2 Wheat

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2.1
Introduction

The wheats (*Triticum* spp.) belong to the Poaceae, the largest family within the monocotyledonous plants. Bread wheat (*Triticum aestivum* L. em. Thell) is one of the most important cereal grain crops of the world and is cultivated over a wide range of climatic conditions. Global production of bread wheat in 2003 was 557 Mt, with an average yield of 2.68 t/ha (http://apps.fao.org/). The world's major bread wheat-producing areas are in northern China, northern India, northern USA and adjoining areas in Canada, northern and central Europe, western Russia, southern Australia, southern Latin America and South Africa. Worldwide, wheat provides nearly 55% of the carbohydrate and 20% of the food calories consumed globally (Breiman and Graur 1995).

Wheat is one of the most extensively studied crop species, particularly in the area of cytogenetics. An extensive catalogue of genetic and cytogenetic stocks was developed in the years following the ground-breaking isolation of aneuploid lines by Sears (1954). This work led to the concept of chromosome engineering, which takes advantage of the effect of the *Ph* genes. These genes restrict pairing and recombination to homologous chromosomes (Riley and Chapman 1958). Wheat provides a model system for the study of polyploid cytogenetics because of the ease of chromosome manipulation. The pioneering cytogenetic work by Kihara, Sakamura, Sax, Sears, Riley and others (Riley and Chapman 1958; Riley 1965) showed that the species of the genus *Triticum* form a polyploid series, with a basic number of $x = 7$. Thus there are the diploid ($2n = 2x = 14$), tetraploid ($2n = 4x = 28$) and hexaploid ($2n = 6x = 42$) species. Most modern cultivated wheat varieties are hexaploid (*T. aestivum*), described as 'common' or 'bread' wheat and valued for bread making. Bread wheat is a segmental allopolyploid containing the three distinct but genetically related (homoeologous) genomes A, B and D. It also has a very large genome (1.8×10^{10} bp), making an average wheat chromosome about 25-fold larger in terms of DNA content than the average rice chromosome (Moore et al. 1995b). Thus three wheat chromosomes carry the same DNA content of the entire haploid maize genome, and half of an average wheat chromosome is equivalent to the haploid rice genome (Gill and Gill 1994). The large genome size of bread wheat is due to extensive regions of retrotransposon-type elements such that over 80% of the genome consists of repetitive DNA sequence (Schulman et al. 2004). In contrast to the suitability of bread wheat for cytogenetic studies, the application of molecular techniques has been slow (Lagudah et al. 2001; Langridge et al. 2001). Many molecular markers are unable to detect an adequate and useful polymorphism for the construction of molecular maps, and consequently applications of marker-assisted selection (MAS) applications have been limited. However, despite these problems, some success has been achieved in recent years, and molecular genetic as well as physical maps have become available for the chromosomes of all homoeologous groups (Gupta et al. 1999; Varshney et al. 2004a). Molecular markers are increasingly being used to tag genes or QTLs (quantitative trait loci) of agronomic importance, offering the possibility of their use in marker-assisted selection (MAS) for wheat breeding (Gupta et al. 1999; Jahoor et al. 2004). In addition to their use in MAS, molecular markers have begun to be used to isolate genes via map-based cloning (Stein and Graner 2004). Some molecular markers detect homoeoloci; that is, the same sequence is present

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on all three members of a homoeologous group. Such homoeoloci have helped in the construction of comparative maps in different cereals, and these sometimes demonstrate the presence of major translocations thought to have occurred during speciation. In this article, we review recent progress related to the generation of genetic and physical maps in wheat and their applications for a variety of purposes including gene tagging for MAS, map-based cloning, diversity studies and comparative mapping in cereals. The impact of functional genomics and other recent approaches such as association mapping and genetical genomics on wheat breeding in the near future is also discussed.

2.2
Molecular Markers – Types and Availability

Recent advances in molecular techniques have led to the development of assays based on variation in DNA sequence, broadly referred to as DNA (or molecular) markers (Langridge and Chalmers 2004). DNA markers provide good resolutio because, unlike most non-DNA-based markers (morphological, biochemical or physiological), they are (1) unlimited in number, (2) independent of environment, developmental stage and complex genetic interactions, (3) frequently free of dominant and recessive effects and (4) easy to score, analyse and interpret. The DNA markers that have been used for the construction of molecular maps are broadly classified into three groups: the first-generation markers, RFLPs (**r**estriction **f**ragment **l**ength **p**olymorphisms) and RAPDs (**r**andomly **a**mplified **p**olymorphic **D**NAs); the second-generation markers, SSRs (**s**imple **s**equence **r**epeats or microsatellites) and AFLPs (**a**mplified **f**ragment **l**ength **p**olymorphisms); and the third-generation markers, SNPs (**s**ingle **n**ucleotide **p**olymorphisms) and InDels (**in**sertion-**del**etions) (for details see Gupta et al. 2002b; Varshney et al. 2004a; Mohler and Schwarz 2004). In addition, an array of marker types have been developed amongst which are STSs (**s**equence **t**agged **s**ites), SCARs (**s**equence **c**haracterized **a**mplified **r**egions), ISSRs (**i**nter**s**imple **s**equence **r**epeats), and SAMPL (**s**elective **a**mplification of **m**icrosatellite **p**olymorphic **l**oci). More recently, EST (**e**xpressed **s**equence **t**ag)-based markers (EST-SSRs and EST-SNPs) have been developed in wheat (Varshney et al. 2004a). Retrotransposon sequences (which are present in high-copy numbers), both alone or in combination with microsatellites or AFLPs, have been exploited to generate IRAPs (**i**nterretrotransposon **a**mplified **p**olymorphisms), REMAPs (**re**trotransposon-**m**icrosatellite **a**mplified **p**olymorphisms) and SSAPs (**s**equence-**s**pecific **a**mplified **p**olymorphisms) (Schulman et al. 2004). Each marker system has particular advantages and disadvantages (Gupta et al. 2002b) and user choice is best based on objective, convenience and cost. All these marker types, except the SNPs, have been incorporated into current molecular maps, and efforts are currently under way to construct SNP maps of wheat (Varshney et al. 2004a).

The accepted nomenclature for DNA marker loci and alleles in wheat and related species is published every 4 years in the Proceedings of the International Wheat Genetics Symposium (for the most recent edition see Proc of the 10th Int Wheat Genet Symp, Paestum, Italy, 2003), and an annual supplement is published in the Annual Wheat Newsletter (http://wheat.pw.usda.gov/ggpages/awn/). The catalogue lists all *Triticum* genes, RFLPs, SSRs, STSs, AFLPs, etc. that have been localized to a chromosome or chromosome arm, all known alleles of *Triticum* genes and prototype strains for each allele, the chromosomal locations of genetic markers, the linkage position of mapped genes, literature citations and other relevant information.

2.3
Construction of Molecular Maps

Early genetic maps were based entirely on morphological and biochemical markers. However, these maps had poor resolution, as marker number was limited and allelic variants were frequently restricted to exotic germplasm, precluding their usefulness in breeding programmes. Molecular markers detect both sequence (for example SNPs, resulting in RFLPs, RAPDs, AFLPs, etc.) and length polymorphisms (polymorphisms due to length variation of a sequence, as in SSRs and sometimes also in RFLPs). These loci usually segregate in a Mendelian manner, so that the conventional basis of linkage and recombination can be used for constructing these maps. A major advantage of molecular mapping is the possibility of analysing a large number of markers in a single mapping population. Therefore, DNA-based markers have been used for the construction of maps with a high marker density in almost all major crops including cereals (Varshney et al. 2004a). These maps have found application for gene tagging, QTL identification, and for the characterization of germplasm collections (Gupta et al. 1999; Langridge and Chalmers 2004). The aneuploid and deletion stocks in the type variety Chinese Spring have allowed the alignment of physical and genetic maps, and this has provided an insight into the physical and genetic organization of the wheat genome.

2.3.1
Genetic Maps

RFLPs were developed for mapping in the human genome (Botstein et al. 1980). Subsequently, they were adapted for use in mapping plant genomes (Bernatzky and Tanksley 1986; Weber and Helentjaris 1989) including bread wheat (Chao et al. 1989; Liu and Tsunewaki 1991). Disappointingly, RFLPs have only been able to detect a low level of polymorphism in wheat. This has been attributed variously to its polyploid nature, its high proportion of repetitive DNA, its large genome size and its recent origin (ca. 10,000 years ago). Thus in an effort to maximize the diversity between the parents of mapping populations, a standard hexaploid variety was crossed with a synthesized hexaploid (a chromosome-doubled hybrid of the wide cross tetraploid *T. turgidum* x diploid *Aegilops tauschii*) to produce a reference mapping population known as the ITMI population (Langridge et al. 2001). Alternatively, the three constituent genomes have been analysed at the diploid level. This involves generation of populations from specimen diploids *Ae. tauschii* (D genome) (Boyko et al. 1999, 2002) and *T. monococcum* (A genome) (Dubcovsky et al. 1996). Mapping populations have included F_2 populations, F_3 families, bulked F_4 families and recombinant inbred line (RIL) populations, and, in some cases, doubled haploids (DHs) and recombinant substitution lines (RSLs). RSLs, DHs and RILs have the particular advantage of being immortal, while F_2 populations, F_3 families and bulked F_4 families are easier to produce.

Using various mapping populations, a number of RFLP-based maps have been constructed both for individual chromosomes and for the entire wheat genome (Table 1). RFLP genotyping is time consuming and labour intensive and is therefore unsuitable for the rapid evaluation of large segregating populations typically encountered in commercial breeding programmes (Gale et al. 1995). The first replacement PCR-based technology was RAPDs, and these have been used for mapping many species including *Arabidopsis* (Reiter et al. 1992), barley (Giese et al. 1994) and rye (Masojć et al. 2001). In wheat, RAPDs have been of limited use, partly because of the low level of polymorphism that they uncover, but also because of poor reproducibility. Critically, RAPD alleles are usually dominant, and therefore a heterozygous genotype cannot be distinguished from one of the related homozygotes. A more profound disadvantage of the system is that a given pair of similarly sized RAPD products amplified from two genotypes may not represent homologous sequences (Devos and Gale 1992). As with RAPDs, AFLPs are commonly dominant markers. However, AFLP is a superior platform, due both to its greater robustness, and to its delivery of a far higher multiplex ratio (the number of distinct loci analysed per primer pair and per gel lane) (Ma and Lapitan 1998). AFLP has found its greatest application in fingerprinting studies (see later), but also to some extent in mapping. A number of genetic maps have incorporated AFLP loci, but usually associated with an RFLP and/or SSR backbone (Table 1). More recently, microsatellites (SSRs) have become the favoured markers. Their advantages include multi-allelism, codominant inheritance, relative abundance and extensive genome coverage (Gupta and Varshney 2000). Microsatellite markers for wheat have been generated from a number of sources, including the John Innes Centre (JIC), Norwich, UK (Stephenson et al. 1998), IPK, Gatersleben, Germany (Röder et al. 1998b), the Wheat Microsatellite Consortium (WMC; Varshney et al. 2000a; Gupta et al. 2002a), Beltsville Agricultural Research Centre (BARC; Song et al. 2002a,b) and the Genoplante/INRA Wheat SSR Club (http://wheat.pw.usda.gov/ggpages/SSRclub/; Guyomarc’h et al. 2002; Nicot et al. 2004). To date the densest microsatellite-based map of wheat contains 1,238 loci covering 2,569 cM with an average interval distance of 2.2 cM (Somers et al. 2004). In addition, wheat ESTs have also been exploited to generate the microsatellite (EST-SSR) markers in wheat (see later). A detailed account on development and application of microsatellite markers in wheat is available in a recent review by Röder et al. (2004).

Emphasis in marker research is now beginning to shift to the development of SNP markers, which are biallelic and are extremely abundant. SNPs have the potential to deliver very high throughput and

Table 1. A list of some important genetic maps constructed in wheats[a]

Map type	Population used for mapping	Number of loci mapped	Genetic map length (cM)	Reference
RFLP maps				
Wheat (Group 1)	ITMI RILs (W7984 × Opata85)	98	146 to 344	Van Deynze et al. (1995a)
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 (*T. aestivum* var. Chinese Spring × *T. spelta* var. Duha)	197	–	Liu and Tsunewaki (1991)
Wheat	DHs (Chinese Spring × Courtot)	264	1,772	Cadalen et al. (1997)
Wheat	RILs (*T. aestivum* cv. Chinese Spring × *T. spelta* var. *duhamelianum* K19-1)	320	3,451	Sasakuma and Shindo (2003)
Wheat-durum	RILs (*T. durum* var. Messapia × *T. turgidium* var. MG4343)	245	–	Blanco et al. (1998)
Wheat-diploid	F2s (*T.monococcum* KT3-5 × *T. Boeoticum* KT1-1)	115	1,250	Sasakuma and Shindo (2003)
SSR maps				
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)	65		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	RIL (Courtot × Chinese Spring)	84	–	Guyomarc'h et al. (2002)
Wheat	ITMI RILs (W7984 × Opata85)	168	–	Song et al. (2002a,b)
Wheat	F2:3s (ND3338 x F390)	247	3,067	Liu et al. (2003)
Wheat	3 DHs (RL4452 × AC Domain, Wuhan × Maringa, Superb × BW278) and ITMI RILs (W7984 × Opata85)	1,235	2,569	Somers et al. (2004)
Wheat	ITMI RILs (W7984 × Opata85)	825	–	Nicot et al. (2003a)
Wheat	ITMI RILs (W7984 × Opata85)	61 (eSSRs)	–	Nicot et al. (2003b)
Wheat	ITMI RILs (W7984 × Opata85)	126 (eSSRs)	–	Nicot et al. (2004)
Wheat	ITMI RILs (W7984 × Opata85)	101 (eSSRs)	–	Gao et al. (2004)
Wheat	ITMI RILs (W7984 × Opata85)	149 (eSSRs)	–	Yu et al. (2004b)
Wheat	ITMI RILs (W7984 × Opata85)	876 (eSSRs)	–	Peng et al. (2004a)
Wheat	ITMI RILs (W7984 × Opata85)	638	–	Röder et al. (2004b)
Wheat-durum	RILs (*T. Durum* var. Messapia × *T. Turgidium* var. MG4343)	79	–	Korzun et al. (1999)
Wheat-durum	RILs (*T.turgidum* subsp. *Durum*)	112	–	Jurman et al. (2003)

Table 1. (continued)

