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A consensus linkage map of rye (*Secale cereale* L.) including 374 RFLPs, 24 isozymes and 15 gene loci

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Abstract Consensus linkage maps were constructed for all seven rye chromosomes using 12 basic RFLP maps. The maps presented contain a total of 413 markers. The number of markers per chromosome varies from 41 (chromosome 3R) to 83 (chromosome 1R). In addition to 374 RFLP and 24 isozyme markers 15 gene loci were incorporated, determining the traits reduced plant height, self fertility, male sterility restoration, vernalization response, resistance against powdery mildew, chlorophyll deficiency, hairy leaf sheath, hairy peduncle, waxy endosperm, waxless plant and absence of ligules. The maps presented allow the selection of markers for the fine mapping of certain regions of the rye genome. In terms of the known chromosomal rearrangements within the *Triticeae* its utilization can also be extended for mapping in wheat and barley.

Key words Consensus map · Isozymes · RFLP · Rye · *Secale cereale* L.

Introduction

For the mapping of agronomically important major genes or quantitative trait loci (QTLs) well-saturated genetic maps are required. The development of DNA markers, such as restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD) and more recently microsatellites, has resulted in the construction of molecular maps in most of the cereal species including rye (*Secale cereale* L.). Generally, the published molecular maps can be divided into two categories. On one hand, there are several maps available covering most of all the seven rye chromosomes, as reported by Devos et al. (1993), Philipp et al. (1994), Loarce et al. (1996), Senft and Wricke (1996) and Korzun et al. (1998), whereas other authors used only selected RFLP markers for the tagging of genes affecting traits of interest. In that case only single chromosomes or chromosome regions were mapped (Plaschke et al. 1993, 1995; Korzun et al. 1996, 1997; Voylokov et al. 1998). Comparisons among certain regions of chromosomes mapped with common markers in different populations indicate that, in most cases, the order of molecular markers on the linkage maps is identical, although the distances are different. Consequently, the construction of consensus maps becomes possible by using common markers as anchors and extrapolating the positions of markers mapped between these anchors.

In the present paper we attempt to summarize the present status of molecular mapping in rye. Consensus maps are constructed for all seven rye chromosomes by combining published data from several individual linkage maps consisting of RFLP, isozyme and gene loci. The figures presented will help to select as many markers as possible from those available in defined regions for the fine mapping of particular genes.

Materials and methods

The consensus maps were constructed using 12 RFLP maps published during the last 6 years (Table 1). In total these basic maps consist of 537 RFLP, 38 RAPD, 33 isozyme and seven C-band markers. The basic mapping sets were obtained from analyzing F_2 and/or F_3 populations of 13 different rye crosses. In addition to the markers, 15 different gene loci have been mapped on five different chromosomes including genes determining reduced plant height (*ct1*, *ct2*, *Ddw1*) on chromosomes 7R and 5R (Devos et al. 1993; Plaschke et al. 1993, 1995; Korzun et al. 1996), self fertility (*S*, *Z*, *S5*) on chromosomes 1R, 2R and 5R (Senft and Wricke 1996; Voylokov

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Table 1 References, crosses, mapped chromosomes and number of markers of the basic mapping sets used for the construction of the consensus maps

Reference	Cross	Chromosomes	Number of markers
Devos et al. (1993)	Ds2 × R × 10	1R, 2R, 3R, 4R, 5R, 6R, 7R	156
Plaschke et al. (1993)	Petka × Moskovskij Karlik	5R	21
Plaschke et al. (1995)	Halo × Gülzow kurz	7R	11
Wanous and Gustafson (1995)	UC90 × E-line	1R	31
Wanous et al. (1995)	UC90 × E-line	6R, 7R	30
Korzun et al. (1996)	R1620 × R347/1	5R	16
Loarce et al. (1996)	E × R	1R, 3R, 4R, 5R, 6R, 7R	89
Senft and Wricke (1996)[a]	I-line × I-line	1R, 2R, 3R, 4R, 5R, 6R, 7R	127
Korzun et al. (1997)	SI × N6	2R, 4R, 7R	21
Börner et al. (1998)	R1620 × R347/1	4R	8
Korzun et al. (1998)	P87 × P105; P105 × P87	1R, 2R, 3R, 4R, 5R, 6R, 7R	91
Voylokov et al. (1998)	V × l6; V × l454; V × l2	1R, 2R, 5R	35

[a]The map for chromosome 2R was modified (Saal, unpublished data)

et al. 1998), vernalization response (*Sp1*) on chromosome 5R (Plaschke et al. 1993), resistance against powdery mildew (*Pm*) on chromosome 1R (Senft and Wricke 1996; Wricke et al. 1996), chlorophyll deficiency (*Chl*) and hairy leaf sheath (*Hs*) on chromosome 5R (Senft and Wricke 1996), hairy peduncle (*Hp1*) on chromosome 5R (Korzun et al. 1996), male fertility restoration (*Rfg1*) on chromosome 4R (Börner et al. 1998), absence of ligules (*al*), waxy endosperm (*Wx*) and waxless plant (*wa1*) on chromosomes 2R, 4R and 7R, respectively (Korzun et al. 1997).

