Chapter 3

MOLECULAR MAPS IN CEREALS: METHODOLOGY AND PROGRESS

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1. INTRODUCTION

Cereals provide for our major food crops, and therefore have been a subject of detailed genetic and cytogenetic studies during major part of the last century. These studies led to the preparation of linkage maps, which were also assigned to individual chromosomes, thus leading to the construction of chromosome maps in all major cereals. In some cases, the availability of cytogenetic stocks (e.g. deletion stocks in bread wheat) also allowed construction of physical maps. In the past, a major limitation in the construction of genetic maps has been the non-availability of mutants for majority of individual genes, so that only handful of genes could be mapped. However, during 1980s, the availability of molecular markers and the high level of DNA polymorphism, which they detect, led to renewed emphasis on genetic and physical mapping of genomes in many plant/animal systems, and cereals were no exception. Consequently, not only genetic and physical maps were constructed for all major cereal genomes, but these maps were also put to a variety of uses, so that crop improvement programmes are now undergoing a paradigm shift, making use of genes and technologies, hitherto not available to plant breeders. With the advent of genomics, the physical maps have also been found useful for high quality whole genome sequencing (Sasaki and Burr, 2000). For construction of these molecular maps, a variety of molecular markers have been used, which have received detailed treatment elsewhere (for molecular markers, consult in this book, Chapter 2 by Somers).

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The molecular markers that have been used for construction of molecular maps in cereals can be broadly classified in three groups, the first generation markers, the RFLPs (restriction fragment length polymorphisms) and RAPDs (randomly amplified polymorphic DNA), the second generation markers, the SSRs (simple sequence repeats or microsatellites) and AFLPs (amplified fragment length polymorphisms) and the third generation markers, the SNPs (single nucleotide polymorphisms) and InDels (insertion-deletion) (for a reveiew see Gupta *et al.,* 2002b). In addition to above, some other classes of molecular markers (i.e. derivatives of RFLPs, SSRs, AFLPs) such as STSs (sequence tagged sites), ISSRs (inter simple sequence repeats), SAMPL (selective amplification of microsatellite polymorphic loci), etc. have also been used. More recently, EST (expressed sequence tag)-based markers (EST-SSRs and EST-SNPs) are also being developed in all major cereals (see Sreenivasulu *et al.,* 2002). All these marker types except the recently developed SNPs have been utilized for the construction of molecular maps, and efforts are being made to construct SNP maps also in all major cereals. In this chapter, we first briefly describe the methods involved in the construction of these molecular maps, and then discuss the present status of these maps (including transcript maps) and the future prospects of developing high-density maps, which are needed both for map based cloning and marker-assisted selection (MAS). In addition, towards the end of this chapter, we also describe some special issues of applying molecular techniques to genome analysis and molecular breeding of cereal species. The various uses of these maps will be dealt with elsewhere in this book.

2. MOLECULAR GENETIC MAPS

Molecular markers detect both sequence polymorphisms (e.g. SNPs, resulting in RFLPs, RAPDs, AFLPs, etc.) and length polymorphisms (polymorphisms due to length variation of a sequence, as in SSRs and sometimes in RFLPs also), which are ubiquitous and abundant in all living organisms. These polymorphisms would segregate, majority of times, in a Mendelian manner, so that the conventional basis of linkage and recombination can be used for constructing these maps like the classical maps prepared during the middle of the last century. A major advantage of molecular mapping is the possibility of analyzing a large numbers of DNA-markers in a single mapping population. However, the systematic construction of these maps requires a mapping population and software, which facilitates the construction of map utilizing the large amount of data that is generated using the molecular genotyping of the mapping population.

2.1. Mapping Populations

Molecular markers are used for constructing genetic maps by recording co-segregation of markers in defined populations. Several types of mapping populations can be derived from crosses involving any two diverse parents. For instance, an F_2 population or backcross population can be derived from F_1 plants through selfing or backcrossing them to one of the parents; recombinant inbred lines (RILs) can be derived by single seeds descent for at least five or more generations, and doubled haploids (DHs) can be derived from haploid obtained from F_1 plants through anther/egg cell/ovule culture or distant hybridization. The simplest of these mapping populations are the F_2 populations or the backcross (BC) populations. For the majority of cereal species, populations such as these are easy to construct although sterility in the F_1 hybrid may limit some combinations of parents, particularly in wide crosses. A major drawback of using F_2 and BC populations is that they are ephemeral, that is, seed derived from selfing these individuals will not breed true (Young, 2001). The RILs and DHs, on the other hand, are immortal and can be permanently maintained and evaluated in repeated experiments. RILs have an additional advantage of being the product of several meioses, so that each RIL contains a different combination of linkage blocks from the original parents. However, generation of RILs is time-consuming, and some regions of genome tend to stay heterozygous longer than expected from theory (Burr and Burr, 1991). Therefore, in several mapping projects, DHs were preferred, because they can be used for linkage mapping with many of the same advantages of RILs and take less time in production (Heun *et al.,* 1991). In addition to the above, some other mapping populations such as recombinant inbred substitution lines (RISLs), recurrent intermated populations, etc. were also used for increasing the efficiency and genetic resolution of genome mapping in cereals (Araki *et al.,*1999; Rousset *et al.,* 2001;Sharopova *et al.,*2002). For instance in maize, an intermated population has been generated from a common population (B73 × Mo17) after five generations of intermating. Genotyping of this population before and after intermating with the same set of 190 RFLP loci resulted in nearly a four-fold increase in the genetic map distance and increased the potential for improved genetic resolution in 91% of the intervals evaluated (Lee *et al.,* 2002).

In cereals, sometimes only a few markers could be mapped with a specific segregating population (as described above) due to low levels of polymorphism between the parents of the mapping population. In wheat, to overcome this problem, either synthetics, created by combining tetraploids (A and B genomes) with *Aegilops tauschii* (D genome) were used in crosses, or else mapping of individual genomes was done at the diploid level, so that

mapping populations were constructed using the diploid progenitors *Aegilops tauschii* – (D genome) (Boyko *et al.,* 1999) and *Triticum monococcum* – (A genome) (Dubcovsky *et al.,* 1996). In some cases, wild species were included in crosses with cultivated species for preparing mapping populations. For instance, in barley *Hordeum spontaneum* was crossed with *Hordeum vulgare* (Ramsay *et al.,* 2000; Chang *et al.,* 2001) and in case of rice, *Oryza glaberrima* or *Oryza glumaepatula* was crossed with *Oryza sativa* (Lorieux *et al.,* 2000; Brondani *et al.,* 2001). Use of such strategies enhanced the level of polymorphism of markers thus facilitating the mapping of a much larger number of markers.

2.2. Computer Programmes

In principle, linkage mapping with DNA markers does not differ from mapping with classical genetic markers, so that genetic distances between DNA markers are based on frequencies of genetic crossing over, and are represented on the genetic map in centiMorgans (cM). However, the number of markers, to be analyzed in a single mapping population used for mapping, can reach several thousands, thus necessitating the use of computer programmes; many such programmes have been developed and used in the past for constructing genetic maps in a variety of plant genomes.

The most widely used mapping software is 'Mapmaker' (Lander *et al.,* 1987), which is based on the concept of a LOD score, the "log of the odds-ratio" (Morton, 1955). Mapmaker performs multipoint analysis of many linked loci, which is essential to sort out the many different possible marker orders. In the same species, several maps can be prepared using different mapping populations. In such cases it is useful to relate the maps derived from different mapping populations, to produce an integrated or consensus map. The computer programme 'JoinMap' is often used for this purpose (Stam, 1993). 'Map Manager' is another programme which helps to keep track of markers data in a population of interest (Manly and Olson, 1999).

2.3. Whole Genome Genetic Maps in Cereals

Over the last two decades, using a variety of molecular markers high-density molecular linkage maps have been developed for all major cereal species. A summary of these maps is presented in Table 1. Phillips and

Table 1. A list of some important genetic (including transcript) maps* available in cereals

Map type /crop	Population used for mapping	Number of loci mapped	Genetic map length (cM)	Reference
RFLP maps				
Barley	DHs (Proctor × Nudinka)	154	1,091	Heun *et al* (1991)
Barley	DHs (Igri × Franka; *Hordeum vulgare* ssp Vada × *H vulgare* ssp. *spontaneum*line 1B-87)	226	1,453	Graner *et al* (1991)
Barley	DHs (Steptoe × Morex)	295	1,250	Kleinhofs et al (1993)
Barley	DHs (Harrington × TR306)	898	1,060	Kasha *et al* (1994)
Barley	F2s (Ko A × Mokusekko)	222	1,389	Miyazaki *et al* (2000)
Maize	F2s (CO159 × T× 303)	215	-	Gardner *et al* (1993)
Maize	F2s (CO159 × T× 303)	92	-	Chao *et al* (1994)
Maize	Intermated RILs (B73 × M017)	180	5,917	Lee *et al.* (2002)
Oat	F2s/ F3s (*Avena atlantica* (M66/3) × *A hirtula* (Cc7050 - CAV4490)	192	614	O'Donoughe *et al.* (1992)
Oat (2×)	F2s (*Avena strigosa* Shreb × *A. wiestii* Sleud)	208	2,416	Rayapaty *et al.* (1994)
Oat	RILs (*Avena byzantina* cv Kanota × *A sativa* cv Ogle)	561	1,482	O'Donoughe *et al* (1995)
Oat (2×)	F2s (*Avena strigosa* CI3815 × *A wiestii* CI1994)	181	880	Kremer *et al* (2001)
Rice	BC lines (*Oryza sativa* × *O longistaminata*)	726	1,491	Causse *et al* (1994)
Rice	F2s/ F3s (*indica* var. IR24 × *japonica* marker stocks)	83	-	Yoshimura *et al* (1997)
Rice-wild	F2s (*Oryza sativa* var. Johnson × *Zizania palustris* L.)	121	1,805	Kennard *et al* (2000)
Rye	F2s (DS2 × R×L10)	~50	-	Devos *et al.* (1993a,b)
Rye	F2s (P87 × P105)	88	660	Korzun *et al.* (1998)
Sorghum	F2s (BSC35 × BT× 631)	71	633	Ragab *et al* (1994)