Map type	Population used for mapping	Number of loci mapped	Genetic map length (cM)	Reference
AFLP maps				
Wheat	DHs (Garnet × Saunders)	426	–	Penner et al. (1998)
Wheat	ITMI RILs (W7984 × Opata85)	140	–	Hazen et al. (2002)
Composite maps				
Aegilops tauschii	F2s [*Ae. tauschii* var *meyeri* (TA1691) × *Ae. tauschii* var *typical* (TA1704)]	732	–	Boyko et al. 2002
Wheat-einkorn	F2s (*T. monococcum* × *T. boeoticum* ssp. *boeoticum*)	81 (RFLPs, RAPDs, ISSRs)	–	Kojima et al. (1998)
Wheat-einkorn	F2s/ F3s (*T. monococcum* ssp. *monococcum* DV92 × *T. monococcum* ssp. Aegilopoides C3116)	335 (mainly RFLPs)	714	Dubcovsky et al. (1996)
Wheat-durum	RILs [*T. durum* (Messapia) × *T. turgidium* (MG4343)]	88 (AFLPs, RFLPs)	2,063 (total)	Lotti et al. (2000)
Wheat-durum	F2s (*T. dicoccoides* acc. Hermon H52 × *T. durum* cultivar Langdon (Ldn)	545 (AFLPs, RAPDs, SSRs)	3,169–3,180	Peng et al. (2000b)
Wheat-durum	RILs (Jennah Khetifa × Cham1)	306 (RFLPs, SSRs , AFLPs)	3,598	Nachit et al. (2001)
Wheat-durum	RILs (Omrabi5 × T.dioccoides 600545 × Ombrabi 5)	279 (RFLP, SSR, SSP)	2,289	Elouafi and Nachit (2004)
Wheat-emmer	RILs	549 (SSRs, AFLPs, RAPDs)		Nevo (2001)
Wheat	DHs (Schomburgk × Yarralinka)	147 (RFLPs, SSRs, AFLPs)	–	Parker et al. (1998)
Wheat	RILs (*T. aestivum* L. var. Forno × *T. spelta* L. var. Oberkulmer)	230 (RFLPs, SSRs)	2,469	Messmer et al. (1999)
Wheat	DHs (Cranbook × Halbred, CD87 × Katepwa, Sunco × Tasman)	355 to 902 (RFLPs, SSRs, AFLPs)	–	Chalmers et al. (2001)
Wheat	DHs (Courtot × Chinese Spring)	380 (RFLP, SSRs, AFLPs)	2,900	Sourdille et al. (2000b)
Wheat	DHs (Courtot × Chinese Spring)	659 (RFLP, SSRs, AFLPs)	3,685	Sourdille et al. (2003)
Wheat	F5s (Arina × Forno)	396 (RFLPs, SSRs)	3,086	Paillard et al. (2003)
Wheat	DHs (Beaver x Soissons)	241 (AFLPs, SSRs)	2,290	Verma et al. (2004)

[a] Details and updated version of these maps are available at GrainGenes (http://wheat.pw.usda.gov/GG2/maps.shtml)

automation. In the human genome, 1.8 million SNPs have been documented (http://snp.cshl.org/). In an international consortium, an attempt has been made to mine for SNPs from the massive amounts of wheat EST sequence available on public databases (http://wheat.pw.usda.gov/ITMI/2002/WheatSNP.html). Using this approach, Somers et al. (2003b) estimated SNP frequency as 1 every 540 bp, and efforts are under way to develop SNP markers in wheat (Mochida et al. 2003; Ogihara 2003).

Integrated (or 'composite') maps including more than one type of molecular marker (particularly RFLPs, SSRs and AFLPs) have also been prepared (Table 1). These maps typically have higher resolution than those based on a single marker type because they exploit a larger number of loci.

Comparisons between specific chromosomal regions across related species usually show that locus order (but not map distance) is highly conserved. Consequently, the construction of 'consensus maps' has become possible, where common markers are used as anchors and the position of other loci mapping in interstitial positions is extrapolated (for example, in barley, see Varshney et al. 2004b). In this way, 4,000 loci from 16 independent maps have been integrated into a single map (Appels 2003). This consensus map has been aligned with physical maps (see later) and has recently been put forward as the backbone for a long-range wheat genomic sequencing proposal. More rigorous consensus maps that use the linkage data from multiple populations can also be constructed using computer packages such as JoinMap (Stam and Van Ooijen 1995), but this method has not yet been used to develop a consensus map of wheat.

2.3.2
Transcript Genetic Maps or Functional Maps

A large amount of EST data has been generated in wheat, and 587,088 sequences are currently available in the public domain (http://www.ncbi.nlm.nih.gov/dbEST/dbEST_summary.html; 12 November 2004). From these, 44,630 TCs (tentative consensi) and 79,008 EST singletons have been identified (Sect. 3.5.1[TS1]). The integration of these loci into genetic maps would generate a "stranscript map"/'gene map' or 'functional map' (Schuler et al. 1996). To achieve this, each EST has to be converted into an effective marker assay. This could be in the form of RFLP, STS, CAPS (cleaved amplified polymorphic sequences), SSR or SNP. For instance, a given EST could be amplified from genomic DNA and the PCR product obtained used as an RFLP probe in a Southern hybridization (Smilde et al. 2001); or it could be tested directly for length or sequence polymorphism between the parents of a mapping population (Gilpin et al. 1997). Sequence variation between homologous PCR products can be detected directly by sequencing, indirectly by digestion with restriction enzymes (CAPS), or by heteroduplex analysis. Many ESTs contain microsatellites, which can be targeted by conventional SSR technology (Kantety et al. 2002; Varshney et al. 2002, 2004c, 2005a). Software search programmes have been developed to identify such situations, for example MISA (Thiel et al. 2003; available at http://pgrc.ipk-gatersleben.de/misa). The frequency of SSRs in wheat ESTs has been variously reported to be as high as 1 in 1.33 kb (Morgante et al. 2002) to as low as 1 in 17.42 kb (Gao et al. 2003). Discrepancies in the estimates of frequency and distribution of SSRs across different studies are probably an artefact of varying identification criteria and data quantity (Varshney et al. 2005a). Some ESTs via SSR assay (EST-SSRs) have been placed in genetic maps (Gao et al. 2004; Nicot et al. 2004; Peng et al. 2004a; Yu et al. 2004b), but they have not been integrated, to any great extent, in wheat in the way that has been done in rice (Harushima et al. 1998) and maize (Davis et al. 1999). An important feature of EST-SSR markers is their applicability across species (Holton et al. 2002; Gupta et al. 2003; Yu et al. 2004a; Varshney et al. 2005b), which makes them valuable for comparative mapping.

2.3.3
Physical Maps

Physical maps are based on the actual separation between markers, in terms of base pairs (or linear length, measured cytologically on metaphase mitotic chromosomes). This is in contrast with genetic distances, which are based on recombintaional frequencies. At the chromosome level, a physical map can be generated by hybridizing a labelled DNA *in situ* to a cytological preparation. Sites of hybridization can then be directly visualized microscopically (Schwarzacher 2003; Jiang and Gill 1994). A comparison has been made between physical and genetic distances between adjacent markers in hexaploid wheat using in situ

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hybridization (ISH) with 21 RFLP probes from linkage groups 5 and 6 (Zhang et al. 2000). Although the linear order and linkage relationships between DNA probes on these physical maps were generally conserved, a significant difference between the genetic and the physical distances was observed. However, this technique is laborious and not practicable on a genome-wide scale (Varshney et al. 2004a). An alternative strategy to physically mapping single and low-copy sequences is to generate and characterize chromosomal deletion stocks (Endo and Gill 1996). Chromosomal segments defined by these deletions have been labeled 'bins', and a large number of molecular markers including functional markers have been assigned to these bins (Table 2). In the USA a National Science Foundation-funded consortium has assigned 16,099 EST loci to 159 bins (http://wheat.pw.usda.gov/NSF/progress_mapping.html, Qi et al. 2003, 2004). This 'transcriptome map' has an average of 766 loci per chromosome and an expected average of 95 loci per chromosome bin or 1 EST locus per 1 Mb of wheat DNA (Gill et al. 2003; Qi et al. 2004).

Comparing across wheat homoeologues, synteny appeared to decrease with the distance of a chromosome region from the centromere and with an increase in recombination rates along the average chromosome arm (Akhunov et al. 2003a). Furthermore, 31 paralogous sets of loci were observed with perturbed synteny. In a separate study, the physical mapping data were also 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. 2003b; Dvorák et al. 2003).

In another project in France, a total of 725 microsatellite loci were assigned to 94 breakpoints in a homozygous (88 terminal deletions, 6 interstitial) and 5 in a heterozygous state representing 159 deletion bins with an average of 4.97 SSR/bin (Sourdille et al. 2004). Assignment of ESTs and genetically mapped SSRs to deletion bins in the above studies will be useful not only for verification of deletion stocks but also for allocating associated QTLs to deletion bins.

Physical mapping of wheat genomes using deletion lines suggests a non-random distribution of cDNA markers and ESTs (Gill et al. 1996a,b; Faris et al. 2000; Qi et al. 2003, 2004). The lower number or complete absence of cDNA markers in the centromeric region parallels the absence of recombination in these regions and suggests the presence of 85% of wheat genes in less than 10% of the genome. The small gene-rich regions are thought to be interspersed by large blocks of repetitive DNA (Gill et al. 1996a,b; Sandhu and Gill 2002a; Sandhu et al. 2003; Sidhu et al. 2003). It is believed that about three to four major and four to five minor gene-rich regions are present in each wheat chromosome (Sandhu and Gill 2002b). The gene-poor regions, in contrast, mainly contain retrotransposon-like repetitive sequences (Feuillet and Keller 1999; Schulman et al. 2004). Interestingly, physical location, structural organization and gene densities of the gene-rich regions are similar across the three genomes of hexaploid wheat (Gill et al. 1996a; for a review see Gill 2004). The resolution of this physical localization was, however, low due to a limited number of deletion lines and should improve in future with the availability of more deletion lines.

The availability of genome-wide BAC-contigs has been a prerequisite for sequencing the model genomes of *Arabidopsis* and rice (TAGI 2000, Sasaki and Burr 2000). Similar efforts are currently under way to prepare contig maps of the genomes of sorghum (Klein et al. 2000) and maize (Gardiner et al. 2004; http://www.maizemap.org/iMapDB/iMap.html). As a resource for contig construction, several large insert DNA libraries have been constructed for wheat (Stein and Graner 2004). However, the large size of the wheat genome presents serious problems for the development of a full genome contig map. Nevertheless, efforts are under way to prepare a contig map of the D genome of wheat to produce a detailed picture of gene distribution in the wheat D genome and enhance our understanding of the evolution of large genomes (http://wheat.pw.usda.gov/PhysicalMapping/). To date a total of 215,645 genomic fragments, cloned in BAC and BiBAC vectors, of an *Ae. tauschii* line (the D-genome progenitor of wheat) have been fingerprinted (Luo et al. 2003). As a result, 10,035 contigs were obtained at a Sulston score of 1×10^{-30} and a tolerance of 0.4 bp, corresponding to about 3,200 Mb (http://wheatdb.ucdavis.edu:8080/wheatdb/). Recent developments on construction of chromosome specific BAC library would facilitate preparation of individual physical maps of wheat in the near future (Safar et al. 2004).

As an alternative to the resource-intense development of contig maps, subgenomic physical maps of wheat can also be developed using radiation hybrid

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Table 2. Some physical maps of wheat prepared after using the deletion lines

Genome	Marker loci mapped	Cytogenetic stocks used	Reference
Wheat (homoeologous group 1)	19 RFLP	18 DLs[a]	Kota et al. (1993)
Wheat (homoeologous group 1)	50 RFLPs	56 DLs	Gill et al. (1996a)
Wheat (homoeologous group 1)	2,212 loci (944 ESTs)	101 DLs	Peng et al. (2003, 2004a)
Wheat (homoeologous group 2)	30 RFLPs	21 DLs	Delaney et al. (1995a)
Wheat (homoeologous group 2)	43 SSRs	25 DLs	Röder et al. (1998a)
Wheat (homoeologous group 2)	2,600 loci (1,110 ESTs)	101 DLs	Conley et al. (2004)
Wheat (homoeologous group 3)	29 RFLPs	25 DLs	Delaney et al. (1995b)
Wheat (homoeologous group 3)	2,266 loci (996 ESTs)	101 DLs	Munkvold et al. (2004)
Wheat (homoeologous group 4)	40 RFLPs	39 DLs	Mickelson-Young et al. (1995)
Wheat (homoeologous group 4)	1,918 loci (938 ESTs)	101 DLs	Miftahudin et al. (2004)
Wheat (homoeologous group 5)	155 RFLPs	65 DLs	Gill et al. (1996b)
Wheat (homoeologous group 5)	245 RFLPs, 3 SSRs	36 DLs	Faris et al. (2000)
Wheat (homoeologous group 5)	2,338 loci (1,052 ESTs)	102 DLs	Linkiewicz et al. (2003, 2004)
Wheat (homoeologous group 5S)	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)	5,154 loci (7,965 ESTs)	101 DLs	Randhawa et al. (2004)
Wheat (homoeologous group 6S)	82 RFLPs	14 DLs	Weng and Lazar (2002a)
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 (homoeologous group 7)	2,148 loci (919 ESTs)	101 DLs	Hossain et al. (2004a)
Wheat (chromosomes 6B, 2D and 7D)	16 SSRs	13 DLs	Varshney et al. (2001)
Wheat (chromosome 1D)	32 SSRs	11 DLs	Huang and Röder (2003)
Wheat (chromosome arm 1BS)	24 AFLPs	8 DLs	Zhang et al. (2000)
Wheat (chromosome arm 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) TS2
Wheat (chromosome arm 6BL)	32 AFLPs	–	Dieguez et al. (2003)
Wheat (whole genome)	121 expresses candidate resistance genes	339 DLs	Dilbirligi and Gill (2003)
Wheat (whole genome)	94 loci for genes involved in N-uptake, bread making quality or disease resistance	97 DLs	Benard et al. (2003)
Wheat (whole genome)	59 loci for 14 candidate ESTs for FHB	91 DLs	Han et al. (2003)
Wheat (whole genome)	16,099 loci (7,104 ESTs)	101 DLs	Gill et al. (2003) Qi et al. (2003, 2004)
Wheat (whole genome)	725 SSRs	159 DLs	Sourdille et al. (2004)

[a] DLs = deletion lines

(RH) populations (Cox et al. 1990) or by the so-called HAPPY (**hap**loid genome; **poly**merase chain reaction) mapping procedure (Dear and Cook 1989). Neither method relies on the availability of BAC-contigs or cloned DNA fragments and may be suitable for the high-throughput mapping of PCR-based markers independent of the presence of polymorphism (Waugh et al. 2002; Thangavelu et al. 2003; Wardrop et al. 2002). RH mapping of one scs^{ae} (species cytoplasm specific) gene in durum wheat is already in progress (http://cropandsoil.oregonstate.edu/cgb/projects.html). RH mapping permitted the localization of the *scs*^{ae} gene on the long arm of chromosome 1D along with eight linked markers (Kianian et al. 2003; Hossain et al. 2004b).

2.4
Application of Molecular Markers in Wheat Genetics and Breeding

In the last decade the generation of molecular markers and their mapping has offered new opportunities for plant breeding and has become a key component of what is now popularly termed *molecular breeding*. These resources allow the tracking of specific loci and alleles through the identification of markers linked to major genes, analysis of quantitative trait loci (QTLs), positional cloning of genes and characterization of genetic variation in germplasm. In addition, mapped markers can often be used in related species to analyse syntenic relationships.

