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Molecular-genetic maps for group 1 chromosomes of Triticeae species and their relation to chromosomes in rice and oat

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Abstract: Group 1 chromosomes of the Triticeae tribe have been studied extensively because many important genes have been assigned to them. In this paper, chromosome 1 linkage maps of *Triticum aestivum*, *T. tauschii*, and *T. monococcum* are compared with existing barley and rye maps to develop a consensus map for Triticeae species and thus facilitate the mapping of agronomic genes in this tribe. The consensus map that was developed consists of 14 agronomically important genes, 17 DNA markers that were derived from known-function clones, and 76 DNA markers derived from anonymous clones. There are 12 inconsistencies in the order of markers among seven wheat, four barley, and two rye maps. A comparison of the Triticeae group 1 chromosome consensus map with linkage maps of homoeologous chromosomes in rice indicates that the linkage maps for the long arm and the proximal portion of the short arm of group 1 chromosomes are conserved among these species. Similarly, gene order is conserved between Triticeae chromosome 1 and its homoeologous chromosome in oat. The location of the centromere in rice and oat chromosomes is estimated from its position in homoeologous group 1 chromosomes of Triticeae.

Key words: Triticeae, RFLP, consensus, comparative.

Résumé : Les chromosomes du groupe 1 de la tribu des Triticeae ont été étudiés en détail car plusieurs gènes importants y ont été assignés. Dans ce rapport, les cartes génétiques du chromosome 1 chez le *Triticum aestivum*, le *T. tauschii* et le *T. monococcum* sont comparées à celles existant chez l'orge et le seigle, facilitant ainsi dans cette tribu la cartographie de gènes importants au plan agronomique. La carte consensuelle qui en résulte est composée de 14 gènes d'importance agronomique, de 17 marqueurs d'ADN provenant de clones dont la fonction est connue et 76 marqueurs d'ADN provenant de clones anonymes. Il existe 12 inconsistances dans l'ordre des marqueurs parmi sept cartes du blé, quatre cartes de l'orge et deux cartes de l'avoine. Une comparaison entre la carte consensuelle des chromosomes du groupe 1 des Triticeae et les cartes des chromosomes homéologues du riz indique que les cartes génétiques du bras long et de la partie proximale du bras court des chromosomes du groupe 1 sont conservées parmi ces espèces. De même, l'ordre des gènes est maintenu entre les chromosomes 1 des Triticeae et le chromosome homéologue de l'orge. La position du centromère du chromosome 1 chez le riz et l'avoine est estimée à partir des chromosomes homéologues du groupe 1 chez les Triticeae.

Mots clés : Triticeae, RFLP, carte génétique consensuelle, cartographie comparative.

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Introduction

The Gramineae family contains approximately 10 000 species, including the two most important food crops in the world, wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.). Other economically important members of this family include barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), and rye (*Secale cereale* L.). These species represent a great diversity in reproductive habit, ploidy level, and DNA content. Despite their familial relationships, these crops have been studied in relative isolation from each other.

Restriction fragment length polymorphisms (RFLPs) have been assigned to wheat chromosome arms (Anderson et al. 1992; Devey and Hart 1993) and RFLP linkage maps exist for hexaploid wheat (Chao et al. 1989; Liu and Tsunewaki 1991; Devos et al. 1992; Devos et al. 1993*b*) and its D-genome progenitor, *Triticum tauschii* (Coss) Schmal. (Gill et al. 1991, 1993; Lagudah et al. 1991). Physical maps constructed using C-bands as genetic markers (Curtis and Lukaszewski 1991) and deletion stocks (Werner et al. 1992; Kota et al. 1993) have given important insights into the relationship between physical and genetic distances in wheat. RFLP linkage maps also exist for barley (Heun et al. 1991; Kleinhofs et al. 1993; Schondelmaier et al. 1993; Graner et al. 1994), rice (Causse et al. 1994), oat (O'Donoughue et al. 1992; L.S. O'Donoughue, in preparation), and rye (Baum and Appels 1991; Devos et al. 1993*a*; Philipp et al. 1994).

The feasibility of using a common set of DNA probes to develop comparative linkage maps in crop plants was first demonstrated with tomato and potato (Bonierbale et al. 1988). Similar work confirmed substantial conservation of gene order among chromosomes of wheat, barley, and rye (Devos et al. 1992, 1993*a*, 1993*b*). Recently, comparative maps have been developed for rice, maize, and wheat (Ahn and Tanksley 1993; Ahn et al. 1993; Kurata et al. 1994) and a surprising degree of genome conservation was detected among these diverse species.

Each cereal crop has unique characteristics that can be exploited to enhance the understanding of the genetics of the Gramineae family and for increasing the ability to manipulate grass genomes for plant improvement. Wheat has an extensive collection of aneuploid stocks that are ideal for mapping, because virtually every DNA marker can be assigned to a specific chromosome arm or part of an arm without requiring intragenomic polymorphism between the parents (Sears 1966; Sears and Sears 1978; Gale and Sharp 1988; Anderson et al. 1992; Devey and Hart 1993; Kota et al. 1993). The large number of species in the Triticeae tribe that can be hybridized with cultivated wheat offers a vast stock of genetic resources. The gene order in wheat and barley is generally conserved (Devos et al. 1992, 1993*b*); therefore, information gained in one crop can be applied directly to the other. The small genome of rice, combined with a well-developed RFLP map and transformation system (Kothari et al. 1993), makes it an ideal candidate for map-based gene cloning.

Chromosome 1 of wheat has been studied extensively both at the classical and molecular level. Many important genes, such as those controlling rust resistance and bread-making quality, have been assigned to this chromosome (Gill et al. 1991; Baum and Appels 1991). Our objectives for the present research were (*i*) to develop species-specific maps for chromosome 1 of Triticeae using a common set of DNA probes, (*ii*) to develop a consensus map for chromosome 1 of Triticeae, and (*iii*) to assess the conservation of gene order among Triticeae species, oat, and rice.

Materials and methods

Definitions

In this manuscript, the following definitions will be used: *homologous*: of chromosome segments identical with respect to their constituent loci; *homoeologous*: partially homologous, referring to residual homology of originally completely homologous chromosomes (Huskins 1932); *orthologous*: of genes present in different species that descended from a common ancestral gene (Fitch and Margoliash 1970).

Plant materials

The populations used in this study and their characteristics are listed in Table 1. The *T. aestivum* (Ta) population consists of 114 F_7 lines derived by single-seed descent from the cross W-7984, an amphihexaploid wheat synthesized from *T. tauschii* (Tt) and Altar84 durum, with Opata85, a Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT)-bred spring wheat that does not contain the 1B/1R translocation. The *T. monococcum* / *T. aestivum* (Tm/Ta) population is a population of monosomic recombinant substitution lines from the cross $DS1A^m(CS1A) \times CS$ in the absence of the *Ph1* gene. Nullitetrasomic (Sears 1966) and ditelosomic (Sears and Sears 1978) lines were used to assign polymorphic DNA fragments to specific chromosome arms and to determine the positions of the centromeres in Ta.

Probes

Group 1 clones were selected based on previously published aneuploid and linkage data from Gramineae species. The cDNA and genomic DNA probes used to develop the different maps were derived from wheat (CS, GLK, KSU, PSR, TAM, WG), barley (ABC, ABG, BCD, MWG), oat (CDO), and rice (RZ). The probes were described by the following authors: BCD, CDO, and WG, Heun et al. 1991; RZ, Causse et al. 1994; KSU, Gill et al. 1991; PSR, Chao et al. 1989; GLK, Liu and Tsunewaki 1991; TAM, Devey and Hart 1993; CS, Lagudah et al. 1991; MWG, Graner et al. 1991; and ABC and ABG, Kleinhofs et al. 1993. The WHS179 probe was supplied by L. Hartl, Institute of Agronomy and Plant Breeding, Freising-Weihenstephan, Germany; ADH (p3'NTR), 5SDNA (pTA794), and NOR1 (pTA17) by J. Peacock, Canberra, Australia; ATPase (cNP5) by J. Chua, Rockefeller University, New York; CAB2 (pKG1490) by K. Gausing, University of Aarhus, C.F. Møllers Allé, Århus C, Denmark; DOR2 (pMA1959) by K. Walker-Simmons, United States Department of Agriculture, Pullman, Wash., U.S.A.; EM (p1015) by R.S. Quatrano, University of North Carolina, N.C., U.S.A.; PGK (PGK) by M. Gale, Cambridge Laboratory, Norwich, U.K.; ESI47 (pESI47) by J. Dvořák, University of California, Davis, Calif., U.S.A.; LEC (pNVR1) by N.V. Raikhel, Plant Research Laboratory, Department of Energy, Michigan State University, Mich., U.S.A.; AGA (WE:AGA.7) by M.R. Olive, Division of Plant Industry,

Table 1. The mapping populations and their characteristics.

