting following four different vernalization treatments (at 5°, applied to seedlings under 12-hr artificial lighting) of 0, 1, 2, and 4 weeks. Days to ear emergence were recorded in the field and greenhouse trials. In the field, severity of natural leaf-rust infection (density of foliar uredinia on an increasing scale from 0 to 9) were recorded after heading, at *ca.* 85 days from sowing. For scoring coleoptile color, 8–10 seeds of each line were germinated and grown on wet filter paper in Petri dishes in a growth chamber at 20° under constant fluorescent and incandescent lighting. On the seventh day, the coleoptiles were visually rated for intensity of red color on a scale of 0–5 (the synthetic parent was colored, the cultivated parent green). For scoring kernel hardness, several hundred greenhouse-grown kernels from each line in turn were placed on white paper and rated independently by two observers for the proportion of vitreous kernels. For all characters, the phenotypic scores for each line were regressed on the number of paternal RFLP alleles present in that line (0, 2, or rarely 1 for heterozygotes) at each RFLP locus in turn. The resulting *F* statistics were viewed by plotting along an axis on which the loci were placed as adjacent points in order of mapping. To show the parental source of the phenotypic effect, the statistic was plotted above or below the horizontal axis according to the sign of the regression slope.

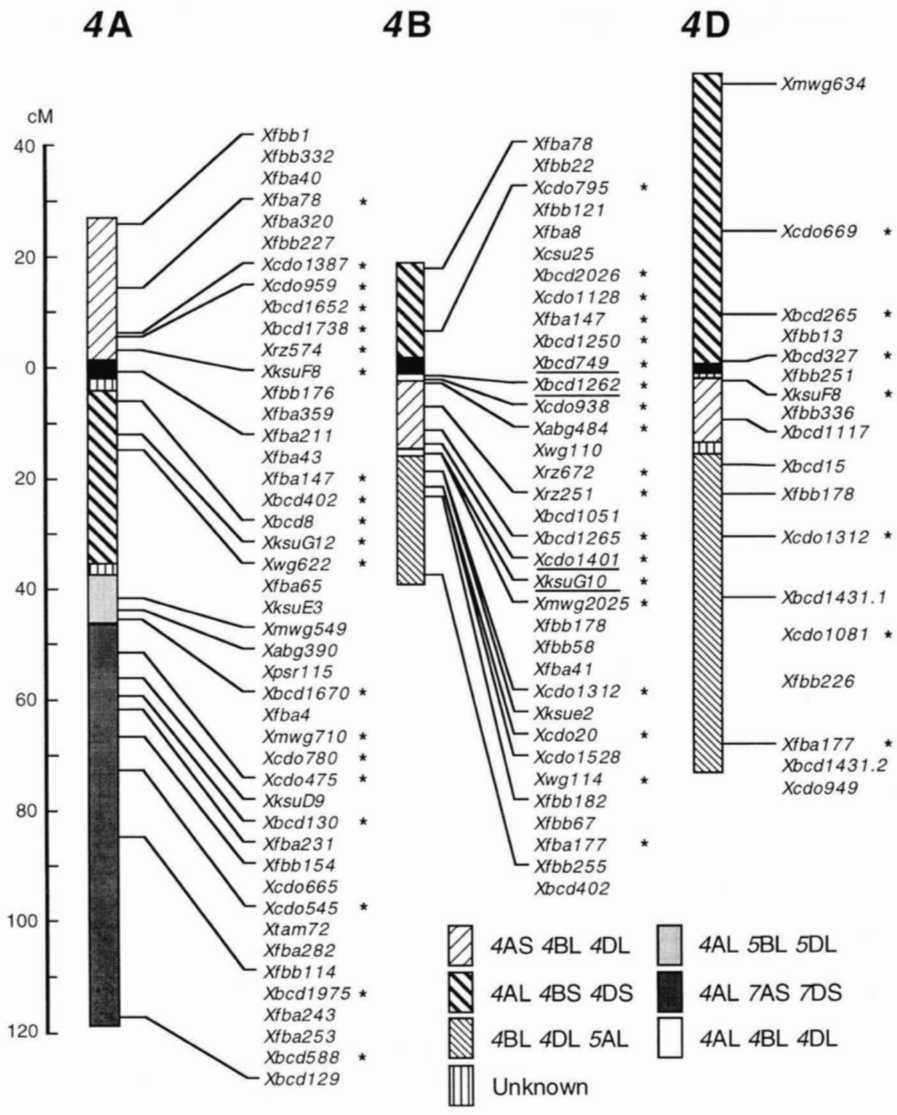
Regression of the score on the genotype expected from flanking-marker genotypes at 1-cM intervals along the chromosomes (HALEY and KNOTT 1992) was also used to localize putative genes in intervals between RFLP loci. The resulting *F* tests were plotted along chromosome maps to indicate regions of influence on the traits analyzed. A description of the software and calculations used for these analyses appears in NELSON (1994). Briefly, multipoint map-distance estimates calculated with Mapmaker for a recombinant-inbred population are converted to estimates of gametic recombination R by inverse application of the mapping function (KOSAMBI 1944) and these estimates are transformed via the function $r = 2R/(1 + 2R)$ (HALDANE and WADDINGTON 1931) to estimates of the expected recombination r after selfing to homozygosity. The resulting r are used to calculate genetic expectation at any desired locus between flanking markers **A** and **B**. Let r_A and r_B represent the recombination frequency between the locus and either of the flanking markers; then, after scaling by the expected frequencies of the four possible flanking-marker classes, the expected genetic effect for a locus in each genotype class in a homozygote will be AABB, aabb: $\pm a[(1 - r_A - r_B)/(1 - r)]$ and AAbb, aaBB: $\pm a[(r_B - r_A)/r]$ where a represents the additive effect of the locus upon the phenotype, a constant m representing the midparent mean may be ignored, and no dominance term need be fitted for this population type. The coefficient of a is computed at 1-cM intervals and the phenotype is regressed upon it to give the plotted *F* statistic.