Table 1. Continued

Sorghum	F2s (*Sorghum bicolor* × *S propinquum*)	276	1,445	Chittenden *et al* (1994)
Sorghum	F2s (*Sorghum bicolor* ssp bicolor IS3620 × BT× 623)	190	1,789	Xu *et al* (1994)
Sorghum	RILs (*Sorghum bicolor* BT× 623 × IS3620C)	323	1,347	Peng *et al* (1999)
Wheeat (D-genome)	*T tauschii* (TA1691 var meyeri × TA1704 var typica)	152	1,554	Gill *et al* (1991)
Aegilops tauschii	F2s [*Aegilops tauschii* var *meyeri* (TA1691) × *Ae tauschii* var *typica*(TA1704)]	546	-	Boyko *et al* (1999)
Wheat (Group 1)	ITMI RILs (W7984 × Opata85)	98	146 to 344	Van Deynze *et al* (1995)
Wheat (Group 2)	F2/F3s (Chinese Spring × SyntheticTimgalen)	114	-	Devos *et al* (1993b)
Wheat (Group 2)	ITMI RILs (W7984 × Opata85)	173	~ 600	Nelson *et al* (1995b)
Wheat (Group 3)	F2/F3s (Chinese Spring × SyntheticTimgalen)	~60	-	Devos *et al* (1992) Devos and Gale (1993)
Wheat (Group 3)	ITMI RILs (W7984 × Opata85)	160	~ 660	Nelson *et al* (1995c)
Wheat (Group 4)	ITMI RILs (W7984 × Opata85)	98	-	Nelson *et al* (1995a)
Wheat (Group 5)	F2/F3s (Chinese Spring × SyntheticTimgalen)	~50	-	Xie *et al* (1993)
Wheat (Group 5)	ITMI RILs (W7984 × Opata85)	118	-	Nelson *et al* (1995a)
Wheat (Group 6)	ITMI RILs (W7984 × Opata85)	154	516	Marino *et al* (1996)
Wheat (Group 6)	F2/F3s (Chinese Spring × Synthetic)	62	317	Jia *et al* (1996)
Wheat (Group 7)	ITMI RILs (W7984 × Opata85)	109	-	Nelson *et al* (1995a)
Wheat	F2s (*Triticum aestivum* var Chinese Spring × *Triticum spelta* var duha	197	-	Liu and Tsunewaki (1991)
Wheat	DHs (Chinese Spring × Courtot)	264	1,772	Cadalen *et al* (1997)
Wheat- durum	RILs (*T durum* var Messapia × *T turgidum* var MG4343)	245	-	Blanco *et al* (1998)

Table 1. Continued

SSR maps				
Barley	DHs (*Hordeum vulgare* var. Lina × *H. spontaneum* Canada Park)	242	1,173	Ramsay *et al.* (2000)
Barley	F2s (Lerche × BGRC41936), DHs (Igri × Franka)	57	840	Pillen *et al.* (2000)
Barley	Consensus map- DHs (Igri × Franka; Steptoe × Morex; OWB Dom × OWB Rec)	76	-	Thiel *et al.* (2003)
Barley	Consensus map – DHs (Igri × Franka; Steptoe × Morex)	127	-	Li *et al.* (2003)
Maize	Intermated RILs (B73 × Mo17)	978	4,906	Sharopova *et al.* (2002)
Rice	DHs (*indica* var. IR64 × *japonica* var. Azucena)	120	-	McCouch *et al.* (1997)
Rice	DHs (IR64 × Azucena, ZYQ × JX), RILs (Milyang 23 × Gihobyeo)	121	~ 1,900	Chen *et al.* (1997)
Rice	DHs (IR64 × Azucena), RILs (Milyang 23 × Gihobyeo; Lemont × Teqing)	312	1,822	Temnykh *et al.* (2000)
Rye	Consensus map- F2s (P87 × P105; N6 × N2; N7× N2; N7 × N6)	99	-	Khelestkina *et al.* (2004)
Wheat	ITMI RILs (W7984 × Opata85)	279	-	Roder *et al.* (1998b)
Wheat	F2s (Chinese Spring × Synthetic)	53		Stephenson *et al.* (1998)
Wheat	ITMI RILs (W7984 × Opata85)	55		Pestsova *et al.* (2000)
Wheat	DHs	172	-	Harker *et al.* (2001)
Wheat	ITMI RILs (W7984 × Opata85)	65	-	Gupta *et al.* (2002a)
Wheat	4 mapping populations (W7984 × Opata85, Courtot × Chinese Spring, Eureka × Renan; Arche × Recital)	533	-	Gandon *et al.* (2002)
Wheat	ITMI RILs (W7984 × Opata85) Chromosomal assignment by using nulli-tetrasomic lines	144 173	-	Song *et al.* (2002)
Wheat- durum	RILs (*Triticum durum* var. Messapia × *T. turgidium* var. MG4343)	79	-	Korzun *et al.* (1999)

Table 1. Continued

AFLP maps				
Barley	DHs (Proctor × Nudinka)	118	1,096	Becker *et al.* (1995)
Barley	RILs (L94 × Vada)	566	1,062	Qi *et al.* (1998)
Barley	DHs (Proctor × Nudinka)	511	2,673	Castiglioni *et al.* (1998)
Maize	RILs (B73 × Mo17)	1539	1,178	Vuylsteke *et al.* (1999)
Maize	F2s (D32 × D145)	1355	1,376	Vuylsteke *et al.* (1999)
Maize	F2s (B73 × A7)	246	2,057	Castiglioni *et al.* (1999)
Rice	DHs (IR64 × Azucena)	208	3,058	Maheswaran *et al.* (1997)
Rye	F2s (synthetic I0.1 lines)	71	215 (total 1100)	Saal and Wricke (2002)
Bread wheat	DHs (Garnet × Saunders)	426	-	Penner *et al.* (1998)
Wheat	ITMI RILs (W7984 × Opata85)	140	-	Hazen *et al.* (2002)
Composite maps				
Aegilops tauschii	F2s (*Aegilops tauschii* var. *meyeri* (TA1691) × *Ae. tauschii* var. *typical* (TA1704) (marker loci- defense related genes, REMAPs/ SREMAPs, IRAPs, SSRs, ISSRs, RFLPs)	732	-	Boyko *et al.* (2002)
Barley	Consensus map from 7 maps (marker loci- mainly RFLPs)	587	1,087	Langridge *et al.* (1995)
Barley	Consensus map from 4 maps (marker loci- mainly RFLPs)	880	-	Qi *et al.* (1996)
Barley	F2s (*Hordeum chilense*) (marker loci- RAPDs, SSRs, RFLPs, SCARs, STS, etc.)	123	694	Hernandez *et al.* (2001)
Barley	DHs (OWBDom × OWB Rec) (marker loci- RFLPs, RAPDs, SSRs, AFLPs)	~ 720	1,387	Costa *et al.* (2001)

Table 1. Continued

Barley	RILs (Azumamugi × Kato Nakate Gold) (marker loci AFLPs, STSs, etc)	272	926	Mano *et al* (2001)
Barley	DHs (*Hordeum vulgare* var Lina × *H spontaneum* var Canada Park) (marker loci- IMPs)	88	-	Chang *et al* (2001)
Maize	F2/F5-6s (I0 × F2, I252 × F2) (marker loci- ESTs and RFLPs)	275	1,765	Causse *et al* (1996)
Maize	F2 (T×303 × CO159) (maiker loci- ESTs , RFLPs, SSRs, etc.)	1736	1,727	Davis *et al* (1999)
Maize	RILs (B73 × Mo17) (marker loci- MITE- HBr)	213	1,092	Casa *et al* (2000)
Maize	F2 (T1 × T2)	~310	-	Maisan *et al* (2001)
Maize	Several mapping populations (maiker loci- RFLPs and SSRs)	> 1800	-	http.//www maizemap.org/ maps.htm
Oat (6×)	RILs (Kanota × Ogle; Clintland64 × IL86-5698) (marker loci- AFLPs and RFLPs)	300	2,351	Jin *et al* (2000)
Oat (6×)	RILs (Ogle × TAM O-301) (marker loci- RFLPs, AFLPs, RAPDs, STSs, etc)	441	2,049	Portyanko *et al* (2001)
Rice	BCs (*Oryza sativa* × *O longistaminata*) (marker loci- cDNA/RFLPs, SSRs, etc.)	726	1,491	Causse *et al* (1994)
Rice	F2s (Nipponbare × Kasalath) (marker loci- ESTs, RFLPs, RAPDs, etc)	1383	1,575	Kurata *et al* (1994)
Rice	F2 population (Nipponbare × Kasalath) (marker loci- ESTs, RFLPs, RAPDs, etc.)	2275	1,522	Harushima *et al* (1998)
Rice	RILs (Milyang 23 × Gihobyeo) (marker loci- AFLPs, RFLPs, SSRs, etc)	~530	1,814	Cho *et al* (1998)