Species	Parents	Population Type	Population Size	Number of loci	Length of map (cM)	References
Triticum aestivum	W-7984/Opata85	RI	114	39, 59, 28[a]	164, 136, 154	Present study
T. monococcum	G1777/G2528	F_2	76	40	116	Present study
T. monococcum/T. aestivum	DSTm1A(CS1A)/ Chinese Spring	RSL	96	77	112	Present study
T. tauschii	2 crosses (consensus)	F_2 F_2	39 45	19	143	Lagudah et al. 1991
T. tauschii	TA1691/TA1704	F_2	60	37	344	Gill et al. 1993
T. aestivum		Deletion stocks	16	19		Kota et al. 1993
T. dicoccoides	3 crosses (consensus)	BC		18	141	Curtis and Lukaszewski 1991; present study
Hordeum vulgare	Steptoe/Morex	DH	150	51	152	Kleinhofs et al. 1993, 1994
H. vulgare	Proctor/Nudinka	DH	113	20	163	Heun et al. 1991
H. vulgare	Igri/Franka	DH	71	38	163	Graner et al. 1994
H. vulgare/H. spontaneum	Vada/1B-87	F_2	135	26	165	Schondelmaier et al. 1993
Secale cereale	3 crosses (consensus)	—	—	30	190	Baum and Appels 1991
S. cereale	DS2/R×L	F_2	60	14	106	Devos et al. 1993*a*
S. cereale	Imperial	Translocation stocks	8	62		Rogowsky et al. 1993
S. cereale	6 crosses (consensus)	BC		7	203	Alonso-Blanco et al. 1993, 1994
S. cereale	5 crosses (consensus)	Translocation stocks	3	5		Sybenga et al. 1990
S. cereale	2 crosses (consensus)	BC		6		Lukaszewski 1992
(*Oryza sativa/O. longistaminata*) × *O. sativa*		BC	113	54, 20[b]	147, 80	Causse et al. 1994; present study
Avena atlantica/A. hirtula		F_2	44	58	115	O'Donoughue et al. 1992; present study

NOTE: The linkage maps for *T. aestivum* (Ta) and oat were constructed in the laboratories of M. Sorrells; *T. monococcum* (Tm) and Tm/Ta, J. Dvořák; *T. dicoccoides*, R. Appels; and rice, S. McCouch. RI, recombinant inbred; RSL, recombinant substitution lines; BC, backcross; DH, doubled haploid.

[a]Number of loci for 1A, 1B, and 1D, respectively.

[b]Number of loci for chromosomes 5 and 10, respectively.

Commonwealth Scientific and Industrial Research Organization, Canberra, Australia; GLU3 (pTDUCD1) by B.G. Cassidy, University of California, Davis, Calif., U.S.A.; CHS (CHS) by W. Rohde, Max-Planck-Institut für Züchtungsforschung, Köln, Germany; and GLB1 (λHV29) by R.L. Rodriguez, Department of Genetics, University of California, Calif., U.S.A. XGli1 and XGli3 were assayed with HOR1,2 (pCP387, P. Shewry) supplied by A. Kleinhofs, Washington State University, Pullman, Wash., U.S.A. In the *T. aestivum* (Ta) population, GLU1 was assayed by E. Autrique at the wheat quality laboratory, CIMMYT, Mexico, as described by William et al. (1993). In rice, BCD1434 was assayed using PCR with primers developed from the same probe (35 cycles of 94°C for 1 min, 45°C for 1 min, and 72°C for 2 min).

DNA extraction, Southern blotting, and hybridization

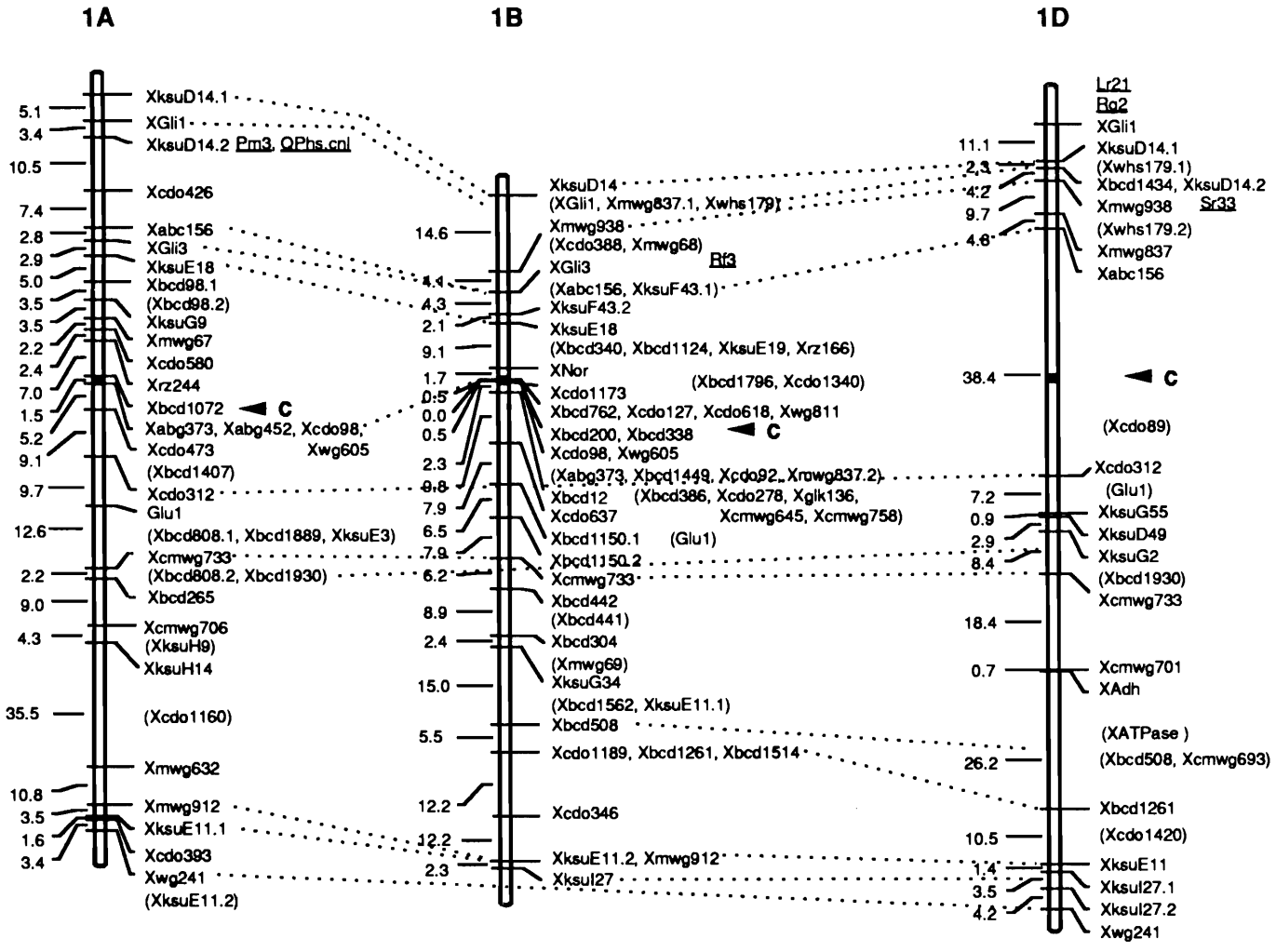
The procedures used for RFLP analyses for the Ta population were described by Heun et al. (1991). The restriction enzymes used to digest DNA for the Ta population were *Eco*RI, *Eco*RV, *Dra*I, *Hin*dIII, and *Xba*I, and up to 40 restriction enzymes were used in the Tm and Tm/Ta populations. RFLP procedures for the *T. monococcum* (Tm) and the Tm/Ta maps were as described by Dubcovsky et al. (1994).