The threshold of $F = 15.0$ shown in the plots represents the approximate experimentwise $P = 0.05$ Type-I error threshold for a population of 114 lines subjected to 320 independent tests, this being the number of markers in a framework set from all 21 chromosomes used to locate regions of interest by regression of phenotype on marker genotype. Because of linkage such tests are not independent, so that this threshold is conservative.

RESULTS AND DISCUSSION

General observations: RFLP maps of the A-, B-, and D-genome chromosomes of homoeologous groups 4, 5, and 7 are shown in Figures 1–3. Loci in homoeologous regions were presumed to be orthologous if detected by the same probe in the map positions expected from prior evidence including aneuploid analysis, maps of related species, and linkage to other such markers. The homoeologies within groups 4, 5, and 7 are affected by several rearrangements known to have occurred in chromosomes *4*A, *5*A, and *7*B. The Chinese Spring aneuploid hybridization patterns of probes detecting markers on these chromosomes are indicated by fill patterns in the figures and show the true homoeologous relationships among regions on otherwise nonhomoeologous chromosomes.

The paucity of markers, presumably due to lower DNA polymorphism, in the D-genome chromosomes of all three groups relative to the marker density in the A and B genomes echoes the experiences of CHAO *et al.* (1989) and LIU and TSUNEWAKI (1991) with other wheat mapping crosses and of the present authors with homoeologous groups 1 and 3 (but not 2) in this cross (NELSON *et al.* 1995ab; VAN DEYNZE *et al.* 1995). Of 325 marker loci mapped in these groups, only 68 (21%) mapped to D-genome chromosomes. This deficiency in D-genome polymorphism may arise from the choice of *T. tauschii* accession used to produce the synthetic



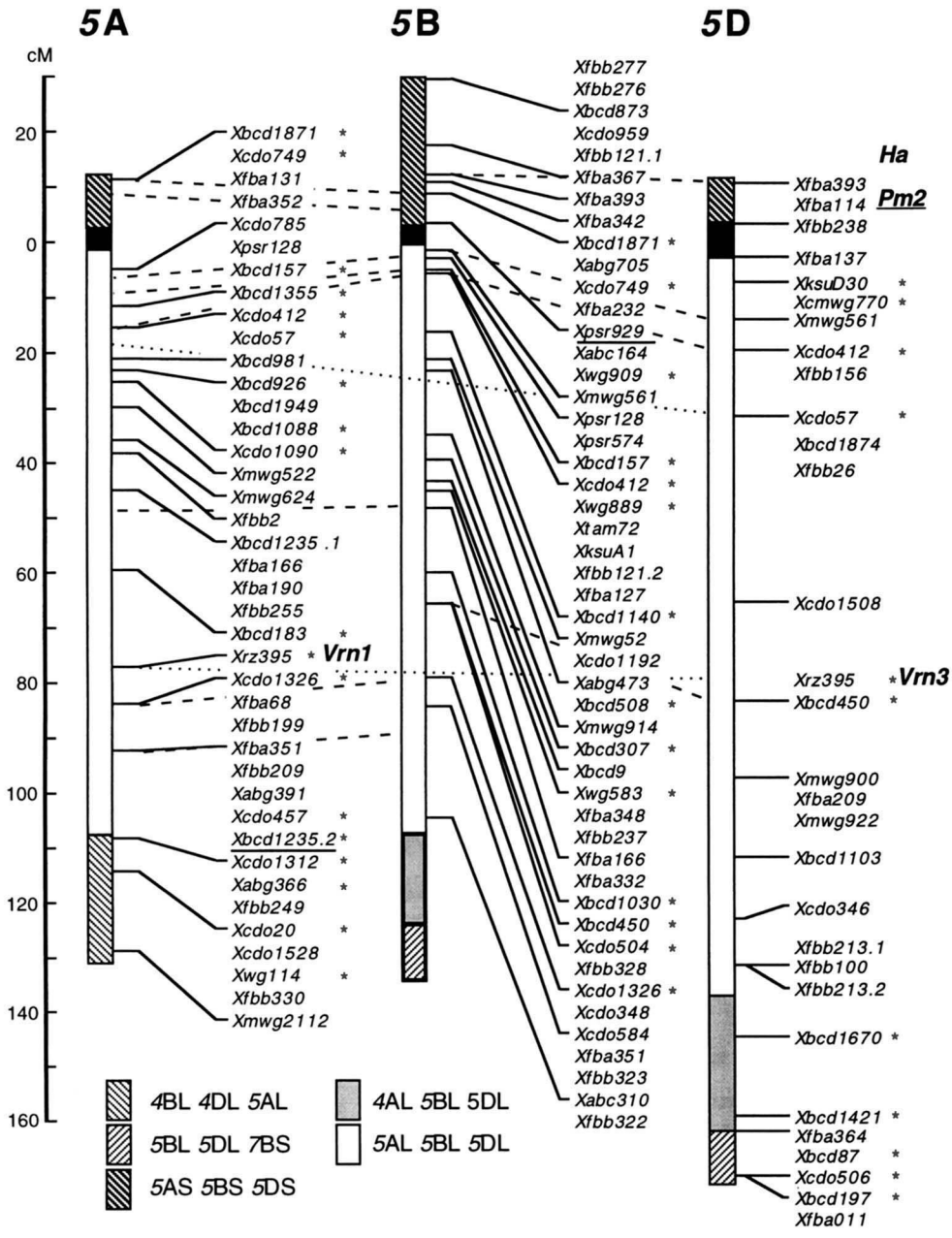
FIGURES 1–3.—RFLP maps of wheat homoeologous groups 4, 5, and 7. Short arms of chromosomes are at top. Markers accompanied by chromosome tick marks are in LOD 3.0 order. Chromosomal segments are coded according to the hybridization patterns, on Southern blots of Chinese Spring (CS) nullitetra- and ditelosomic stocks, of the probes identifying loci on the segments. Asterisked (*) markers identify these probes; see text for discussion. Segments on 5BL and 7BS outlined in bold are inferred but not mapped with RFLP markers. Broken lines drawn between chromosomes connect presumed orthologous loci; dotted lines connect loci on the *A* and *D* chromosomes. Centromeres, shown as black bands on chromosomes, are placed between marker loci assigned to arm on the basis of ditelosomic analysis. Marker loci are shown coincident with centromeric bands or translocation breakpoints if assignments to either adjoining region were not made for them. Line segments separating marker names indicate cutoff points where ambiguous. Boldfaced symbols to right of chromosome maps denote genes; those not mapped in this cross but inferred from other reports (see text) are underlined. Boxed markers at base of group-7 chromosomes were placed at <LOD 3.0.