Table 1. Continued

Rice	BCs (*Oryza sativa* × *O. glaberrima*) (marker loci- SSRs, STSs, AFLPs, RAPDs, etc.)	129	1,923	Lorieux *et al.* (2000)
Rice	BCs (*Oryza glumaepatula* RS-16 × *O. sativa* BG-90-2) (marker loci- SSRs, STSs)	162	1,500	Brondani *et al.* (2001)
Rice	DHs (IR64 × Azucena), BCs (*Oryza sativa* × *O. longistaminata*) (marker loci- RFLPs, SSRs)	630	1,491	McCouch (2001)
Rice	F2s (Nipponbare × Kasalath) (marker loci- RFLPs, RAPDs, STSs, etc.)	3267	-	http://rgp.dna.affrc.go.jp/publicdata/geneticmap2000/index.html
Rice	F2s (Nipponbare × Kasalath) (marker loci- STSs, CAPS, etc.)	332	-	http://rgp.dna.affrc.go.jp/publicdata/caps/index.html
Rye	F2s (E × R) (marker loci- RFLPs, RAPDs)	99		Loarce *et al.* (1996)
Rye	F2s (synthetic I0.1 lines I-line × a genebank accession) (marker loci- RFLPs, RAPDs)	92	760	Senft and Wricke (1996)
Rye	consensus map from 13 mapping populations (marker loci- mainly RFLPs)	415	-	Börner and Korzun (1998)
Rye	F2s (P87 × P105) (marker loci- RFLPs, SSRs, etc.)	183	1,063	Korzun *et al.* (2001)
Rye	F2s (UC-90 × E-line, King II × Imperial) (marker loci- RFLPs, SSRs, etc.)	184	727	Ma *et al.* (2001)
Rye	F2s (DS2 × R×L10) (marker loci- RFLPs, RAPDs, etc.)	282	1,140	Masojć *et al.* (2001)
Sorghum	RILs (IS2807 × 379; IS2807 × 249) (marker loci- RFLPs, AFLPs)	443	1,899	Boivin *et al.* (1999)

Table 1. Continued

Sorghum	RILs (BT×623 × IS3620C) (marker loci- RFLPs, SSRs)	470	1,406	Bhattramakki *et al.* (2000)
Sorghum	RILs (B35 × T×7000) (marker loci- RFLPs, SSRs)	214	1,200	Subudhi and Nguyen (2000)
Sorghum	RILs (BT×623 × IS3620C) (marker loci- AFLPs, SSRs, RFLPs, etc.)	2926	1,713	Menz *et al.* (2002)
Wheat-durum	F2s/ F3s (*T. monococcum* ssp. *monococcum* DV92 × *T. monococcum* ssp. *Aegilopoides* C3116) (marker loci- mainly RFLPs)	335	714	Dubcovsky *et al.* (1996)
Wheat- einkorn	F2s (*T. monococcum* × *T. boeoticum* ssp. *boeoticum*) (marker loci- RFLPs, RAPDs, ISSRs)	81	-	Kojima *et al.* (1998)
Wheat-durum	RILs [*T. durum* (Messapia) × *T. turgidium* (MG4343)] (marker loci- AFLPs, RFLPs)	88	2,063 (total)	Lotti *et al.* (2000)
Wheat-durm	RILs (Jennah Khetifa × Cham1) (marker loci- RFLPs, SSRs, AFLPs, etc.)	206	3,598	Nachit *et al.* (2001)
Wheat	RILs (*Triticum aestivum* L. var. Forno × *T. spelta* L. var. Oberkulmer) (marker loci- RFLPs, SSRs)	230	2,469	Messmer *et al.* (1999)
Wheat	DHs (Cranbook × Halbred, CD87 × Katepwa, Sunco × Tasman) (marker loci RFLPs, SSRs, AFLPs,etc.)	355 to 902	-	Chalmers *et al.* (2001)
Wheat	DHs (Courtot × Chinese Spring) (marker loci- RFLP, SSRs, AFLPs)	659	3,685	Sourdille *et al.* (2003)
Wheat	F5s (Arina × Forno) (marker loci- RFLPs, SSRs)	396	3,086	Paillard *et al.* (2003)

*only maps comprising >50 loci are listed. Details and updated version of these maps are available at Graingenes website http://wheat.pw.usda.gov/ggpages/map_summary.html

Vasil (1994, 2001) also compiled details of many maps and this information is available on-line at GrainGenes (http://wheat.pw.usda.gov /ggpages/maps), which is regularly updated.

It is evident from Table 1, that genetic maps were prepared in the past mainly by using co-dominant RFLP markers in different cereals like wheat (see Gupta *et al.,* 1999), barley (see Varshney *et al.,* 2004), maize (http://www.maizemap.org/) and rice (http://rgp.dna.affrc.go.jp/Public data.html). RFLP analysis, however, is time consuming, labour intensive and is too slow for rapid evaluation of large segregating populations used in commercial breeding programmes (Gale *et al.,* 1995). Subsequently, other marker systems such as RAPDs, because of the ease of analysis, were also used for mapping (Giese *et al.,* 1994; Harushima *et al.,* 1998; Masojć *et al.,* 2001). However, RAPDs were not found suitable for preparation of genome-wide dense molecular map, since they exhibited low level of reproducibility between laboratories due to variation in PCR conditions and/or due to the use of different models of thermal cyclers (Devos and Gale, 1992; Penner *et al.,* 1993). Like RAPDs, AFLPs are also assumed to represent a dominant marker system, but these were found to be superior, due to high multiplex ratio (number of different genetic loci that may be analysed per primer pair and per gel lane), so that they were included in genetic maps in many cereals (Maheswaran *et al.,* 1997; Qi *et al.,* 1998; Castiglioni *et al.,* 1998; Vuylsteke *et al.,* 1999). During 1990s, microsatellites became the markers of choice due to a variety of attributes including their multiallelic nature, co-dominant inheritance, relative abundance and extensive genome coverage (Powell *et al.,* 1996). In the past, it was expensive and cumbersome to generate microsatellites, even though they were generated for many plant species including cereals (see Gupta and Varshney 2000; Table 1). In cereals a large number of microsatellites have been developed and mapped. For instance in wheat, several microsatellite maps are already available (Röder *et al.,* 1998b; Pestsova *et al.,* 2000; Varshney *et al.,* 2000; Gupta *et al.,* 2002) and an integrated map with ~1000 SSR loci will become available soon (D. Somers, Canada, personal communication). Similarly more than 1800 mapped microsatellite loci are available in maize (Sharopova *et al.,* 2002; http://www.agron.missouri.edu/ssr.html). In rice, a set of >2700 SSRs are available in public domain, as bioinformatics-based approach facilitated mapping of 2240 SSR loci after utilizing the draft sequence of rice generated by Monsanto (McCouch *et al.,* 2002). However, in barley, only ~700 SSR loci have been mapped (Ramsay *et al.,* 2000; Pillen *et al.,* 2000; Li *et al.,* 2003; Varshney *et al.,* unpublished). Over the last five years, emphasis has shifted to SNP markers, which are biallelic in nature and are abundant in any genome. Efforts have been initiated to develop SNP maps in barley (Kota *et al.,* 2001), maize (Batley *et al.,* 2003), rice (Nasu *et al.,* 2002), wheat

(http://wheat.pw.usda.gov/ITMI/2002/WheatSNP.html). It is believed that dense SNP maps will be available soon especially as the cost SNP assays continues to come down.

Due to availability of different marker assays, 'integrated' or 'composite' maps involving more than one type of molecular marker (particularly the SSRs, AFLPs, InDels) have been prepared (see Table 1). In some cases, molecular marker maps have included mapped genes for economic traits also. In most cereals especially barley, wheat, rice and maize, a large number of markers have been mapped in different mapping populations. Comparisons among certain regions of chromosomes mapped with common markers in different populations indicate that the order of molecular markers on the linkage maps is similar, although the distances may differ. Consequently, the construction of 'consensus maps' becomes possible by using common markers as anchors and extrapolating the positions of markers mapped between the anchors. For instance, a consensus genetic linkage map for rye chromosome 7R could be generated from seven different genetic maps (Börner and Korzun, 1998; Fig. 1). Similarly in barley, availability of common markers, mapped in different mapping population, allowed several groups to construct consensus maps (see Varshney *et al.,* 2004; Table 1). These consensus maps display higher marker densities than their individual components, which make them highly useful resources. On the other hand, the reliability of consensus maps may decrease over distances of a few centiMorgans, or where marker densities are high and the number of common markers is low. To increase the genetic resolution, Kleinhofs and Graner (2001) divided the barley genome in approximately 10 cM intervals ("BINs"). Each BIN is defined by its two flanking markers, which have been anchored in the Steptoe/Morex and the Igri/Franka maps. Such BINs, each BIN encompassing a 20 cM interval, are already available in maize (Gardiner *et al.,* 1993; Coe *et al.,* 2001). BIN maps readily allow the placement of markers mapped in different mapping populations. Although their genetic resolution is limited, they accommodate the information from a large number of maps. Thus availability of BIN maps facilitates identification of a large number of markers for a given chromosomal region.

