African Journal of Biotechnology Vol. 5 (25), pp. 2569-2587, 29 December 2006
Available online at http://www.academicjournals.org/AJB
ISSN 1684–5315 © 2006 Academic Journals

Review

Principles, requirements and prospects of genetic mapping in plants

K. Semagn[1*], Å. Bjørnstad[2] and M. N. Ndjiondjop[1]

[1]Africa Rice Center (WARDA), 01 BP 2031, Cotonou, Benin.
[2]Norwegian University of Life Sciences, Department of Plant and Environmental Sciences, P.O. Box 5003, N-1432, Ås, Norway

Accepted 24 November, 2006

Genetic mapping (also known as linkage mapping or meiotic mapping) refers to the determination of the relative position and distances between markers along chromosomes. Genetic map distances between two markers are defined as the mean number of recombination events, involving a given chromatid, in that region per meiosis. Genetic map construction requires that the researcher develop appropriate mapping population, decide the sample size and type of molecular marker(s) for genotyping, genotype the mapping population with sufficient number of markers, and perform linkage analyses using statistical programs. The construction of detailed genetic maps with high levels of genome coverage is a first step for localizing genes or quantitative trait loci (QTL) that are associated with economically important traits, marker assisted selection, comparative mapping between different species, a framework for anchoring physical maps, and the basis for map-based cloning of genes. Highly reproducible, high throughput, codominant, and transferable molecular markers, especially developed from expressed regions, are sought to increase the utility of genetic maps. This article reviews the principles, requirements, and future prospects of genetic mapping in plants.

Key words: Crop improvement, JoinMap, linkage mapping, meiotic mapping, molecular markers, physical map.

INTRODUCTION

Since the early 1950s, the development of genetics has been exponential with several milestones, including determination of DNA as the genetic material in 1944, discovery of the double-helix structure of DNA in 1953, the development of electrophoretic assays of isozymes (Markert and Moller, 1959) and a wide range of molecular markers that reveals differences at the DNA level (see Semagn et al., 2006 for review). Each of these milestones had led to a huge wave of progress in genetics. Consequently, our understanding of organismal genetics now extends from phenotypes to molecular levels, which can lead to new or improved screening methods for selecting superior genotypes more efficiently and improve decision-making process in breeding strategies. Genetic mapping (also known as linkage mapping or meiotic mapping) is one of the various applications of molecular markers in any species. It refers to the determination of the relative positions of genes on a DNA molecule (chromosome or plasmid) and of their distance between them. Genetic map indicates the position and relative genetic distances between markers along chromosomes, which is analogous to signs or landmarks along a highway where the genes are “houses” (Paterson, 1996; Collard et al., 2005). The first genetic map was published in 1911 by T. H. Morgan and his student, Alfred Sturtevant, who showed the locations of 6 sex-linked genes on a fruit fly chromosome. The principles of genetic mapping and linkage analyses are still used in much the same way but with far more advanced methodologies. During the past two decades, the step from the quite limited polymorphism in morphological traits/mutants and isozymes to the high pace of develop-

*Corresponding author. E-mail: k.semagn@cgiar.org or semagnk@yahoo.com; Fax (229) 21 35 0556; Tel (229) 21 35 01 88.

ment of molecular markers resulted in extensive genetic mapping experiments in many species.

The construction of detailed genetic maps with high levels of genome coverage is a first step for some of the applications of molecular markers in plant breeding (Tanksley et al., 1989) and serves five purposes:

a) Allow detailed genetic analysis of qualitative and quantitative traits that enable localization of genes or quantitative trait loci (QTL) (Mohan et al., 1997; Doerge, 2002; Yim et al., 2002).
b) Facilitate the introgression of desirable genes or QTLs through marker-assisted selection.
c) Allow comparative mapping between different species in order to evaluate similarity between genes orders and function in the expression of a phenotype (Ahn and Tanksley, 1993; Paterson et al., 2000).
d) Provide a framework for anchoring with physical maps based on chromosome translocations, DNA sequence or other direct measures (Yim et al., 2002).
e) Constitute the first step towards positional or map-based cloning of genes responsible for economically important traits (Mohan et al., 1997; Vuysteke et al., 1999).

To be useful for all these purposes, a genetic linkage map has to follow technical and methodological criteria such as simplicity, robustness, transferability, speed and cost effectiveness (Lorieux et al., 2000). This article reviews the principles, requirements, and future prospects of genetic linkage mapping as a prerequisite for plant improvement programs.

PRINCIPLES OF GENETIC MAPPING

Genetic mapping is based on the principle that genes (markers or loci) segregate via chromosome recombination during meiosis (i.e. sexual reproduction), thus allowing their analysis in the progeny (Paterson, 1996). During meiosis, chromosomes assort randomly into gametes, such that the segregation of alleles of one gene is independent of alleles of another gene. This is stated in Mendel's second law and is known as the law of independent assortment. The law of independent assortment always holds true for genes that are located on different chromosomes, but it does not always hold true for genes that are on the same chromosome. When two genes are close together on the same chromosome, they do not assort independently and are said to be linked. Genes that are closer together or tightly-linked will be transmitted together from parent to progeny more frequently than those genes located far apart.

At the beginning of meiosis, a homologous chromosome pair may intertwine – form so called chiasma, plural chiasmata – and exchange sections of chromosome (Figure 1). Such process or set of processes is called recombination (also called cross-over or strand exchange) by which DNA molecules interact with one another to bring a rearrangement of the genetic information in an organism. The pair then breaks apart to form gametes with new combination of genes that differs from either of the parents. The observed recombination fraction between two loci is an estimate of one-half the number of chiasmata or crossover events between two loci because crossing over occurs at the four-strand stage and for single crossover events, only two of the four strands participate in the recombination. Two non-sister chromatids participate in the cross-over and the other two chromatids do not exchange chromosome segments (Figure 1). Such process produces two types of gametes:

a) If crossing over does not occur, the products are parental gametes.
b) If crossing over occurs, the products are recombinant gametes.

The allelic composition of parental and recombinant gametes depends upon whether the original cross involved genes in coupling or repulsion phase. In diploid species, the most prevalent gametes in a coupling phase will be those with two dominant alleles or those with two recessive alleles. For repulsion phase crosses, gametes containing one dominant and one recessive allele will be most abundant (Figure 1).