Data analyses

The data for individual maps developed in this study were analyzed using MAPMAKER version 2.0 (Lander et al. 1987). Markers were placed with a LOD threshold of 3.0 to develop the linkage maps. The Kosambi mapping function (Kosambi 1944) was used to convert recombination frequency to centimorgans (cM).

A consensus map for the Triticeae tribe was developed using wheat as a base. Loci were included in the consensus map only when their order agreed among maps within a species and they were present in at least two linkage maps

Fig. 1. Linkage maps for group 1 chromosomes of *Triticum aestivum*. Short arms are at the top. Map distances are in centimorgans. Markers preceded by an X are DNA markers and those without an X indicate genes encoding traits or isozymes that were assayed within the population. The marker preceded by a Q is a quantitative trait locus (QTL). Underlined markers were mapped in different populations. Markers in parentheses are assigned to intervals at a LOD <3.0. Dotted lines indicate orthologous loci. The boldfaced C and the darkened region of the chromosomes mark the positions of the centromeres.



of group 1 chromosomes of Triticeae species. The relative position of markers was determined by the location of common markers in the individual linkage maps. Spearman's rank correlation was used to compare this consensus map with one developed using JOINMAP software (Stam 1993) for group 1 chromosomes of Triticeae.

Results

Chromosome 1 of *Triticum aestivum*

The linkage maps (LOD 3) for group 1 chromosomes of *T. aestivum* (Fig. 1) comprise 131 markers representing 98 loci. The markers shown in parentheses map to the respective intervals at a LOD threshold less than 3.0. The locations of six known-function genes (underlined) that were mapped in different populations, *Pm3*, resistance to powdery mildew (*Blumeria graminis* f.sp. *tritici*; Ma et al. 1994); *Lr21*, leaf rust (*Puccinia recondita* f.sp. *tritici*) and *Rg2*, red glume colour (Jones et al. 1990); *Sr33*, resistance to stem rust (*P. graminis* f.sp. *graminis*; Jones et al. 1991); *QPhs.cnl*, resistance to preharvest sprouting (Anderson et al. 1993), and male-fertility restoration, *Rf3* (Z.Q. Ma, in preparation), are included. The chromosomal arm locations of the polymorphic loci and centromere positions were determined using the DNA from the ditelosomic lines digested with the same restriction enzyme used for mapping. The centromeres were placed at the midpoints between the most proximal short arm and long arm markers.

Chromosomes 1A, 1B, and 1D consist of 39, 58, and 28 DNA/biochemical markers and have genetic lengths of 164, 136, and 154 cM, respectively. Although 1B is the shortest genetically, it is represented by the most loci. Six probes (ABC156, GLI, GLU, KSUD14, KSUE11, and CMWG733) detected polymorphisms for loci on three genomes and 13 probes (BCD508, BCD1261, BCD1930, CDO98, CDO312, KSUE18, KSUI27, MWG837, MWG912, MWG938, WG241, WG605, and WHS179) detected polymorphic loci on two genomes. The relative order of these markers in the A, B, and D genomes is the same. This is

Fig. 2. Linkage maps for group 1 chromosomes of *Triticum* species. Short arms are at the top. The lengths of the individual linkage maps were normalized so that the distance between *XGli1* and *XGlu1* would equal 75 cM for comparison purposes. Markers preceded by an X are DNA markers and those without an X indicate genes encoding traits or isozymes that were assayed within the population. The marker preceded by a Q is a QTL. Underlined markers were mapped in different populations. Markers in parentheses are assigned to intervals at a LOD <3.0. The darkened regions of the chromosomes at 75 cM indicate the positions of the centromeres. Dotted lines indicate orthologous loci. In the Tm/Ta map, *Xbcd446*, *Xbcd762*, *Xbcd1796*, *Xcdo658*, *Xcdo1188*, *Xpsr161*, *Xpsr168*, *Xpsr381*, *Xpsr937*, *Xtam52*, and *Xwg789* cosegregate with *Xbcd1072*; and *Xbcd207*, *Xbcd386*, *Xbcd921*, *XEsi47*, *Xcmwg758*, *Xpsr158*, *Xpsr1201*, *Xwg180*, and *Xwg605* cosegregate with *Xabg452*.