2.4. Transcript Genetic Maps

Due to current emphasis on functional genomics in cereals, large-scale EST sequencing projects have generated a large amount of sequence data (Sreenivasulu *et al.,* 2002; Rudd, 2003). Since each EST corresponds to an

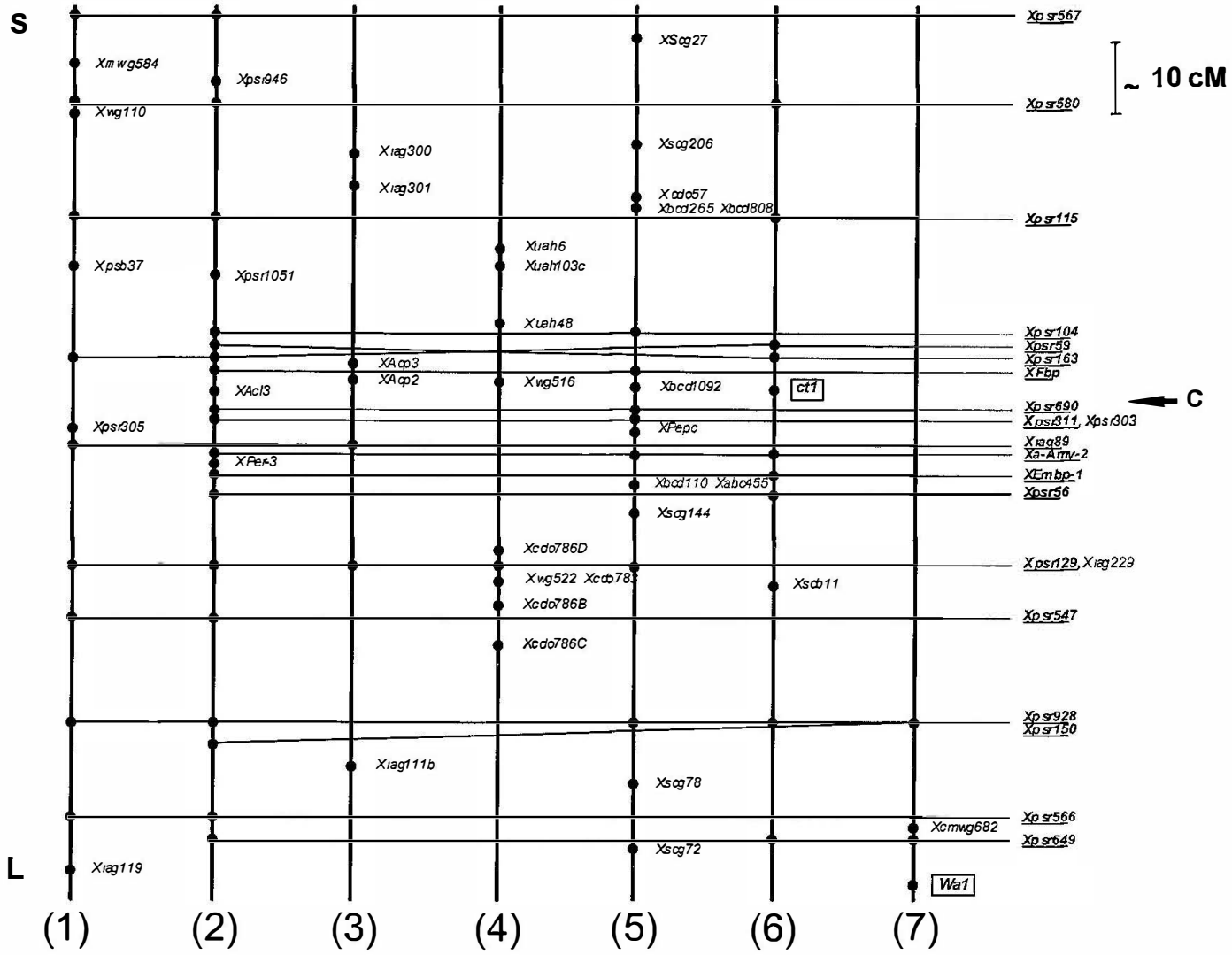

Figure 1. Preparation of a consensus linkage map of chromosomes 7R. This map was constructed (Borner and Korzun 1998) by using the followmg basic maps (1) Korzun *et al* (1998), (2) Devos *et al* 1993a, (3) Senft and Wricke (1996), (4) Loarce *et al* (1996), (5) Wanous *et al* 1995, (6) Plaschke *et al* (1995), (7) Korzun *et al* (1997a) 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

mRNA, these ESTs are being mapped, and will be integrated in genetic maps. Such genetic maps are termed 'functional map'/'transcript map' or 'gene map' (Schuler *et al.,* 1996). For placing ESTs (transcripts/genes) onto genetic map, ESTs can be converted into different marker assays like RFLPs, STSs, CAPSs (cleaved amplified polymorphic sequences), SSRs or SNPs. For instance, an EST can be amplified by using genomic DNA as a template with the help of PCR primers designed from this EST. The PCR products obtained thus can either be used as RFLP probes in Southern hybridization (Smilde *et al.,* 2002) or may be directly tested for length or sequence polymorphism in parents of a mapping population (Gilpin *et al.,* 1997). Sometimes, PCR products can also be digested with a set of restriction enzymes to test restriction polymorphism in parents of mapping populations for mapping ESTs as CAPS.

ESTs have also been used for developing EST-SSRs or even EST-SNPs, if ESTs for the same region are available from two or more genotypes (see Sreenivasulu *et al.,* 2002). Many software packages or algorithms are available for mining SSRs or SNPs in ESTs (Table 2) and corresponding PCR primers may be designed from the EST sequences (Kota *et al.,* 2001; Varshney *et al.,* 2002; Batley *et al.,* 2003). Thus, EST-derived SSRs or SNPs are a free by-product of EST sequencing projects. Mapping of ESTs via these marker assays is important, since QTLs or genes for different disease resistance or other agronomic traits associated with these ESTs may provide the 'candidate genes' for the trait in question. Potential of these 'candidate genes' can be further assessed in RCSLs (recombinant chromosome substitution lines) that carry variants of the 'candidate gene'. Thus direct gene markers for different traits may be generated which will be of great value in marker-assisted breeding (see later), although it does not conclusively prove function (Thomas, 2003). The above functional maps are also very useful for comparative mapping studies (see Varshney *et al.,* 2004).

'Functional maps' are already available in some cereals like rice (Harushima *et al.,* 1998) and maize (Davis *et al.,* 1999). Recently, in barley more than 1000 ESTs have been placed on the genetic map (A. Graner, Germany,

Table 2. Some algorithms/ programmes for mining SSRs and SNPs in ESTs

Programme	Source
SSR	
*MI*croS*A*tellite	http://pgrc.ipk-gatersleben.de/misa
SSRIT	http://www.gramene.org/gramene/searches/ssrtool
SPUTNIK	http://espressosoftware.com:8080/esd/pages/sputnik.jsp
SNP	
SniPpER	http://mips.gsf.de/proj/sputnik
AutoSNP	http://www.cerealsdb.uk.net/discover.htm
Jalview	http://www.ebi.ac.uk/~michele/jalview/

personal communication) In wheat, though deletion-based physical mapping by using ESTs is in progress (discussed later), some efforts have been initiated for the genetic mapping of ESTs in the form of SSRs also (Holton *et al.,* 2002; M. Sorrells, USA, personal communication). In other cereal species also, ESTs have been screened for presence of SSRs (Hackauf and Wehling, 2002; Kantety *et al.,* 2002; Varshney *et al.,* 2002; Gao *et al.,* 2003; Gupta *et al.*, 2003). Mapping of SSR-ESTs (SSR containing ESTs) is also in progress in rye (Khelestkina *et al.*, 2004; B. Hackauf and P. Wehling, Germany, personal communication).

3. PHYSICAL MAPS

Physical maps of whole genomes are based on physical distances between genes or molecular markers measured either in terms of base pairs (megabasepairs = 10^6 base pairs) or in terms of relative physical lengths of chromosome segments. For instance, the distance of a gene/marker from the centromere may be represented as a fraction of the whole arm. While genetic maps are based on recombination frequencies, physical maps rely on direct size estimates, whether measured at the chromosome level under the microscope or else measured in terms of DNA sequence, if complete sequence of the chromosome or a part thereof is available. Physical maps provide virtually unlimited numbers of DNA markers from any chromosomal region for gene tagging and manipulation. They provide an framework for studies in genome molecular structure, organization and evolution, gene regulation, and gene interaction. Physical maps, therefore, are central tools to every type of genetic and molecular enquiry and manipulation including genome analysis, gene isolation and eventually crop

improvement. The following methods can be utilized for preparation of physical maps.

3.1. Physical Maps based on FISH

Physical maps can be generated through *in situ* hybridization (ISH), where chromosome sites that are homologous to a known labelled DNA probe can be directly visualized under the microscope. The technique initially proved useful for DNA probes that were at least a few kilobases in length. Several improvements were made to make the technique suitable for smaller DNA fragments (reviewed by Jiang and Gill, 1994; Maluszynska, 2002). For instance, fluorescence *in situ* hybridization (FISH), including DNA fibre FISH, was successfully utilized for physical mapping of centromeric and other small DNA sequences in rice (Dong *et al.,* 1998; Cheng Z.K. *et al.,* 2002).

ISH was used in many studies in cereals with different objectives. A comparison was made between the physical distances and genetic distances (between adjacent markers) in hexaploid wheat using ISH with 21 RFLP probes from linkage groups 5 and 6 (Zhang X.Q. *et al.,* 2000). The linear order and linkage relationships between DNA probes on these physical maps were generally the same as those on the RFLP-based genetic maps, but there was a significant difference between the genetic or recombinational distances on a linkage map and the physical distances obtained using ISH. The results also showed that the available linkage map did not completely cover the physical length of all the chromosomes. Similarly FISH mapping has been conducted in some other cereals using randomly selected or RFLP marker-anchored BAC (bacterial artificial chromosome) clones (Jiang *et al.,* 1995; Zwick *et al.,* 1998; Cheng *et al.,* 2001a,b). In rice, for cytological characterization of the genome and for identification of each chromosome arm, a set of 24 chromosome arm-specific BACs was used (Cheng *et al.,* 2001a). A standardized rice karyotype was also constructed which was anchored by centromere-specific and chromosome arm-specific cytological landmarks. This karyotype fully matched to the rice genetic map.

The potential of fibre FISH was successfully used to determine the size of seven segmental physical gaps, measuring 30 to192kb, and two telomere gaps on rice chromosome 10, measuring 80 and 30kb (The Rice Chromosome 10 Sequencing Consortium, 2003). Some details of physical mapping, using ISH/ FISH technology, are summarized in Table 3.