How can we decide how close two genes are on a chromosome? Whereas genes located on different chromosomes assort independently (unlinked) and have a recombination frequency of 50%, linked genes have a recombination frequency that is less than 50% (Hartl, 1988). The chance of a crossover producing recombination between genes is directly related to the distance between two genes - the lower the frequency of recombination between two markers, the closer they are situated on a chromosome (conversely, the higher the frequency of recombination between two markers, the further away they are situated on a chromosome).

REQUIREMENTS FOR GENETIC MAPPING

Genetic linkage map construction requires that the researcher;

1) Develop appropriate mapping population and decide the sample size.
2) Decide the type of molecular marker(s) for genotyping the mapping population.
3) Screen parents for marker polymorphism, and then genotype the mapping population (parents plus all progenies).
4) Perform linkage analyses (calculate pairwise recombination frequencies between markers, establish linkage groups, estimate map distances, and determine

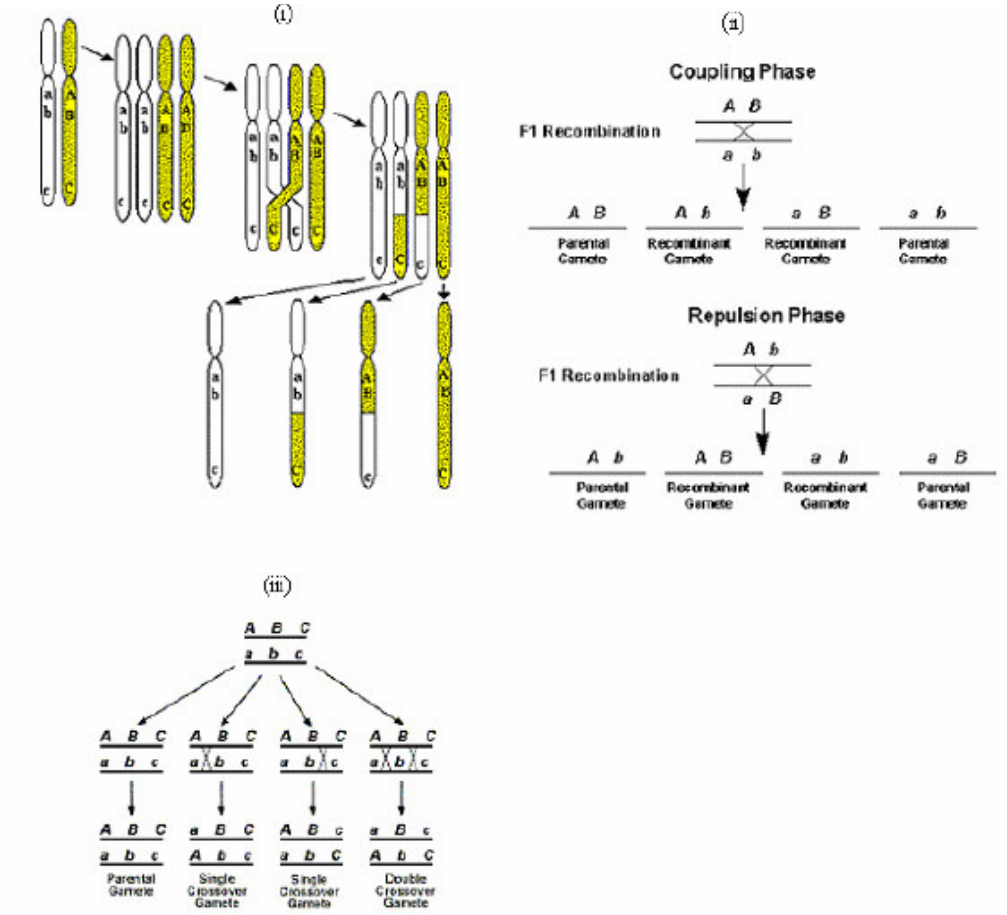


Figure 1. Different steps involving two strands during meiosis: (i) single recombination between genes that are far apart, and two types of gametes are produced after the completion of meiosis: parental type (abc and ABC) and recombinant type (abC and ABc); (ii) single recombination between two genes at the coupling and repulsion phase; (iii) single and double recombination between genes.

map order) using statistical programs.

A detail of each of these requirements is provided below.

Mapping population

The first step in producing a mapping population is selecting two genetically divergent parents, which show clear genetic differences for one or more traits of interest (e.g., the recipient or recurrent parent can be a highly productive and commercially successful cultivar but lacks disease resistance, which is present in another donor parent). The parents should be genetically divergent enough to exhibit sufficient polymorphism and at the same time they should not be too genetically distant so as to:

a) Cause sterility of the progenies and/or
b) Show very high levels of segregation distortion during linkage analysis.

In self-pollinating species, mapping populations originate from parents that are both highly homozygous (inbred). In cross pollinating (outcrossing) species, the situation is more complicated since most of these species do not tolerate inbreeding. Two-way pseudo-testcross, half-sib and full-sib families derived from controlled crosses have been proposed for mapping in outcrossing species. As shown in Figure 2, progenies from the second filial generation (F_2), backcross (BC), recombinant inbred lines (RILs), double haploids (DHs), and near isogenic lines (NILs) can be used for genetic mapping in self pollinating species (Burr et al.,1988; He et al., 2001; Doerge, 2002). Selection of populations is critical to successful linkage mapping. F_2 populations are developed by selfing F_1 hybrids derived by crossing the two parents while BC population is produced by crossing F_1 back into one of the parents (the recipient or recurrent parent). RILs are developed by single-seed selections from individual plants of an F_2 population; such selections continue for six to eight generations. If backcross selection is repea-