hexaploid. Recent chromosomal maps (DEVOS *et al.* 1992, 1993b; XIE *et al.* 1993) made in another synthetic × bread-wheat cross do not show a comparable deficiency of D-genome RFLPs.

The choice of a stringent LOD threshold of 3.0 for ordering of markers suggests comparison with other genome maps. Maps cited above have been based on F_2 and other early-generation populations and LOD thresholds of 2.0–2.5 have commonly been reported. At LOD 3.0, two-thirds of the markers scored on the full population and one-third of those scored on half of the lines could be assigned to map positions and the remainder only to intervals. In a much larger (252 line) recombinant inbred population of *A. thaliana* (REITER *et al.* 1992) only 126 of 225 markers could be ordered at LOD 3.0. In the present study, relaxing the LOD threshold to 2.0 allowed a further 54 markers to be placed on the maps (data not shown). Clusters of markers shown on the maps (*e.g.*, on chromosome arms 7AL and 4BS) commonly display only one or two recombinations between any two markers in the cluster and fall, in indeterminate order, within an interval of <10 cM.

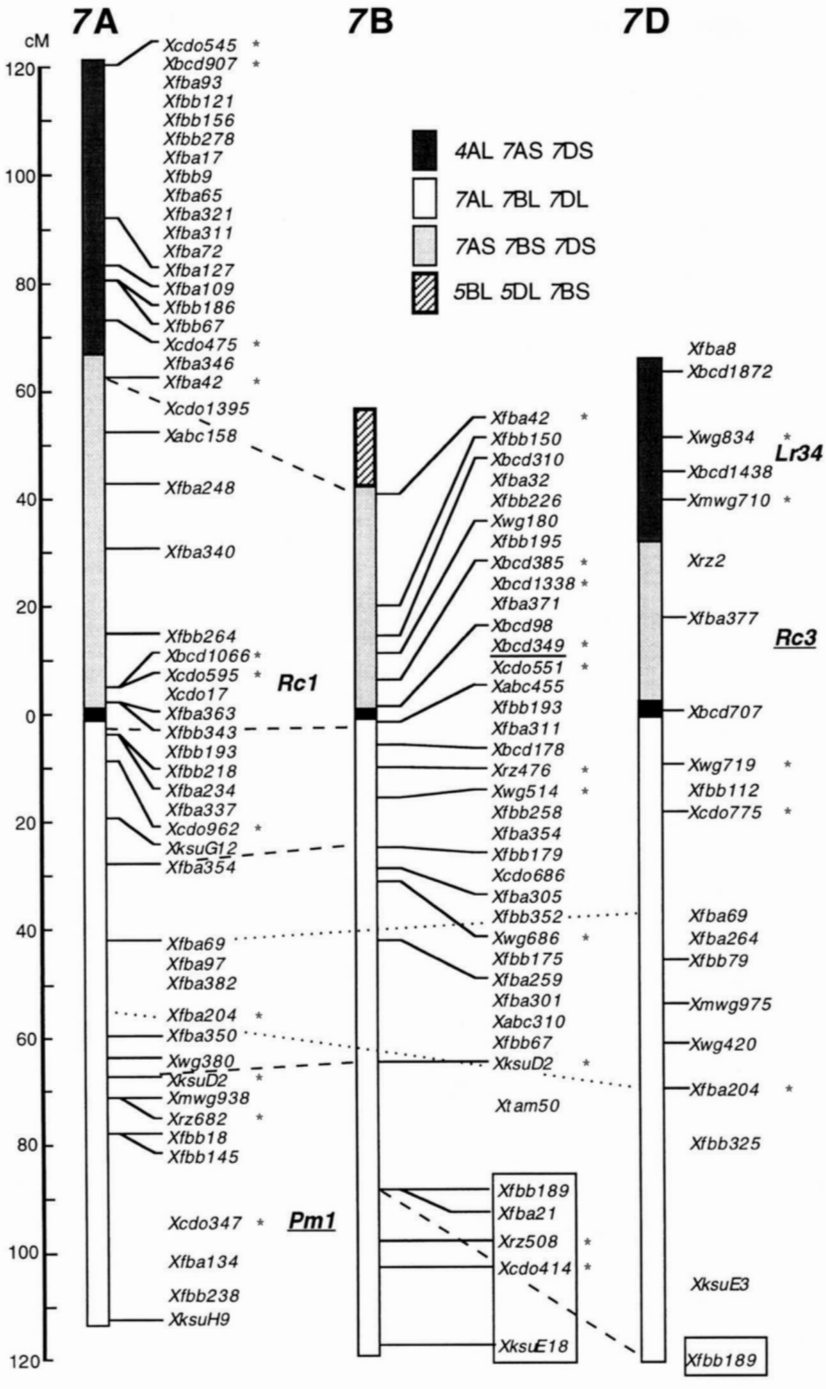
With respect to the relative genetic lengths of chromosomes, those in all three groups are comparable with their counterparts in existing wheat and barley maps, the group-4 homoeologues being the shortest (except for chromosome 4A, much of which is not native to this chromosome) and the group-7 homoeologues the longest. The group-5 maps are comparable with those of XIE *et al.* (1993) in having no markers more than 25 cM distal to the centromeres on the short arms. The cytological L/S arm-length ratios for these chromosomes are the highest of any wheat chromosome (GILL 1987).