Table 3. Some examples of physical mapping in cereals using ISH/FISH

Cereal specie	Probes used for ISH/FISH	Target region	Reference
Aegilops	pSc119.2, pAs1, PSR907	Wheat-alien breakpoints (BPs) along the 3 BS and 3 DS arms	Biagetti *et al.* (1999)
Barley	BAC clones	Telomere	Lapitan *et al.* (1997)
Barley	Germin-like cDNAs with 26 BAC clones	Chromosomes 2H, 3H, 4H, 7H	Druka *et al.* (2002)
Rice	Telomeres and telomere- associated satellites	Chromosomes 9, 11	Wu and Tanksley (1993)
Rice	14 RFLPs	Chromosomes 7, 8, 11, 12	Song and Gustafson (1995)
Rice	24 chromosomal arm specific BAC clones (containing 24 RFLP markers)	Cytological characterization of rice genome	Cheng *et al.* (2001a)
Rice	Chromosome 10 specific 18 BAC clones	Chromosome 10	Cheng *et al.* (2001b)
Maize	4 markers (umc105a, csu145a, Cent C, pZm4-21)	Chromosome 9	Sadder and Weber (2002)
Oats (*6x*)	*Lrk10*-like receptor kinase sequences	Linkage groups 4, 12, 5, 6, 13	Cheng D. W. *et al.* (2002)
Sorghum	BAC clones contatining markers	Chromosome 1	Islam-Faridi *et al.* (2002)
Sorghum	22 BAC clones (encompassing 10 linkage groups)	Integrated karyotyping of Sorghum	Kim *et al.* (2002)
Tritordium*	Glu-1 loci	Chromosome arms 1AL, 1 BL, 1H(ch)L	Cabrera *et al.* (2002)
Wheat	47 RFLPs	*In situ* hybridization	Chen and Gustafson (1995)
Wheat	Rice markers	Homoeologous group 5 chromsomomes	Sarma *et al.* (2000)
Wheat	*Glu-1* loci	Homoeologous group 1 long arms (1 AL, 1 BL and 1 DL)	Cabrera *et al.* (2002)
Wheat	HSP70 gene homologue	Chromosome 1 B	Francki *et al.* (2002)

*Tritordeum- an amphiploid between *Triticum turgidum* cv. *durum* and *Hordeum chilense*

3.2. Physical Maps based on Deletion Stocks

Cytogenetic stocks can also be used for generating physical maps by locating genetically mapped DNA markers to specific chromosomal segments. Different types of cytogenetic stocks, are available for this purpose, including B-A translocations in maize (Weber and Helentjaris, 1989) and maize chromosome additions to oat genome (Riera-Lizarazu *et al.,* 2000), deletion stocks in wheat (Endo and Gill, 1996) and chromosomal translocation stocks in barley (Künzel *et al.,* 2000). These stocks were extensively used for physical mapping of the genomes of these cereals, in particular wheat and barley, genomes.

In bread wheat availability of a set of more than 400 deletion stocks facilitated preparation of physical maps for all the seven homoeologous groups (reviewed by Gupta *et al.,* 1999; P.K. Gupta, India, personal communication). It was shown that the deletion lines from three chromosomes of each of the seven homoeologous groups could be pooled together, so that each of the seven consensus chromosomes representing seven homoeologous groups can be divided into approximately 62 different 'physical bins', each bin with an average size of 40 Mb. By assuming a uniform distribution of recombination, these bins each represents a segment of 10 cM on the genetic map, so that the average ratio of physical to genetic distance becomes 4 Mb/cM (Lagudah *et al.,* 2001). A consortium of 13 laboratories in USA funded by National Science Foundation, USA, is engaged in assigning 10,000 unique ESTs to physical locations on chromosomes by using deletion lines (http://wheat.pw.usda.gov/NSF/progress_mapping.html, Qi *et al.,* 2003). When physical mapping data were used to assess organizational and evolutionary aspects of the wheat genome, it was found that recombination has played a central role in the evolution of wheat genome structure. The gradients of recombination rates along chromosome arms promoted more rapid rates of genome evolution in distal, high-recombination regions (hot spots of recombination) than in the low recombination proximal, regions (Akhunov *et al.,* 2003). In another project in France, a total of 725 microsatellite loci were assigned to 94 breakpoints in a homozygous (88 distal delitions, 6 interstitial) and 5 in a heterozygous state representing 159 delition bins with an average of 4.97 SSR/bin (Sourdille *et al.,* 2004). Assignment of ESTs and genetically mapped SSRs to deltion bins in above studies will be useful not only for deletion stock verifications but also for allocating associated QTLs to deletion bins as numerous ESTs that could be potential candidate genes have been assigned.

Table 4. A summary of physical mapping in wheat and barley using various cytogenetic stocks

Cereal species	Marker loci mapped	Cytogenetic stocks used	Reference
Barley (whole genome)	301 STSs	240 TLs	Künzel *et al.* (2000)
Barley (chromosome 7H)	28 STSs, 17 AFLPs	22 TLs	Serizawa *et al.* (2001)
Barley (chromosome 3H)	24 SSRs	14 TLs	Künzel and Waugh (2002)
Wheat (Homoeologous group 1)	19 RFLP	18 DLs	Kota *et al.* (1993)
Wheat (Homoeologous group 1)	50 RFLPs	56 DLs	Gill *et al.* (1996a)
Wheat (Homoeologous group 2)	30 RFLPs	21 DLs	Delaney *et al.* (1995a)
Wheat (Homoeologous group 2)	43 SSRs	25 DLs	Roder *et al.* (1998a)
Wheat (Homoeologous group 3)	29 RFLPs	25 DLs	Delaney *et al.* (1995b)
Wheat (Homoeologous group 4)	40 RFLPs	39 DLs	Mickelson-Young *et al.* (1995)
Wheat (Homoeologous group 5)	155 RFLPs	65 DLs	Gill *et al.* (1996b)
Wheat (Homoelogous group 5)	245 RFLPs, 3 SSRs	36 DLs	Faris *et al.* (2000)
Wheeat (short arm of homoeologous group 5)	100 RFLPs	17 DLs	Qi and Gill (2001)
Wheat (chromosome 5A)	22 RFLPs	19 DLs	Ogihara *et al.* (1994)
Wheat (Homoeologous group 6)	24 RFLPs	26 DLs	Gill *et al.* (1993)
Wheat (Homoeologous group 6)	210 RFLPs	45 DLs	Weng *et al.* (2000)
Wheat (Homoeologous group 6-short arm)	82 RFLPs	14 DLs	Weng and Lazar (2002)
Wheat (Homoeologous group 7)	16 RFLPs	41 DLs	Werner *et al.* (1992)
Wheat (Homoeologous group 7)	91 RFLPs, 6 RAPDs	54 DLs	Hohmann *et al.* (1995)
Wheat (chromosomes 6B, 2D and 7D)	16 SSRs	13 DLs	Varshney *et al.* (2001)
Wheat (1 BS)	24 AFLPs	8 DLs	Zhang H.N. *et al.* (2000)
Wheat (chromosome 4DL)	61 AFLPs, 2 SSRs, 2 RFLPs	8 DLs	Milla and Gustafson (2001)
Wheat (chromosome arm 1BS)	22 expressed sequences	DLs	Sandhu *et al.* (2002)
Wheat (whole genome)	7,697 unique ESTs	101 DLs	http://wheat.pw.usda.gov/NSF/progress_mapping.htm ; Qi *et al.* (2003)
Wheat (whole genome)	725 SSRs	159 DLs	Sourdille *et al.* (2004)

TLs= translocation lines ; DLs= deletion lines

In barley, translocation breakpoints were used for the preparation of a physical map for all the seven chromosomes (Künzel *et al.,* 2000). Deletion-based physical mapping has also been conducted in barley for some chromosomes including 7H (Serizawa *et al.,* 2001). The status and future prospects on physical mapping of the barley genome has been discussed in a recent review (Varshney *et al.,* 2004), and available information on physical mapping in wheat and barley is summarized in Table 4. Based on physical mapping of wheat and barley by using cytogenetic stocks, it has been speculated that the Triticeae genomes contain gene-rich regions (Sandhu and Gill 2002; for detail see Chapter 12 by K.S. Gill in this book).

3.3. Physical Maps Based on Contigs

The availability of genome wide DNA-contigs and their physical mapping has been a prerequisite for high quality sequencing of the genomes of model organisms, Arabidopsis and rice (TAGI 2000; Sasaki and Burr, 2000). DNA contigs can be assembled and physical maps prepared (through fingerprints of the BACs) using large insert DNA clones, such as yeast artificial chromosomes (YACs) and bacterial artificial chromosomes (BACs). The above contig assembly is dependent on a high density genetic map and/or high-quality large insert DNA libraries. Physical maps generated through contig assembly are then used to find the minimum tilling path for sequencing.

As a prerequisite for whole genome sequencing (WGS), physical maps using BACs, YACs and contigs have been prepared in several crops including some of the cereals. Among cereals, YAC libraries were prepared initially in maize (Edwards *et al.,* 1992), barley (Kleine.*et al.,* 1993) and rice (Umehara *et al.,*1995). These libraries were used for a number of studies but their general use has been limited by the high frequency of chimeric and unstable clones. Therefore, BAC libraries became popular due to ease of handling, relative simplicity in their development and a low frequency of chimeric clones. BAC libraries in many cereals have been constructed using Texas A & M GENEfinder Genomic Resources (http://hbz.tamu.edu/bacindex.html) and the BAC/EST Resource Centre at Clemson University Genomics Institute (http://www.genome.clemson.edu/groups/bac/). A gene-enriched BAC library has also been prepared in maize for cloning allele-specific fragments (Fu and Dooner, 2000). In hexaploid wheat, a library in Chinese Spring has been constructed using a newly developed transformation-competent artificial chromosome (TAC) vector, pYLTAC17 (Liu *et al.,*2000). These libraries are useful resources for physical mapping, positional cloning, WGS, genomic structural analysis and comparisons of

specific regions in different cereal species (for details see Chapter 11 by Stein and Graner, Chapter 13 by Yu and Wing).