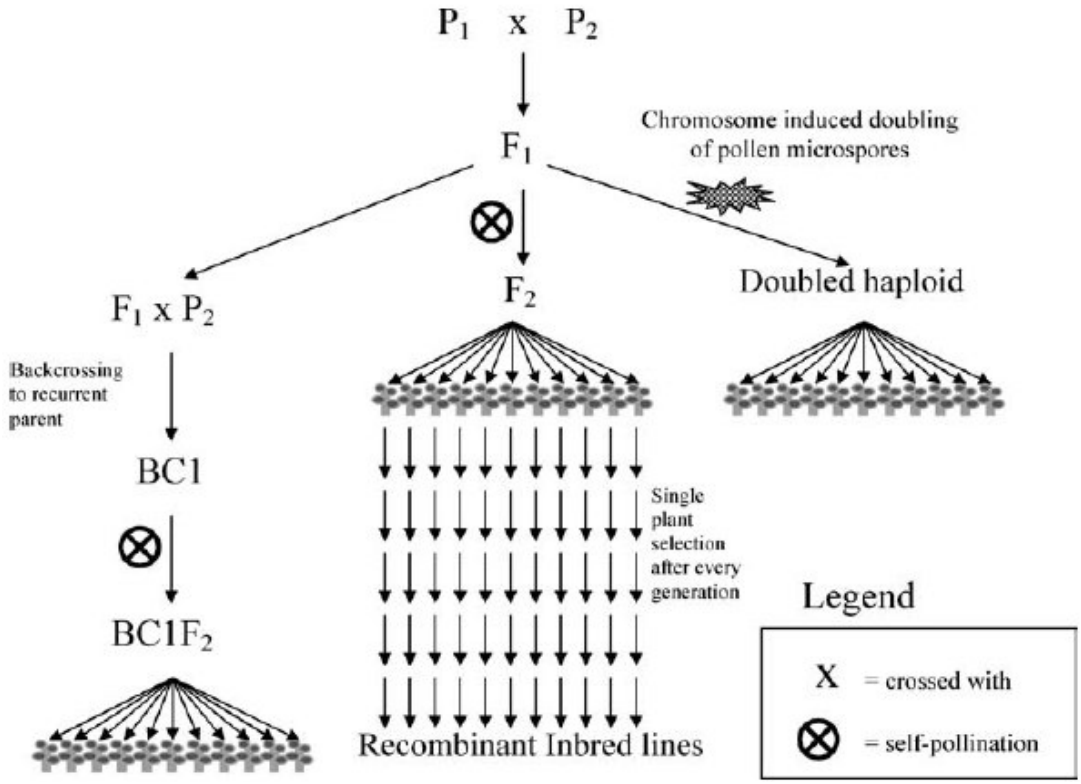


Figure 2. Diagram of the main types of mapping populations for self-pollinating species. (Collard et al., 2005).

ted at least for six generations, more than 99% of the genome from BC_6 and above will be derived from recurrent parent (Babu et al., 2004). Selfing of selected individuals from BC_7F_1 will produce BC_7F_2 lines that are homozygous for the target gene, which is said to be nearly isogenic with the recipient parent (NILs). NILs are frequently generated by plant breeders as they transfer major genes between varieties by backcross breeding (Tanksley et al., 1995). A DH population is produced by doubling the gametes of F_1 or F_2 population. Plants will be regenerated using tissue culture techniques after induction of chromosome doubling from pollen grains or haploid embryos resulting from species crosses.

Currently available literature shows that genetic maps are constructed using different types and sizes of mapping populations, marker systems, statistical procedures and computer packages (Ferreira et al., 2006). Each factor can affect the efficiency of the mapping process because of differences in the genetic distances between markers that can occur by variations in the degree of recombination observed in different crossings (Liu, 1998), and this is true even if different maps are generated for different populations of the same species (Paterson et al., 2000). For example, He et al. (2001) compared linkage maps between DH and RIL populations derived from the same rice cross. Map length per chromosome in the RIL population was shorter than that in the DH population, and the total map length for all chromosomes in the RIL population (1465 cM) was 70.5% of that in the DH population (2079 cM), although the opposite should have been expected due to the higher amount of recombination possible in RILs. Each mapping population has advantages and disadvantages (McCouch and Doerge, 1995; Paterson, 1996) and the research needs to decide the appropriate population for linkage mapping depending on project objective, time available for developing the population, and whether the molecular markers to be used for genotyping are dominant or codominant. Both F_2 and BC are the simplest types of mapping populations because they are easy to construct and require only a short time to produce. However, F_2 and BC populations are considered to be temporary populations because they are highly heterozygous and cannot be propagated indefinitely through seeds. RILs, NILs and DHs are permanent populations because they are homozygous or 'true-breeding' lines that can be multiplied and reproduced without genetic change occurring. Seeds from RILs, NILs and DHs can be transferred between different laboratories for linkage mapping to ensure that all collaborators examine identical material (Young, 1994; Paterson, 1996; He et al., 2001). DH populations are quicker to generate than RILs and NILs but the production of DHs is only possible

for species with a well established protocol for haploid tissue culture. The time required for developing RILs and NIL populations is a major constraint in mapping studies.

In spite of the availability of various papers on genetic mapping, specific studies relating to the ideal number of individuals in a given population required to establish accurate genetic maps have yet been inconclusive. Simulation studies performed using a sample size ranging from 50 to 1000 individuals of F_2, BC, RILs and DHs populations have shown that the type and size of mapping populations can exert an influence on the accuracy of genetic maps (Ferreira et al., 2006):

I. Populations' size with the lowest number of individuals provided several fragmented linkage groups and inaccurate locus order.
II. More accurate maps were obtained for RIL and F_2 population with co-dominant markers, while maps constructed from F_2 with dominant marker was less accurate.
III. The higher the number of individuals, the more precise was the map.
IV. For all population types, a total of 200 individuals were required to construct reasonably accurate linkage maps.

In practice, the population size used in preliminary genetic mapping studies varied from 50 to 250 individuals (Mohan et al., 1997) but a larger population size is needed for high resolution fine mapping.