Delineating a pericentric inversion on chromosome 4A: The chromosomal designation 4A used here is that agreed upon at the Seventh International Wheat Genetics Symposium (MILLER and KOEBNER 1987) to designate the chromosome formerly called 4B. NARANJO *et al.* (1987) observed a pattern of rare and heterogeneous pairing of the short arm of this chromosome and inferred an ancestral structural modification of this arm.



FIGURES 1–3.—*Continued*

DNA probes in wheat commonly hybridize to orthologous loci on all three chromosomes of a homoeologous group. If one of the loci lies in a region that has been rearranged by inversion or translocation, genotyping a series of nullisomic or ditelosomic stocks may be used to identify the chromosomes and arms involved in the rearrangement (LIU *et al.* 1992; ANDERSON *et al.* 1992). For example, several isozymes identify loci on chromosomes *4*AL, *4*BS, and *4*DS and one (*Acph*) identifies loci on *4*AS, *4*BL, and *4*DL (HART and LANGSTON 1977; HART 1987). It has been suggested on this basis and on pairing evidence (NARANJO *et al.* 1987) that a pericentric inversion on this chromosome took place in the evolution of hexaploid wheat. The aneuploid analysis and RFLP mapping data reported here are consistent with an inversion that involved some part of the short arm of chromosome *4*A but left at least one unrearranged segment on the long arm proximal to the genomic region involved in the inversion. Figure 1 shows the three group-4 chromosomes of the present map and indicates the preinversion arm origin of the pericentromeric segments on chromosome *4*A based on aneuploid analysis of many of the probes mapped in group 4. The patterns drawn on the *4*B and *4*D chromosomes are not intended to suggest ancestral rearrangements of these chromosomes, but to show the map distribution of orthologous loci identified by probes having the indicated CS hybridization patterns. All probes that identified loci on the short arm of wheat chromosome *4*A hybridized to the long arms of chromosomes *4*B and *4*D as revealed by linkage or aneuploid analysis, a pattern reported also by LIU *et al.* (1992) for



FIGURES 1–3.—*Continued*

all 19 of their group-4 probes. In the present study probe FBA147 identified loci on both *4*AL and *4*BS and probe KSUF8 identified loci on both *4*AS and *4*DL (Figure 1). Although FBA78 appears to detect a homoeologous relationship between *4*AS and *4*BS, the RFLP fragment mapped from this multicopy probe on chromosome *4*BS was a minor one not present on the CS blots, while the major fragments on CS showed the *4*AS-*4*BL-*4*DL hybridization pattern diagnostic for the inversion. The available data do not reveal the orientation of the *4*AS segment with respect to its homoeologous counterparts on *4*BL and *4*DL.

Probe BCD1262 was first reported by ANDERSON *et al.* (1992) to hybridize to *4*AL, *4*BL, and *4*DL on CS, thus identifying a region appearing not to have been involved in an inversion. In the present cross, the only RFLP identified by this probe mapped to chromosome *4*BL close to the centromere. Another probe, KSUG10, gave the same *4*AL-*4*BL-*4*DL hybridization pattern. However, *XksuG10* lies 13 cM distal to *Xbcd1262* on chromosome *4*BL (Figure 1) and several *4*AS-*4*BL-*4*DL markers map at >LOD 3.0 between the two loci in the linkage map. The indication is that only an interstitial segment of *4*AL was involved in the pericentric inver-

sion. Left unclear are the locations on chromosome arm *4*AL to which *Xbcd1262* and *XksuG10* map, because of the three orthologous loci identified by either probe on CS, only the B-genome locus was polymorphic with the restriction enzymes used. In Figure 1, candidate locations have been suggested by the inclusion of regions given the pattern labeled "Unknown."

Probe WG622, a *4*AL-*4*BS-*4*DS probe on CS that in this cross identified a locus on chromosome *4*AL, has provided the terminal marker on barley chromosome arm *4HS* in the maps of KLEINHOFS *et al.* (1993), HEUN *et al.* (1991), and GRANER *et al.* (1994) and on *T. tauschii* chromosome *4*D (GILL *et al.* 1993). A presumed telomere-specific marker has been reported (KLEINHOFS *et al.* 1993) to map *proximal* to *Xwg622* in barley. The relative orientation of *Xwg622-4A* and *Xbcd402-4A* in the present map and the map of KLEINHOFS *et al.* (1993) suggests that the pericentric inversion of the ancestral *4*AS segment resulted in the distal end remaining distal, as would be expected from a pairing and exchange of segments on opposing arms.