The consensus maps presented here were constructed by drawing all published maps for chromosomes of one particular homologous group side by side. Small unlinked groups present in the maps of Senft and Wricke (1996) or Loarce et al. (1996) were excluded. Only RFLP, isozyme and gene loci were considered. All the loci actually mapped on the chromosomes were marked with a point. If there were at least two loci in common, they were used as anchors and connected with a continous horizontal line. For all the loci between the anchors the relative map position has been extrapolated. Because the distance between common markers in different mapping populations varies, only a rough estimate of the genetical distance is given. A detailed description of the basic maps (size of mapping populations, source of DNA clones, etc.) is provided by the authors listed in Table 1.

Table 2 Number of markers placed on the consensus maps of the seven rye chromosomes

Chromosome	Number of markers			
	RFLPs	Isoenzymes	Gene loci	Total
1R	77	4	2	**83**
2R	44	4	2	**50**
3R	39	2	–	**41**
4R	48	–	2	**50**
5R	68	7	7	**82**
6R	40	7	–	**47**
7R	58		2	**60**
Total	374	24	15	**413**

Results and Discussion

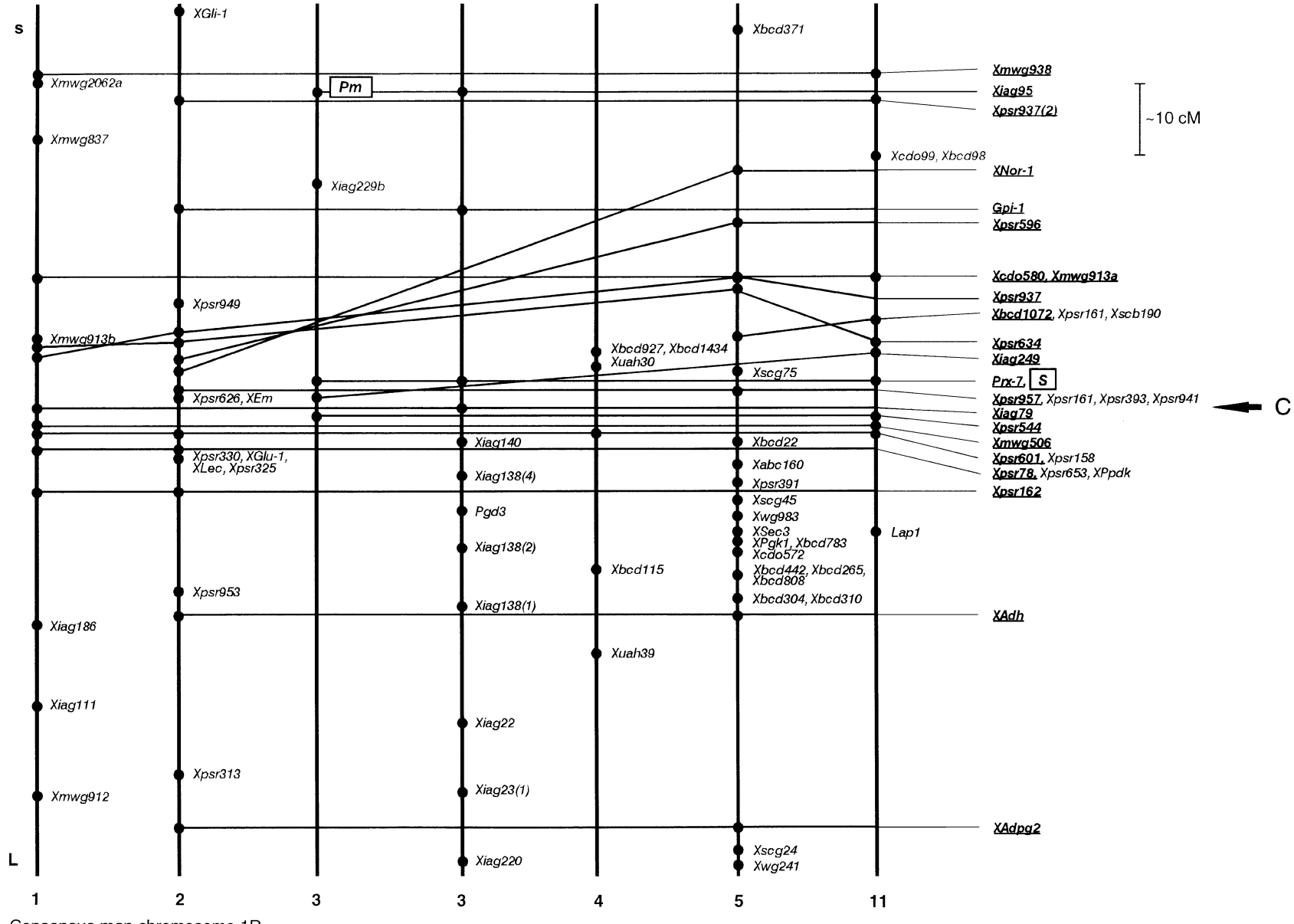
The consensus linkage maps for the seven rye chromosomes are shown in Fig. 1 (a–g). In total 413 markers are shown including 374 RFLPs, 24 isozymes and 15 gene loci. Considering the total number of RFLP markers in the basic maps (537) it could be concluded that about one-third of them have been successfully used in mapping studies more than once. On average the consensus maps consist of about 60 markers per chromosome with a maximum of 83 on chromosome 1R and a minimum of 41 on chromosome 3R. The chromosomal distribution of the markers, divided into RFLPs, isozymes and genes, is shown in Table 2.