Staub and Serquen (1996) reviewed the genetic information for different types of mapping populations in relation to dominant versus codominant markers. Maximum genetic information is obtained from F_2 population using a codominant marker system. Dominant markers supply as much information as codominant markers in RIL, NILs and DHs (Burr et al., 1988; Figure 3) because all loci are homozygous, or nearly so. BC populations can be useful for mapping dominant markers if all loci in the recurrent parent are homozygous, and the donor and recurrent parent have contrasting polymorphic marker alleles (Reiter et al., 1992). Information obtained from BC populations using either codominant or dominant markers is less than that obtained from F_2 populations because one, rather than two, recombinant gametes are sampled per plant. If the phenotypic variation is known to be controlled by QTLs which all exhibit complete dominance in the same direction, then a backcross to the recessive parent results in the QTL segregating in two classes (heterozygote and recessive homozygotes; Figure 3) and this cross is a more powerful means of locating QTLs than F_2. F_2 is more powerful for detecting QTLs of additive effect, and can also be used to estimate the degree of dominance for detected QTLs. RILs, NILs and DHs may be powerful tools for QTL detection in some circumstances but provide no information on dominance relationships for any QTL (Haley and Andersson, 1997).

Selection of molecular markers for mapping

Restriction fragment length polymorphisms (RFLPs), microsatellites or simple sequence repeats (SSRs), expressed sequence tags (ESTs), cleaved amplified polymorphic sequence (CAPS), random amplified polymerphic DNA (RAPD), amplified fragment length polymorphisms (AFLPs), inter simple sequence repeat (ISSR), diversity arrays technology (DArT), and single nucleotide polymorphism (SNP) have been used for map construction in several plants. Each marker system has advantages and disadvantages, and the various factors to be considered in selecting one or more of these marker systems have been described in another review (Semagn et al., 2006). The first large scale efforts to produce genetic maps were performed mainly using RFLP markers, the best known genetic markers at the time (Helentjaris et al., 1986; 1988; Burr et al., 1988; Beavis and Grant, 1991; Shoemaker et al., 1992; Gardiner et al., 1993; Coe et al., 1995). The major strength of RFLP markers includes codominant inheritance, good transferability between laboratories, locus-specificity that allows synteny (conserved order of genes between related organisms) studies, and high reproducibility. There are, however, several limitations for RFLP analysis:

a) It requires high quantity and quality of DNA.
b) It depends on the development of specific probe libraries for the species.
c) The technique is not amenable for automation.
d) The level of polymorphism is low.
e) It is time consuming and laborious.
f) It usually requires radioactively labeled probes.

With the development of polymerase chain reaction (PCR)-based markers, the strategy in linkage mapping dramatically shifts to this new type of marker. Currently, microsatellite markers remain a standard for linkage map construction. The advantages of SSRs are well documented (Powell et al., 1996; Gupta et al., 1999) and these include: high information content, co-dominant inheritance, reproducibility, locus specificity, highly transferability, and ease for automation for high throughput screening. However, the high development cost and effort required to obtain working SSR primers for a given species has restricted their use to only a few of the agriculturally important crops (Squirrell et al., 2003). ESTs are attractive for marker development since they represent coding regions of the genome. ESTs have been used for efficient development of EST-based RFLP, CAPS, SSRs and SNP markers (Harushima et al., 1998; Davis et al., 1999; Cho et al., 2000; Eujayl et al., 2002). There are a number of advantages for markers developed from EST-based sequences. First, if an EST marker is

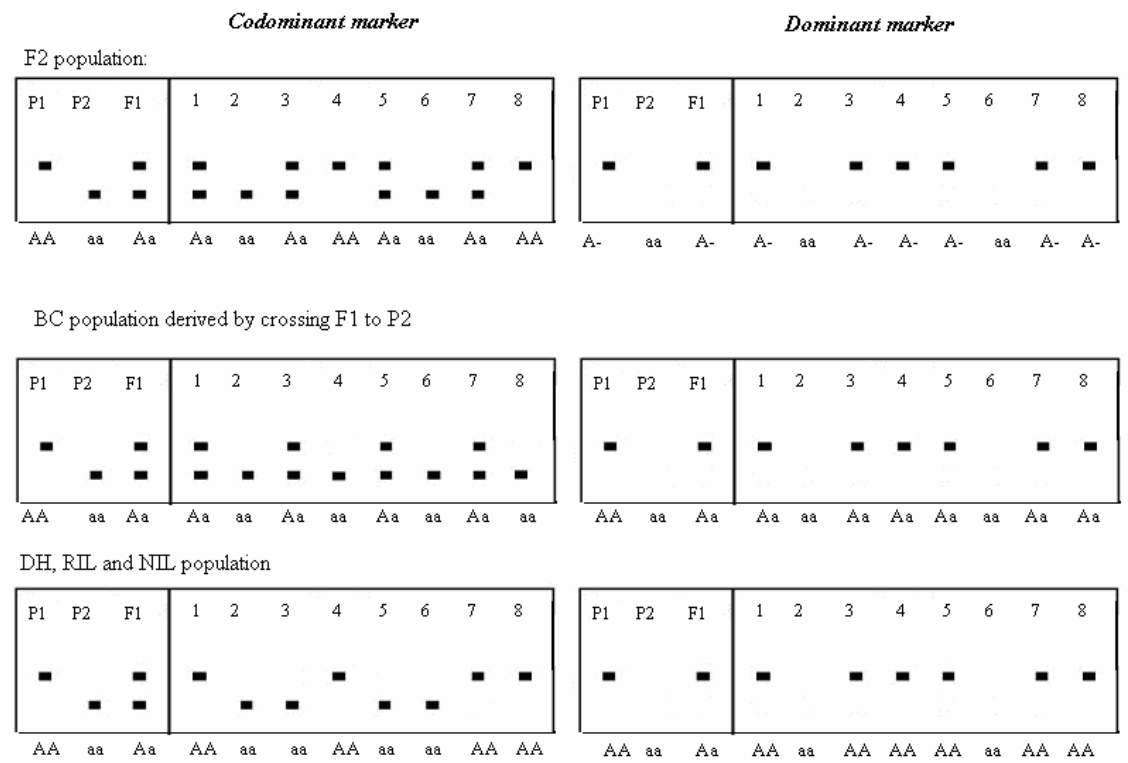


Figure 3. An example of a hypothetical gel showing segregation patterns for codominant (left- hand side) and dominant (right-hand side) markers for five types of mapping populations (Collard et al., 2005). In contrast to codominant markers, dominant markers cannot discriminate between heterozygous and dominant-homozygous genotype in F_2 populations. P_1 and P_2 are the two parents, and the eight progenies derived from the two parents are numbered from 1 to 8.