Translocation among groups 4, 5, and 7: NARANJO *et al.* (1987) concluded from meiotic pairing affinities in material deficient for the *Ph1* gene suppressing homoeologous pairing (RILEY and CHAPMAN 1958) that the evolution of wheat had involved reciprocal translocations of chromosomal segments between chromosomes *4*AL, *5*AL, and *7*BS. It is currently thought (NARANJO 1990; LIU *et al.* 1992) that in an AA diploid or early AABB tetraploid ancestor of wheat, chromosomes *4*AL and *5*AL exchanged short terminal segments. In the tetraploid, the distal portion of the *5*AL segment on *4*AL was then exchanged with a terminal segment from *7*BS, leaving behind an interstitial *5*AL-native segment on *4*AL.

LIU *et al.* (1991) presented a skeleton map of chromosome *4*A bearing loci detected by three probes shown by aneuploid analysis to hybridize to chromosomes *7*AS, *7*DS, and *4*AL and thus identifying the translocated *7*BS segment on the end of *4*AL. To these was linked a single locus, *Xpsr115-4A,* inferred to hybridize to the interstitial *5*AL segment. We have mapped this and three further markers (Figure 1) on the interstitial segment. Its distal breakpoint is thereby defined to within a few centimorgans, while the proximal one, representing the union of this segment with the *4*AL arm, lies in the 27-cM region between *Xmwg549* and *Xwg622.* Probes identifying loci distal to *Xbcd1670* on chromosome *4*AL show that the distal segment originated in chromosome *7*B, in the form of orthologous loci on the maps of chromosome arms *7*AS and *7*DS as well as on the maps of homoeologous chromosomes of other grass species (Figure 4). The orientation of the marker loci common to these maps indicates that the *7*BS-*4*AL translocation preserved the orientation of the *7*BS segment with respect to the centromere. This finding agrees with that of WERNER *et al.* (1992) based on deletion mapping.

The *5*A-*4*A translocation breakpoint on chromosome arm *5*AL (Figure 2) may be delimited to a 2-cM interval between markers on either segment. The terminal portion of *5*AL carries four markers whose orthologous counterparts appear on wheat *4*BL. Also on this segment lie *Xmwg2112* and *Xabg366,* mapped to chromosome *4*HL of barley by GRANER *et al.* (1994) and KLEINHOFS *et al.* (1993), respectively.

In this cross, no markers could be placed on the terminal segment of ancestral *5*AL now residing on chromosome *7*BS. Clones (BCD87, CDO506, and BCD197) giving the corresponding CS pattern (*5*BL-*5*DL-*7*BS) diagnostic for the *5*AL-*7*BS translocation identified loci only on chromosome *5*DL. The positions of *Xfba42* on chromosome arms *7*AS and *7*BS and the CS pattern of probes identifying loci distal to *Xfba42-7AS* (Figure 3) suggest that the translocation breakpoint on *7*BS lies just distal to the present terminus of the RFLP map of *7*BS.

Once the ancestral rearrangements in wheat have been delineated with molecular markers having orthologous counterparts in other grass genomes, it is of interest to know whether homoeologous regions in other species have undergone similar changes. Such knowledge may shed light on the chronology and the physical and genetic mechanisms of these events. Similar rearrangements in the rye genome have been documented (LIU *et al.* 1992; DEVOS *et al.* 1993b) and some close wild relatives of wheat exhibit the *4*A-*5*A translocation (KING *et al.* 1994). However, our inspection of published RFLP maps has yielded no evidence in other species for translocations analogous to those in wheat. The probes that hybridize to translocated segments of wheat and have been mapped in barley, *T. tauschii,* or rice identify loci on the foreign chromosomes homoeologous to the unrearranged chromosomes of wheat to which the probes hybridize in Chinese Spring; *cf.* Figure 4. Even in the relatively more rearranged maize and diploid or hexaploid oat genomes (O'DONOUGHUE *et al.* 1992, 1995; AHN *et al.* 1993), none of the rearrangements appears analogous to those in wheat. Available evidence is consistent with the proposal of NARANJO (1990) that the *4*AL-*5*AL translocation first occurred in the A-genome progenitor of wheat and the inversion in a primitive AABB tetraploid before or after the second (*4*AL-*7*BS) translocation.

Comparative mapping: The broad homoeologies between the molecular maps of wheat, barley, *T. tauschii,* and rice, described in works cited above, held as expected for the present nine chromosomes based on >50 probes used in common on two or more of the maps, and are not detailed here.

Inferences about gene location based on comparative mapping must be made cautiously, not only because of intragenomic rearrangements but because of nonhomoeologous duplication of loci. Figure 4 shows the homoeology between the interstitial *5*A segment on wheat