2.4.1
Gene Tagging and QTL Analysis for MAS

The potential value of genetic markers, linkage groups and their association with agronomic traits has been known for more than 80 years. The usefulness of marker-assisted selection (MAS) was recognized as early as 1923 when Sax demonstrated in beans an association between seed size and seed coat pigmentation. The first molecular-marker based (RFLP) map in plants was made in tomato and consisted of 57 loci (Bernatzky and Tanksley 1986). Since then, maps have been constructed for nearly all crop plants (summarized by Philips and Vasil 2001), allowing, in principle, the application of MAS in plant breeding, as originally proposed by Sax (1923) and Thoday (1961). The concept of selection based on genotype rather than phenotype created strong interest among plant breeders (Tanksley et al. 1989; Paterson et al. 1994). The rationale relies on the discovery of phenotype/genotype associations between genome regions (as assayed by molecular markers) and traits in segregating populations (such as F_2s, RILs, DHs, etc.). These are derived by analysis of segregation of simply inherited traits and by QTL analysis for complex traits (Lee 1995). The identification of markers sufficiently tightly linked to target genes/QTLs and their conversion, if necessary, to a PCR platform has made MAS feasible in some plant breeding programmes (Langridge and Chalmers 2004). MAS can increase the efficiency and accuracy of selection, especially for traits that are difficult to phenotype or are recessive. The time-lag between the advent of DNA-marker technologies and their practical application for MAS has been, and remains, attributable to the high unit cost in the context of a relatively low value end product (Koebner et al. 2001).

In wheat, a significant number of major genes and QTLs for different traits have been tagged. Markers for more than 36 traits were already developed by 1999 (Gupta et al. 1999). Recent progress and significant achievements in the area of mapping disease resistance genes and the identification of QTLs and major genes for some agronomically important traits are summarized in Tables 3 and 4, respectively. A variety of molecular markers (RFLP, RAPD, AFLP, SSR) have been used for gene tagging and QTL analysis, but the consensus is that SSRs are best suited for this purpose (Gupta et al. 2002b). RFLP is not readily adapted to high sample throughput and RAPD assays are not sufficiently reproducible or transferable between laboratories. While both SSRs and AFLPs are efficient in identifying polymorphisms, SSRs are more readily automated (Shariflou et al. 2003). While RFLPs and AFLPs can in principle be converted into a simple PCR assay (STS), AFLP conversion is complicated by the observation that in large genome templates, individual bands are generally composed of multiple fragments (Shan et al. 1999; Carter et al. 2003). The inclusion of many microsatellite markers on genetic maps (Röder et al. 1998b; Gandon et al. 2002; Somers et al. 2004; Peng et al. 2004a) will ease their use for tagging for marker-assisted wheat breeding.

Status of MAS in Wheat Breeding

Prior to their use in plant breeding, the markers need to be validated, a process where functionality is tested in a range of genetic backgrounds (Langridge and Chalmers 1998; Gupta et al. 1999). For instance, marker validation studies were conduced for QTL for grain protein content by using NILs (Singh et al. 2001), for *Lr10* by using 16 wheat cultivars (Blazkova et al. 2002), for QTL for Fusarium head blight (FHB) resistance by using the progeny of crosses between the FHB-resistant spring wheat line and five European wheat varieties (Angerer et al. 2003; Liu and Anderson 2003a) or NILs from existing breeding populations (Pumphrey and Anderson 2003) and in germplam

Table 3. Some examples of gene tagging or QTL identification for resisiatnce to important diseases of wheat

Disease	Gene/QTLs	Chromosome	Marker type	Reference
I. Fungal resistances				
Black (stem) rust/ Septoria trici bloch (STB)	*Stb1*	5BL	AFLP, RAPD	Adhikari et al. (2004b)
	Stb2	3BS	SSR	Adhikari et al. (2004c)
	Stb3	6DS	SSR	Adhikari et al. (2004c)
	Stb4	7DS	AFLP, SSR	Adhikari et al. (2004a)
	Stb5	7DS	SSR	Arraiano et al. (2001)
	Stb6	3AS	SSR	Brading et al. (2002)
	Stb7	4AL	SSR	McCartney et al. (2003)
	Stb8	7BL	SSR	Adhikari et al. (2003)
	QStb.risø–2B	2BL	SSR	Eriksen et al. (2003a)
	QStb.risø–3A.1, *QStb.risø–3A.2*	3AS	SSR	Eriksen et al. (2003a)
	QStb.risø–3B	3BL	AFLP	Eriksen et al. (2003a)
	QStb.risø–6B.1, *QStb.risø–6B.2*	6B	AFLP	Eriksen et al. (2003a)
	QStb.risø–7B	7B	AFLP	Eriksen et al. (2003a)
	QStb	1DS	RFLP/SSR	Börner et al. (2003)
	QStb	6BS	RFLP/SSR	Börner et al. (2003)
	QStb	7BL	RFLP/SSR	Börner et al. (2003)
Powdery mildew	*Pm1*	7AL	RFLP	Ma et al. (1994) Hartl et al. (1995)
		7AL	STS	Hu et al. (1997)
	Pm1c	7AL	AFLP	Hartl et al. (1999)
	Pm1e (formerly *Pm22*)	7AL	SSR	Singrün et al. (2003)
	Pm2	5DS	RFLP	Ma et al. (1994), Hartl et al. (1995)
	Pm3a, b, c	1AS	RFLP	Hartl et al. (1993)
	Pm3b	1AS	RFLP	Ma et al. (1994)
	Pm3g (Mlar)	1AS	Gliadin	Sourdille et al. (1999)
	Pm3	1AS	SSR	Bougot et al. (2002)
	Pm4a	2AL	RFLP	Ma et al. (1994)
		2AL	AFLP	Hartl et al. (1999)
		2AL	STS	Ma et al. (2003)
	Pm5e	7BL	SSR	Huang et al. (2003c)
	Pm6	2BL	RFLP	Tao et al. (2000)
	Pm8/Pm17 (allelic)	1BL/1RS; 1AL/1RS	STS	Mohler et al. (2001)
	Pm13	3DS	STS	Cenci et al. (1999)
	Pm18	7A	RFLP	Hartl et al. (1995)
	Pm21	6AL/6VS	RAPD	Qi et al. (1996)
		6AL/6VS	SCAR	Liu et al. (1999a)
	Pm24	1DS	SSR, AFLP	Huang et al. (2000)
	Pm25	1A	RAPD	Shi et al. (1998)
	Pm26	2BS	RFLP	Rong et al. (2000)
	Pm27	6B-6G	SSR	Järve et al. (2000)
	Pm29	7DL	RFLP	Zeller et al. (2002)
	Pm30	5BS	SSR	Liu et al. (2002b)
	Qpm.vt–1B	1B	SSR, RFLP	Liu et al. (2001a)
	Qpm.vt–2A	2A	SSR	Liu et al. (2001a)

Table 3. (continued)

Disease	Gene/QTLs	Chromosome	Marker type	Reference
	Qpm.vt–2B	2B	RFLP, SSR	Liu et al. (2001a)
	QTL	5A	RFLP	Keller et al. (1999b)
	QTL	7B	RFLP	Keller et al. (1999b)
Yellow (stripe) rust	*Yr5*	2BL	RGAP/CAPS	Yan et al. (2003a), Chen et al. (2003)
	Yr7	2BL	AFLP	Bariana et al. (2001)
	Yr9	1BL/1RS	RGAP	Shi et al. (2001)
		1BL/1RS	SCAR	Mago et al. (2002)
	Yr10/ Yr10vav	1BS	SSR	Wang et al. (2002), Bariana et al. (2002)
	Yr10	1BS	SCAR	Shao et al. (2001)
	Yr15	1BS	RFLP	Sun et al. (1997, 2002)
		1BS	SSR	Chagué et al. (1999), Peng et al. (2000a)
	Yr17	2AS	SCAR	Robert et al. (1999)
		2AS	STS	Seah et al. (2001)
		2AS	CAPS	Helguera et al. (2003)
	Yr18	7DS	RFLP	Singh et al. (2000)
		7DS	SSR, AFLP	Bariana et al. (2001)
		7DS	SSR	Suenaga et al. (2003)
	Yr26	1BS	SSR	Ma et al. (2001)
	Yr28	4DS	RFLP	Singh et al. (2000)
	Yr29	1BL	RFLP, AFLP	Bariana et al. (2001)
		1BL	AFLP	William et al. (2003c)
	Yr30	3BS	SSR	Suenaga et al. (2003)
	Yr32	2AL	AFLP, SSR	Eriksen et al. (2003b)
	YrKat	2DS	SSR	Bariana et al. (2001)
	Yrns–B1	3BS	SSR	Börner et al. (2000)
	YrH52	1BS	SSR	Peng et al. (2000a)
	YrMoro	Group 1	STS	Smith et al. (2002)
	YrQz	2B	AFLP, SSR	Deng et al. (2004)
	QTL	3BS	RFLP	Singh et al. (2000)
	QTL	3DS	RFLP	Singh et al. (2000)
	QTL	5DS	RFLP	Singh et al. (2000)
	QYR1	2BL	SSR	Boukhatem et al. (2002)
	QYR2	2AL	SSR	Boukhatem et al. (2002)
	QYR3	2BS	RFLP	Boukhatem et al. (2002)
	QYR4	7DS	RFLP	Boukhatem et al. (2002)
Brown (leaf) rust	*Lr1*	5DL	RFLP, SSR	Ling et al. (2003)
	Lr3	6BL	AFLP	Dieguez et al. (2003)
	Lr9	6B	RFLP	Autrique et al. (1995)
	Lr10	1AS	RFLP	Nelson et al. (1997)
		1AS	STS	Schachermayr et al. (1997)
	Lr19	7DL	RFLP	Autrique et al. (1995)
		7DL	STS	Prins et al. (2001)
		7DL	SCAR	Cherukuri et al. (2003)
	Lr21/Lr40	1DS	STS	Huang and Gill (2001)
	Lr23	2BS	RFLP	Nelson et al. (1997)
	Lr24	3DL	RFLP	Autrique et al. (1995)
	Lr25	4A/2R	SCAR	Procunier et al. (1995)

Table 3. (continued)

Disease	Gene/QTLs	Chromosome	Marker type	Reference
	Lr26	1BL/1RS	SCAR	Mago et al. (2002)
	Lr27	3BS	RFLP	Nelson et al. (1997)
	Lr28	4AL	STS	Naik et al. (1998)
		4AL	SSR	Vikal et al. (2004)
	Lr29	7DS	SCAR	Procunier et al. (1995)
	Lr31	4BL	RFLP	Nelson et al. (1997)
	Lr32	3DS	RFLP	Autrique et al. (1995)
	Lr34	7DS	RFLP	Nelson et al. (1997)
		7DS	SSR	Suenaga et al. (2003)
		7DS	SSR	Schnurbusch et al. (2003b)
	Lr35	2B	STS	Seyfarth et al. (1999)
		2B	SCAR	Gold et al. (1999)
	Lr37	2AS	SCAR	Robert et al. (1999)
		2AS	STS	Seah et al. (2001)
		2AS	CAPS	Helguera et al. (2003)
	Lr39	2DS	SSR	Raupp et al. (2001)
	Lr41	2D	SSR	Singh et al. (2004b)
	Lr46	1BL	SSR	Suenaga et al. (2003)
		1BL	AFLP	William et al. (2003c)
	Lr47	7AS	STS, CAPS	Helguera et al. (2000)
	Lr50	2BL	SSR	Brown–Guedira et al. (2003)
	Lr-undesignated	BSA[a]	AFLP	Craven et al. (2003)
	QTLs	7BL	RAPD	Nelson et al. (1997)
Durable broad spectrum stem rust	*Sr2*	3BS	SSR	Spielmeyer et al. (2003)
	Sr2	3BS	ESTs	Spielmeyer and Lagudah (2003)
Fusarium head blight/ Scab	QTL	1B	Glutenin	Buerstmayr et al. (2002)
	QTL	1B	SSR	Shen et al. (2003a)
	QFhs.ndsu–2A	2AL	RFLP	Waldron et al. (1999)
	QFhs.inra–2A	2A	SSR	Gervais et al. (2003)
	QTL	2BL	SSR	Zhou et al. (2002)
	QFhs.inra–2B	2B	SSR	Gervais et al. (2003)
	QTL	2DS	SSR	Shen et al. (2003b)
	QTL	2DL	SSR	Somers et al. (2003a)
	QTL	3AL	RFLP	Anderson et al. (2001)
	QTL	3AS	SSR	Bourdoncle and Ohm (2003), Shen et al. (2003a)
	QFhs.ndsu–3AS	3AS	SSR	Otto et al. (2002)
	QFhs.inra–3A	3A	RFLP	Gervais et al. (2003)
	QTL	3A	SSR	Steiner et al. (2003)
	QFhs.ndsu–3B	3BS	RFLP	Waldron et al. (1999), Liu and Anderson (2003b)
	QTLs	3BS	SSR	Anderson et al. (2001), Liu and Anderson (2003b), Buerstmayr et al. (2002, 2003), Zhou et al. (2002), Bourdoncle and Ohm (2003), Shen et al. (2003b), Somers et al. (2003a)
	QTL	3BS	STS	Guo et al. (2003)
	QTL	3BL	SSR	Bourdoncle and Ohm (2003)

Table 3. (continued)

Disease	Gene/QTLs	Chromosome	Marker type	Reference
	QFhs.inra–3B	3B	SSR	Gervais et al. (2003)
	QTL	4BS	RFLP	Anderson et al. (2001)
	QTL	4BS	SSR	Somers et al. (2003a)
	QFhs.ifa–5A	5A	SSR	Buerstmayr et al. (2002, 2003)
	QFhs.inra–5A.1, QFhs.inra–5A.2	5A	SSR	Gervais et al. (2003)
	QFhs.inra–5A.3	5A	Awns	Gervais et al. (2003)
	QTL	5A	SSR	Ma et al. (2003)
	QTL	5AS	SSR	Somers et al. (2003a)
	QTL	5BL	SSR	Bourdoncle and Ohm (2003)
	QFhs.inra–5D	5D		Gervais et al. (2003)
	QTL	6AS	RFLP	Anderson et al. (2001)
	QTL	6BS	RFLP	Waldron et al. (1999), Anderson et al. (2001)
	QTL	6BS	SSR	Anderson et al. (2001), Shen et al. (2003b)
	QFhs.inra–6D	6D		Gervais et al. (2003)
	QTLs (2)	3B	SSR	del Blanco et al. (2003)
	QTLS	11	AFLP	Bai et al. (1999)
	QTLs(3)	BSA	RAPD	Sun et al. (2003)
	QTLs(3)	3	AFLP	Schmolke et al. (2003)
Eyespot	*Pch1*	7D	SSR	Groenewald et al. (2003)
	Pch2	7A	RFLP	de la Pena et al. (1996, 1997)
Karnal bunt	Unspecified	4B	SSR, AFLP	Singh et al. (1999, 2003)
Loose smut	Major gene		STS from AFLP	Knox et al. (2002)
Bunt	*Bt10*	BSA	SCAR (RAPD)	Laroche et al. (2000)
Septoria nodorum	*snbTM*	BSA	SCAR (RAPD)	Cao et al. (2001)
Leaf or glume blotch (Stagonospora nodorum)	*QSng.sfr-3BS*	3B	SSR	Schnurbusch et al. (2003a)
	QSng.sfr-34BL	4B	SSR	Schnurbusch et al. (2003a)
	QTLs (2)	5A	SSR	Toubia-Rahme et al. (2003)
	QTLs (1)	3B	SSR	Toubia-Rahme et al. (2003)
Pyrenophora tritici repentis	*Pti2*	1A/4A	RFLP	Faris et al. (1997)
	Pti2	1AS	RFLP	Effertz et al. (2002)
II. Viral resistances				
Barley yellow dwarf virus	*Bdv2*		STS (RAPD)	Stoutjesdijk et al. (2001)
	BYDV	7DL	SSR	Ayala et al. (2001)
Wheat streak mosaic virus	*Wsm1*	Group 4	STS (RAPD)	Talbert et al. (1996)
Wheat spindle streak mosaic virus	*WSSMV*	2D	RFLP	Khanet al. (2000a)
		2DL	SSR	Wang et al. (2003)
III. Nematode resistances				
Cereal cyst nematode	*Cre1*	–	STS	Ogbonnaya et al. (2001)
	Cre3	–	STS	Ogbonnaya et al. (2001)
	Cre6	–	STS	Ogbonnaya et al. (2001)
Root lesion nematode	*Rlnn1*	7A	RFLP	Williams et al. (2002)
Root knot nematode	*Rkn-mn1*	TLs[b]	RAPD	Barloy et al. (2000)
		TLs	SCAR (RAPD)	Yu et al. (2003)