found to be genetically associated with a trait of interest, it is possible that the mapped gene directly affects the trait. Second, ESTs that share homology to candidate genes or differentially expressed ESTs in a tissue of interest, can be specifically targeted for genetic mapping. Third, EST-based markers are very useful for comparative mapping across different species because they generally have high degree of sequence conservation, and are more likely to be transportable across pedigree and species than are markers derived from non-expressed sequences. Fourth, if DNA sequence information is lacking for a target species, ESTs derived from other species could be used as the basis for genetic mapping in other species of interest. Hence, marker development and map-based cloning in one species will profit from data available in any other species. Genetic mapping with ESTs would thus enable a more rapid transfer of linkage information between species (Cato et al., 2001). However, the scope of EST-derived marker development is limited to species for which sequencing databases already exist (Eujayl et al., 2004). In some cases, CAPS markers have been used for genetic mapping (Iwata et al., 2001; Tani et al., 2003) and they have several advantages:

I. CAPS are much easier and less time-consuming than RFLPs.
II. CAPS primers developed from ESTs are more useful as genetic markers for comparative mapping study than those markers derived from non-functional sequences such as genomic microsatellite markers.
III. CAPS markers are inherited mainly in a co-dominant manner (Matsumoto and Tsumura, 2004), and the development of CAPS markers is only possible where mutations disrupt or create a restriction enzyme recognition site.

AFLP markers have been used extensively in genetic mapping for increasing marker density in several species (e.g., Barrett and Kidwell, 1998; Parker et al.,1998; Huang et al., 2000; Schwarz et al., 2000; Chalmers et al., 2001). AFLP markers are highly polymorphic, reproducible, and can be used for any organism without initial investment in primer/probe development and sequence information. They generally provide good genome coverage, but clustering of AFLP markers especially from the methylation insensitive EcoRI-enzyme may aggravate clustering in the highly methylated centromere and surrounding heterochromatin regions of the genome. Ulti-

mately the position of AFLP markers is dependent on the location of the restriction sites of the enzymes used in their production (King et al., 2002). RAPD markers have been used to construct linkage maps in several species but has not found wide acceptance (e.g., Demeke et al., 1997; Yang et al., 1996). Non-reproducibility and comigration of RAPD markers limited their application in mapping. Inter simple sequence repeat (ISSR) markers have also been used in some cases (Dirlewanger et al., 1998; Kojima et al., 1998; Davila et al., 1999; Arcade et al., 2000). High polymorphism and simplicity are interesting characteristics of ISSR markers for mapping purposes (Kojima et al., 1998). Like RAPDs, comigration and non-reproducibility are limitations for ISSRs (Moreno et al., 1998), although some authors claim a reproducibility of ISSR fragments over 99% on polyacrylamide gels (Fang and Roose, 1997). AFLPs, RAPDs and ISSRs share a common limitation for linkage mapping in that;

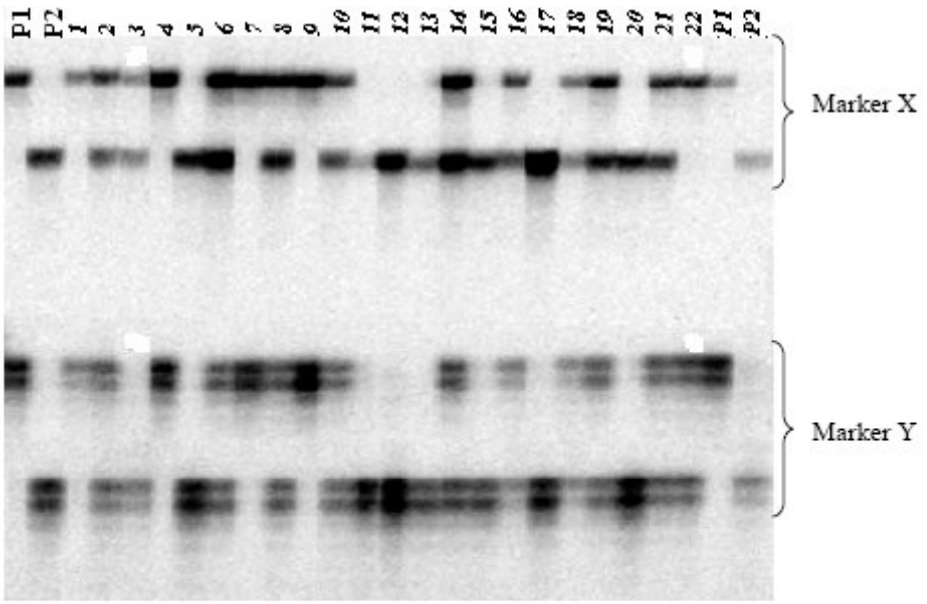
a) The chromosomal location of markers scored from one cross cannot be extrapolated to others unless indirectly determined using other known markers, such as RFLPs and microsatellites.
b) They all are dominant markers, and unable to show differences between dominant homozygous and heterozygous individuals. Hence, these markers are less valuable for mapping F_2 or BC populations.

DArT has recently been used in genetic mapping and fingerprinting studies in wheat (Akbari et al., 2006; Semagn et al., 2006), Arabidopsis (Wittenberg et al., 2005), and barley (Wenzl et al., 2004). DArT is a high-throughput, quick, and highly polymorphic and reproducible method but their dominant inheritance is still a limitation for mapping. DArT markers have a great potential for genetic mapping in a number of 'orphan' crops relevant in Third World countries (see www.cambia.org or http://www.diversityarrays.com for information). DArTs, however, have not yet been tested in a wide range of species by different researchers, and the chromosomal location of DArT markers remains to be established in each target species. SNPs are numerous, can be quite polymorphic when defined on the haplotype level (500 - 1000 bp length of DNA), should be highly transferable if assayed for conserved orthologous set genes (Fulton et al., 2002), can be restricted to coding DNA thus allowing quantitative trait nucleotide (QTN) studies, and can be codominant (although this depends upon the technique used to assay the SNPs). SNP genotyping technologies have been developed rapidly in the last few years. As a result, a great variety of different SNP typing protocols and facilities have become available for researchers, and there is no single protocol that meets all research needs. Different aspects should be taken into account to determine the best suitable SNP technology in terms of sensitivity, reproducibility, accuracy, capability of multiplexing for high throughput analysis, cost effectiveness in terms of initial investment for equipment and cost per datapoint, flexibility of the technology for uses other than SNP discovery, and time-consumption for analysis (Semagn et al., 2006 for review). In general, the use of SNP demands extensive investment for highly specialized equipment and skilled manpower.