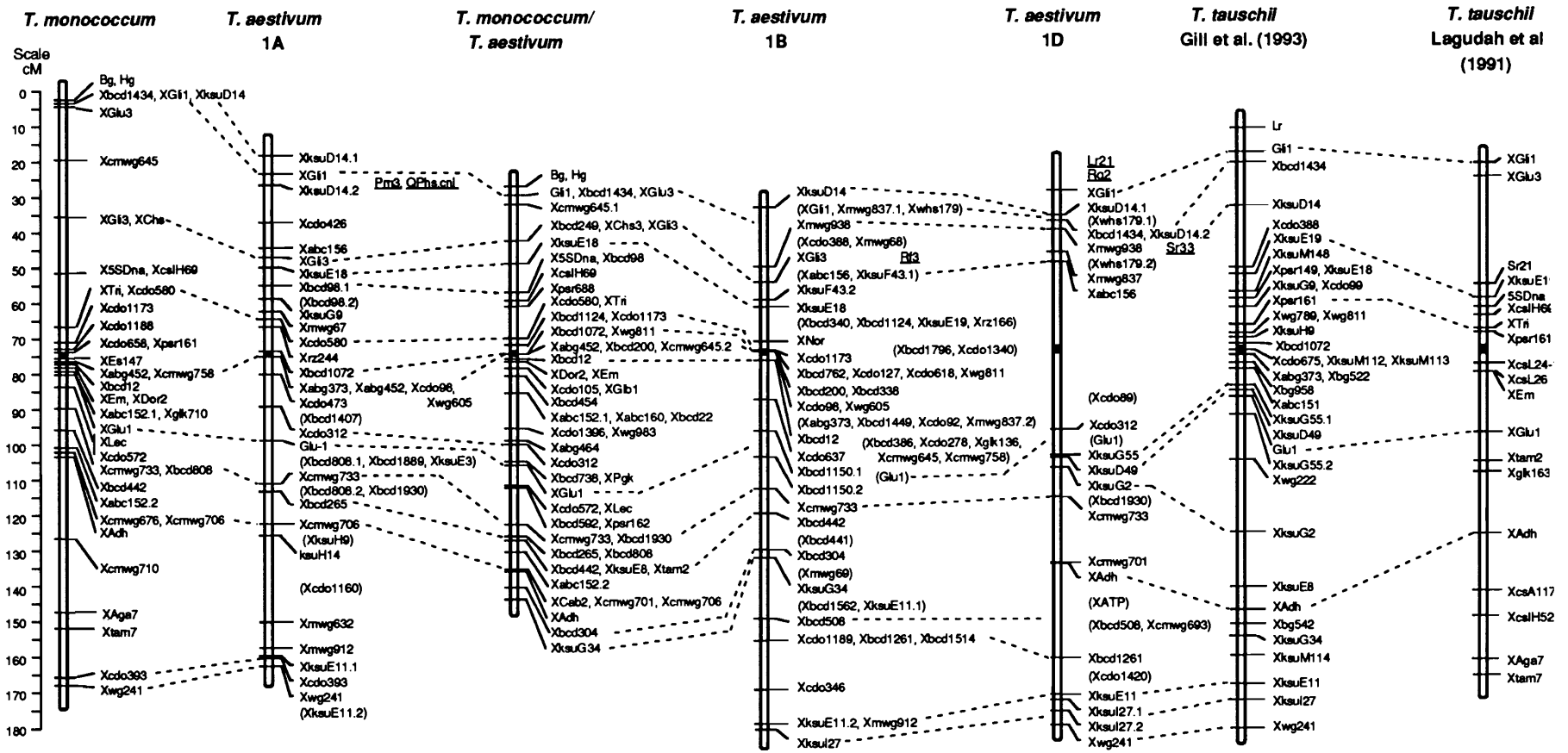
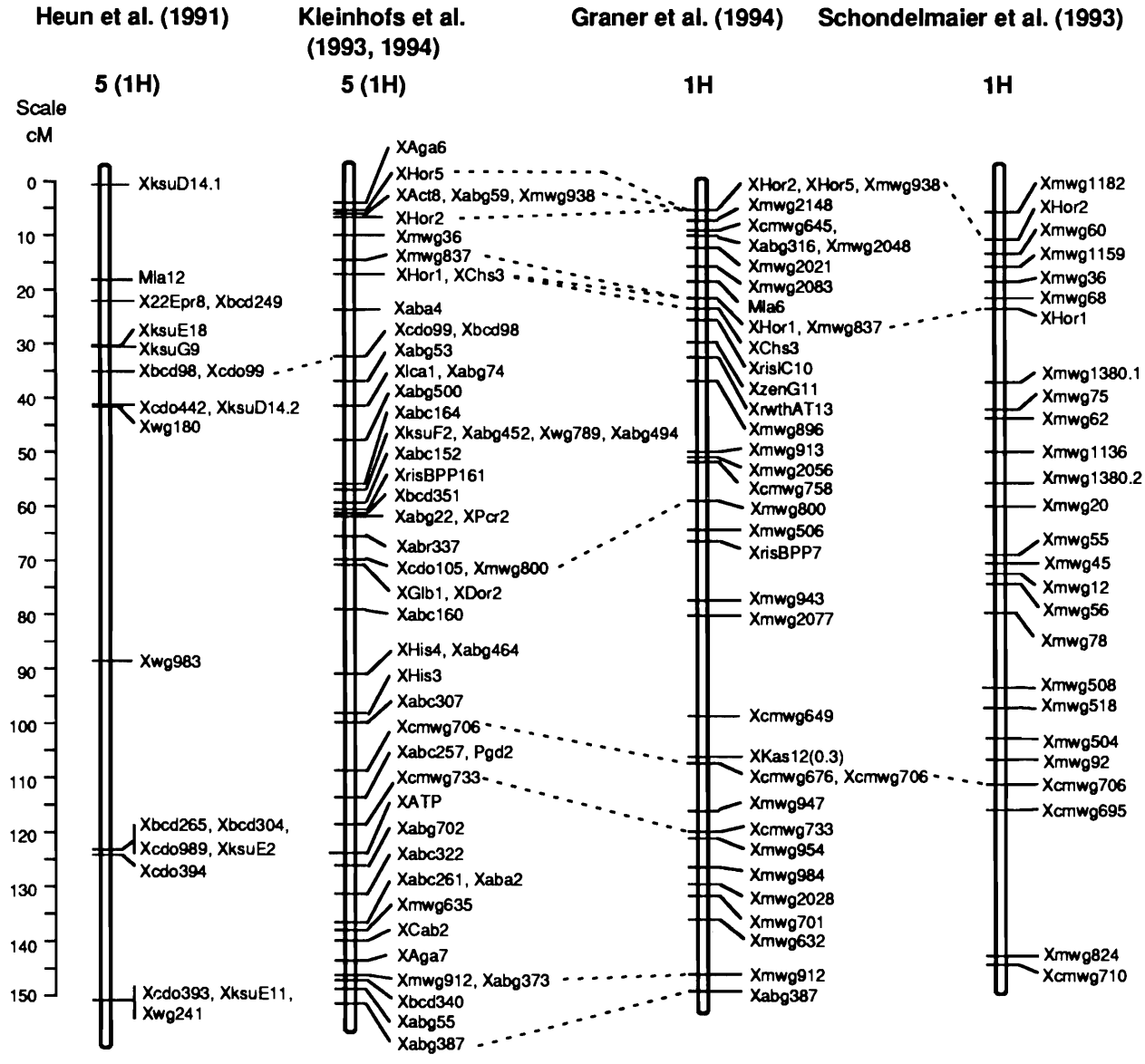


Fig. 3. Linkage maps for *Hordeum* species chromosome 5 (1H), homoeologous to group 1 chromosomes of *Triticum* species. Short arms are at the top. Markers preceded by an X are DNA markers. Those without an X indicate genes encoding traits or isozymes that were assayed within the population. Dotted lines indicate orthologous loci.



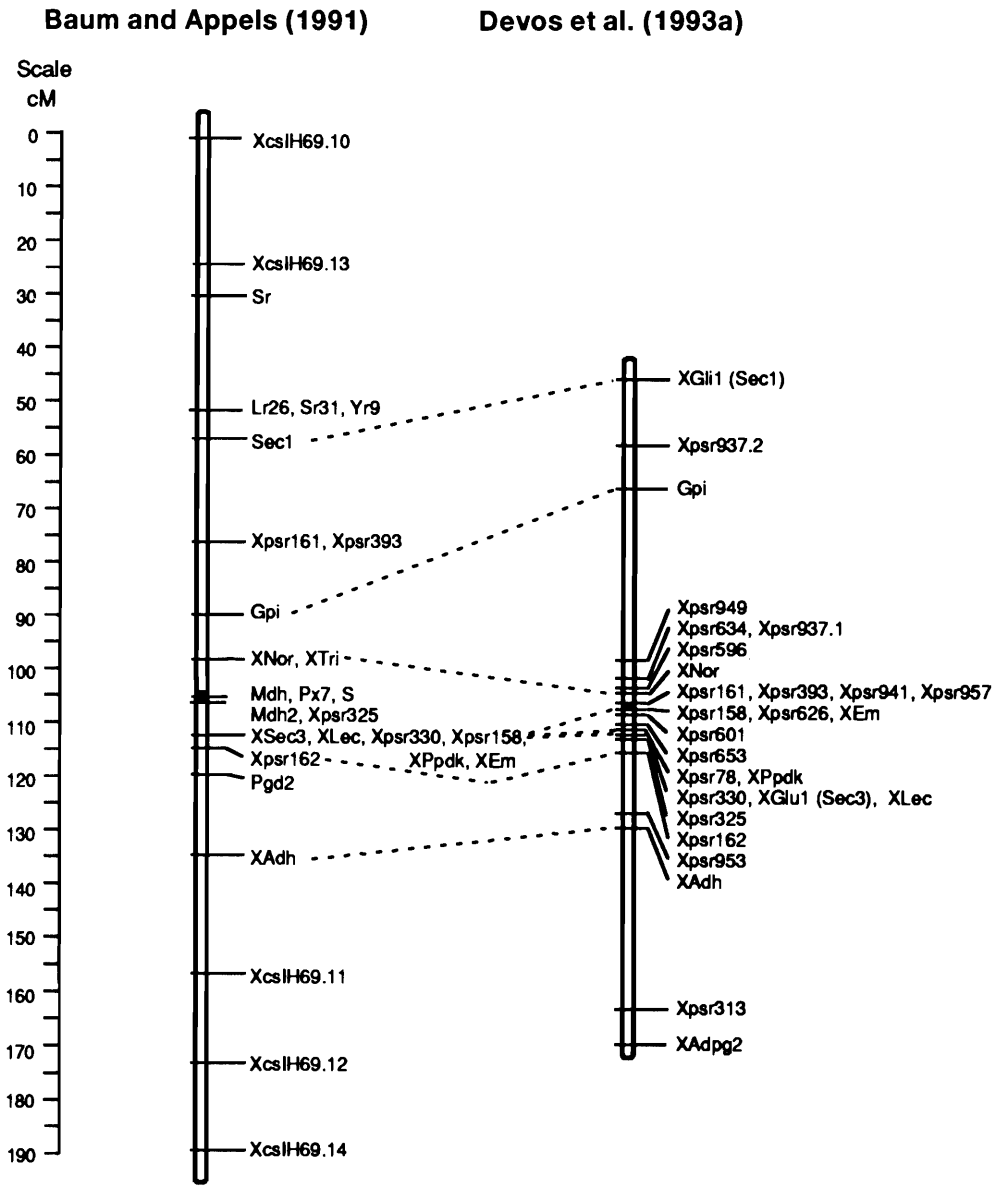
substantiated by comparing maps from the different *Triticum* species in Fig. 2. The only inconsistencies involve markers that were mapped at LOD < 3.0.