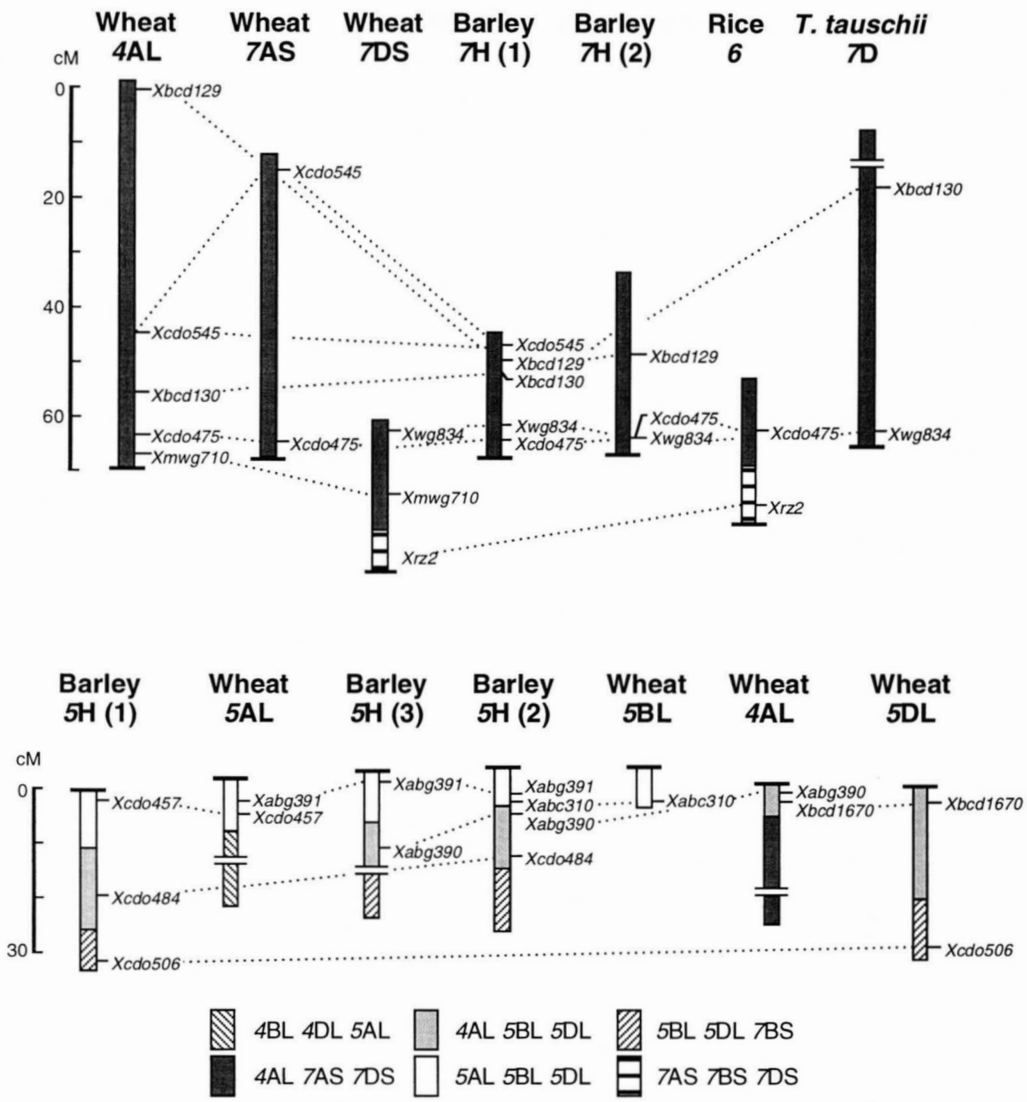


FIGURE 4.—RFLP homoeology of barley, rice, and *T. tauschii* chromosomes with wheat chromosomes involved in the ancestral 4-5-7 translocation. Solid crossbars at ends of segments indicate proximal chromosomal regions not drawn. Sources: for barley maps, (1) HEUN *et al.* (1991), (2) KLEINHOFS *et al.* (1993), (3) GRANER *et al.* (1994); for rice map, AHN and TANKSLEY (1993); for *T. tauschii* map, GILL *et al.* 1991; GILL *et al.* 1993).

chromosome 4A with the other chromosomes of wheat homoeologous group 5 and with the corresponding barley chromosomes. One probe, however, violates this correspondence; MWG549 identifies a barley chromosome 5H locus well proximal to the region expected from homoeology and also identifies other loci on barley chromosomes 3H and 6H (GRANER *et al.* 1994). While it may be that this genomic clone hybridizes to corresponding sites in the wheat genome without producing RFLPs in the present cross, the more desirable clones for comparative mapping are those that identify only loci in homoeologous regions. The maps of homoeologous groups 1–3 made with this cross have each contained >20 pairs of such orthologous loci, while groups 4, 5, and 7 together, although their marker density is similar, contain only 35. Eight of the pairs are not shown connected in Figures 1–3 because one member of each lies in a region translocated to a different homoeologous group. The conventional test of clones for the detection of orthology is hybridization to the CS aneuploid series (*e.g.*, ANDERSON *et al.* 1992). Markers from clones whose hybridization patterns on nullitetra- or ditelosomic CS blots showed fragments missing from stocks lacking three homoeologous chromosomes or arms are indicated in Figures 1–3 by asterisks. Because such loci, when mapped in wheat or in a related species, almost invariably bear out the evidence of orthology supplied by aneuploid analysis (NELSON *et al.* 1995a,b; VAN DEYNZE *et al.* 1995), construction of a plausible consensus order for a set of homoeologous wheat chromosomes does not require that all orthologous loci actually be mapped as RFLPs in the chromosomes unless rearrangements are suspected.

Among other multicopy probes giving potentially

misleading hybridization patterns were FBB67, which identified RFLPs on *1*BS (not shown), *4*BL, 7AS, and 7BL; BCD402, which identified a RFLP on *4*BL (Figure 1) that if orthologous to *Xbcd402-4A* would not agree with the other evidence for the rearrangement of chromosome *4*A; and FBA78, mentioned above. Probe ABC310 identified an RFLP on 7BL that corresponds to a locus on barley chromosome 7H in the map of KLEINHOFS *et al.* (1993) and another RFLP on 5BL that corresponds to a locus on barley chromosome 5H in the map of GRANER *et al.* (1994).

Mapping vernalization genes: The winter habit of wheat is characterized by delayed ear emergence in the absence of vernalization (cold treatment after germination). The character is measured under nonvernalizing conditions as the days between sowing and the time the ear emerges from its enveloping flag leaf. SEARS (1944) identified an earliness gene on chromosome *5*A of Chinese Spring and later studies (*e.g.,* LAW *et al.* 1975; SNAPE *et al.* 1985) established the approximate positions and likely orthology of two major controlling genes *Vrn1* and *Vrn3* on the long arms of chromosomes *5*A and 5D.