Polymorphism screening and genotyping of the mapping population

The third step in the construction of a linkage map is to identify sufficient number of markers that reveal differentces between parents (i.e., polymorphic markers). It is critical that sufficient polymorphism exists between parents in order to construct a linkage map. In general, cross pollinating species possess higher levels of polymorphism compared to inbreeding species. Once sufficient numbers of polymorphic markers have been identified between parents, they must be used to genotype the entire mapping population. Examples of DNA markers screened across different populations are shown in Figures 3 and 4. The progenies will inherit a marker from either of the parents (homozygous dominant or homozygous recessive) or both parents (heterozygous) but the scoring method is different between codominant and dominant markers, as the latter is not able to show differences between dominant homozygous and heterozygous individuals.

A genetic map is as good as the data that were used to construct it. Researchers construct a linkage map assuming no errors present in the data and then look for improbable genotypes, such as those originating from double recombinations (Figure 1). Therefore, the data must be critically checked for all possible errors, such as typographical error, missing data, genotype coding error, order of genotypes along all loci, etc. It is absolutely essential that the order of the individuals is identical over all loci in the data file. As discussed by several authors (e.g. Shields et al., 1991; Hackett and Broadfoot, 2003), a low frequency of typing errors can have a substantial impact on the order and length of a linkage map. The most likely effect of a typing error is to introduce a double recombination, so that an individual's genotype at three neighboring loci might change from a true genotype of ABA to ABB. This is increasingly the case as the marker density increases and the proportion of true recombinations between neighboring markers falls. Individuals with too much missing data will contribute very little information in the map calculations; in fact they might even cause problems (Van Ooijen and Voorrips, 2001). The presence of missing values in the marker data means that information about the number of true recombination that has taken place along the chromosome is lost. Hackett and Broadfoot (2003) performed a simula-



Marker	F_2 individuals																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
X	a	h	h	a	b	h	a	h	a	h	b	b	b	h	b	h	b	h	h	b	h	a
Y	a	h	b	a	b	h	a	h	a	h	b	b	b	h	b	h	b	h	h	b	h	h

Figure 4. A polyacrylamide gel showing segregation patterns for the two parents and 22 F_2 progenies. F_2 individuals are subjected to amplification with the primer pair belonging to markers X and Y and the two reactions are run simultaneously on a same gel. F_2 individuals that show a recombination event in the region flanked by X and Y can easily be distinguished from non-recombinants because they produce three PCR fragments instead of two (homozygous F_2 non-recombinants) or four (heterozygous F_2 non-recombinants). In this example, only individuals 3 and 22 have recombination between marker X and Y. The table shows the genotypic data for the F_2 individuals coded as follows: a (same allele as P_1), b (same alleles as P_2), and h (heterozygous for the two alleles) (Modified from Peters et al., 2004).

tion study to investigate the effects of typing errors and missing values on the construction of linkage maps and concluded that missing values had less effect than typing errors, but they reduced the number of correctly ordered markers and produced shorter map lengths for more widely separated markers.

Linkage analyses and map construction

Linkage analyses and mapping are computerized. Several computer packages are presently available for genetic linkage mapping but the most widely used are JoinMap (Stam, 1993a), MAPMAKER/EXP (Lander et al., 1987), GMENDEL (Echt et al., 1992), LINKAGE (Suiter et al., 1983), and Map Manager QTX (Manly et al., 2001). JoinMap is a commercial program while all others are freely available from the internet. The basic principles in map construction are basically the same for the different statistical programs, and the major steps in linkage analyses are described using JoinMap as an example.

a) Test for segregation distortion

For each segregating marker, a chi-square analysis needs to be performed to test for deviation from the expected segregation ratio for the mapping population (1:1 for both dominant and codominant markers in BC, RIL, DH and NIL; 1:2:1 for codominant markers in F_2; 3:1 for dominant markers in F_2). A deviation of the observed genotypic frequencies from the expected in a given genotypic class within a segregating population is called segregation distortion (Sandler and Novitski, 1957; Sandler and Golic, 1985; Lyttle, 1991). Segregation distortion can occur due to different reasons: statistical bias, genotyping and scoring errors (Plomion et al., 1995) and biological reasons like chromosome loss, competition among

gametes for preferential fertilization, gametocidal or pollen-killer genes (abortion of male or female gametes), incompatibility genes, chromosome arrangements or non-homologous pairing (Strauss and Conkle, 1986; Lyttle 1991; Bradshaw and Stettler, 1994; Lefebvre et al., 1995). Segregation distortion is a problem often encountered in mapping studies (Wendel and Parks, 1984; Torres et al., 1985; Lyttle, 1991; Schon et al., 1991; Zivy et al., 1992). It has been shown that the analysis of linkage may be influenced by deviations of single-locus segregation ratios from expected frequencies, and several authors have discussed methods to test for linkage or to estimate recombination frequencies between genes showing segregation distortion (Bailey, 1949; Garcia-Dorado and Gallego, 1992; Lorieux et al., 1995a,b). The effects of inclusion of loci with significant segregation distortion in the final linkage map seem contradictory. According to Hackett and Broadfoot (2003), segregation distortion had very little effect both on marker order and map length but others have reported reduction in map length due to the presence of loci with significant segregation distortion. Segregation distortion is a normal phenomenon in wide crosses, and one should be careful in removing loci with segregation distortion from further calculation. It is better to study these loci after calculating the map, as markers distorted towards the same direction clustered in a small chromosome region (Byrne et al., 1995; Lefebvre et al., 1995; Harushima et al., 1996; Lu et al., 2002; Matsushita et al., 2003; Sibov et al., 2003).