Linkage maps for chromosome 1 in *Triticum* species

Linkage maps for group 1 chromosomes of *Triticum* species are shown in Fig. 2. The lengths of the maps range from 116 cM in Tm to 344 cM in Tt (Table 1). The Tm/Ta map is 112 cM but is incomplete due to the nature of the cross. The lengths of the linkage maps in Fig. 2 were adjusted in order to have the same distance (75 cM) between *XGli1* on 1S and *XGlu1* on 1L for comparison purposes. Although interlocus distances varied, the relative order of markers and centromere locations for Ta and related species is conserved (Fig. 2). Duplicated loci within chromosome 1A were detected for GLI, BCD98, BCD808, KSUD14, and KSUE11 in the Ta population; ABC152 in the Tm population and the Tm/Ta cross; and CMWG645 in the Tm/Ta cross. Within chromosome duplications were also detected in 1B (represented only in Ta) for BCD1150, KSUE11, KSUF43, and MWG837; and for WHS179 (Ta) and KSUG55 (Tt; Gill et al. 1993) in 1D.

Loci for resistance to leaf rust (*Lr*, Gill et al. 1991; *Lr21*, Jones et al. 1990), stem rust (*Sr21*, Lagudah et al. 1991; *Sr33*, Jones et al. 1991), powdery mildew (*Pm3*; Ma et al. 1994), preharvest sprouting (*QPhs.cnl*; Anderson et al. 1993), male-fertility restoration (*Rf3*; Z.Q. Ma, in preparation), gliadins (*XGli1*, *XGli3*), glutenins (*XGlu1*, *XGlu3*), triticin protein (*XTri*), lectin (*Lec*), chlorophyll a/b proteins (*XCab*), early methionine-labelled polypeptide (*XEm*), dormin 2 (*Dor2*), alcohol dehydrogenase (*XAdh*), ATPase (*XATP*), wheat endosperm ATP-dependent glucose-

Fig. 4. Linkage maps for chromosome 1R of rye (*Secale cereale*). Short arms are at the top. Markers preceded by an X are DNA markers. Those without an X indicate genes encoding traits or isozymes that were assayed within the population. The darkened regions of the chromosomes at 105 cM indicate the position of the centromeres. Dotted lines indicate orthologous loci.



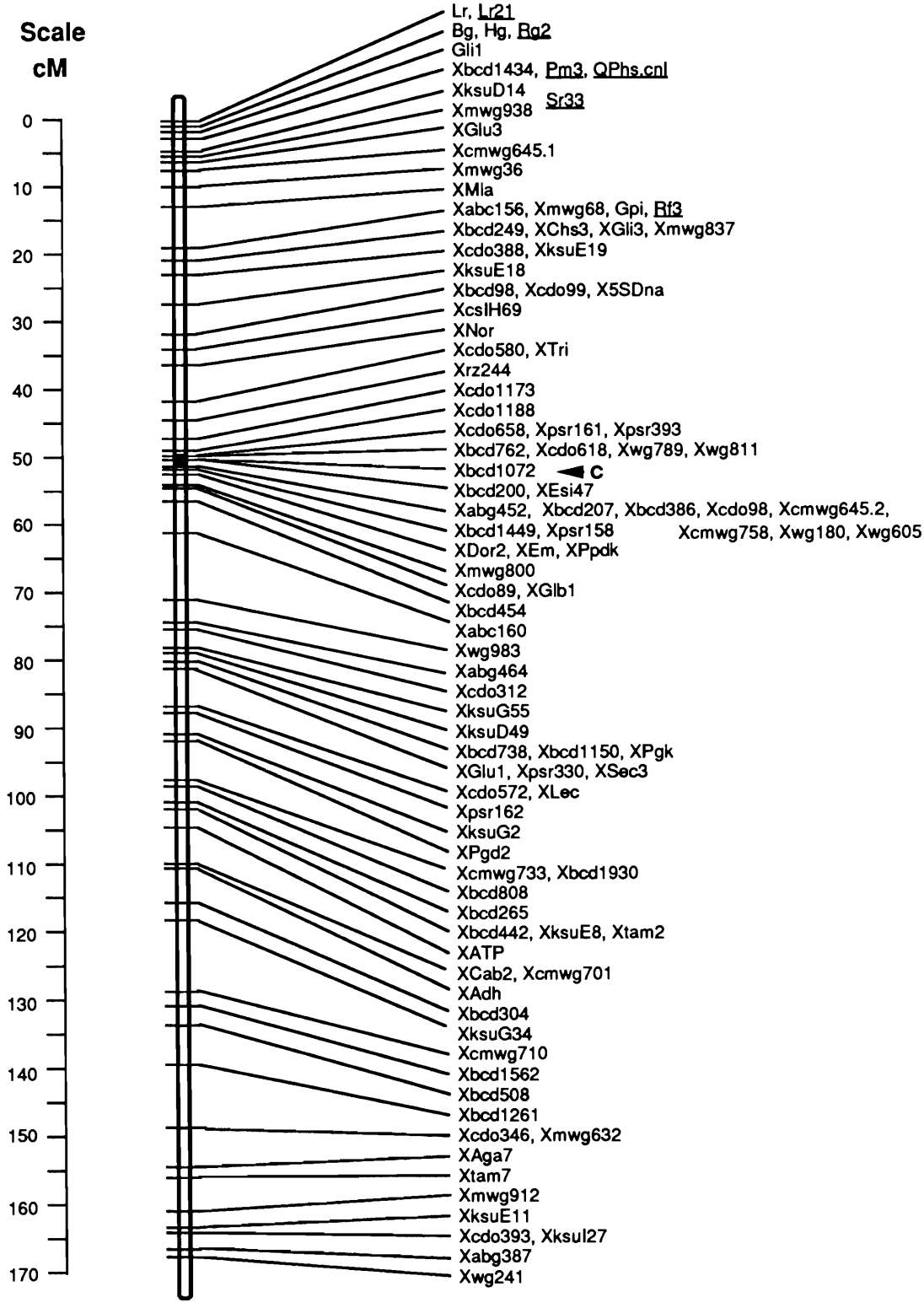
1-phosphate adenosyltransferase (*XAga*), chalcone synthase (*XChs*), 1,3-1,4-β-glucanase (*XGlb*), phosphoglycerate kinase (*XPgk*), early salt-stress induced gene (*XEsi47*), hairy glume (*Hg*), black glume (*Bg*), red glume (*Rg2*; Jones et al. 1990), 5S ribosomal DNA (*X5SDna*), and 45S ribosomal DNA (*XNor*) have been assigned to one or more of the *Triticum* linkage maps (Fig. 2).

A consensus map for group 1 chromosomes of Triticeae

There were only three inconsistencies in the order of common loci in the seven wheat maps presented, both involving markers that were placed at LOD <3.0. The position of *Xbcd1796* relative to *Xcdo1173* and of *Xbcd12* relative to *Xcmwg758* is different between Ta (1B) and the Tm/Ta cross (Fig. 2). The different positions of *XksuH9* on the Tt and Ta maps suggest that there may be more than one *XksuH9* locus in *Triticum* genomes.