Table 3. (continued)

Disease	Gene/QTLs	Chromosome	Marker type	Reference
IV. Insect resistances				
Russian wheat aphid	*Dn1*	7D	SSR	Liu et al. (2001b)
		7DS	RGA	Swanepoel et al. (2003)
	Dn2	NILs	SCAR (RAPD)	Myburg et al. (1998)
		7D	STS (RFLP)	Ma et al. (1998)
		7D	SSR	Liu et al. (2001b), Miller et al. (2001)
	Dn4	1D	RFLP	Ma et al. (1998)
		1D	SSR,	Liu et al. (2002a), Arzani et al. (2003)
	Dn5	7D	SSR	Liu et al. (2001b)
	Dn6	7D	SSR	Liu et al. (2002a)
	Dn8	7D	SSR	Liu et al. (2001b)
	Dn9	7D	SSR	Liu et al. (2001b)
	Dnx	7D	SSR	Liu et al. (2001b)
	Unspecified	NILs	SCAR (RAPD)	Venter and Botha (2000)
Hessian fly	11 loci	1A, 5A	RAPD	Dweikat et al. (1997)
	H31	5BS	AFLP/STS	Williams et al. (2003)
Wheat curl mite	*Cmc3*	T1AL.1RS	SSR, RFLP	Malik et al. (2003)
	Cmc4	6D	SSR, RFLP	Malik et al. (2003)
Greenbug	*Gb3*	7DL	SSR, AFLP	Weng and Lazar (2002a)
Sawfly cutting	*Sc*	3B	SSR	Houshmand et al. (2003)

[a] BSA = bulked segregant analysis
[b] TLs = translocation lines

collections (Zhou et al. 2003). Similarly, markers associated with preharvest sprouting (Kato et al. 2001; Mares and Mrva 2001), plant height (Ellis et al. 2002), and barley yellow dwarf virus (Ayala et al. 2001) were validated and used for enriching favourable allele frequency in early generation segregating populations and tracking donor parent alleles during backcrossing (Cakir et al. 2003). Microsatellite markers were linked to two major QTLs for FHB and were subsequently used in a marker-assisted backcross scheme to transfer these QTLs from bread wheat to durum wheat (Gladysz et al. 2003). Similarly, STS markers were used in the marker-assisted introgression of *Pm13* into 18 bread wheat cultivars, where BC_5 lines had already been developed (Reffo et al. 2003). Two effective leaf rust resistance genes *Lr29*+ *Lr24* were also successfully transferred into registered wheat cultivars with the assistance of molecular markers (Kraic et al. 2003). Molecular markers have also facilitated the pyramiding of multiple disease resistance genes in wheat as demonstrated by Liu et al. (2000), who integrated three powdery mildew resistance gene combinations (*Pm2*+*Pm4a*, *Pm2*+*Pm21*, *Pm4a*+*Pm21*) into an elite wheat cultivar 'Yang158'.

The use of MAS in wheat has a history of about 20 years and also involves the exploitation of non-DNA-based assays. For example, the correlation between bread-making quality and allelic status at the *Glu-1* (endosperm storage protein subunit glutenin) loci (Payne et al. 1983, 1987; Rogers et al. 1989) has been widely used in breeding programs. Some more recent examples of the utilization of MAS for glutenin alleles include Ahmad (2000), de Bustos et al. (2001), Radovanovic and Cloutier (2003), among others. More recently, a particular effort to use MAS in wheat breeding has been initiated in Australia. Over 1,000 marker assays covering five loci were performed at the University of Adelaide in the fiscal year 1999–2000 (Eagles et al. 2001), rising to >6,000 assays for 10 loci in 2002 and to ∼20,000 assays in 2003 (Kuchel et al. 2003) and around 50,000 assays in 2004 (SP Jefferies, Australia, pers. commun.). Loci

Table 4. A list of some grain quality traits of wheat for which genes or QTLs have been identified with molecular markers

Trait	Chromosome	Molecular marker	Number of QTLs/gene identified	Per cent phenotypic variation explained	Reference
Awn length	4A	SSR	*Hd*	8.5	Sourdille et al. (2002)
	6B	SSR	*B2*	45.9	Sourdille et al. (2002)
Coleoptile length	4B	RFLP		27–45	Rebetzke et al. (2001)
Culm thickness	2A	RFLP	1		Keller et al. (1999a)
	2B	RFLP	1	13.2	Keller et al. (1999a)
	3A	RFLP	1	21	Keller et al. (1999a)
	3B	RFLP	1	11.3	Keller et al. (1999a)
	4A	RFLP	1	16	Keller et al. (1999a)
	4B	RFLP	1	12.9	Keller et al. (1999a)
	5A	RFLP	1	37.6	Keller et al. (1999a)
	5B	RFLP	1	11.1	Keller et al. (1999a)
Dormancy	2AL	RFLP	1	–	Mares et al. (2002)
	2DL	RFLP	1	–	Mares et al. (2002)
	4AL	RFLP	1	–	Mares et al. (2002)
Grain length	3B	RFLP	1	21.9	Campbell et al. (1999)
Ear compactness	2B	RFLP	*Ppd2* region	9–22	Sourdille et al. (2000a)
Floral fertility	1B	SSR	1	10	Rousset et al. (2003)
Flour colour	3A	RFLP	1	13	Parker et al. (1998)
	7A	RFLP/AFLP	1	60	Parker et al. (1998)
	7A	STS/AFLP	1	60	Parker and Langridge (2000)
Flowering time	1Am	RFLP	*Eps-Am1*	47	Bullrich et al. (2002)
	2A	SSR	1	11.5	Huang XQ et al. (2003a)
	2A	RFLP	1	14.1–16.6	Ahmed et al. (2000)
	2B	RFLP	*Esp-2BS*	13.5–13.7	Ahmed et al. (2000)
	2D	SSR	1	15	Huang XQ et al. (2003a)
	2D	RFLP	*Ppd-D1*	29–31	Li et al. (2002a)
	6A	SSR	2	13.7–16.9	Huang et al. (2003b)
	7A	RFLP	*Esp-7A*	14.5–20.9	Ahmed et al. (2000)
	2A	SSR	*Ppd-A1*	10–11	Li et al. (2002a)
Grain protein content	2A	SSR	1	20.8	Prasad et al. (2003)
	2A	SSR	1	13.4–19.6	Prasad et al. (2003)
	2D	SSR	1	18.7	Prasad et al. (1999, 2003)
	3D	SSR	1	13.9–16.2	Prasad et al. (2003)
	4A	SSR	1	8.2–13.6	Prasad et al. (2003)
	6B	RFLP	1	72	Mesfin et al. (1999), Chee et al. (2001), Distelfeld et al. (2004)
	6B	STS/SSRs	–	up to 16.4	Khan et al. (2000b), Prasad et al. (2003)
	BSA	ISSR, RAPD	9	13.4– 13.5	Dholakia et al. (2001)
	5A	SSR	1	6.2	Singh et al. (2001)
	7A	SSR	1	32.4	Prasad et al. (2003)
	7D	SSR	1	15.9	Prasad et al. (2003)
Grains/spike	3A	RFLP	2	12.3– 18.3	Shah et al. (1999)
	4A	RFLP	1	12– 27	Araki et al. (1999)
	5A	RFLP	3	10– 42	Kato et al. (2000)

Table 4. (continued)

Trait	Chromosome	Molecular marker	Number of QTLs/gene identified	Per cent phenotypic variation explained	Reference
Grain weight	1A	RFLP	1	11.8	Campbell et al. (1999)
	1A	SSR	1	15.1	Varshney et al. (2000b)
	1B	RFLP	1	11.1	Campbell et al. (1999)
	2A	SSR	1	17.2	Huang et al. (2003b)
	2D	SSR	1	15.4	Huang et al. (2003b)
	3A	RFLP	1	12.2	Shah et al. (1999)
	3A/3B	RFLP	1	10.9	Campbell et al. (1999)
	3B	RFLP	1	12.2	Campbell et al. (1999)
	3B	AFLP	2	6	Elouafi and Nachit (2004)
	4B	AFLP	1	3	Elouafi and Nachit (2004)
	4D	SSR	1	14.3	Huang et al. (2003b)
	4D	SSR	1	6.8–13.1	Liu et al. (2003)
	5A	RFLP	1	11.0–19.0	Kato et al. (2000)
	5B	SSR	1	16	Huang et al. (2003b)
	6B	SSR	2	28	Elouafi and Nachit (2004)
	7A	SSR	1	14.5	Huang et al. (2003b)
	7B	SSR	2	20.6–25.9	Huang et al. (2003b)
	7D	SSR	1	17.3	Huang et al. (2003b)
Heading time	2BS	RFLP	Ppd-B1	23.4–44.4	Sourdille et al. (2000a)
	7BS	RFLP	*earliness per se*	7.3–15.3	Sourdille et al. (2000a)
Leaf angle	1A	RFLP	1	12.1	Keller et al. (1999a)
	3B	RFLP	1	11.1	Keller et al. (1999a)
	4A	RFLP	1	16.4	Keller et al. (1999a)
	5A	RFLP	1	11.2	Keller et al. (1999a)
	7D	RFLP	1	16.4	Keller et al. (1999a)
Leaf width	1B	RFLP	1	14	Keller et al. (1999a)
	3B	RFLP	1	19.7	Keller et al. (1999a)
	5A	RFLP	1	14.9	Keller et al. (1999a)
	5B	RFLP	1	11.2	Keller et al. (1999a)
Milling yield	3A, 7D	AFLP	2	19–22	Parker et al. (1999)
Number of spikeltes	2D	SSR	1	–	Rousset et al. (2003)
	5B	SSR	1	–	Rousset et al. (2003)
Pre-harvest sprouting tolerance (PHST)	2B	RFLP/SSR	2	4–16.2	Kulwal et al. (2004)
	2D	RFLP/SSR	1	14.9	Kulwal et al. (2004)
	3A	RFLP	1	5.6	Groos et al. (2002)
	3B	RFLP/SSR	2	24.9	Groos et al. (2002)
	3B	RFLP/SSR	5	3–20	Kulwal et al. (2004)
	3D	SSR	1	11.6	Groos et al. (2002)
	3D	RFLP	3	3.2–17.4	Kulwal et al. (2004)
	4A	rice sequence (*in GA20-oxidase-silico* analysis)			Li et al. (2004a)
	5A	RFLP	1	10.7	Groos et al. (2002)
	5B	SSR	1	–	Kulwal et al. (2004)
	5D	RFLP	1	–	Kulwal et al. (2004)
	6A	RFLP	1	–	Kulwal et al. (2004)
	6B	SSR	1	–	Roy et al. (1999)

Table 4. (continued)

Trait	Chromosome	Molecular marker	Number of QTLs/gene identified	Per cent phenotypic variation explained	Reference
	7A	RFLP	1	5.6	Groos et al. (2002)
	7B	RFLP/SSR	1	–	Kulwal et al. (2004)
	7D	STS	1	–	Roy et al. (1999)
Plant height	1B	RFLP	1	15–30	Cadalen et al. (1998)
	1B	SSR	1	13.3	Keller et al. (1999a)
	2A	PCR	1	29.3	Keller et al. (1999a)
	2B	SSR	1	17.4	Huang et al. (2003b)
	2D	SSR	*Rht8*	∼ 100	Korzun et al. (1998)
	3A	Gene	*Eps*	42.4	Shah et al. (1999)
	3A	RFLP	1	10.4	Shah et al. (1999)
	4A	RFLP	2	20–29	Araki et al. (1999)
	4A	SSR	1	23	Keller et al. (1999a)
	4B	RFLP	2 (*Rht-B1*)	10–20	Cadalen et al. (1998)
	4B	SSR	*Rht-B1*	11.8	Huang et al. (2003b)
	4D	RFLP	*Rht-D1*	9–15	Cadalen et al. (1998)
	4D	SSR	*Rht-D1*	29.5	Huang et al. (2003b)
	5A	RFLP/SSR	*Rht-12*	–	Korzun et al. (1997b)
	5A	PCR	1	31	Keller et al. (1999a)
	5B	PCR	1	20	Keller et al. (1999a)
	6A	SSR	1	16.5	Huang et al. (2003b)
	6B	PCR	1	7	Keller et al. (1999a)
	7A	RFLP	1	10.3–11.7	Cadalen et al. (1998)
	7B	RFLP	1	7.7–16.5	Cadalen et al. (1998)
	7B	PCR	1	7	Keller et al. (1999a)
Spike length	1AL	RFLP	–	12	Sourdille et al. (2000a)
Spikes/plant	2D	Gene-Ppd-D1	1	16–22	Li et al. (2002a)
	4A	RFLP	1	46–52	Araki et al. (1999)
	5A	RFLP	1	26–39.1	Kato et al. (2000)
	7A	RFLP	1	16–22	Li W et al. (2002)
Test weight	6B	SSR	1	9	Elouafi and Nachit (2004)
	7A	SSR	1	17	Elouafi and Nachit (2004)
Tiller angle	2A	RFLP	1	12–14	Li et al. (2002a)
	3A	RFLP	1	14–19	Li et al. (2002a)
Tiller number	1D	RFLP	1	14–15	Li et al. (2002a)
	2D	RFLP	1	11–15	Li et al. (2002a)
	5A	RFLP	*Vrn1*	7–37	Kato et al. (2000)
	5A	RFLP	1	10–19	Kato et al. (2000)
	6A	RFLP	1	12–31	Li et al. (2002a)
Vernalization sensitivity	5B	RFLP	*Vrn1/Fr1*	–	Galiba et al. (1995)
	5B	SSR	*Vrn-B1*	–	Salina et al. (2003)
	5B	SSR/AFLP	*Vrn-B1*	–	Barrett et al. (2002)
	SB	dCAPs	*Vrn2* (=*Vrn-B1*)	–	Iwaki et al. (2002)
	5B	SSR	*Vrn2* (=*Vrn-B1*)	–	Iwaki et al. (2002)
	5B	AFLP	*Ppd-B1*	–	William et al. (2003b)

Table 4. (continued)