In plants, the percentage, degree, origin and genetic effects of segregation distortion vary significantly with species, population types, crosses and marker types. DH and RIL populations usually have high segregation distortion while BC populations usually have relatively fewer segregation distortions. For DH, non-Mendelian segregation may arise due to the various reasons mentioned above plus selection associated with the *in vitro* DH production process and fixation of recessive lethal genes into homozygous. In view of molecular marker types, Lorieux et al. (1995a, b) indicated that the estimation of recombination fractions in codominant markers is less affected by segregation distortion than that of dominant markers. In most cases, however, the scale and extent of segregation distortion for codominant versus dominant markers varied significantly among different data.

b) Establishing linkage groups

Markers are assigned to linkage groups using the odds ratios, which refers to the ratio of the probability that two loci are linked with a given recombination value over a probability that the two are not linked. This ratio is called a logarithm of odds (LOD) value or LOD score (Risch, 1992; Stam, 1993a). The critical LOD scores used to establish linkage groups and calculate map distances are called 'linklod' and 'maplod', respectively (Stam, 1993b; Ortiz et al., 2001). Marker pairs with a recombination LOD score above a critical 'linklod' are considered to be linked whereas those with a LOD score less than 'linklod' are considered unlinked. Several researchers used a 'linklod' value of 3 as the minimum threshold value in order to decide whether or not loci were linked. A LOD value of 3 between two markers indicates that linkage is 1000 times more likely than no linkage (Stam, 1993a). Experience with modern data sets with many markers, especially those species with large numbers of chromosomes, shows that even using a 'linklod' of $\geq$ 6 may lead to false positive linkage (Stam, 1993b; O'Donoughue et al., 1995). Higher critical LOD values will result in more number of fragmented linkage groups, each with smaller number of markers while small LOD values will tend to create few linkage groups with large number of markers per group. Two markers are placed in distinct linkage groups if they are not linked to any member of the other group. At any stage in the calculation, there is a group of markers which have been assigned to a linkage group and a group of free markers which have not yet been assigned.

Various options (e.g., changing the parameters of analyses, excluding loci or individuals, generation of additional marker data for linkage groups with few number of markers, etc.) can be tested until researchers establish satisfactory linkage groups. Ideally one would like to arrive at a number of linkage groups that is the same as the haploid chromosome numbers of the species under study. In practice, determining number of linkage groups is usually not a straightforward task because;

a) Loci on different chromosomes may appear to be linked by chance (spurious linkage).
b) Two or more linkage groups can be obtained for each chromosome (Figure 5), which results to the total number of linkage groups much higher than the haploid chromosome numbers.

If a linkage group consists of loci from different chromosomes, this often leads to many suspect linkages and to a poor goodness-of-fit of the resulting map. Therefore, it is important to critically check every marker in each linkage group before proceeding to the next step. Furthermore, the number of linkage groups, especially in polyploid species (e.g., O'Donoughue et al., 1995; Wight et al., 2003; Semagn et al., 2006), can be higher than the number of haploid chromosomes if the molecular markers are not well-distributed across all chromosomes and don't sufficiently cover the genome. In hexaploid wheat, for example, the International Triticeae Mapping Initiative (ITMI) population (Synthetic/Opata) is one of the most extensively mapped population (Nelson et al., 1995a,b,c; Van Deynze et al., 1995; Marino et al., 1996; Roder et al., 1998; Song et al., 2005) with 1468 markers scored for 115 recombinant inbred (RI) lines (http://wheat.pw.us-

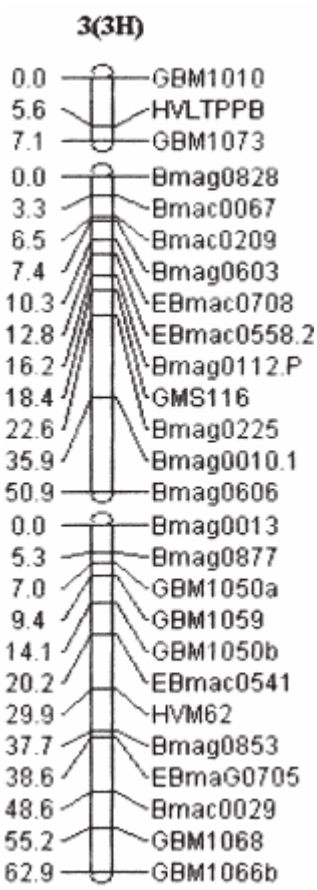


Figure 5. Linkage map of barley chromosome 3H constructed using 104 recombinant inbred lines (RILs) derived from a cross between accession OUH602 and cultivar Harrington. The map is developed using 26 simple sequence repeat (SSR) markers, which are given on the right side of each chromosome. Map distances in centimorgan are given on the left side (Yun et al., 2005). Note that the chromosome is fragmented into 3 linkage groups with each linkage group consisting of 3, 11 and 12 markers. This is an example of a poor map that doesn't representative the entire chromosome for large scale application.

da.gov/GG2/index.shtml). Such data set, however, were created by combining results from various research groups. One of the problem Semagn et al. (2006) encountered in the ITMI dataset was the difficulty to establish 21 linkage groups corresponding to the 21 hexaploid wheat chromosome (2n=6x=42). A total of 56 to 63 linkage groups were obtained depending on the LOD score used to establish linkages. The number of linkage groups per chromosome varied from 1 for chromosomes 4B and 4D to 5 for chromosomes 7A, 7B and 7D. Hexaploid wheat has a very large genome, 16 million kb/haploid cell (Bennett and Smith, 1976), and the large number of linkage groups compared to haploid chromosome numbers suggest that several areas of the genome remain undetected even in markers as high 1468 loci. Therefore, linkage mapping in species with high genome size could be much more complex and problematic even in the presence of large number of markers.