Regression analysis revealed a region on chromosome *5*A in which the synthetic-parent RFLP alleles were associated with a 3-day advance in heading under the field growing conditions at Ithaca and another region on chromosome 5D in which the Opata alleles were associated with a similar effect. In the greenhouse trial, the 4-week vernalization produced a 5-day advance and the 2-week a 3-day advance in heading date associated with the *5*A factor, in comparison with the unvernalized controls. In some cases, there were significant effects (data not shown) from the short arms of group-2 chromosomes, consistent with the known influence of these chromosomes on earliness in wheat (*e.g.,* WORLAND *et al.* 1987) and barley (*e.g.,* BARUA *et al.* 1993). This and other associations with chromosomes that are not the subject of this paper will be discussed elsewhere.

Regression analysis (Figure 5) indicates that the factors on *5*AL and 5DL are orthologous genes, in the form of their close linkage with orthologous loci identified by probe RZ395 on both chromosomes. Marker *Xrz395-5D* was not used in this analysis because its position with respect to the closely linked marker *Xbcd450* was uncertain, but its estimated location is shown. The loci in evidence here are certainly *Vrn1* and *Vrn3*. The *Vrn1* allele resides in Altar durum, the A-genome donor to the synthetic parent. *Vrn3* is contributed by the wheat parent and is absent in the D-genome donor, *T. tauschii,* which flowers late or not at all in the absence of vernalization. The wheat and synthetic parents, which both display a spring growth habit, thus carry one *Vrn* allele each.

The distance of the *Vrn1* locus from the centromere of *5*A is ~80 cM on the RFLP map in comparison with the 100-cM estimate of SNAPE *et al.* (1985). The probable rye counterpart of the *Vrn* genes, *Sp1,* has been placed by PLASCHKE *et al.* (1993) on the RFLP map of rye chromosome *5*R.

Mapping a coleoptile-pigmentation gene: A gene for red coleoptile on chromosome 7A was reported by SEARS (1954) and TAHIR and TSUNEWAKI (1969); the latter also detected a color-promoting gene on 7D. The 7D locus (*Rc3*) has been placed 10–16 cM from the centromere (ROWLAND and KERBER 1974; SUTKA 1977; CHAO *et al.* 1989); however, the 7A locus, *Rc1,* has not previously been mapped. In the present cross, regression analysis (Figure 5) showed marker *Xcdo17* to account for 44% of the variation in color in the population, with the durum A genome contributing the effect. This marker lies on 7AS within 10 cM of the centromere. Other regions of chromosome 7A may influence the trait (Figure 5), and a marker on 2AS (*Xbcd348,* data not shown) accounted for 9% of the variation in coleoptile color, an effect that may coincide with the suppressor influence on color detected by TAHIR and TSUNEWAKI (1969) in group 2.

Mapping a leaf-rust resistance gene: Leaf-rust disease was quantified by density of foliar uredinia (ROELFS *et al.* 1992) under the assumption that the natural inoculum was a mixture of avirulent pathotypes; host resistance was thus treated as the result of quantitative action of major and minor genes. In the 1993 field trial, a region on the short arm of chromosome 7D was strongly associated with disease (Figure 5). The Opata allele at locus *Xwg834* accounted for 22% of the variation in disease, the lines with this allele having a mean disease score of 2.6 as compared with 5.1 for those with the *T. tauschii* allele. A multiple-regression model (not shown) also including a locus on chromosome 2B (NELSON *et al.* 1995b) accounted for 45% of the variation. Although the Ithaca rust pathotypes are unknown, Opata possesses the widespread resistance gene *Lr34* (SINGH 1992), recently shown (DYCK *et al.* 1994) to lie on chromosome arm 7DS. *Lr34* was estimated to lie 30 cM distal to *Rc3,* a position in agreement with that of the resistance gene detected here.

Mapping kernel hardness: Kernel hardness, a character of importance to milling quality of wheat, is commonly assayed by milling. MATTERN *et al.* (1973) and FORSTER and ELLIS (1990) assigned a softness factor respectively to 5D and to 5DS of Chinese Spring. Regression analysis of kernel vitreousness in the mapping population revealed two regions of strong positive association with *T. tauschii* marker alleles, one on chromosome arm 5DS as shown in Figure 5 (marker *Xfbb238* accounting for 33% of phenotypic variation) and the other, of somewhat less effect, on chromosome 2D (not shown). The 5DS gene is likely to be *Ha* (MORRISON *et al.* 1989). Only minor factors were detected in the durum A and B genomes; however, Opata is classified as a hard red spring wheat and may already possess durum hardness alleles. In barley, the homoeologous region