In an Chapter 13 of this book, the methodology for preparation of contig-based physical map is described by Yu and Wing. The physical maps that have been prepared using YAC and BAC clones are summarized in Table 5. In some cases BAC libraries have been screened with genetically mapped ESTs or EST-derived markers, so that the physical maps can be compared with EST maps or transcript maps (discussed above). For example, for the preparation of a physical map, the CUGI (Clemson University Genomics Institute) collected the fingerprint data of two rice (Nipponbare) BAC libraries (20 fold coverage) (Soderlund *et al.,* 2000) and assembled contigs from 127,459 BAC end sequences (Mao *et al.,* 2000). With the availability of Monsanto working draft of the rice genome (Barry, 2001) and fingerprinted contig map from CUGI, a comprehensive physical map of the entire rice genome was prepared (Chen *et al.,* 2002). Using genetically mapped markers, most of the rice genome (~90.6%) was anchored through overgo hybridization, DNA gel blot hybridization and *in silico* anchoring. This physical map consists of 66,384 fingerprinted BAC clones (including 2,278 singletons) representing 20 fold coverage of the genome (http://www.genome.clemson.edu/projects/rice/fpc/integration). Simultaneously in an EST-project at RGRP (Rice Genome Research Programme), Japan, specific primers were designed for 6,713 unique (non-redundant) ESTs derived from 19 cDNA libraries. Subsequently, these primers were screened against 4,387 YAC clones and a comprehensive YAC-based rice transcript map was prepared. This map contains 6,591 EST sites and covers 80.8% of the genome (Wu *et al.,* 2002). In another recent study, 28,000 cDNA clones were physically mapped onto a *japonica* rice (Kikuchi *et al.,* 2003). As part of the International Rice Genome Sequencing Project (IRGSP), a fine physical map of the rice (*Oryza sativa japonica* Nipponbare) chromosome 4 has been prepared using 114 BAC clones from a taxonomically related subspecies *Oryza sativa indica* Guangluai 4 with 182 RFLP and 407 EST markers (Zhao *et al.,* 2002). In another recent study, rice sequence data from 2,251 ordered BAC/PAC clones was compared with 4,485 wheat ESTs. This study suggested that numerous translocations will complicate the use of rice as a model for cross-species transfer of information (Sorrells *et al.,* 2003).

Physical mapping by anchoring BAC clones with markers in cereals other than rice is also in progress. For instance, in maize 2,036 Mb of the 2500 Mb has already been covered (release 1/27/03) (http://www.maizemap.org /iMapDB/iMap.html; http://www.genome.arizona.edu/fpc/maize/; Coe *et*

Table 5. Contig-based physical mapping in some cereals

Cereal species	Approach	Clones (library) used	Markers used	Genome coverage and contigs	Reference
Rice (chromosome 1)	Screening YAC library with markers	476 YAC clones found positive	182 markers	284 YACs defined 69 contigs, coverage 60% of the chromosome length	Wang *et al.* (1996)
Rice	BAC fingerprinting	20, 682 BAC clones used	565 (RFLPs, SSRs, cDNAs and anchor probes)	120 kb resolution contig map, 631 contigs, genome covered 398 Mb (92%)	Hong *et al.* (1997)
Rice	Screening YAC library with markers	7,000 YAC clones used; 2,443 YAC clones found positive	1,285 (RFLPs and RAPDs)	222 Mb (52%)	Kurata *et al.* (1997)
Rice (chromosome arms 11 S and 12 S)	Screening YAC library with markers	7,000 YAC clones used; 38 YAC clones were identified as positive clones	46 genetic markers	Chromosome arm 11S- 2.09 Mb/ 2.51 Mb; chromosome arm 12S- 2.29 Mb/ 2.48 Mb	Wu *et al.* (1998)
Rice	*In silico* anchoring	80,143 BAC end sequences (54.2 Mb, 11.8% of rice genome)	2,152 DNA markers (spanning sequence length of 0.78 Mb) used and 418 markers were anchored to BAC clones	0.09 Mb (11.5% of total marker length)	Yuan *et al.* (2000)
Rice	BAC fingerprinting	21,087 BAC clones used	16 DNA markers associated with 2 or more contigs were used for analysis	298 BAC contigs; genome covered 419 MB (95%)	Tao *et al.* (2001)

Table 5. Continued

Rice	Screening YAC library with DNA markers	7,606 YAC clones used; 1,892 YAC clones identified as positive	1,439 DNA markers	297 YAC contigs and 142 YAC islands; genome covered 270 Mb (63%)	Saji *et al.* (2001)
Rice (Chromosome 9)	Screening BAC library	6 BAC ends, 1 YAC end	3 RFLPs	6.8 cM interval	Kamolsukyunyong *et al.* (2001)
Rice	Screening YAC library with ESTs	4,387 YAC clones	6,591 ESTs	384 YAC contigs; genome covered 347.3 Mb (80.8%)	Wu *et al.* (2002)
Rice	BAC fingerprinting (overgo hybridization, DNA gel blot hybridization, *in silico* anchoring)	65,287 BAC clones	1,704 markers (3,199 probes)	362.9 Mb (90.6%)	Chen *et al.* (2002)
Rice (Chromosome 4)	Screening BAC library with RFLPs and *in silico* anchoring of ESTs with BAC-end sequence database	566 BAC clones identified positive; 13,000 BAC-end sequences were used for *in silico* anchoring	182 RFLPs, 407 ESTs	11 contigs with 34.5 Mb (94% of estimated chromosome size)	Zhao *et al.* (2002)
Sorghum	Screening of BAC pools	2,400 BACs	32 different AFLP primer combinations	3,366 contigs, each containing an average of 5 BACs	Klein *et al.* (2000)
Sorghum	Screening of BAC pools with RFLP probes	38,016 BAC clones were used; 550 BAC clones were identified as positive	156 probes (160 loci)	103 contigs containing an average of 1.6 markers and 5.3 BACs)	Draye *et al.* (2001)

al., 2002; Cone *et al.,* 2002; Yim *et al.,* 2002). Efforts are also underway in sorghum (http://www.genome.arizona.edu/fpc/sorghum/; Klein *et al.,*2000; Draye *et al.,* 2001), and in the D-genome of wheat (http://wheat.pw. usda.gov/PhysicalMapping/). However, physical mapping of the complete hexaploid wheat genome using large insert libraries has yet to be undertaken. In barley some preliminary work has been conducted in this direction after anchoring BAC clones by using EST-derived SSR markers (Varshney *et al.,* unpublished results). *al.,* 2000). With the availability of Monsanto working draft of the rice genome (Barry, 2001) and fingerprinted contig map from CUGI, a comprehensive physical map of the entire rice genome was prepared (Chen *et al.,* 2002). Using genetically mapped markers, most of the rice genome (~90.6%) was anchored through overgo hybridization, DNA gel blot hybridization and *in silico* anchoring. This physical map consists of 66,384 fingerprinted BAC clones (including 2,278 singletons) representing 20 fold coverage of the genome (http://www.genome.clemson.edu/projects/rice/fpc/integration). In parallel, in an EST-project at RGRP (Rice Genome Research Programme), Japan, specific primers were designed for 6,713 unique (non-redundant) ESTs derived from 19 cDNA libraries. Subsequently, these primers were screened against 4,387 YAC clones and a comprehensive YAC-based rice transcript map was prepared. This map contains 6,591 EST sites and covers 80.8% of the genome (Wu *et al.,* 2002). In another recent study, 28,000 cDNA clones were physically mapped onto a japonica rice (Kikuchi *et al.,* 2003). As part of the International Rice Genome Sequencing Project (IRGSP), a fine physical map of the rice (*Oryza sativa japonica* Nipponbare) chromosome 4 has been prepared using 114 BAC clones from a taxonomically related subspecies *Oryza sativa indica* Guangluai 4 with 182 RFLP and 407 EST markers (Zhao *et al.,* 2002). In another recent study, rice sequence data from 2,251 ordered BAC/PAC clones was compared with 4,485 wheat ESTs. This study suggested that numerous translocations will complicate the use of rice as a model for cross-species transfer of information (Sorrells *et al.,* 2003).

Physical mapping by anchoring BAC clones with markers in cereals other than rice is also in progress. For instance, in maize 2,036 Mb of the 2500 Mb has already been covered (release 1/27/03) (http://www.maizemap.org /iMapDB/iMap.html; http://www.genome.arizona.edu/fpc/maize/; Coe *et al.,* 2002; Cone *et al.,* 2002; Yim *et al.,* 2002). Efforts are also underway in sorghum (http://www.genome.arizona.edu/fpc/sorghum/; Klein *et al.,*2000; Draye *et al.,* 2001), and in the D-genome of wheat (http://wheat.pw. usda.gov/PhysicalMapping/). However, physical mapping of the complete hexaploid wheat genome using large insert libraries has yet to be undertaken. In barley some preliminary work has been conducted in this direction after anchoring BAC clones by using EST-derived SSR markers.

Anchoring of genetically mapped SSR markers to BAC clones also gave a clue about the presence of gene-rich regions in barley genome (Varshney *et al.,* unpublished results).

3.4. Novel Strategies

Although preparation of contig-based physical maps is underway in larger genomes such as maize and diploid progenitors of hexaploid wheat, full genome contig physical maps could not be developed in barley or hexaploid wheat. As an alternative, efforts are underway to establish subgenomic physical maps from radiation hybrid (RH) panels (Cox *et al.,* 1990) or by "HAPPY" mapping (Dear and Cook, 1989). These methods do not rely on the availability of BAC-contigs or cloned DNA fragments and may be suitable for the high throughput mapping of PCR-based markers even in the absence of polymorphism (Waugh *et al.,* 2002).