Trait	Chromosome	Molecular marker	Number of QTLs/gene identified	Per cent phenotypic variation explained	Reference
	5D	SSR	*Vrn4* (=*Vrn-D1*)	–	Kato et al. (2003)
	7A	AFLP	*VrnA-2*	–	William et al. (2003b)
Yield	2D	SSR	1	11.5	Huang et al. (2003b)
	3B	SSR	2	9.6–21.6	Huang et al. (2003b)
	4A	RFLP	1	17–27	Araki et al. (1999)
	4D	SSR	2	10.1–12.3	Huang et al. (2003b)
	5A	Gene-*q*	1	23–27	Kato et al. (2000)
Others					
Alpha-amylase	1B	SSR	1	7.9–14.7	Zanetti et al. (2000)
	3B	RFLP	1	7–15.5	Zanetti et al. (2000)
	5A	RFLP	2	13.0–38.5	Zanetti et al. (2000)
	6A	RFLP	1	13.5–17.7	Zanetti et al. (2000)
	7B	RFLP	1	7.7–25.0	Zanetti et al. (2000)
Starch quality	4A	AS-PCR[a]	*Wx-B1*	–	McLauchlan et al. (2001)
	7A	AS-PCR	*Wx-A1*	–	McLauchlan et al. (2001)
	7D	AS-PCR	*Wx-D1*	–	McLauchlan et al. (2001)
	4A	GS-PCR[b]	GBSS[c]	–	Briney et al. (1998)
Polyphenol oxidase	2D	RFLP	1	23	Demeke et al. (2001)
	2A	RFLP	1	12–16	Demeke et al. (2001)
	3B	RFLP	1	11–14	Demeke et al. (2001)
	6B	RFLP	1	12–14	Demeke et al. (2001)
Anther culturability	5B	SSR	2	76.7	Zhang et al. (2003a)
Crossability (wheat-rye)	5B	RFLP	*Kr1*	65	Tixier et al. (1998)
Flag leaf senescence	2B	AFLP/SSR		10.2–11.4	Verma et al. (2004)
	2D	AFLP/SSR	1	21.7–32.9	Verma et al. (2004)
Glume colour	1D	SSR	*Rg2*	–	Arzani et al. (2003)
Species cytoplasm specific (scs)	1A	RFLP	scs^{ti}	–	Simons et al. (2003)
	1A	RH mapping	scs^{ae}	–	Kianian et al. (2003), Hossain et al. (2004)
Thermosensitive genic male sterlity (TGMS)	2B	AFLP/SSR	*wtms1*	–	Xing et al. (2003)
Photoperiod temperature sensitive genic malesterlity (PTSGMS)	–	ISSR	*ptms1*	–	Cao et al. (2003)
	3A	ISSR	*ptms2*	–	Cao et al. (2003)

[a] AS-PCR = allele-specific PCR
GS-PCR = gene-specific PCR
GBSS = granule bound starch synthetase

for which markers have been successfully tested within experimental populations in Australia include tolerance to high soil boron (*Bo1*), tolerance to late-maturity α-amylase (LMA) (7BL), barley yellow dwarf virus resistance (*Bdv2)* (7DL), cereal cyst nematode resistance *Cre1* (2BL), *Cre8* (6BL), waxy or granule-bound starch synthase (*Wx-B1)* (4A), high-molecular-weight glutenin subunits (*GluD1)*

(1DL), leaf rust resistances (*Lr46)* (1BL), (*Lr34)* (7DS), height or dwarfing genes (*Rht1)* (4BS), (*Rht2)* (4DS), (*Rht8)* (2DS), root lesion nematode resistance (*Rlnn1)* and yellow flour colour (7AL), stem rust resistances (*Sr2)* (3BS), (*Sr36)* (2B) and VPM (Ventricosa x Persicum x Marne), a source for eyespot resistance gene *Pch1*, obtained by introgrossion) segment (2AS). Additional loci for which markers are under investigation include aluminium toxicity tolerance (4B), *Glu-A3* (1AS), *Glu-B3* (1BS), *Lr1* (5DL), *Lr13* (2B), *Lr19* (7DL) and polyphenol oxidase activity (2D) (Pallotta et al. 2003). At CIMMYT (Mexico), marker implementation in wheat breeding involves the routine deployment of markers for the four genes *Cre1*, *Cre3*, BYDV resistance, *ph1b* mutant, and for the *Ae. ventricosa* segment carrying *Yr17*, *Lr37*and *Sr38* translocated 2AS. Approximately 7,000 marker assays are performed annually (William et al. 2003a).

With the availability of many more markers than in earlier years, the potential for uptake is now much greater than in the past. Reflecting this, a consortium of 12 wheat-breeding and research programmes across the US named 'MASwheat' (http://maswheat.ucdavis.edu/index.htm) has recently been launched, aiming to 'transfer new developments in wheat genomics and biotechnology to wheat production'. However, with a unit assay cost in the range of US$1–2 (Dreher et al. 2003; Koebner and Summers 2003), the widespread application of MAS must compete with alternative assay methods for the scarce funds available to most breeding programs. Although it was recently suggested that the bulk of MAS uptake remains restricted to low volume applications, such as genotype construction by backcrossing, and to the development of niche genotypes such as waxy wheats (Koebner 2004), this is clearly not the case for some breeding programmes such as the Australian programme described above. As the unit assay costs fall with the development of automated platforms and high-throughput marker systems, one can anticipate that MAS assays will become increasingly feasible for commercial wheat breeding.

2.4.2
Map-Based Cloning (MBC) of Genes in Wheat

In addition to their use for indirect selection of genes or QTLs of agronomic importance (including resistance to diseases), molecular markers offer the possibility of isolating genes of interest by positional cloning with an ultimate objective of producing transgenic plants for crop improvement. There are three major requirements for positional gene isolation: (i) a high-resolution, high-density genetic map spanning the gene or region of interest; (ii) availability of a large insert genomic YAC, BAC or PAC library for preparation of a physical map to isolate the candidate gene; and (iii) multiple independent mutant stocks, an efficient transformation system for use in functional complementation or an alternative technique for functional analysis of candidate genes. All these resources have become available in wheat (Lagudah et al. 2001; Stein and Graner 2004).

However, long-distance chromosome walking is not efficient in wheat because of the large amount of repetitive DNA and the physical size of the genome. To overcome this problem, several strategies have been developed for isolating genes from wheat.

Genome Collinearity

The gene order appears to be well conserved among various species of grass. This is referred to as synteny. Since the rice genome has been sequenced, it can be used as an intergenomic vehicle in cereals including wheat (Moore et al. 1995a; Keller and Feuillet 2000). This approach was used for the isolation of the vernalization response gene *Vrn1* from *Triticum monococcum* (Yan et al. 2003b). Complete marker/gene collinearity was observed for the putative orthologous regions on *T. monococcum* chromosome $5A^m$ and rice chromosome 3, and a BAC contig of the target region was constructed from a *T. monococcum* BAC library. It was collinear to two BACs representing the orthologous locus in rice. However, both physical maps showed a gap between the same two collinear genes. Interestingly, screening of a sorghum BAC library revealed a collinear BAC that bridged the gap in the other two species leading to a consensus physical map across three cereal species. The most promising candidate gene for *Vrn1* proved to be an orthologue in all three species. Similarly, using the genome collinearity approach, Sutton et al. (2003) have identified candidate meiotic genes at the *Ph2* locus of wheat. They identified the rice genomic region syntenous to the region deleted in wheat chromosome pairing mutant *ph2a*. With the help of markers known to reside within the region deleted in *ph2a* and data from wheat, barley and rice genetic maps, markers delimiting the region deleted on wheat chromosome 3DS in the *ph2a* mutant were used to locate the syntenous region on rice chromosome 1S. A 6.58-Mb rice contig generated from 60 overlapping rice PAC clones spanning the syntenous rice region has enabled identification of 218 wheat ESTs putatively located in the region deleted in *ph2a*. The candidate gene approach may sometimes also fail, as suggested by the reports of variation in the content and order of orthologous genomic sequences from several cereal species (for a review see Bennetzen and Ramakrishna 2002; Feuillet and Keller 2002). In particular, the identification of candidate genes for race-specific disease resistance loci, which are less conserved between species and prone to genomic rearrangements (Leister et al. 1998), has proved problematic, and the earlier optimism regarding the use of the model genome strategy has diminished recently (Brueggeman et al. 2002; Bennetzen and Ma 2003).

Subgenome Chromosome Walking

In addition to the high proportion of repetitive DNA in wheat, polyploidy poses another level of complexity to positional cloning. As mentioned earlier, the three homoeologous subgenomes A, B and D are highly collinear and most of the functional loci occur as triplicate genes. Therefore, screening of a large insert library will yield two thirds of clones, which are not related to a target locus in a specific subgenome. In order to tackle this problem, large insert libraries were constructed from diploid and tetraploid wheat species (Stein and Graner 2004). Therefore an approach called 'subgenome chromosome walking', employing these libraries, has been used to isolate disease resistance genes. The first successful example of this approach involved map-based cloning of the *Lr10* leaf rust resistance locus (located on chromosome 1AS) of bread wheat. A three-step chromosome walk in a *T. monococcum* BAC library initiated from a closely linked RFLP marker allowed a BAC contig to be established, which contained the flanking markers and two candidate resistance genes (Stein et al. 2000; Wicker et al. 2001). Markers cosegregating with the gene were derived from the initial contig, and additional markers were developed from low-copy sequences obtained after low-pass shotgun sequencing of neighbouring BAC clones. All markers derived from the *T. monococcum* contig mapped to collinear segments of the *T. aestivum* genetic map. The *T. aestivum* orthologues of the two candidate genes were subsequently isolated. One of the candidate genes, *Rga1*, proved to be *Lr10* as confirmed after sequence analysis of mutant alleles and complementation *via* transformation into a susceptible genotype (Feuillet et al. 2003).

Similarly, the powdery mildew resistance gene *Pm3b* was isolated from *T. aestivum* using a subgenomic BAC library. Since chromosome walking in *T. monococcum* was not successful due to a gap in the BAC library, a BAC library of the tetraploid relative *T. turgidum* ssp. *durum* (Cenci et al. 2003) was used, allowing construction of a contig covering *Pm3b*. Resistance conferred by transient expression was monitored in the epidermis of detached wheat leaves of a susceptible *T. aestivum* cultivar after biolistic bombardment with the homoeologue of the identified candidate gene and subsequent powdery mildew infection (Yahiaoui et al. 2003). The *Q* locus of *T. aestivum*, conferring free-threshing and square-headed spikes, was physically delimited by the same strategy (Faris et al. 2003) and should lead to the isolation of the *Q* locus.

Another gene conferring resistance to wheat leaf rust was isolated through the use of a *Aegilops tauschii* (D genome) subgenomic cosmid library (Huang et al. 2003a). *Lr21* was previously introgressed into *T. aestivum* via synthetic wheat derived from a cross between *T. turgidum* and the resistant *Ae. tauschii* accession TA1649. A closely linked RFLP probe was used to screen the cosmid library. A single cosmid clone harbouring the closely linked RFLP fragment could be isolated. The *Lr21* gene spans 4,318 bp and encodes a 1,080-amino-acid protein containing a conserved nucleotide-binding site (NBS) domain, 13 imperfect leucine-rich repeats (LRRs), and a unique 151-amino-acid sequence missing from known NBS-LRR proteins at the N terminus. The whole cosmid was used for complementation via stable transformation, and resistance was achieved.

However, unlike disease resistance, many agronomically important traits are controlled by QTLs (Table 3). In recent years, significant progress has been made in the isolation of QTLs such as those controlling fruit weight (*fw*2.2) in tomato (Alpert and Tanksley 1996) and photoperiod sensitivity (*Hd1*, *Hd3a*, *Hd6*) in rice (Yano et al. 2000; Takahashi et al. 2001; Kojima et al. 2002). Due to systematic development of resources in wheat, it is now becoming possible to clone QTLs for some important traits in wheat for crop-improvement programs.

2.4.3
Allelic Diversity

An understanding of germplasm diversity and genetic relationships among breeding materials is an invaluable aid for crop-improvement strategies. Conventional analyses of genetic diversity in germplasm accessions, breeding lines and populations have relied on pedigree information and morphological and agronomic performance data. The advent of biochemical and particularly DNA marker technology has improved the accuracy and number of lines that can be assessed in germplasm collections (Tanksley and McCouch 1997; Mohammadi and Prasanna 2003).

For practical reasons many of the early attempts to study diversity employed RAPDs (Vierling and Nguyen 1992; Joshi and Nguyen 1993). However, it soon became clear that the greater reproducibility of RFLPs was advantageous (for example, Siedler et al. 1994; Autrique et al. 1996). Now, SSRs and AFLPs have largely replaced these for genetic diversity studies (Table 4). In particular, some SSR loci can show such high levels of variability that even closely related genotypes can be distinguished from one another (Plaschke et al. 1995; Prasad et al. 2000; Stachel et al. 2000). On the other hand, AFLPs have the advantage of delivering a much higher multiplex ratio and are particularly useful for fingerprinting and the assessment of genetic diversity (Law et al. 1998; Bohn et al. 1999; Schwarz et al. 2000). As some differences in AFLP pattern have been found to be specific for particular plant organs (Donini et al. 1997), it is important to extract template DNA from physiologically uniform tissues. Recently developed genic microsatellites (or EST-SSRs) have been found to be superior to genomic SSRs due to improved quality of banding pattern (Eujayl et al. 2001; Leigh et al. 2003). Although the informativeness of genic SSRs is generally lower than for genomic SSRs, their origin from the conserved proportion of a genome have made them more suitable as a tool to assess genetic diversity across species (Gupta et al. 2003; Bandopadhyay et al. 2004; for a review see Varshney et al. 2005a). Recently, retrotransposon-based molecular markers have also been used for diversity studies in wheat by using the S-SAP (**s**equence-**s**pecific **a**mplification **p**olymorphism) assay (Queen et al. 2004). A summary of some genetic diversity studies involving with different marker systems in *Triticum* species is given in Table 5.

Molecular-marker evaluations have indicated that genetic diversity among varieties or inbred lines is higher than expected, although it is lower than that among landraces (Chen et al. 1994; Autrique et al. 1996; Zhang et al. 2002; Röder et al. 2003). For example, Röder et al. (2003) found 198 alleles across 19 SSR loci in 502 European varieties, 280 alleles in 450 European landraces and 323 alleles in 544 non-European landraces. Of the 339 alleles found in 994 landraces, 147 are present only in landraces but not in varieties, suggesting a genetic similarity of 57%.

Evidence of temporal flux in genetic diversity has been observed in wheat varieties released at different times within a country or region. Genetic diversity appears to be decreasing in Iranian wheats (Sayed-Tabatabaei and Shahnejat-Bushehri 2003), increasing in Italian durum wheats (Maccaferri et al. 2003), but has remained constant in the wheat varieties of Argentina (Manifseto et al. 2001), UK (Donini et al. 2000; Koebner et al. 2003) and the Yaqui Valley of Mexico (Souza et al. 1994). Interestingly, genetic diversity in Nordic spring wheat was enhanced by plant breeding in the first quarter of the 20th century and, following a decrease during the second quarter, increased again by plant breeding (Christiansen et al. 2002).

The use of molecular markers has also shown that diversity within a genome is largely shaped by recombination and selection and is not homogenous. In *Aegilops*, the polymorphism level of a locus has been correlated with recombination rate along the centromere to telomere axis (Dvorák et al. 1998b). Intraspecific nuclear genome variation appears lower in einkorn wheats and higher in *Ae. speltoides*, while this pattern is reversed for chloroplast DNA (Mizumoto et al. 2002). Comparison of landraces and improved varieties of Chinese wheat revealed a significant difference in the level of diversity within the D genome (Zhang et al. 2003b), indicating that high selection pressure has been applied to the D genome during the breeding process.