The highest density is seen on chromosomes 1R and 5R. Both consensus maps are based on the seven available mapping sets, including single chromosome maps constructed with the aim of tagging genes for self fertility on chromosomes 1R and 5R (Voylokov et al. 1998) or for reduced plant height and vernalization response on chromosome 5R (Plaschke et al. 1993; Korzun et al. 1996). Surprisingly, only 10 of the 80 loci of chromosome 5R map to the short arm. A similar situation was observed for the homoeologous group-5 chromosomes of wheat (Gale et al. 1995).

Chromosomes 3R and 6R, comprising four and five mapping sets respectively, show the lowest density of mapped loci in rye. On both chromosomes, RFLPs and isozymes, but no gene loci, have been mapped, although several agronomically important genes have been localized in the past, e.g. two genes for powdery mildew resistance, designated *Pm3* and *Pm5*, on chromosomes 3RS and 6RL respectively (Melz et al. 1992).

Common to all seven chromosomes is the clustering of mapping points in the centromeric regions due to the fact that recombination occurs more frequently in the distal chromosome regions. Mainly in these regions the order of a few markers common to the basic mapping sets is changed (Fig. 1).

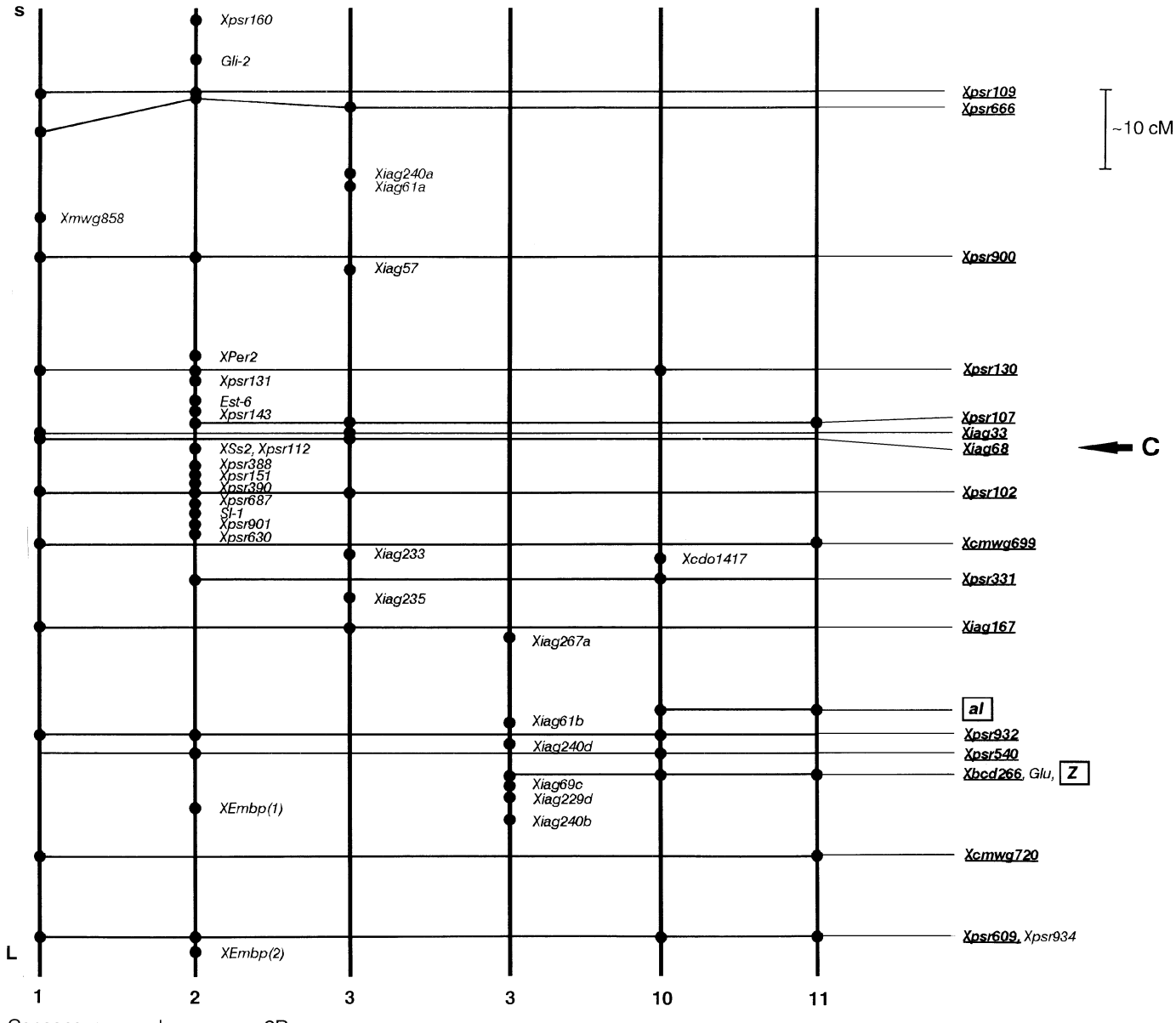
Although there may be some uncertainity in the order of mapping points extrapolated from the different mapping sets the consensus map presented will enable potential users to choose markers in regions of interest