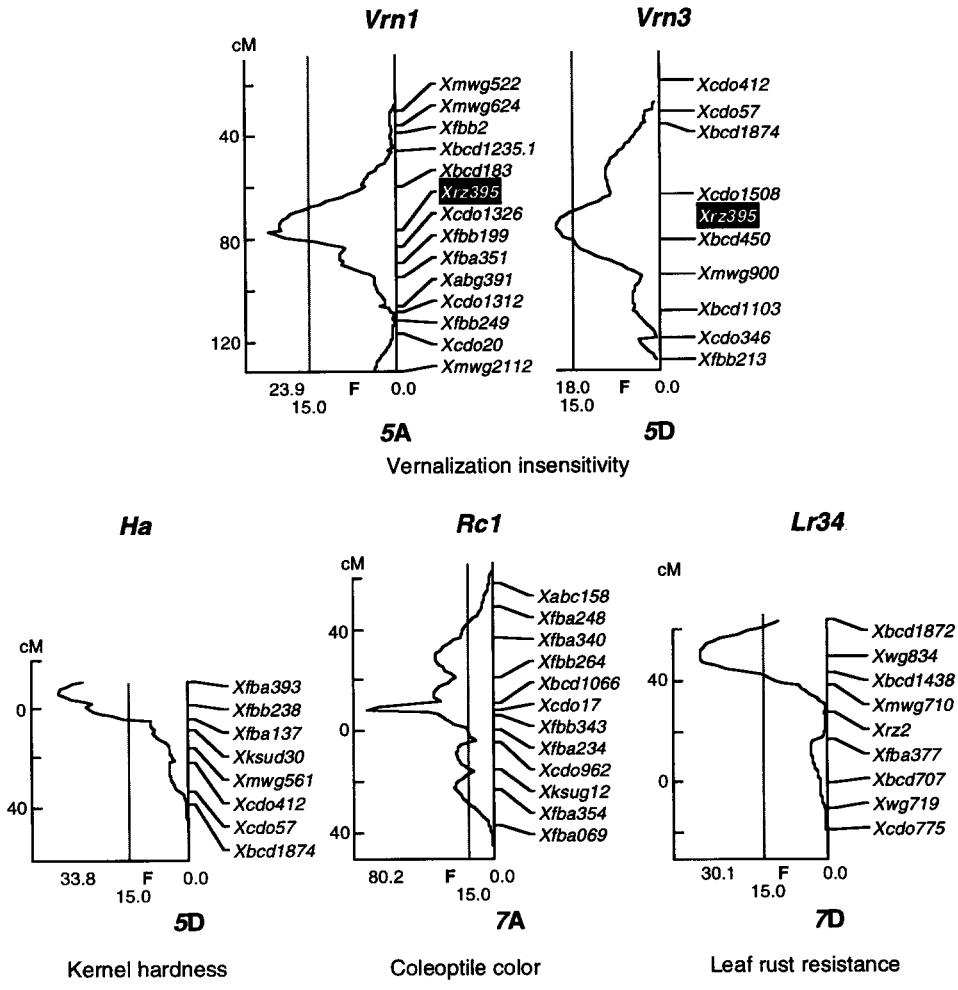


FIGURE 5.—Interval regression analysis of several characters controlled by major wheat genes. Plots show *F* tests for regression of phenotype on expected genotype at 1-cM intervals along chromosomes and are scaled to the maximum value of the statistic, shown at lower left. Short arms of chromosomes are toward top. Highlighted labels in the vernalization plots show orthologous marker loci linked to the *Vrn* genes on chromosomes 5A and 5D. Centimorgan scales originate at centromeres.

on chromosome 5H is associated with milling-energy requirement (CHALMERS *et al.* 1993).

RFLP tags for other genes: Probe BCD1871 has been shown (MA *et al.* 1994) to identify a marker locus within 3.5 cM of the powdery-mildew resistance gene *Pm2* on chromosome arm 5DS near the centromere. In the present cross, this clone identified orthologous loci on chromosomes 5AS and 5BS (Figure 2) and the linkage of marker *Xfba393-5B* to *Xbcd1871-5B* suggests that its orthologous locus *Xfba393-5*DS lies near *Pm2*. Probe CDO347 was found in the same study (Ma *et al.* 1994) to identify a locus cosegregating with *Pm1* in the distal region of chromosome arm 7AL (Figure 3). This is the same location to which this locus mapped in our cross and on barley chromosome 7H of HEUN *et al.* (1991). Mildew-resistance genes in the parents have not yet been characterized by inoculation studies.

CONCLUSIONS

We demonstrate the characterization of chromosomal rearrangements in wheat by combining linkage and aneuploid analysis with molecular marker evidence. The ancestral translocations between chromosomes 4A, 5A, and 7B may have been somewhat more complicated than has been thought. There are two separate regions on the long arm of chromosome 4A in which either no rearrangement, or perhaps an even number of rearrangements resulting in the appearance of none, has occurred. A clearer picture of these events may be expected from further linkage mapping and physical mapping methods such as the use of terminal deletion stocks (WERNER *et al.* 1992). Comparative mapping between the hexaploid and the unrearranged diploid Triticeae genomes may elucidate the physical and genetic bases for the occurrence and fixation of the inversion and translocations.

The availability of a wheat map now containing ~1100 marker loci has simplified the placement of classical genes formerly requiring crossing experiments and cytological analysis using monosomic and telocentric stocks. Because of the wide cross that formed the basis of the mapping population, many mono- and polygenic characters have segregated in this set of inbred lines. Besides those reported here, major genes mapped to date in this cross include the kernel-color genes *R1* and *R3* and *W²I, Inhibitor of waxy* (NELSON *et al.* 1995a,b) and several other disease-resistance and morphological genes yet to be reported. The allohexaploidy of wheat has hitherto complicated the dissection of characters

controlled by sets of orthologous genes because of the difficulty of determining progeny genotypes at all the loci at which genes are segregating. With DNA markers one may not only localize several such genes simultaneously, but also, with a sufficiently saturated map, accurately genotype the progeny for the genes in question, *e.g.*, the *R* and *Vrn* genes in this population. As one application of this capability to studies of gene action and interaction, molecular markers for vernalization and photoperiod-sensitivity genes invite an elucidation of the interactions between vernalization, temperature, and photoperiod in plant development. In practical terms, introgression of chromosomes and chromosomal regions into breeding material can be brought under fine control by the use of maps detailing the positions of desired genes and the genomic regions into which they are apt to be incorporated by homoeologous recombination.

Marker and phenotypic data will be placed in the GrainGenes database (GrainGenes, the Triticeae Genome Gopher; accessible via Internet Gopher, host greengenes.cit.cornell.edu, port 70, menu "Grains files to browse"). The software used for gene localization runs on a Macintosh computer and is available from the senior author.

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