Genetic diversity studies involving germplasm from different countries or regions often allow separation of accessions into distinct groupings (Stachel et al. 2000; Bai et al. 2003; Pester et al. 2003). Among wild emmer wheats from Israel and Turkey, DNA polymorphisms have been associated with microclimatic stress (Fahima et al. 1999, 2002; Li et al. 1999, 2002). Associations between allelic constitutions at marker loci with agronomically important traits have been proposed in some diversity studies (Kobiljski et al. 2002; Roy et al. 2002; Bai et al. 2003). However, although suitable genotypes for hybridization were identified in this way (Roy et al. 2004), the overall ge-

Table 5. Details on some important allelic diversity studies using molecular markers in wheat

Markers	Material	Outcome	Reference
RFLP-based diversity			
58 probes	52 winter wheat, 9 spring wheat and 20 spelt (*T. spelta*) lines representing part of European breeding germplasm	A clear separation of wheat and spelt germplasm was possible. Novel spelt lines with various proportions of wheat germplasm were positioned between wheat and traditional spelt lines. The spring wheat lines formed a distinct group	Siedler et al. (1994)
39 probes	113 improved cultivars and landraces of diverse ecogeographical origin	Lower genetic distances were observed for the improved cultivars and some landraces from Morocco and Jordan while genetic distances were larger for the remaining landraces. Narrower genetic diversity in breeding lines suggested the need for the use of other sources of variation	Autrique et al. (1996)
48 probes	11 red and 11 white wheat lines from eastern USA soft wheat germplasm pool	Actual genetic similarity among unrelated lines in eastern USA soft wheat genepool appreared to be higher than that observed for unrelated landraces from southwest Asia. It also suggested that the ancestral landrace parents of this gene pool were themselves drawn from a base population where inbreeding was greater	Kim and Ward (1997)
20 probes	22 accessions representing 11 species of cultivated emmer and timopheevi wheat, 16 accessions of wild emmer wheat, 14 accessions of wild Timopheevi wheat and 1 accession of common wheat	Large genetic diversity in *T. Dicoccum*, the non-free threshing species, supported the archeological evidence that *T. dicoccum* was the earliest domesticated tetraploid wheat	Mori et al. (1997)
98 probes	124 accessions of all major Australian wheat varieties and lines	RFLP analysis can be used for the characterization and grouping of elite breeding material of wheat. Associations were derived for a range of stem rust, leaf rust and yellow rust resistance genes	Paull et al. (1998)
75 probes	Chinese accessions of *T. tauschii*, *T. aestivum* from Sichuan white (SW), Yunnan hulled (YH), Tibetan weedrace (TW) and Xinjiang rice (XR) wheat groups	Chinese landraces had a higher degree of genetic relatedness to the southwest Asian *T. tauschii*, particularly to accessions from Iran rather than to the Chinese *T. tauschii*. Chinese Spring was most related to Chendu-guang-tou, a cultivar from the southwest wheat group	Ward et al. (1998)
9 probes	202 wild wheat relative (*Ae. geniculata* Roth) genotypes belonging to 151 populations originating from different ecogeographical regions	Efficiency of RFLP markers in building core collection of *Ae. genicula* was demonstrated	Zaharieva et al. (2001)
11 probes	17 populations of wild emmer wheat sampled from southeastern Turkey	Narrow genetic variability was recorded among 17 populations studied	Tanyolac et al. (2003)

Table 5. (continued)

Markers	Material	Outcome	Reference
RAPD-based diversity			
40 primer pairs	20 accessions of wild tetraploid durum wheat and 10 genotypes of cultivated tetraploid durum wheats selected from geographically diverse locations	A higher level of polymorphism among different accessions of wild emmer wheat from Israel, Turkey and Jordan than the group of cultivated American, Turkish and Syrian durum wheats	Joshi and Nguyen (1993)
26 primer pairs (182 loci)	7 accessions of Tibetan wheat, 22 cultivars of common wheat and 17 lines of spelt wheat	European spelt wheat and the Tibetan wheat showed much higher genetic diversity than Chinese common wheat which could be used to diversify the genetic basis for common wheat breeding	Sun et al. (1998)
31 primer pairs (136 loci)	29 accessions of two *Ae. tauschii* species	Divergence between the two subspecies of *Ae. tauschii* was greater than than within one subspecies from different geographical regions	Kong et al. (1998)
87 primer pairs (304 loci)		Information regarding the genetic diversity of the parental lines was not helpful for predicting F1 performance	Perenzin et al. (1998)
6 primer pairs (54 loci)	20 wheat lines	It was possible to differentiate wheat lines with different performances and the classification of parents from these markers is of predictive value for developing superior hybrids	Liu et al. (1999b)
20 primer pairs (97 loci)	118 registered individuals of wild emmer wheat	DNA polymorphisms appeared to be assocaited with microclimatic stress. Microclimatic selection appears to play an important role in DNA differentitation	Li et al. (1999)
10 primer pairs (59 loci)	110 genotypes of wild emmer wheat from 11 populations sampled in Israel and Turkey	Natural selection causes adaptive RAPD ecogeographical differentiation. RAPD markers are useful for estimation of genetic diversity in wild wheats and the identification of suitable parents for the development of mapping populations for the tagging of agronomically important tarits derived from wild wheat	Fahima et al. (1999)
10 primer pairs (48 loci)	15 accessions of 5 groups of hexaploid wheat: common, spelta, macha, vavilovii, and semi-wild wheat (SWW)	Common wheat is most closley related to SWW followed by spelta, vavilovii, and macha	Cao et al. (2000)
4 primer pairs (17 loci)	11 Italian local varieties of emmer wheat	High variability was found within landrace populations underlying the values of landraces as an irreplaceable bank of genetically diversified and highly co-adapted genotypes	Barcaccia et al. (2002)
17 primer pairs	35 spring wheat cultivars and lines with different levels of Fusarium resistance	A collection of unrelated genotypes can be used to identify markers linked to an agronomically important trait as three RAPD markers, significantly associated with FHB, were identified in the study	Sun et al. (2003)

Table 5. (continued)

Markers	Material	Outcome	Reference
SSR-based diversity			
23 primer pairs	40 wheat cultivars and lines comprising European elite material	Relatively small number of microsatellites can be used for estimation of genetic diversity and cultivar identification in elite material of bread wheat	Plaschke et al. (1995)
14 loci	65 wheat varieties chosen to represent the bulk of area sown in UK over past 70 years	Potential of microsatellites for high-throughput genetic diversity assement was demonstrated	Donini et al. (1998)
23 primer pairs	21 accessions of *T. dicoccoides* (19 resistant and 2 susceptible to yellow rust) originating from centre of origin and diversity in Upper Galilee and Hermon Mountain in Israel	All the wild emmer wheat could be distinguished. Genetic diversity of wild emmer wheat is correlated with geographical distribution	Fahima et al. (1998)
20 primer pairs	55 elite exotic wheat genotypes originating in 29 countries representing 6 continents	A set of 12 primer pairs could distinguish 48 genotypes. One genotype from Portugal was found unique and diverse as it was a single member of a subcluster	Prasad et al. (2000)
42 primer pairs	60 wheat cultivars originating from three agroecological areas: Germany, Austria and Hungary	Excellent resolving power of microsatellites was demonstrated for varietal identification, which arises through breeding under specific environmental conditions and for different end use	Stachel et al. (2000)
24 primer pairs (26 loci)	15 Libyan wheat genotypes	Relatively small number of primer pairs can be used to distinguish all genotypes used	Ben Amer et al. (2001)
24 chloroplast SSR loci	43 accessions from *Triticum* and *Aegilops* species involved in wheat polyploid evolution	Results suggested that the two types of chloroplast genomes of common wheat might have independently originated from the corresponding types of wild and cultivated emmer wheat species	Ishii et al. (2001)
19 loci	124 wheat cultivars and lines	Level of genetic diversity in Australian wheat cultivars has increased over time and the introduction of semi-dwarf germplasm resulted in an increase in the overall diversity	Parker et al. (2002)
43 loci	13 wheat genotypes of diverse origin	A wide range of genomic diversity was observed among all the genotypes, providing them to be the prime candidates for selective breeding for specific traits and broadening the genetic base	Ahmad (2002)
47 primer pairs	75 Nordic spring wheat cultivars bred during 20th century	Genetic diversity in Nordic spring wheat was enhanced by plant breeding in the first quarter of the 20th century and following a decrease during the second quarter was increased again by plant breeding	Christiansen et al. (2002)

Table 5. (continued)

Markers	Material	Outcome	Reference
20 primer pairs	135 wild emmeer wheat genotypes representing 15 populations from a wide range of ecological conditions of soil, temperature and water availability in Israel and Turkey	Microsatellite analysis was found to be highly effective in distinguishing genotypes of wild emmer wheat of natural populations and for the tagging of agronomically important traits derived from wild emmer wheat	Fahima et al. (2002)
19 loci	502 recent European wheat varities, mainly of winter type	A database of 502 wheat varieties was prepared. Approximately 25% of the varieties showed some heterogeneities, with the highest level of heterogeneity in southeastern European material. Furthermore, the highest genetic diversity and the highest number of rare alleles were observed in southern European varieties	Röder et al. (2003)
24 loci	998 accessions of common wheat originating from 68 countries of 5 continents	Accessions from the Near East and the Middle East exhibited more genetic diversity than those from any other region. Greater diversity was found in south-east Europe than in northern and south-west Europe	Huang et al. (2002)
46 loci	710 wheat genotypes from Novi Sad Core Collection originating from 38 countries	Some microsatellites were found associated with 6 important traits, i.e. stem height, earliness, resistance to leaf rust and powdery mildew, sedimentation value and protein content, for wheat breeding	Kobiljski et al. (2002)
28 loci	105 individual plants of wild emmer wheat from a microsite, Yehudiyya, northeast of the Sea of Galilee, Israel	Niche-specific and niche-unique alleles and linakge disequlibria were found in the two subpopulations. Effects of ecological stresses and natural selection on SSR diversity resulted presumably in adaptive structures	Li et al. (2002b)
70 loci	58 accessions covering a wide spectrum of genetic diversity of durum wheat gene pool	Large portion of the molecular variation detected within the group of 45 modern cultivars was accounted for by SSR alleles tracking back to 10 foundation genotypes. Level of genetic diversity present in modern durum wheat germplasm was found increased over time	Maccaferri et al. (2003)
33 primer pairs	13 genotypes including 7 new lines and their parents	8 markers in combination differentiated the seven new wheat lines from each other as well as from their parents. Graphic presentation of the genetic constitution of the new plant type lines was developed which can be used as bar-coded molecular tags for identification of the respective seed samples	Mohapatra et al. (2003)
20 primer pairs	100 bread wheat varieties developed in breeding centres of Ukraine during 1912–2002	Changes were noticed in allele distribution in microsatellite loci over time. A high level of intravarietal heterogeneity was also recorded	Cheobtar et al. (2003)

Table 5. (continued)

Markers	Material	Outcome	Reference
19 loci	502 recent European wheat varities, mainly of winter type	A database of 502 wheat varieties was prepared. Approximately 25% of the varieties showed some heterogeneities, with the highest level of heterogeneity in south-eastern European material. Furthermore, the highest genetic diversity and the highest number of rare alleles were observed in southern European varieties	Röder et al. (2003)
20 primer pairs	96 random accessions of common wheat from the ten wheat regions in China including 33 modern varieties and 63 landraces	Modern varieties and landraces were grouped in two different clusters. Data suggested that one locus with good polymorphism should be detected for each 47.35 cM on average to reflect genetic relationships among varieties with more than 90% certainity	Zhang et al. (2003b)
70 SSR loci	134 durum wheat accessions comprising modern varieties and a number of founders	Genetic diversity of the exmained accessions was highly structured in a number of groups or subgroups	Maccaferri et al. (2003)
20 genomic SSRs, 22 EST-SSRs	64 durum lines, landraces and varieties	EST-SSRs produced high-quality markers but were less polymorphic than genomic SSRs. Data provided a platform to develop a genotypic database for durum wheat that will facilitate the exploitation of its genetic resources	Eujayl et al. (2001)
20 EST-SSRs	52 elite exotic wheat genotypes	EST-SSRs proved superior to genomic SSRs for diversity estimation	Gupta et al. (2003)
12 genomic SSRs, 20 EST-SSRs	56 old and new varieties of bread wheat on the UK recommended list	EST-SSRs delivered fingerprints of superior quality, amplifying clear products with few stutter bands	Leigh et al. (2003)
47 genomic SSRs, 52 EST-SSRs	68 advanced CIMMYT wheat lines targeted to different megaenvironments (MEs)	A higher number of alleles were detected for genomic SSRs than EST-SSRs, but gene diversity between MEs was similar for both type of markers. High levels of genetic diversity were found within the germplasm targeted to each ME; however, genotypes could not be separated according to their targeted MEs	Dreisigacker et al. (2003)
64 EST-SSRs	18 *Triticeae* species belonging to *Triticum-Aegilops* complex	EST-SSRs were recommended in studies on DNA polymorphism, genetic diversity, gene mapping and synteny conservation across different species of Triticeae	Bandopadhyay et al. (2004)
AFLP-based diversity			
16 primer combinations (229 loci)	54 adapted, elite wheat cultivars and 2 diploid relatives	Genetic diversity among cultivars was hierarchically arranged as cultivars nested within market class and market class nested within growth habitat	Barrett and Kidwell (1998)
16 primer combinations (229 loci)	43 spring and winter wheat lines from Pacific Northwest	Pedigree and AFLP-based genetic diversity estimates (GDEs) detected a similar hierarchical pattern of genetic diversity in 43 cultivars	Barrett et al. (1998)

Table 5. (continued)

Markers	Material	Outcome	Reference
6 primer combinations (90 loci)	55 wheat varieties commonly grown in UK over past 60 years	Results were analysed to assess the potential of AFLP for DNA profiling and plant variety registration. Higher levels of discrimination were achieved by the inclusion of greater numbers of bands in analysis	Law et al. (1998)
18 primer combinations (189 loci)	9 winter and 6 spring Turkish durum wheat cultivars	Relationships among winter and spring type durum cultivars was in accordance with the known pedigree information. The most distant and closest cultivars were selected	Incirli and Akkaya (2001)
60 primer combinations (6778 loci)	15 soft red winter wheat (SRWW) genotypes	Differences in genetic similarity were found for assessing the genetic diversity and plant variety protection use	Grunberg et al. (2001)
10 primer combinations (89 loci)	13 modern Canadian durum wheat	Level of genetic variation within the most developed cultivar is fairly substantial despite rigorous selection pressure aimed at cultivar purity	Soleimani et al. (2002a)
4 primer combinations (105 loci)	54 synthetic hexaploid wheats and their parents *T. dicoccum; Ae. tauschii*)	Snythetic hexaploids had a considerably higher level of AFLP diversity than normally obersved in cultivated hexaploid wheat, suggesting their use in introducing new genetic diversity into the bread wheat gene pool	Lage et al. (2003)
6 primer combinations	87 biotypes representing 54 Strampelli varieties	Variability found by means of molecular analysis appeared not only due to the incomplete homogeneity and stability of Strampelli's material but also to the use of heterogenous local populations as parents	Boggini et al. (2003)
8 primer combinations (146 loci)	10 Italian populations of 'farro' (*T. dicoccum*) wheat	A good grouping of genotypes in each single population was possible. AFLP analysis was found suitable for an effective chracterization of *T. dicoccum* populations	Talame et al. (2003)
8 primer combinations (615 loci)	55 elite exotic wheat genotypes	A pair of genotypes was recommended for hybridization to develop superior cultivars	Roy et al. (2004)
Miscelleneous			
STS-38 markers	10 elite hard red spring wheat cultivars (Montana and North Dakota), 15 hard red spring wheat cultivars and lines from North American Great Plains, 20 accessions representing a wide range of collection and morphological types	Breeding pool for hexaploid hard red spring wheat was found narrow relative to levels of diversity among and within classes in hexaploid wheat	Chen et al. (1994)
STS-12 markers	13 modern Canadian durum wheat	DNA-based markers can be used as an efficient alternative to morphological traits for cultivar identification and fingerprinting at any stage of plant development	Soleimani et al. (2002b)