Consensus map chromosome 1R

a

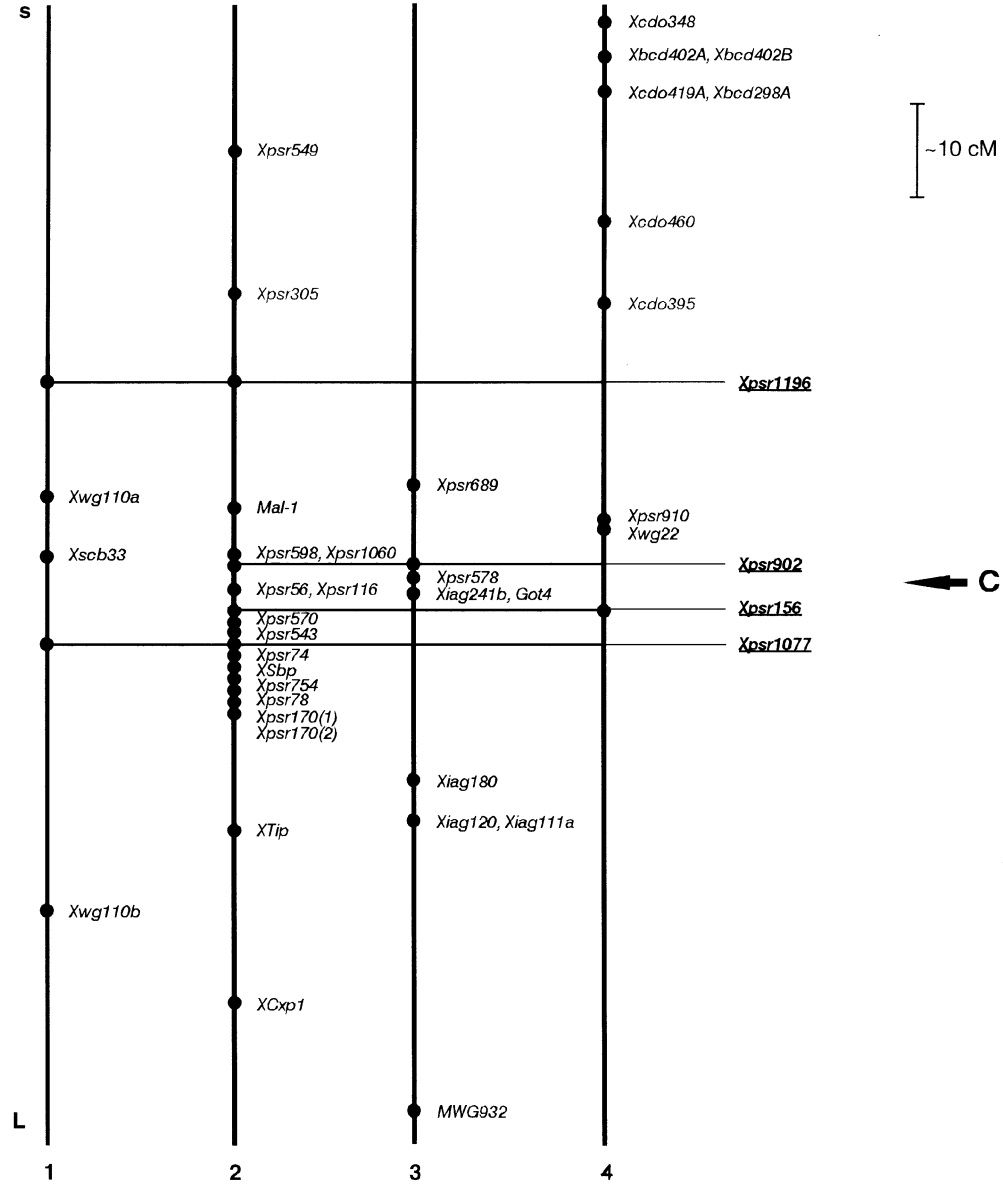
Fig. 1a–g See page 1287 for legend



Consensus map chromosome 2R