3.4.1. Radiation Hybrid (RH) Mapping

In human genetics, RH panels have been constructed by fusing irradiated human cells containing highly fragmented chromosomes in their nuclei with intact hamster cells. Hamster cells selected for the presence of a selectable marker from the human genome, each contains random fragments from human chromosomes. In this way a population of hamster cell lines can be developed, which contain fragments of human chromosomes. The size of the fragments determines the physical resolution, which is a function of the intensity of irradiation used. Mapping is performed on the basis of the presence or absence of PCR-amplicons (Cox *et al.,* 1990). Similar efforts have also been initiated in some cereals. For instance, transgenic barley protoplasts harbouring the bar transgene as a selectable marker was fused with tobacco protoplasts to produce radiation hybrid panels (Wardrop *et al.,* 2002). In maize, individual chromosome additions to hexaploid oat (M9, maize chromosome 9 addition line) were irradiated and a panel of 100 informative M9RHs (maize chromosome 9 radiation hybrids), with an average of 3 breaks per chromosome were prepared (Riera-Lizarazu *et al.,* 2000). This allowed mapping with a resolution of 0.5 to 1.0 Mb. RH mapping of one *scs*^{ae} (species cytoplasm specific) gene in durum wheat is also in progress (Hossain *et al.,* 2002; http://cropandsoil.oregonstate.edu/cgb/projects.html).

3.4.2. HAPPY Mapping

An in *vitro* version of RH mapping is popularly described as HAPPY mapping. In contrast to RH mapping, HAPPY mapping does not require any cell fusion. It is based on the preparation of a series of small aliquots from genomic DNA. Each aliquot contains less than the amount of the haploid genome, hence the term HAPPY (Haploid genome; polymerase chain reaction) mapping. The DNA is sheared either in solution or by irradiation and size fractionated. Presence of physically linked DNA segments can be identified by their co-amplification in a given aliquot. The resolution of the procedure depends on the size of the DNA fragments that are used to prepare the aliquots (Dear and Cook, 1989; for a review see Waugh *et al.,* 2002). HAPPY mapping may be superior to RH mapping, as it does not suffer from problems due to cloning artefacts, or effects of chromosome structure. Using this approach, Thangavelu *et al.* (2003) successfully constructed a high resolution physical map of 1.9 Mbp region around the FCA locus within the genome of of *Arabidopsis thaliana*, and concluded that even in large genomes like that of barley, HAPPY mapping can facilitate the construction of high resolution local physical gene maps, if not the complete genome maps.

4. USES OF MOLECULAR MAPS

Both genetic and physical maps find a variety of uses not only in breeding but also in genomics research. Since several of these uses are discussed in other chapters of this book, only a very brief account will be included in this chapter. Molecular genetic maps have been extensively used for comparative genomic studies, throwing light on genome organization in grasses in general and in cereal crops in particular. The molecular genetic maps are also used for the identification of quantitative trait loci (QTLs) for a number of morphological, physiological and economic traits in several cereals. The QTLs not only help in marker-assisted selection for cereal breeding, but also facilitate the study of changes that the cereal genomes have undergone during breeding and selection. QTL analysis along with transcript maps may also be used for the identification of candidate genes for specific QTLs. Physical maps provide a large number of DNA markers from any chromosomal region for gene isolation. They also provide a framework not only for studies on structure, organization and evolution of the genome, but also for studies on gene regulation and gene interaction (Akhunov *et al.,* 2003; Sorrells *et al.,* 2003). Thus, physical and genetic maps are central to research involving genome sequencing and analysis, gene isolation, and crop

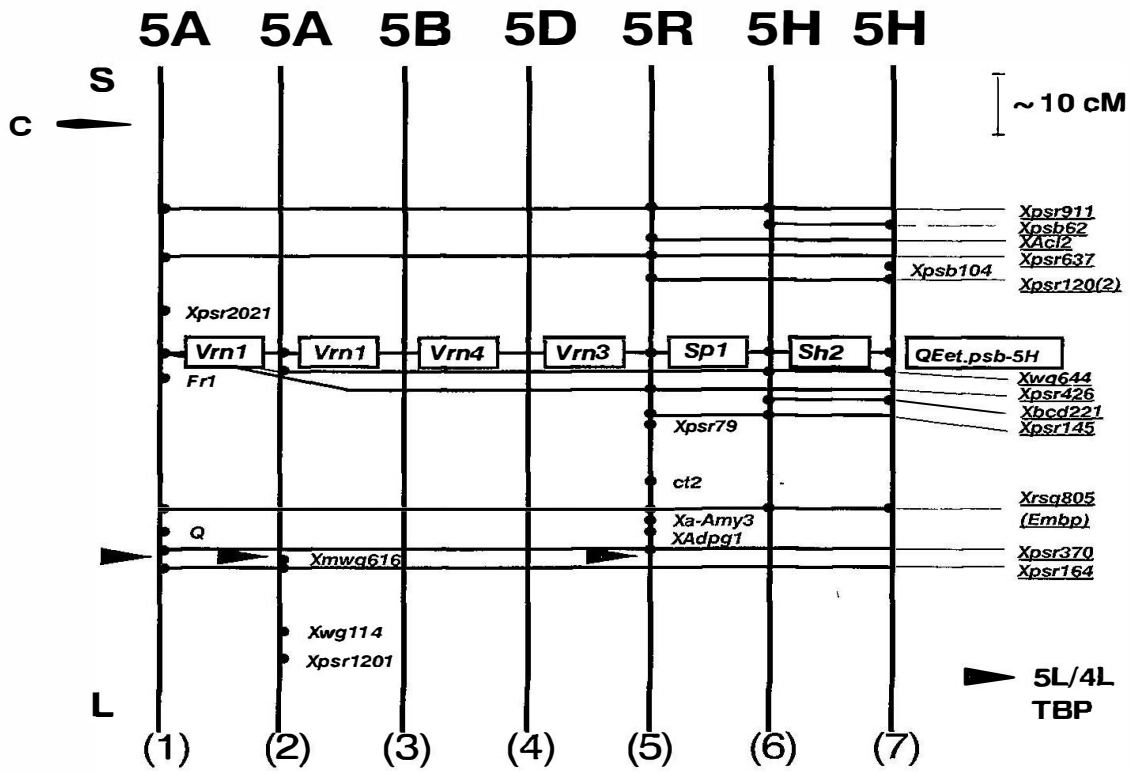

Figure 2: Comparative location of genes determining vernalisation response on chromosomes 5A, 5B and 5D of wheat, 5R of rye and 5H of barley as published by Börner *et al.* (1999). The followmg basic maps were used: (1) Galiba *et al.* (1995), (2) Korzun *et al* (1997b), (3, 4) McIntosh *et al* (1998), (5) Plaschke *et al.* (1993), (6) Laurie *et al.* (1995), (7) Bezant *et al* (1996). Mapped loci are marked with a point. The connecting lines between chromosomes indicate common loci which are underlined. Genetic distances (roughly estimated) are given in centimorgans (cM) The gene loci are boxed. c = estimated centromere position, S = short arm, L = long arm, TPB = translocation break point.

improvement. 'Functional maps' will also prove very useful for comparative mapping and genomics (see Varshney *et al.,* 2004).

4.1. Collinearity and Synteny

RFLP probes allowed cross-species hybridization within the tribe Triticeae, and allowed comparisons among specific regions of homoeologous chromosomes (Devos *et al.,* 1992). Cross-hybridization resolved substantial conservation of the linear order of not only molecular marker loci, but also of gene loci. In these comparisons, although extensive interchromosomal translocations were detected between species, colinearity was retained within the translocated chromosome segments (Devos *et al.,* 1993a). For instance, genes determining vernalization response have not only been identified in linkage groups belonging to all the three homoeologous

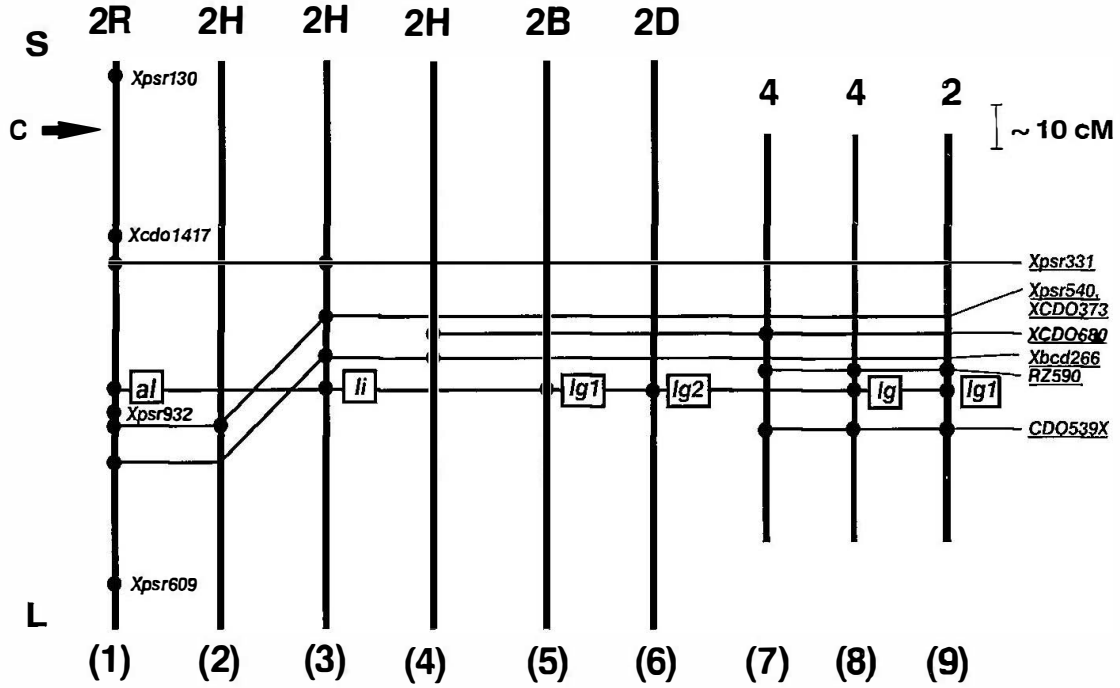

Figure 3. Comparative location of genes determining absence of ligules on chromosomes 2R of rye, 2H of barley, 2B and 2D of wheat, 4 of rice and 2 of maize as published by Börner *et al.* (1999). The following basic maps were used: (1) Korzun *et al.* (1997a), (2) Laurie *et al.* (1993), (3) Pratchett and Laurie (1994), (4) Heun *et al* (1991), (5,6) McIntosh *et al* (1998), (7) Causse *et al* (1994), (8,9) Ahn and Tanksley (1993). Mapped loci are marked with a point. The connecting lines between chromosomes indicate common loci which are underlined. Genetic distances (roughly estimated) are given in centimorgans (cM). The gene loci are boxed c = estimated centromere position, S = short arm, L = long arm.