The linkage maps of chromosome 5 (1H) of barley (*Hordeum* spp.; Heun et al. 1991; Schondelmaier et al. 1993; Kleinhofs et al. 1993, 1994; Graner et al. 1994) (Fig. 3) were compared with the chromosome 1 maps of *Triticum* (Fig. 2). The relative order of the 46 common loci is the same except for *Xabc152*, *Xbcd340*, *Xcdo105*, *XksuG9*, *Xcmwg645*, *Xcmwg676*, *Xcmwg706*, and *Xabg373*. The aberrant position of *Xcmwg645* may be due to the duplication of this locus within 1A in Tm/Ta (Fig. 2). The

Fig. 5. A consensus map for group 1 chromosomes of Triticeae. Short arm is at the top. Markers preceded by an X are DNA markers and those without an X indicate genes encoding traits or isozymes. The marker preceded by a Q is a QTL. The map was constructed so that the distance between *XGli1* and *XGlu1* equaled 75 cM. The darkened region of the chromosome and the arrowhead indicate the location of the centromere.



reason for the anomalous positions of the remaining loci is unclear. The fact that orthologous loci flanking *Xbcd340*, *Xcmwg676*, *Xcmwg706*, and *Xabg373* in the barley and *Triticum* linkage maps show the same order suggests that the aberrant positions of these loci are likely the result of gene duplications. For example, *Xabg373*, which mapped

to the same telomeric position as *Xmwg912* in barley, is located proximally in wheat, while *Xmwg912* remained in its telomeric location (Figs. 2 and 3). The locations of *Xcmwg706* and *Xabg373* in wheat are considered correct, because they are located in these positions in at least two *Triticum* maps (Fig. 2).

With the exception of the loci for *Xpsr161* and *Xpsr393*, and *Xpsr325* the orders of the markers that comprise the two linkage maps for 1R of rye are in agreement (Fig. 4). Based on the maps presented in this paper, it is likely that *Xpsr161* and *Xpsr393* in *Triticum* are orthologous to the *Xpsr161* and *Xpsr393* locus located proximally to XTri in the Devos et al. (1993*a*) map, therefore this position was used in the consensus map. The relative positions of *Xpsr937* on 1R (Devos et al. 1993*a*) and the Tm/Ta map are also inconsistent.

A consensus map (Fig. 5) of group 1 chromosomes for Triticeae species was developed using markers common to two or more linkage maps in Figs. 1–4 as reference points. Based on the above observations for wheat, barley, and rye, a consensus map for group 1 chromosomes of the Triticeae tribe (Fig. 5) can be constructed including *Xcmwg645*, *Xpsr161*, and *Xpsr393* but not *Xabc152*, *Xabg373*, *Xbcd12*, *Xbcd340*, *Xbcd1796*, *Xcdo105*, *XksuG9*, *XksuH9*, *Xcmwg676*, *Xcmwg706*, *Xpsr325*, or *Xpsr937*, because the presence of duplicated loci or ambiguities regarding their relative order were not resolved. Although the Spearman's rank correlation coefficient between the consensus maps based on common loci and JOINMAP (not shown) was 0.97, 17 out of the 83 loci used in the analysis were misplaced by JOINMAP relative to the individual maps.

The locations of nine orthologous loci from agronomically important genes or that were detected from clones of known-function genes, *XCab*, powdery mildew resistance (*Pm3-Mla*), *XATP*, *XDor2*, *XGlb*, *XGli1-XHor2*, *XGli3-XHor1*, *XAga*, and *XChs* in wheat and barley, six orthologous loci, *XNor*, *XGlu1*, *XAdh*, *XGli1-XSec1*, resistance to leaf rust (*Lr21-Lr26*), and *XTri* in wheat and rye, and two orthologous loci, *XPdg2* and *XHor2-XSec1*, in barley and rye, were established.

Physical versus genetic distance

The various approaches for developing physical maps include the use of deletions, translocations, and C-bands as genetic markers. Dramatic distortions in the wheat linkage maps relative to physical landmarks have been reported (Snape et al. 1985; Dvořák and Appels 1986; Curtis and Lukaszewski 1991; Kota et al. 1993). The most detailed physical maps are for chromosome 1B of wheat, with additional information from chromosome 1R of rye (Fig. 6). Comparisons of the genetic linkage maps based on C-banding with those based on physical distance (arbitrary units) indicate that recombination is drastically reduced in the centromere regions of both 1B and 1R. For example, the distance between CucrS4 and CucrL4 is relatively larger in the physical map of 1B (Kota et al. 1993) than in the linkage map (Curtis and Lukaszewski 1991) (Fig. 6A). The order of loci in the linkage maps is also confirmed by their assignment to deletion (1B) or translocation stocks (1R) that have been ordered on the basis of C-band patterns (Fig. 6).

Comparison of the Triticeae consensus map with maps of rice and oat

Figure 7 shows that loci that map to rice chromosomes 5 and 10 are orthologous to loci mapping to the group 1 chromosomes of Triticeae. The order of orthologous loci from the long arm and the proximal portion of the short arm of the linkage maps for group 1 chromosomes of Triticeae is conserved in the linkage maps of rice. The positions of the only loci from the distal portion of the short arm of group 1 Triticeae chromosomes linkage maps (*Xbcd1434*, *Xmwg68*) that could be detected in rice are not conserved relative to Triticeae. Both of these clones detected additional fragments that were monomorphic and thus could not be mapped, leaving open the possibility that the unmapped loci may be orthologous to Triticeae. Loci on chromosome 10 of rice (Fig. 7) are orthologous to the proximal long arm of group 1 chromosomes of Triticeae, and two loci representing the ends of rice chromosome 10 were assigned to the short (*Xrz892*) and long arms (*Xcdo94*) of chromosome 1 of Triticeae using ditelosomics.

The order of 16 orthologous loci in chromosome A of oat and group 1 chromosomes of Triticeae is conserved (Fig. 7). Only loci that were mapped at LOD <2.0 in oat had different positions relative to Triticeae. The oat chromosome A linkage map also includes loci that were assigned to wheat chromosomes 2, 3, 4, and 6 on the distal portion of one arm.

Location of centromeres in rice and oat relative to wheat

In wheat, the position of the centromere can be determined by hybridizing probes to ditelosomic lines. Since the order of orthologous loci in the linkage maps of rice chromosomes 5 and 10 and oat chromosome A seems conserved in the proximal regions of the chromosome arms relative to wheat 1, and since these regions contain loci orthologous to loci from both the short (1S) and long arms (1L) of wheat, an estimate of the location of the centromeres of these chromosomes was made. The best estimate of the centromere location would be between *Xbcd1072* and *Xbcd200* for rice chromosome 5; between *Xrz892* and *Xcdo98* for rice chromosome 10; and at the *Xcdo618* and *Xbcd200* locus for oat chromosome A.

Discussion

Although hexaploid wheat consists of genomes derived from three ancestral species, the genetic mapping of chromosomes 1, 2 (Devos et al. 1993*b*), 3 (Devos et al. 1992), and 7 (Chao et al. 1989) indicate that the relative order of DNA fragments is conserved. The order of genetic loci based on genetic-linkage studies is consistent with the order determined using deletion lines, where virtually all loci can be mapped across three genomes (Werner et al. 1992). This complements the initial evidence based on nullisomic–tetrasomic compensation (Sears 1966) and the detection of homoeoloci in ditelosomic lines (Gale and Sharp 1988; Liu and Gale 1991; Anderson et al. 1992; Devey and Hart 1993). The present data confirm these observations and extend the conservation of gene order in homoeologous group 1 to related Triticeae species.