b

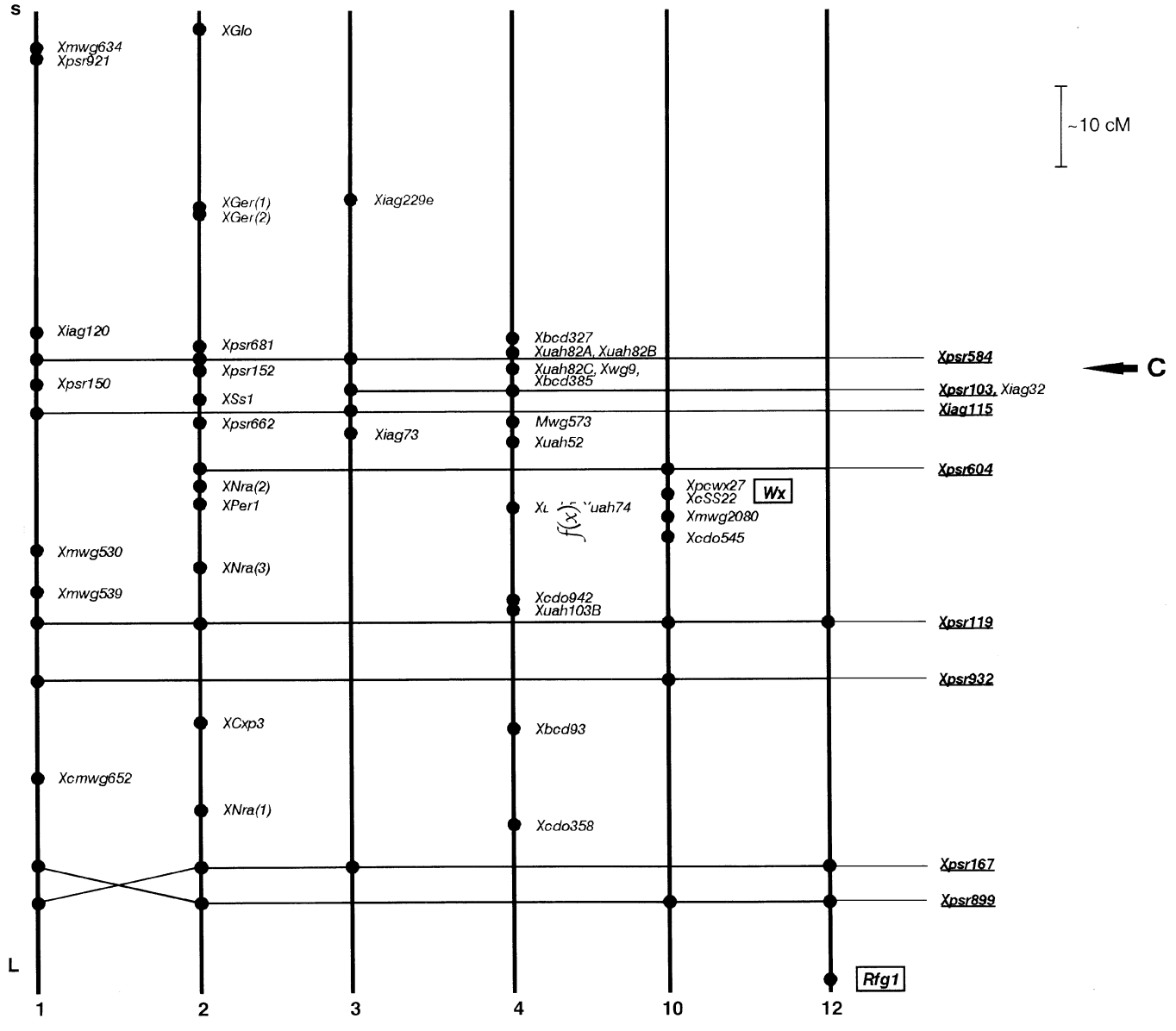
Fig. 1a–g See page 1287 for legend



Consensus map chromosome 3R

c

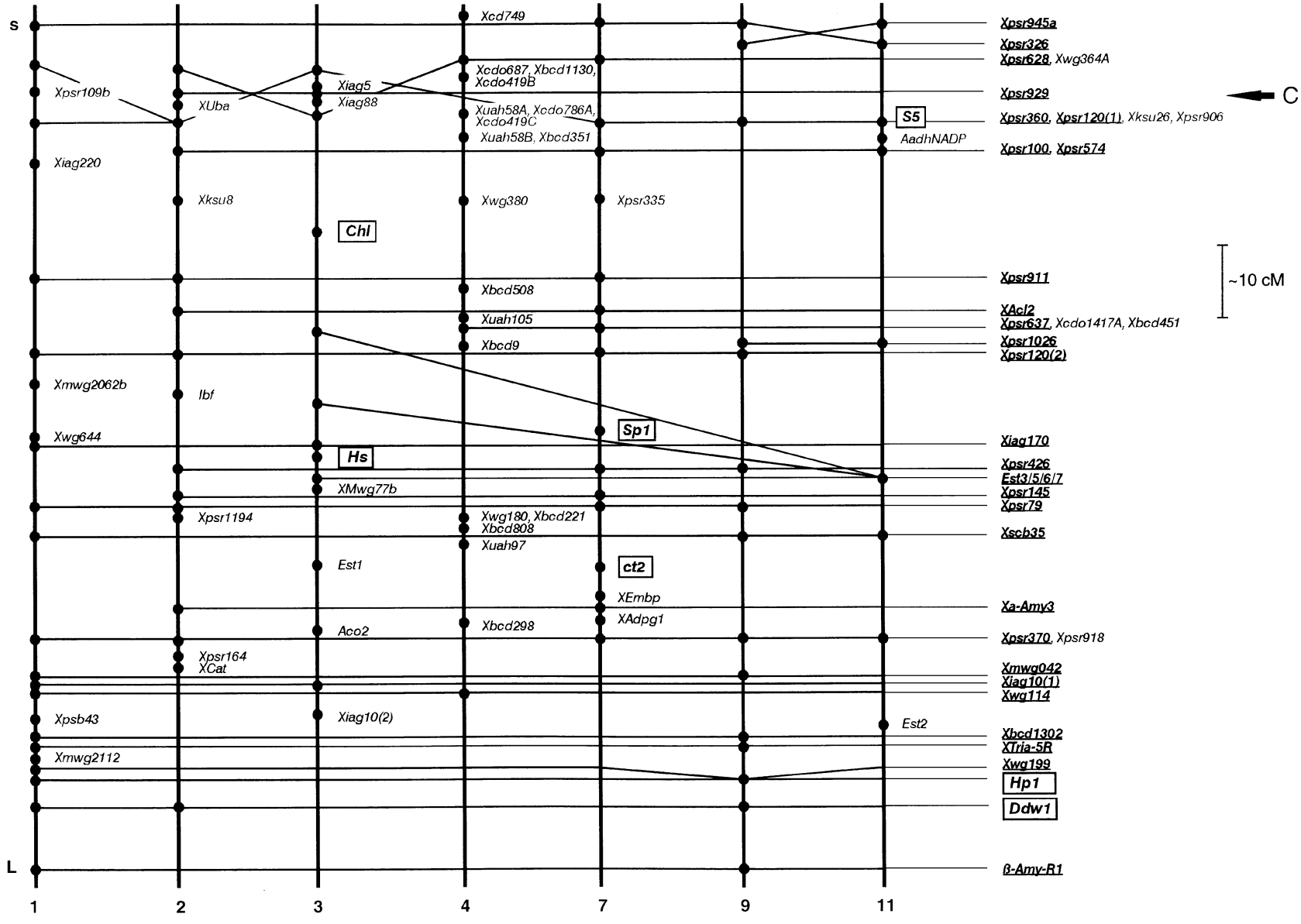