Table 5. (continued)

Markers	Material	Outcome	Reference
RFLP-117 probes, AFLP-16 primer combinations, SSR-21 primer pairs	Two sets of 5 and 6 winter wheat cultivars and lines after mating the above genotypes as per factorial design	Average PIC for polymorphic bands was not significantly different between the three marker systems, whereas the marker index was low for RFLPs and SSRs but high for AFLPs and therefore AFLP was recommended for fingerprinting wheat cultivars. No common pattern between the four dendrograms by using coencestry, RFLP, SSR and AFLP data	Bohn et al. (1999)
AFLP-6 primer combinations (84 loci), SSR-14 loci, SSP-9 loci	Dominant UK winter wheat varieties from 1934 to 1994	Diversity in the time periods overlapped and the most modern group of varieties encompassed the majority of diversity found in earlier decades. Plant breeding has resulted, over time, in a qualitative, rather than quantitative, shift in the diversity of winter wheat grown in the UK	Donini et al. (2000)
SSR-10 primer pairs, AFLP-4 primer combinations (71 loci)	105 Argentine bread wheat cultivars released between 1932 and 1995	Significant differences were observed for both SSR and AFLP only between breeding programmes with large differences in number of released cultivars. The Argentine wheat germplasm has maintained a relatively constant level of genetic diversity during the last half century	Manifesto et al. (2001)
SSR-25 primer pairs, RAPD-31 primer pairs, AFLP-6 primer combination	14 varieties of wheat, 1 of durum and 1 of triticale released for general cultivation since 1920 in India	Most of the cultivars could be uniquely identified with SSR and RAPD markers but not with AFLPs	Garg et al. (2001)
RFLP-338 loci, AFLP-200 loci	40 bread wheat cultivars (central and southern Europe)	Correlations with general and specific combining ability effects for studied traits (grain yield, quality attributes) were statistically significant but too low to be predictive in practical breeding	Corbellini et al. (2002)
AFLP-8 primer combinations (633 loci), SSR-24 cp SSR loci	55 accessions of wild einkorn wheat	Intraspecific nuclear genome variation was lower in einkorn wheats and higher in *Ae spletoides*. In contrast, the chloroplast DNA variation was larger in einkorn wheat and the least in *Ae. speltoides*	Mizumoto et al. (2002)
SAMPL-2 primer combinations (87 loci)	55 elite exotic wheat genotypes	54 genotypes could be distinguished using the SAMPL banding pattern of both primers. An association of six bands with grain protein content, of seven bands with preharvest sprouting tolerance and four bands with 1,000-grain weight was observed using BSA	Roy et al. (2002)

Table 5. (continued)

Markers	Material	Outcome	Reference
AFLP-8 primer combinations, SSR-37 primer pairs	70 spring wheat accessions (32 from CIMMYT and 38 from other breeding programmes worldwide)	AFLP and SSR markers were generally in agreement with estimates of diversity measured using co-efficienty of parentage. CIMMYT accessions were found different from the worldwide group of accessions	Almanza-Pinzon et al. (2003)
AFLP-322 loci, SSR-19 loci	65 wheat cultivars from eight countries varying in head blight resistance levels	US cultivars were found more closley related to cultivars from Europe and Argentina than cultivars from Asia. Integrating FHB resistance QTLs from Asian sources into US wheat, therefore, may increase the genetic diversity in US wheat	Bai et al. (2003)
RAPD-30 primer pairs; AFLP-10 primer combinations (560 loci)	58 accessions of jointed goatgrass (*Ae. cylindrica*) and 6 accessions of the related wild species barb goatgrass	AFLP produced more scorable bands than did RAPD, but both methods revealed limited genetic diversity in jointed goatgrass. AFLPs distinguished among all but 2 of the 16 accessions surveyed	Pester et al. (2003)
SSR-21 loci, AFLP-15 primer combinations (254 loci)	140 wheat landraces, obsolete cultivars and modern cultivars of Czech Republic	A significant drift of genetic basis of modern cultivars in comparison with landraces and obsolete cultivars was recorded. Possibility of reducing number of gene bank accessions to maintain maximum number of alleles by using molecular markers was also demonstrated	Ovesna et al. (2003)
ESTs-6 loci, SSR-6 loci, ISSR-6 loci	20 accessions of Italian emmer wheat (*T. dicoccum* Schübler) populations	Study provided the correct identification of the analysis material to support its registrtaion as varieties	Pagnotta et al. (2003)
SSAP-4 primer pairs	26 *Aegilops* and 9 *Triticum* accessions	SSAP-based diversity tree for *Aegilops* spp. agreed with current classifications; however, the Triticum tree showed several significant differences which may be assocaited with polyploidy in this genus	Queen et al. (2004)

netic diversity of the parental lines was inadequate for predicting either progeny variance or F_1 performance (Perenzin et al. 1998; Bohn et al. 1999; Dreisigacker et al. 2003).

Marker analysis of common wheats with presumptive wild ancestors has provided insights into the crop's domestication and guided strategies for collecting, evaluating and utilizing germplasm. AFLP fingerprinting of einkorn and emmer wheats and barley, along with their wild progenitors, indicated that both einkorn (Heun et al. 1997) and emmer wheats (Özkan et al. 2002) were domesticated in a very small area of southeastern Turkey near the Tigris and Euphrates rivers more than 10,000 years ago. More recently, microsatellite sequences have been used to generate molecular clock estimates of the dates of wheat domestication. These ranged from 9,000 to 19,000 years for the transition from *T. dicoccoides* and *T. aestivum* and 8,705 to 18,414 years between *T. dicoccoides* and *T. durum* (Fahima et al. 2003). Sequence variation at a number of D genome STS loci has suggested that multiple D genome diploid parents were involved in the origin of common wheat (Talbert et al. 1998) and that all wheats share a single D-genome gene pool, which is the *strangulata* form of *Ae. tauschii* (Dvorák et al. 1998a). The *strangulata* gene pool is larger than expected because of gene flow from the *tauschii* form of *Ae. tauschii* (Lubbers et al. 1991; Dvorák et al. 1998a).

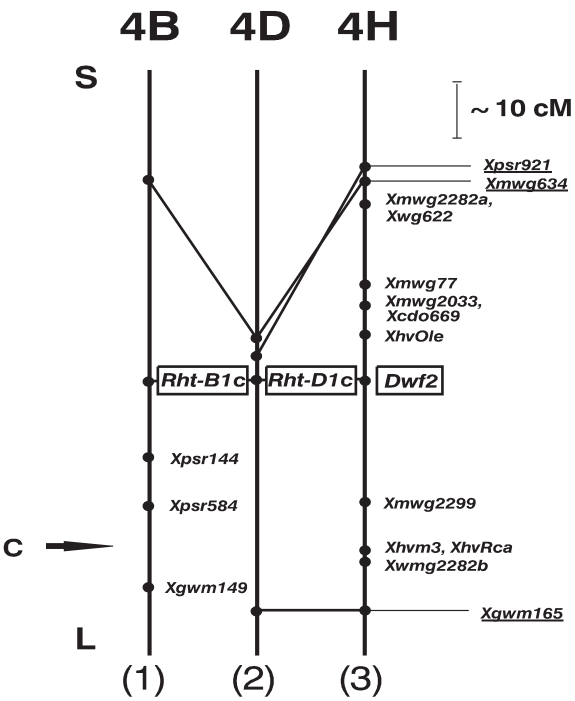

Fig. 1. Comparative location of genes determining dwarfness (GA insensitive) on chromosomes 4B and 4D of wheat and 4H of barley using the following basic maps: (*1*, *2*) Börner et al. (1997), (3) Ivandic et al. (1998). Mapped loci are marked with a *point*. The *connecting lines* between chromosomes 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

2.4.4
Comparative Mapping and Synteny

Molecular mapping of wheat and other grass species suggested that despite more than 60 million years of evolution within the subfamily of the *Poaceae*, the individual grass genomes are characterized by large segments of conserved linkage blocks that display collinear marker orders between different species. Similar to a LEGO-model, grass genomes are considered to be made up of conserved segments (Moore 1995). This model was extended by Gale and Devos (1998), and it was shown that the grass genomes can be displayed in concentric circles in which orthologous genes, which are derived from a common ancestor locus, are located on a radial line. Some reports on comparative mapping dealing with wheat and other cereal species are listed in Table 6. These studies provide important clues about the structural organization of the cereal genomes. For instance, the comparative mapping of GA-insensitive dwarfing genes suggested that the dominant *Rht* genes of wheat and the codominat *Dwf2* gene of barley are members of a homoeoallelic series existing in the triticeae species (Fig. 1). In a similar way, Fig. 2 shows that the *wa1* locus (determining the waxless plant character) of rye is homoeoallelic to the glaucousness (waxiness) loci *w*1 or *w*2^1 of wheat and genes/alleles for glossy sheat/spike (*gs1*, *gs6*, *gs8*) of barley. Furthermore, the alignment of the *gl2* (responsible for altering cuticle wax) gene region of maize with the *w*2^1 of wheat suggests the conservation of genes responsible for similar traits acrosss different cereal genomes. In addition to revealing evolutionary patterns within the *Poaceae* subfamily; comparative mapping provides access to the model genome of rice. An obvious strategy emerging from the concept of syntenous relationships is the transfer of the vast amount of genomic information

Table 6. A list of some important comparative mapping and genomics studies revealing the syntenic relationship of wheat with other cereal species

Species	References
Wheat, barley	Namuth et al. (1994), Hohmann et al. (1995), Dubcovsky et al. (1996), Hernandez et al. (2001), Salvo-Garrido et al. (2001), Weng and Lazar (2002b), Varshney et al. (2005b)
Wheat, maize	Devos et al. (1994)
Wheat, rice	Kurata et al. (1994), Kato et al. (1999), Sarma et al. (1998, 2000), Lamoureaux et al. (2002), Liu and Anderson (2003b), Laubin et al. (2003), Sorrells et al. (2003), Francki et al. (2003), La Rota and Sorrells (2004), Singh et al. (2004a), Li et al. (2004b), Yu et al. (2004b)
Wheat, rye	Devos et al. (1992, 1993a), Khlestkina et al. (2004)
Wheat, barley, rye	Devos et al. (1993b), Devos and Gale (1993), Börner et al. (1998), Gudu et al. (2002)
Wheat, barley, rice	Dunford et al. (1995), Gallego et al. (1998), Kato et al. (2001)
Wheat, maize, rice	Ahn et al. (1993), Moore et al. (1995b)
Wheat, maize, oat, rice	Van Deynze et al. (1995a,b)
Wheat, foxtail-millet, maize, rice	Moore et al. (1995a)

and resources available in rice genome to the wheat genome (see paragraph above, Genome Collinearity).

Our present knowledge of synteny is mainly based on comparative mapping of cross-hybridizing RFLP markers. Comparisons of genetic linkage maps are severely limited in their resolution by the number of orthologous loci detected and by population sizes. Early comparative maps (e.g., Hulbert et al. 1990; Ahn and Tanksley 1993; Ahn et al. 1993; Kurata et al. 1994; Moore et al. 1995a,b; Devos and Gale 1997; Gale and Devos 1998) greatly underestimated the complexity of genome relationships. Those low-resolution comparative maps are biased by the use of single-copy probes that do not sample multicopy regions, simplifying assumptions about collinearity and placing excessive emphasis of gene-rich regions (Bennetzen 2000; Gaut 2001, 2002). *In silico* comparison of DNA sequences among different cereals makes it possible to transfer the sequence information between species to greatly enhance the resolution of comparative maps. For instance, *in silico* comparison of 974 genetically mapped barley ESTs with 524,720 wheat ESTs provided a potential set of 934 (95.4% of the loci tested) EST-derived markers to wheat genetic maps (Varshney et al. 2004c). However, large-scale comparative DNA sequence analysis of physically mapped wheat ESTs with the rice genome suggested that there has been an abundance of rearrangements, insertions, deletions and duplications eroding the wheat-rice genome relationship that may complicate the use of rice as a model for cross-species transfer of information in non-conserved regions (Sorrells et al. 2003; La Rota and Sorrells 2004; see Sect. 2.5.2 below).

2.5
Impact of Genomics Research on Wheat Genetics and Breeding

The publication of the complete genome sequence for *Arabidopsis* (TAGI 2000) and drafts of rice genome (Goff et al. 2002; Yu et al. 2002) provides the basis for elucidating the gene and protein networks that control biological processes. These model systems provide the basis for determining the genes and the respective proteins that control key components of complex traits in crop plants like wheat (Appels et al. 2003; Gupta and Varshney 2004). A large amount of EST data has been generated for wheat, which is being used to study and analyse the transcriptome of wheat (Powell and Langridge 2004). In addition to these advances in wheat genomics, novel approaches such as linkage disequilibrium (LD) analysis and association

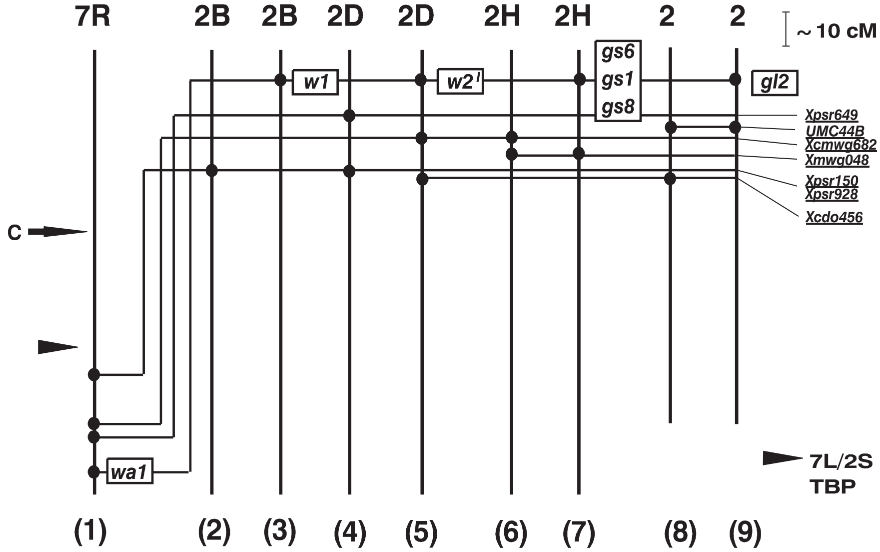

Fig. 2. Comparative location of genes determining waxless plant on chromosomes 7R of rye, 2B and 2D of wheat, 2H of barley and 2 of maize using the following basic maps: (*1*) Korzun et al. (1997a), (*2, 4*) Devos et al. (1993b), (*3*) Driscoll (1966), (*5*) Nelson et al. (1995a), (*6*) Graner et al. (1991), (*7*) Franckowiak (unpublished, cf. Börner 1999), (*8*) Ahn and Tanksley (1993), (*9*) Coe and Neuffer (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, *TPB* = translocation break point

mapping and genetical genomics would have a major impact on wheat genetics and breeding in the near future with the ultimate objective of crop improvement.