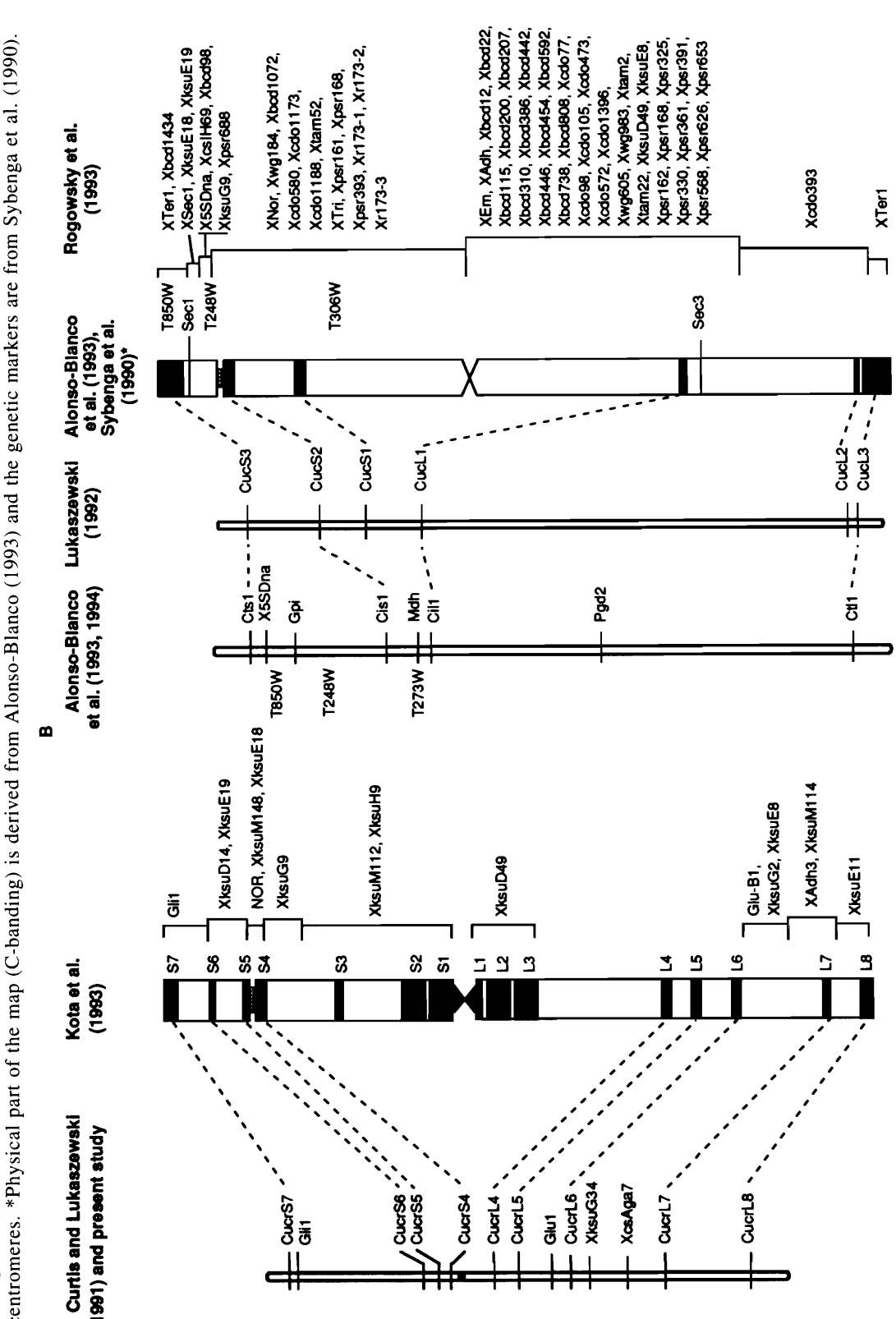


Fig. 6. Genetic and physical maps of chromosome 1B of wheat (A) and chromosome 1R of rye (B). Short arms are at the top. The maps by Kota et al. (1993), Alonso-Blanco et al. (1993), and Rogowsky et al. (1993) were constructed on a physical chromosome length (%) basis. The remaining maps are linkage maps based on C-bands and DNA markers. Markers preceded by an X are DNA markers; C is C-band and T is translocation breakpoint. Dotted lines show orthologous loci. The darkened regions on the linkage maps and the constrictions on the physical maps represent the centromeres. *Physical part of the map (C-banding) is derived from Alonso-Blanco (1993) and the genetic markers are from Sybenga et al. (1990).

As indicated by the number of markers mapped to each genome, the level of polymorphism among genomes in *T. aestivum* is quite variable. The highest degree of polymorphism was detected in chromosome 1B and the lowest in 1D, in spite of the fact that one parent in the *T. aestivum* cross contains 1D from *T. tauschii*, the D genome progenitor of *T. aestivum* (McFadden and Sears 1946). Chao et al. (1989) also reported the lowest level of polymorphism in the D genome of chromosome 7 of *T. aestivum*. High levels of polymorphism have been reported among *T. tauschii* accessions (Gill et al. 1991), but by chance, the accession used to produce the *T. aestivum* synthetic line used in this study is genetically similar to the latter's progenitor. Although polymorphism was not detected in the proximal regions of the 1D chromosome in *T. aestivum*, the data from the nullitetrasomic and ditelosomic lines for loci mapped to 1A and 1B in this region show that homoeologous loci are present on 1D.

Recombination

Except for chromosome 1D in *T. aestivum*, the *Triticum* spp. linkage maps show clustering of markers near the centromere. This has been observed in other studies of wheat (Dvořák and Chen 1984; Snape et al. 1985; Dvořák and Appels 1986; Curtis and Lukaszewski 1991; Chao et al. 1989; Devos et al. 1992, 1993*b*; Werner et al. 1992; Lukaszewski and Curtis 1993), barley (Kleinhofs et al. 1993), rye (Rogowsky et al. 1992; Lukaszewski 1992), and oat (O'Donoughue et al. 1992). Comparisons of the physical (Fig. 6) and linkage (Figs. 1–4) maps outlined in this paper demonstrate the uneven distribution of recombination in these genomes. Genetic and physical distances along chromosomes have been compared using recombination of C-bands (Lukaszewski and Curtis 1993) and deletion stocks (Werner et al. 1992; Kota et al. 1993). In all the studies, the recombination per physical unit of chromosome increased with distance from the centromere. It was estimated that recombination is suppressed in 70–75% and 35–40% of the proximal regions of short and long arms, respectively. Estimates for the number of kilobase pairs (kbp)/cM ranged from 1530 kbp/cM in distal chromosome regions to 234 000 kbp/cM in proximal regions (Lukaszewski and Curtis 1993). Comparisons of the wheat and rice maps in the present study and those of Kurata et al. (1994) suggest that recombination may be suppressed more around the centromeres in Triticeae species than in rice.

Development of a consensus map

A consensus map for Triticeae group 1 chromosomes was established in the present study by constructing individual linkage maps and then defining a common set of markers. A number of factors affect the degree of certainty or error rate associated with the consensus map, including the LOD threshold for the position of loci relative to others in contributing individual maps and the occurrence of duplications and chromosome rearrangements. There were 12 inconsistencies in the relative order of 116 common markers among seven wheat, four barley, and two rye linkage maps. After ruling out errors in scoring, ambiguous loci, such as *Xcmwg645*, were added to the consensus map only when it was clear that a duplication was involved. Loci involved in rearrangements should not be used in consensus maps unless the chromosome region involved is carefully characterized. In view of the chromosomal rearrangements known to be present in other chromosome groups of the Triticeae species analyzed (Devos et al. 1993*a*), group 1 chromosomes seem to be the most highly conserved. It is possible that future more detailed genetic and physical maps may reveal small rearrangements among these species.

Comparisons among diverse species

The same precautions used to develop the consensus map, as well as the possibility of duplications across nonhomoeologous chromosomes, were considered in making comparisons among diverse species. For example, Anderson et al. (1992) reported that 40 of 210 DNA probes hybridized to fragments in more than one homoeologous group of hexaploid wheat chromosomes and that group 1 chromosomes were involved in the majority of these duplications. In the present study, many loci were duplicated between chromosomes 1 and 7 in *Triticum* (data not shown). Some of these loci were also duplicated in homoeologous chromosomes in barley (Kleinhofs et al. 1993, 1994; Schondelmaier et al. 1993; Graner et al. 1994) and oat (O'Donoughue et al. 1992).

Homoeology between wheat chromosome arms and rice was first reported by Ahn et al. (1993), and a more recent study (Kurata et al. 1994) has provided evidence for conservation of gene orders between these two crops. Both studies indicate that rice chromosomes 5 and 10 are homoeologous with group 1 chromosomes of Triticeae. Although the linkage maps for chromosome 10 and part of chromosome 5 in rice are homoeologous to the proximal regions of the linkage maps for group 1 chromosomes of Triticeae, single and multicopy (washing stringency 0.5× SSC (0.15 M NaCl plus 0.015 M sodium citrate) at 65°C) sequences are interspersed throughout these rice chromosomes. The data from the present study indicate that, although orthologous loci span all of rice chromosomes 5 and 10 linkage maps, loci from the distal portion of the linkage maps for the short arm of the Triticeae are not represented in these chromosomes. The only two loci from the distal short arm of the linkage maps of Triticeae that could be detected in rice did not map to homoeologous positions in rice chromosome 5 relative to Triticeae. Kurata et al. (1994) also observed that homoeology between rice and wheat breaks down in the distal regions.