Fig. 1a–g See page 1287 for legend



Consensus map chromosome 4R

d

Fig. 1a–g See page 1287 for legend



Consensus map chromosome 5R

e

Fig. 1a–g See page 1287 for legend

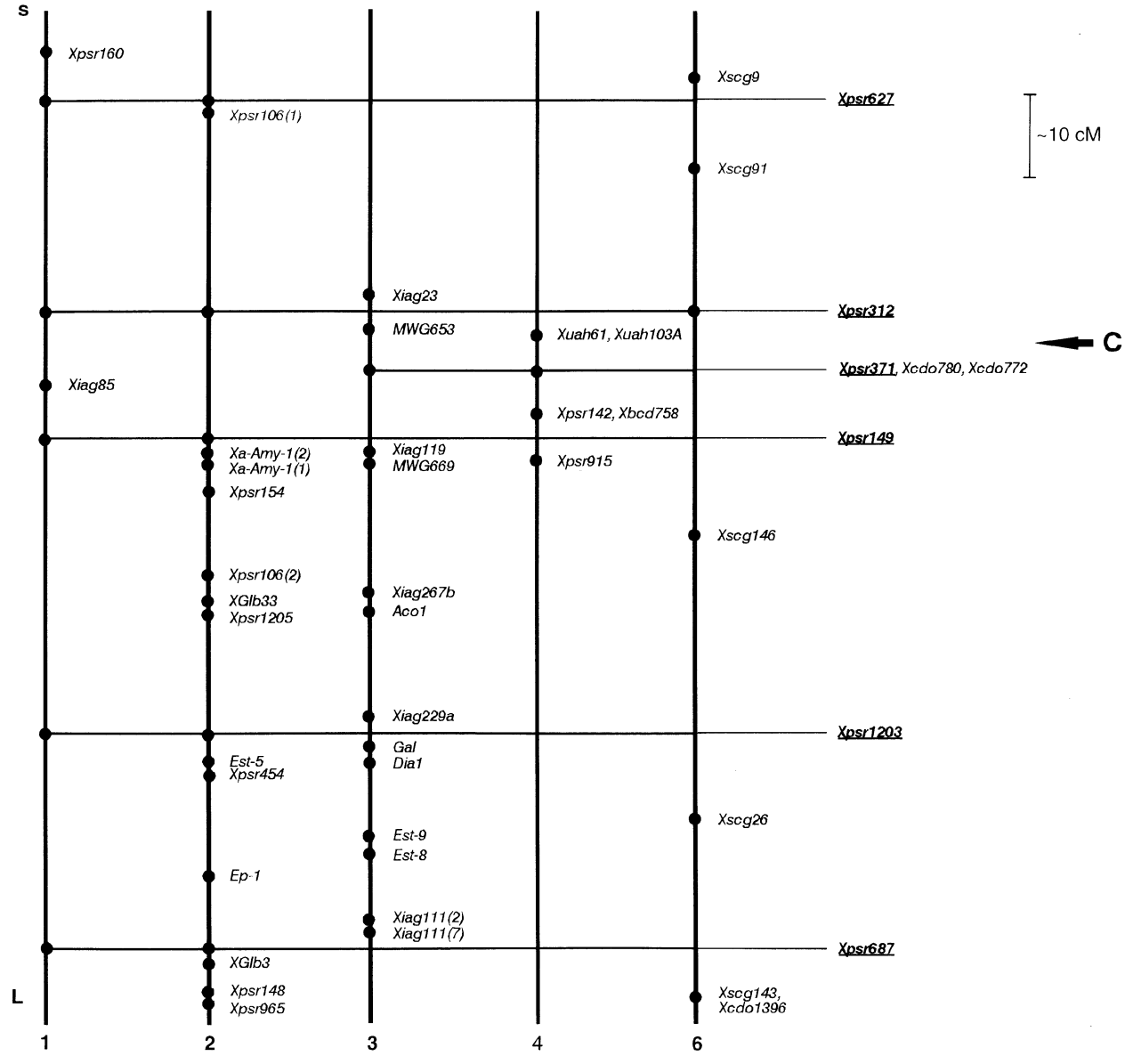
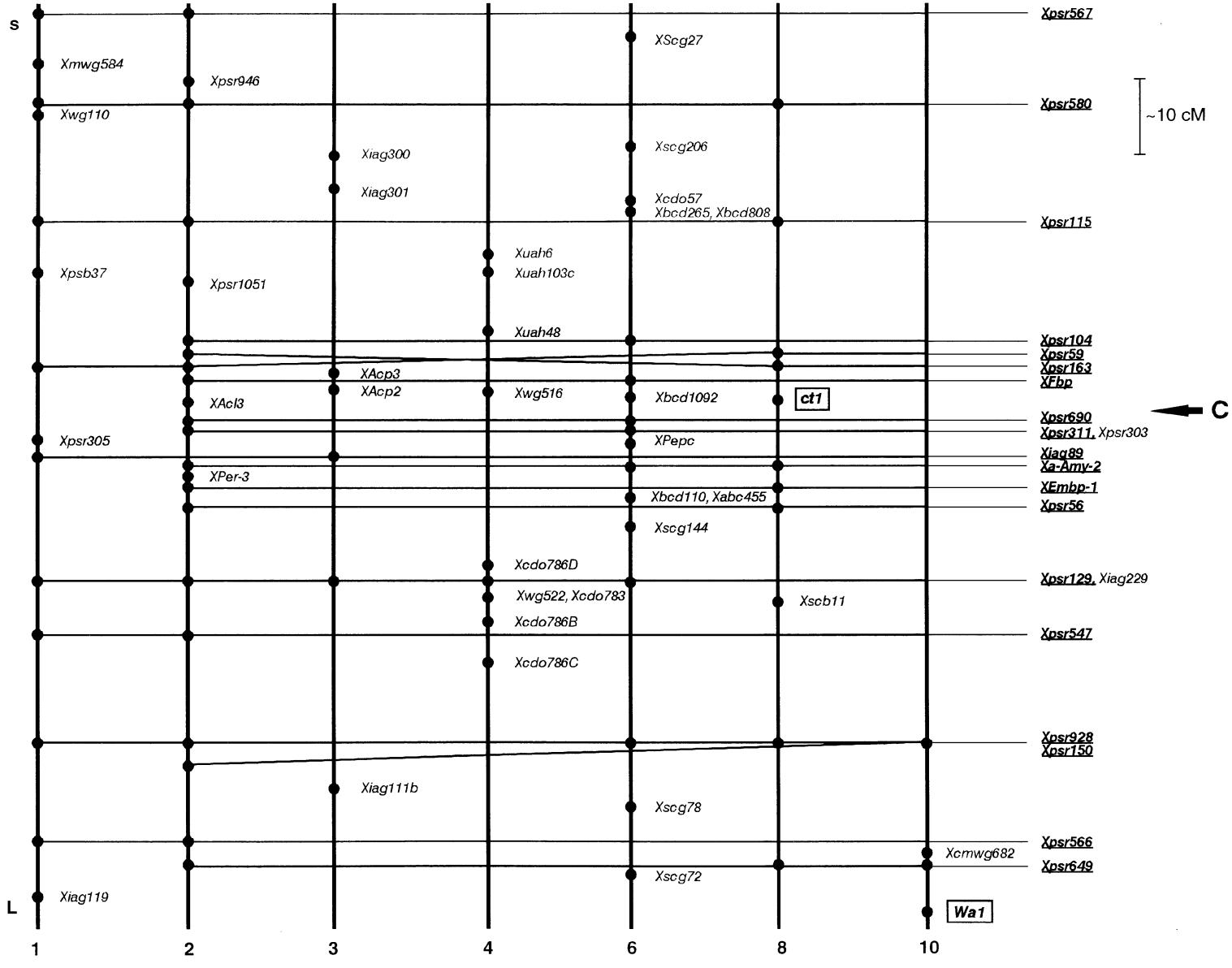