chromosomes of group 5 of wheat (all the 3 genomes) ,but were also identified in the syntenous segments of the corresponding barley and rye chromosomes (Fig. 2). Colinearity was also described between genomes of species belonging to different tribes within the Poaceae (Gale and Devos, 1998). For instance, linkage groups 2R of rye, 2H of barley, 2B and 2D of wheat, 4 of rice and 2 of maize are synteneous, so that the genes determining absence of ligules are located in corresponding chromosome segments in all these species (Fig. 3). This suggested that the information available in maps of one cereal species could be transferred to the map of other species. For instance molecular markers mapped in wheat and barley can be integrated to genetic map of rye. Furthermore, detailed information available for the relatively small genome of rice, can be applied to larger genomes of wheat, barley and rye (Gale and Devos, 1998), although a recent study suggested that the presence of numerous translocations between wheat and rice genomes may complicate the use of rice as a model (Sorrells *et al.*, 2003). More details on synteny and comparative mapping have been described elsewhere in this book (Chapter 5 by Paterson).

4.2. Linkage Disequilibrium and Association Mapping

The above technique of molecular mapping requires a mapping population. The mapping population used for this purpose is the products of just a few cycles of recombinations, limiting the resolution of genetic maps, and often is not representative of germplasm that is being actively used in breeding programs. To oversome these problems, association mapping, based on linkage disequilibrium (LD) is being used for cereal genomics research. LD is the non-random association of markers in a populationand can provide high resolution maps of markers and genes. Association mapping based on LD may also help to resolve QTLs for specific traits (Lai *et al.,* 1994; Buckler and Thornsberry, 2002). LD depends on the evolutionary or selection history, and as a result only gene/marker with tight linkage will be detected (see Wall and Pritchard, 2003). However it is not the case in inbred species, such as wheat or barley, where large linkage blocks (often almost entire chromosome arms) have been maintained over long histories of selection Because of the narrow population structure in many crop plants due to the breeding history, association mapping has not been conducted in many plant systems (for review see Jannick and Walsh, 2002; Flint-Garcia *et al.,* 2003). In cereals so far reports on LD are available only in maize (Remington *et al.,* 2002; Ching *et al.,* 2002), wheat (Paull *et al.,* 1994; 1998) and rice (Garris *et al.*, 2003). Association mapping based on LD has also been demonstrated in maize for *Dwarf8* gene involved in flowering time (Thornsberry *et al.,* 2002) and yellow endosperm colour (Palaisa *et al.,* 2003). Efforts are underway in other cereals like barley (A. Graner, Germany, personal communication), wheat (P. Langridge, Australia, personal communication). Such high resolution mapping of traits/QTLs to the level of individual genes will provide a new possibility for studying the molecular and biochemical basis of quantitative traits variation and will help to identify specific targets for crop improvement. Though LD-based approaches hold great promise for speeding up the fine mapping, conventional linkage mapping will continue to be useful particularly when trying to mendelize QTLs and assessing the effect of a QTL in isolation (Rafalski and Morgante, 2004). In some studies, the utility of an approach involving the use of conventional linkage mapping along with LD has also been recommended for the construction of molecular maps, and for QTL analysis (Nordborg *et al.,* 2002; Zhu *et al.,* 2003). Keeping in view the importance of LD in crop plants in particular cereals, SCRI, Dundee (UK) has organized a workshop on *Gametic Phase Disequilibrium Mapping in Crop Plants* (http://wheat.pw.usda.gov/ggpages/calendar/ SCRI_2004.html) in Australia, recently.

4.3. Marker- Assisted Selection (MAS) for Crop Improvement

In a large number of studies, molecular markers have been used as tools to identify molecular markers associated with major genes and QTLs for agronomically important genes. Among cereals, in wheat alone, molecular markers have been identified for as many as ~40 traits of economic importance (see Gupta *et al.,* 1999 for a review). Similarly in barley, a large number of QTLs and genes for disease resistance, grain quality and physiological traits have been identified; these were compiled by Pat Hayes (Canada) and colleagues (http://www.barleyworld.org/NABGMP/qtlsum.htm). Details on identification of genes and QTLs for biotic and abiotic stresses in cereals are available in Chapter 8 by Jahoor *et al.* and Chapter 9 by Tuberosa and Salvi, respectively in this book.

As an example, some important studies on identification of genes and QTLs with molecular markers in rye are shown in Table 6. Availability of markers associated with these genes offers the possibility to apply marker-assisted selection (MAS) of desirable plants at the juvenile stage from an early generation. For simply inherited traits, PCR-based markers, which require each a small amount of DNA, is becoming very popular for screening large segregating populations. Unfavourable alleles can be eliminated or greatly reduced during the early stages of plant development through marker-assisted selection, focusing the selection in the field on reduced numbers of plants.

Although some examples of utilization of MAS are available in cereals like maize and barley, the promise of MAS at large scale in crop breeding still remains to be realized. The main reasons for this delay are the insufficient number of quality markers (with respect to their predictive and diagnostic value), inadequate experimental design, high costs and complexity of quantitative traits (Koebner and Summers, 2003; Chapter 10 by Koebner in this book). Only close interactions between breeders and biotechnologists will accelerate the effective implementation of MAS in cereal breeding programmes.

6. SUMMARY AND OUTLOOK

Molecular maps are now available for all cereals, and for some cereals such as rice and maize, high density maps are also available. The availability

Table 6. Utilization of molecular markers and genetic maps in identification of gene and QTLs in rye

Traits	Gene/ QTL	Marker type(s)	Location (chromo-some)	Reference
Morphological/Physiological traits				
Reduced plant height (Compactum)	*ct1*	RFLP	7R	Plaschke *et al.* (1995)
	ct2	RFLP	5R	Plaschke *et al.* (1993)
Reduced plant height	*Ddw1*	RFLP	5R	Korzun *et al.* (1996)
Spring growth habit (Vernalisation response)	*Sp1*	RFLP	5R	Plaschke *et al.* (1993)
Flowering time	*QTL*	RFLP	2R,5R, 7R	Börner *et al.* (2000)
Florets per spike	*QTL*	RFLP	6R	Börner *et al.* (2000)
Self fertility	*S*	RFLP, RAPD	1R	Senft and Wricke (1996) Voylokov *et al.* (1998)
	Z	RFLP, RAPD	2R	Senft and Wricke (1996) Voylokov *et al.* (1998)
	S5	RFLP	5R	Voylokov *et al.* (1998)
Fertility restoration	*Rfg1*	RFLP,	4R	Börner *et al.* (1998)
		RAPD,	4R	Miedaner *et al.* (2000)
		RAPD, CAPS AFLP, SCAR	4R	Stracke *et al.* (2003)
Biotic/Abiotic stress response				
Reaction to leaf rust	*Lr-a*	RFLP	6R	Ruge *et al.* (1999)
	Lr-c	RFLP, SSR	1R	Ruge *et al.* (1999)
	Lr-g	RFLP	1R	Ruge *et al.* (1999)
Reaction to powdery mildew	*Pm*	RFLP	1R	Wricke *et al.* (1996)
Resistance against cereal cyst nematode	*CreR*	RFLP, RAPD	6R	Taylor *et al.* (1998)
Aluminium tolerance	*Alt1*	RAPD, SCAR	6R	Gallego *et al.* (1998)
	Alt3	AFLP	4R	Miftahudin and Gustafson (2001)
Quality				
Secalins	*Sec2*	RFLP	2R	Malyshev *et al.* (1998)
	Sec5	RFLP	2R	Malyshev *et al.* (1998)
Waxy endosperm	*Wx*	RFLP	4R	Korzun *et al.* (1997a)

of efficient and cost effective markers will certainly be used in future for improving the available maps of other cereals also. Availability of transcript and functional maps in cereals and comparative genomics of grasses as a

whole will also facilitate transfer of markers from the major cereals to minor species including rye, sorghum, oats and millets. Similarly, physical maps of wheat and barley based on cytogenetic stocks, and thoseof rice, maize and sorghum based on BACs, will be used as a resource for future cereal breeding. Although progress in the construction of contig-based physical maps in wheat and barley is slow due to their large genomes, deletion stocks in wheat and novel approaches such as HAPPY mapping in barley (for local physical maps) are already being used for high resolution mapping in these crops. All these maps offer an opportunity both for understanding the genome organization leading to their use for crop improvement programmes. Advances in bioinformatics will also facilitate integration of information from these maps into genome sequences and gene expression profiles. In the not too distant a future, all this information should be ready on-line to address issues of plant breeding with an ultimate objective of crop improvement.

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