Vedel and Lebacq (1980) reported that the restriction fragment length patterns from digests of oat, barley, and rye chloroplast DNAs were similar. In the present study, the order of loci from the entire length of the linkage maps of group 1 chromosomes of Triticeae is conserved on chromosome A of oat. However, oat chromosome A also contains loci orthologous to chromosomes 2, 3, 4, and 6 of wheat on one of its distal regions (Fig. 7). The close linkage of crown rust (*Puccinia coronata* Cda. f.sp. *avenae*) with avenin genes in oat (Chong et al. 1994) parallels the proximity of the leaf-rust and gliadin loci on the *Triticum* maps. An avenin locus has also been identified on the A chromosome of diploid oat, homoeologous to group 1 of Triticeae (Rayapati et al. 1994).

The homoeology of group 1 chromosomes of Triticeae is noteworthy. With few exceptions, the gene order of this

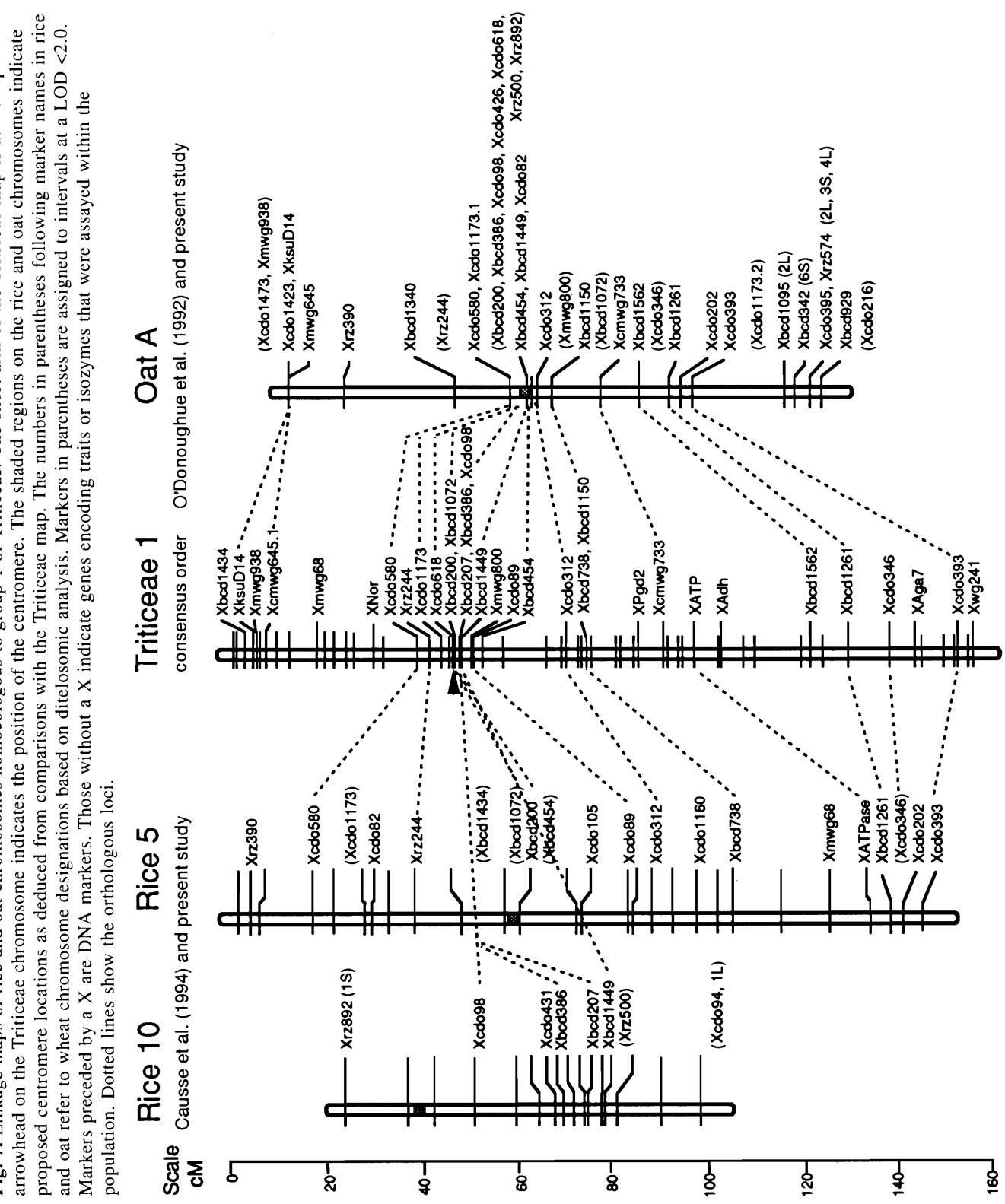


Fig. 7. Linkage maps of rice and oat chromosomes homoeologous to group 1 of Triticeae. The short arm of the Triticeae map is at the top. The arrowhead on the Triticeae chromosome indicates the position of the centromere. The shaded regions on the rice and oat chromosomes indicate proposed centromere locations as deduced from comparisons with the Triticeae map. The numbers in parentheses following marker names in rice and oat refer to wheat chromosome designations based on ditelosomic analysis. Markers in parentheses are assigned to intervals at a LOD <2.0. Markers preceded by a X are DNA markers. Those without a X indicate genes encoding traits or isozymes that were assayed within the population. Dotted lines show the orthologous loci.

group of chromosomes has undergone very little change in gene and DNA sequence order in wheat, rye, and barley at the current resolution of the genetic maps. This is consistent with the observation that chromosome 1R is the only rye chromosome that is not involved in rearrangements relative to wheat (Devos et al. 1993*a*). Comparisons of group 1 chromosomes of Triticeae with their homoeologous chromosomes in rice and oat, suggest that this chromosome is highly conserved, especially in the proximal regions. Blocks of genes may continue to be inherited together because they are critical to survival or performance.

Use of the maps

Genes governing characters such as yield and heterosis, resistance to pests and diseases, or tolerance to environmental stresses have been identified on the genetic maps of wheat, barley, rye, and rice (Anderson et al. 1993; Kleinhofs et al. 1993; Baum and Appels 1991; Causse et al. 1994). We have shown that some of these genes are located in chromosomal regions that have been conserved among these species, suggesting that orthologous genes may confer favorable phenotypes in many of the major cereal crops. The development of consensus and comparative maps with common DNA markers from many species will aid in the efficient identification of markers linked to genes of interest and eventually to isolation of these genes. The efficiency of gene isolation will depend on the level of homology in the regions of interest and the inheritance of the trait. However, the isolation of genes in large genomes with uneven distributions of recombination along chromosomes may be facilitated by first isolating a homoeologous gene in less complex genomes, such as rice.

The number of genes assigned to group 1 chromosomes reflects the agronomic importance of these chromosomes in the Gramineae genome. A partial list of phenotypes encoded by genes located on homoeologous rice chromosomes includes ATPase, calmodulin, bacterial blight resistance, and early flowering (Causse et al. 1994). Although many genes have been identified in oat (Marshall and Shaner 1992), they have not been assigned to chromosomes. Comparative mapping will, therefore, provide a useful approach for defining agronomically important regions of genomes and recovering closely linked DNA markers in order to trace the introgression of genes and chromosome segments in breeding programs. In wheat, the development of consensus maps may circumvent the problem of low polymorphism between mapping parents when targeting specific regions. The consensus map can be used to determine the relative positions of 288 unique markers from the 13 linkage maps presented in this paper. Linkage maps for new crosses can immediately be placed in correspondence to the consensus map by mapping a limited number of common markers. This study has shown that by using a common set of DNA probes to develop genetic linkage maps, a consensus map can be developed among genera of the Triticeae tribe that can be used to make observations about genome organization in the Gramineae family. Most of the data and linkage maps presented in this paper can be obtained via Internet Gopher, host greengenes.cit.cornell.edu, port 70, menu "Grains files to browse."

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