Fig. 1a–g See page 1287 for legend



Consensus map chromosome 7R

g

Fig. 1a–g Consensus linkage maps of chromosomes 1R (**a**), 2R (**b**), 3R (**c**), 4R (**d**), 5R (**e**), 6R (**f**) and 7R (**g**) constructed by using the following basic maps: (*1*) Korzun et al. (1998), (*2*) Devos et al. 1993, (*3*) Senft and Wricke (1996), (*4*) Loarce et al. (1996), (*5*) Wanous and Gustafson (1995), (*6*) Wanous et al. 1995, (*7*) Plaschke et al. (1993), (*8*) Plaschke et al. (1995), (*9*) Korzun et al. (1996), (*10*) Korzun et al. (1997), (*11*) Voylokov et al. 1998, (*12*) Börner et al. (1998). Mapped loci are marked with a *point*. The *horizontal lines* connect common loci used as anchor markers which are *underlined*. The map positions of unique loci were extrapolated. Genetic distances (roughly estimated) are given in centimorgans (cM). The gene loci are *boxed*. *c* = estimated centromere position, *S* = short arm, *L* = long arm

for gene tagging. The utilisation of the markers is not restricted to rye but can be extended to homoeologous chromosome regions of wheat and barley. Although rye has undergone a number of interchromosomal translocations compared to the other *Triticeae* members (Devos et al. 1993) collinearity is retained within the translocated chromosome segments.

Of the 15 gene loci, five (*S*, *Z*, *al*, *Ddw1*, *Hp1*) have been mapped in more than one population. It is shown that the map positions are highly comparable. For *Hp1* on chromosome 5RL Korzun et al. (1996) demonstrated clearly that it is pleiotropic determining both hairy peduncle and hairy leaf sheath, whereas Senft and Wricke (1996) described a gene for hairy leaf sheath (*Hs*) on the same chromosome arm in a position different from *Hp1*. The existence of at least four genes controlling hairy peduncle and/or hairy leaf sheath, however, was previously described by Melz (1987).

Within the *Triticeae* consensus maps have already been constructed for barley (Langridge et al. 1995) and wheat (Gale et al. 1995). The existing collinearity described for the *Triticeae* (Devos et al. 1993; Korzun et al. 1997) or even for species belonging to different tribes within the *Poaceae* (Ahn et al. 1993; Van Deynze et al. 1995a, b), and the fact that most of the RFLP probes allow cross hybridisation within the small-grain cereal genomes, will further increase the number of available markers, allowing for the integration of all these maps in the near future.

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