2.5.1
Transcriptomics and Functional Genomics

In order to establish an inventory of expressed genes in wheat, an international consortium (International Triticeae EST Cooperative) was established to launch the development of a wheat and barley EST database. This effort provided the first serious collection of ESTs and helped lead to other initiatives. In particular a project entitled 'The Structure and Function of Expressed Portion of Wheat Genome' involving 13 laboratories was established in 1999 and funded by the National Science Foundation (NSF), USA (http://wheat.pw.usda.gov/NSF/). The project had as its objective to decipher the chromosomal location and biological function of a large set of wheat genes, to enhance our understanding of the biology of the wheat plant and to create a new paradigm for the improvement of this important crop. To this end, a total of 117,510 ESTs (101,912 are 5′ ESTs and 15,605 are 3′ ESTs, as of July 2003) from 20 cDNA libraries were generated (Zhang et al. 2004). Computational analysis of this dataset yielded 18,876 contigs and 23,034 singletons (http://wheat.pw.usda.gov/NSF/curator/assembly.html; Lazo et al. 2004). In addition to these ESTs, generated in NSF-sponsored projects, other public laboratories and private organizations such as the DuPont Corporation also generated wheat ESTs and submitted them to public databases. As a result, 587,650 wheat ESTs are available in the public domain as of dbEST release 012805 (http://www.ncbi.nlm.nih.gov/dbEST/dbEST_summary.html). A computational analysis of 554,379 wheat ESTs suggested the presence of 44,513 TCs (tentative consensi) and 83,420 singleton ESTs, as per TIGR Wheat Gene Index Release 9.0, 20 September 2004 (http://www.tigr.org).

The extensive EST databases prepared from many different tissues can be used to estimate gene expression levels by measuring the frequency of the appearance of specific sequences, employing computational tools such as Digital Differential Display (http://www.ncbi.nlm.nih.gov/UniGene/info_ddd.shtml) or HarvEST (http://harvest.ucr.edu/). An example of the use of wheat ESTs from multiple cDNA libraries to study developmental processes was shown by Ogihara et al. (2003). After the analysis of 116,232 ESTs, generated from ten wheat tissues, the researchers identified correlated expression patterns of genes across the tissues. Furthermore, relationships of gene expression profiles among the ten wheat tissues were inferred from global gene expression patterns. However, the use of EST databases to study expression profiles is limited by the availability of cDNA libraries used to develop ESTs and by the depth of EST sequencing. There are also problems in tracking genes that may be represented by several partial EST sequences.

Newer techniques allow the estimation of mRNA abundance for large numbers of genes simultaneously. The methods include serial analysis of gene expression (SAGE), microarrays, macroarrays and massively parallel signature sequencing (MPSS). These methods have not been extensively applied in wheat, although nearly all have been applied to some aspects in other cereals such as rice and maize (Milligan et al. 2004).

SAGE (serial analysis of gene expression), a logical extension of EST sequencing, can be used to study expression patterns (Velculescu et al. 1995). Unfortunately, SAGE does suffer from several problems. In particular, SAGE experiments require large amounts of RNA and can be very expensive if many samples are to be analysed, for example from a developmental series. As with MPSS (Brenner et al. 2000; http://www.lynxgen.com/), the signatures generated can be difficult to assign to particular genes when the technique is applied to wheat, where a full genome sequence is not available.

Microarrays and macroarrays offer a technique for screening the expression profile of very large numbers of genes simultaneously (Sreenivasulu et al. 2002). Both types of arrays have been used to study grain development in cereals. Macroarrays have the advantage of ease of manufacture and low cost relative to microarrays, but macroarrays do not provide the same level of gene or probe density for screening. Although macro-/microarrays have been used extensively in some cereals such as maize, rice and barley, use of these technologies in wheat has been limited. Recently cDNA microarrays containing approximately 9,000 wheat cDNAs were used to monitor gene expression during the first 28 d of grain development following anthesis (Leader et al. 2003). This study revealed 66 differentially regulated genes, which showed a sequence similar to transcription factors. Identified genes can be used for gene-specific marker development and synteny with rice to determine if any of the genes map within regions corresponding to QTL for grain yield or quality traits. Similarly, exploitation of cDNA microarrays is under way to identify the genes for endosperm development (Shinbata et al. 2003), for studying the Russian wheat aphid (RWA) defense response mechanisms (Botha et al. 2003) and assessment after fungicide application (Pasquer et al. 2003).

Real-time PCR (RT-PCR) has also been used to study drought stress tolerance (Rampino et al. 2003). Such approaches hold great potential for identifying the genes corresponding to QTLs for use in breeding as recently demonstrated in barley (Potokina et al. 2004). In addition, proteomic approaches have been recently used to assess the relationship between the wheat grain transcriptome and proteome (Branlard et al. 2003). It is hoped that in the near future, the above technologies will be put to extensive use in wheat.

2.5.2
Comparative Genomics and Bioinformatics

The availability of a large number of ESTs of wheat and other cereals and the complete genome sequence of rice has allowed sequence comparisons between wheat and other cereal genomes and opened a new area of comparative genomics. Over the last decade, developments in the field of bioinformatics responded to the needs of wheat (or Triticeae) genomics researchers (Matthews et al. 2004). Several databases and Web sites including GrainGenes (http://wheat.pw.usda.gov/) for Triticeae, GRAMENE (http://www.gramene.org/) for comparative mapping in cereals, and TIGR (http://www.tigr.org/) for genome analysis have been developed. For instance, the GrainGenes database at present contains over 70 map sets and linkage data for *T. aestivum*, *T. turgidum* and diploid species (Carollo et al. 2003). The 'Genomics' page on the GrainGenes website, http://wheat.pw.usda.gov/ggpages/genomics provides resources for wheat genomics researchers such as assemblies of the ESTs, alignment of wheat ESTs to the rice genome sequence, co-operative international projects to develop wheat SNPs and SSRs, an assembly of large DNA clones (BACs) into the physical map of the D genome, and a database of repeat sequences from the Triticeae (TREP) (Matthews et al. 2003).

The use of DNA-sequence-based comparative genomics for evolutionary studies and for transferring information from model species to related large-genome species has revolutionized molecular genetics and breeding strategies for improving these crops (Paterson 2004). Comparative sequence analysis methods provide cross-referencing of genes between species maps, enhance the resolution of comparative maps, study patterns of gene evolution, identify conserved regions of the genomes and facilitate interspecies gene cloning.

A comparison (BLASTN analysis) of 5,780 ESTs that were physically mapped in wheat chromosome bins to 3,280 ordered BAC/PAC clones of rice revealed numerous chromosomal rearrangements that will significantly complicate the use of rice as a model for cross-species transfer of information in non-conserved regions (La Rota and Sorrells 2004). In addition, the physical locations of non-conserved regions were not consistent across rice chromosomes. Some wheat ESTs with multiple wheat genome locations were found associated with the non-conserved regions. An average of 35% of the putative single-copy genes that were mapped to the most conserved bins matched rice chromosomes other than the one that was most similar.

As noted above, interruption of microcollinearity was observed in other studies when extensive comparisons were made across smaller regions between collinear chromosomes (arms) of wheat and rice. For instance, a gene-by-gene BLASTN search of 2,932 genes from rice chromosome 11 (57.3 cM to 116.2 cM) to wheat ESTs and physically mapped wheat ESTs revealed that about one-third of the genes (homologous rice genes) were mapped to the homoeologous group 4 chromosome of wheat, suggesting a common evolutionary origin (Singh et al. 2004a). Location of bin-mapped wheat contigs to chromosomes of all seven homoeologous groups was attributed to the movement of genes (transpositions) or chromosome segments (translocations) within the rice or the hexaploid wheat genomes. In another study on the investigation of microcollinearity between the rice genome and a total of 1,500 kb from physical BAC contigs on wheat chromosome 1AS, a total of 27 conserved orthologous sequences between wheat chromosome 1AS and a region of 1,210 kb located on rice chromosome 5S were identified. However, microcollinearity was found to be frequently disrupted by rearrangements (Guyot et al. 2004). Similarly, microcollinearity was disrupted between a 2.6 cM region (encompassing the grain protein content locus *Gpc-6B1*) on wheat chromosome 6B and a 350 kb region on rice chromosome 2 (Distelfeld et al. 2004). Nevertheless, the region encompassing the *Gpc-6B1* locus showed excellent conservation between the two genomes, which facilitated the saturation of the target region of the wheat genetic map with molecular markers, and the *Gpc-6B1* locus was delimited to 0.3 cM containing five candidate genes in the collinear 64-kb region in rice. Comparative genomics also facilitated the identification of genes controlling seed dormancy and preharvest sprouting in wheat, barley and rice (Li et al. 2004a).

2.5.3
Novel Approaches

AB-QTL Analysis

For the long-term sustainability of wheat production, introduction of alien or exotic genes from wild species is imperative. In the past, many useful genes were transferred from wild relatives into wheat, most of which were single genes or gene clusters conferring resistance to various diseases. Fifty-seven genes for resistance to diseases and pests were introduced into wheat from other genera of the Triticeae family via alien translocations. In many cases, the size of the alien fragments and the translocation breakpoints were precisely determined by genomic in situ hybridization (for review see Friebe et al. 1996). For transferring the QTLs of agronomically important traits from a wild species to a crop variety, an approach named 'Advanced backcross QTL analysis (ABQA)' was proposed by Tanksley and Nelson (1996). In this approach, a wild species is backcrossed to a superior cultivar, and during backcrossing cycles the transfer of a desirable gene/QTL is monitored with molecular markers. The segregating BC_2F_2 or BC_2F_3 population is then used not only for recording data on the trait of interest but also for genotyping with polymorphic molecular markers. These data are then used for QTL analysis, leading to the simultaneous discovery of QTLs, while transferring these QTLs by conventional backcrossing. This approach has been used in wheat recently (Huang et al. 2003b, 2004). After genotyping 72 preselected BC_2F_2 plants derived from a cross between a German variety and synthetic wheat, Hunag et al. (2003b) have identified 40 putative QTLs, including 11 for yield, 16 for yield components, 8 for ear emergence and 8 for plant height. Thus this approach has the potential for direct use in wheat improvement.

Association and Linkage Disequlibrium Analysis

Conventional techniques of molecular mapping require a mapping population based on the products of one (doubled haploids) or two (F_2s) cycles of recombinations, limiting the resolution of genetic maps. In addition, such populations are often not representative of the germplasm that is being actively used in breeding programmes. In contrast, association mapping, based on linkage disequilibrium (LD), does not require a conventional segregating population and may in some cases be more powerful than conventional analysis for identifying the genes responsible for the variation in a quantitative trait (Buckler and Thornsberry 2002; for review see Flint-Garcia et al. 2003). Combined with a consideration of population structure (Pritchard et al. 2000), this association mapping allows for large-scale assessment of allele/trait relationships. A high degree of LD facilitates association analysis of markers linked to a QTL but reduces the resolution of the analysis (for review see Flint-Garcia et al. 2003). For instance, in maize the rapid decay of LD provides a means of mapping candidate genes with high precision and at the same time allows one to associate alleles with phenotypic values (Thornsberry et al. 2001). For those species with high LD, comparative mapping and transcript profiling are necessary for narrowing the list of candidate genes. Various kinds of populations can be designed with the appropriate resolution. For example, segmental introgression lines would have high LD while long-term breeding populations that have been intermated for many generations would have low LD (Sorrells 2004).

In wheat, some studies on association analysis have already been conducted and provided markers linked with some traits (Paull et al. 1994, 1998). Some efforts have been expended to study the association between growth habit and haplotype using a set of 80 hexaploid cultivars and assaying a total of seven SNPs located within a 3-kb region of molecular marker PSR6001, a candidate marker for vernalization responsive gene *Vrn-A1* (Devos and Beales 2003). However, large-scale studies on the estimation of LD in the wheat genome are currently under way in several laboratories. 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 variation in quantitative traits and will help to identify specific targets for crop improvement in wheat. Though LD-based approaches hold great promise for accelerating fine mapping, conventional linkage mapping will continue to be useful particularly when trying to 'mendelize' QTLs and assessing the effect of QTL in isolation (Rafalski and Morgante 2004).

Genetical Genomics

Recently, a new approach, called 'genetical genomics', has also been proposed, where QTL mapping is combined with expression profiling of individual genes in a segregating (mapping) population (Jansen and Nap 2001). In this approach, total mRNA or cDNA of the organ/tissue from each individual of a mapping population is hybridized onto a microarray carrying a high number of cDNA fragments representing the species/tissue of interest and quantitative data are recorded reflecting the level of expression of each gene on the filter. Under the presumption that every gene showing transcriptional regulation is mapped within the genome of the species of interest, the expression data can be subjected to QTL analysis, thus making it possible to identify the so-called 'ExpressQTLs' (eQTLs). The recently developed software tool Expressionview for combined visualization of gene expression data and QTL mapping (Fischer et al. 2003) will be very useful in this connection. Based on segregating populations, eQTL analysis identifies gene products influencing the quantitative trait (level of mRNA expression) in *cis* (mapping of the regulated gene within the QTL) or *trans* (the gene is located outside the QTL). The latter gene product (second-order effect) is of specific interest because more than one QTL can be connected to such a *trans*-acting factor (genes acting on the transcription of other genes) (Schadt et al. 2003). The mapping of eQTLs allows multifactorial dissection of the expression profile of a given mRNA/cDNA, protein or metabolite into its underlying genetic components and also makes it possible to locate these components on the genetic map (Jansen and Nap 2001; Jansen 2003). Eventually, for each gene or gene product analysed in the segregating population (by using expression profiling methodology), eQTL analysis will underline the regions of the genome influencing its expression. This approach has been used in maize (Schadt et al. 2003) and is being investigated by several groups for wheat.

2.6
Concluding Remarks

The development of genomics and genetics resources in wheat has lagged behind that of many other plant species. This has been largely related to concerns about the large size and the polyploid nature of the wheat genome. Therefore, despite its importance as a food crop and the extensive genetic and cytogenetic resources that were available for wheat, genomics programmes were slow to develop. However, over the past few years this situation has changed dramatically. Firstly, several programmes worked together to build a resource base that now allows most genomics approaches to be applied to wheat. Secondly, it has become clear that the behaviour of the wheat genome is different from that of many other species. This means that genomics-based improvement of wheat will be dependent on studies on wheat itself and also that the study of the wheat genome offers some exciting scientific challenges.

A large number of molecular markers have been generated and mapped to produce dense genetic physical maps. Based on the available marker resources, a number of agronomically important genes and an even larger number of quantitative trait loci have been tagged with molecular markers. Further progress in trait mapping will critically depend on the availability of appropriate plant material. The generation and phenotypic analysis of experimental populations (F_2, DH, RIL, etc.) is time consuming and the development of novel approaches of association genetics based on the exploitation of linkage disequilibrium (LD) may lead to the verification of candidate genes in natural populations or collections of various genotypes (Rafalski 2002).

While the isolation of a given gene is usually a prerequisite to understanding its cellular function, the identification and subsequent introgression of superior alleles will be of seminal importance to breed-improved cultivars. The launch of several new initiatives to analyse the wheat genome structure will facilitate the systematic development of wheat genetic and genomic resources.

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