The next step, after establishing linkage groups, is to assign them to a chromosome based on previous available information for anchoring markers (markers with known chromosomal location) and/or using aneuploid lines. Of course, the former is not possible if one starts from scratch. If there are no previously mapped anchoring markers, one needs to determine the chromosomal location of selected markers in a linkage group using aneuploid lines, such as nullisomics, monosomics, and chromosome deletion stocks (Fox et al., 2001). Aneuploid is the condition in which the chromosome number of the cells of an individual is not an exact multiple of the typical haploid set for that species. If a marker is missing from a certain chromosome (piece) in aneuploid lines, it is strong evidence for its physical location. Aneuploids are very useful for assigning linkage groups of genetic markers to both physical chromosomes as well as for merging two or more linkage groups that belong to the same chromosome. However, one should remember that a single probe or primer-pair may produce multiple loci, especially in polyploids, and the different loci may map to different chromosomes.

c) Determining map distance and locus order

For calculating map distances and determining locus order, the researchers need to specify several parameters, including a recombination threshold value, minimum 'maplod', jump threshold value, and mapping function (m.f.). Only information for marker pairs with a LOD score above 'maplod' is used in the calculation of map distances. The choice of 'maplod' values is arbitrary and it can be as low as 0.01 to as high as 3.0. If the value of 'maplod' equal to 0.01, the program uses even very weak linkage information (usually corresponding to recombination values slightly less than 50%). If one is dealing with large linkage groups (i.e., over 50 markers per linkage group), various marker pairs will show insignificant linkage, if at all. In such cases, the 'maplod' value should be set between 0.5 and 1.0 to ensure that no information is used which comes from distant markers (Stam, 1993b). The mapping procedure is basically a process of building a map by adding loci one by one, starting from the most informative pair of loci (loci pair with most linkage information). If the order of sets of (at least three) markers is known in advance, this information can be provided to the program as a "fixed order" (Stam, 1993b; van Ooijen and Voorrips, 2001; Vision et al., 2000). At each step, a marker is added to the map on the basis of its total linkage information with the markers that were placed earlier on the map. For each added locus the best position is searched and a goodness-of-fit measure is calculated. When the goodness-of-fit reduces too sharply

(too large a jump), or when the locus gives rise to negative distances, the locus is removed again. This will continue until all loci have been handled once. This is the end of the so-called first round. Subsequently, all loci previously removed are attempted to be added to the map a second time. This can be successful since the map will contain more loci than at the first attempt. But it may also be unsuccessful again through too large a jump or negative distances, so that a locus will be removed once more. This is the second round. After that, all loci previously removed are attempted a final time to be added to the map by ignoring the requirements of maximum allowed reduction in goodness-of-fit and no negative distances. This is the final round and gives genetic map as shown in Figures 5 and 6. The former is an example of a map that partially represents a chromosome while the latter is a well saturated map that covers the entire chromosome. Of course, when all loci are fitted in the first or second round, there will not be subsequent rounds. Therefore, the researcher needs to critically check the various statistical analyses outputs in calculating map distance and locus ordering.

When map distances are small (<10 cM), the map distance equals the recombination frequency (Figure 7). However, this relationship does not apply for map distances that are greater than 10 cM. Hence, the researcher must select one of the two genetic mapping functions (Haldane or Kosambi), which translates recombination frequencies into map distances and vice versa. Haldane's mapping function (Haldane, 1931) assumes absence of interference between crossovers in meiosis, whereas Kosambi's mapping function (Kosambi, 1944) assumes a certain degree of interference. Interference is the effect in which the occurrence of a crossover in a certain region reduces the probability of a crossover in the adjacent region. Such mapping functions convert recombination fractions into map units called centimorgans (cM) in honor of the geneticist Thomas Hunt Morgan. By definition, one map unit (m.u.) is equal to one percent recombinant phenotypes or 1 cM. For recombination frequentcies above 10%, Haldane mapping functions gives higher map distance than Kosambi; hence, the total map length of a species will be much higher for the Haldane's than Kosambi's mapping function.

The statistical programs perform locus ordering using one of the locus-ordering criteria: weighted least squares, maximum likelihood and minimum sum of adjacent recombination fractions. Hackett and Broadfoot (2003) performed a simulation study to compare the performance of these three locus-ordering criteria in the presence of missing values, typing errors and distorted segregation ratios. The authors concluded that map inflation was more extreme using the maximum likelihood criterion than using weighted least squares. The advantage of the weighted least-squares approach is that the distances between markers are calculated from the map distances between all pairs of markers on a chromosome, and hence the impact of typing errors on the distance between adjacent markers is less severe. JoinMap uses the weighted least squares procedure as described by Stam (1993a), with one modification: the squares of the LODs are used as weights, thereby putting relatively more weight on more informative data (Van Ooijen and Voorrips, 2001).

All markers generated for a particular segregating population may not establish linkage groups. For example, Semagn et al. (2006) genotyped 93 DH lines derived from a cross between hexaploid wheat parents (Arina x NK93604) for 904 DNA markers (271 DArTs, 290 AFLPs, and 343 SSRs) but only 624 markers were finally incurporated into their respective linkage maps. Therefore, a large number of markers will be discarded before constructing the final linkage map.

Vision et al. (2000) proposed two experimental phases in the construction of a high-density genetic map: the first is to construct a high-confidence framework and the second is to add new markers to this framework. This two-phased strategy allows many markers to be placed on a well-measured map with a minimum of genotyping and avoids the loss in map resolution that would result from arbitrarily shrinking mapping population size. In the first phase of the proposed strategy, the breakpoints for each individual in the full mapping population are located using a limited number of the available markers, which are referred to as the framework markers. Preferably, these markers are chosen on the basis of prior knowledge concerning their even distribution throughout the genome, as measured by breakpoint density. The map constructed in this first phase, in which the framework markers are placed confidently and precisely is referred to as the framework map. In the second phase, the genotypes for all subsequent markers are scored in a small sample of individuals that have been selected on the basis of the information obtained during the first phase. The data obtained in this second phase allow the mapping of new markers relative to the fixed framework.

RELATIONSHIP BETWEEN GENETIC AND PHYSICAL MAPS

The order of markers in a high density genetic map remains the same as that of the physical map (Figure 8). However, there is no direct linear relationship between units of genetic distances in centimorgan (cM) and physical distances in kilobase pairs (kb). [Note that 1 megabase pair (Mb) = 10^3 kilobase pair (kb) = 10^6 bp]. For chromosome 4 of Arabidopsis, for example, the kilobase pair to centimorgan ratio varied from 30 to 550 kb per cM (Schmidt et al., 1995). In rice 1 cM on average equals to 258.5 kb (The Rice Genome Sequencing Project, 2005) but this figure actually varies from 120 to 1000

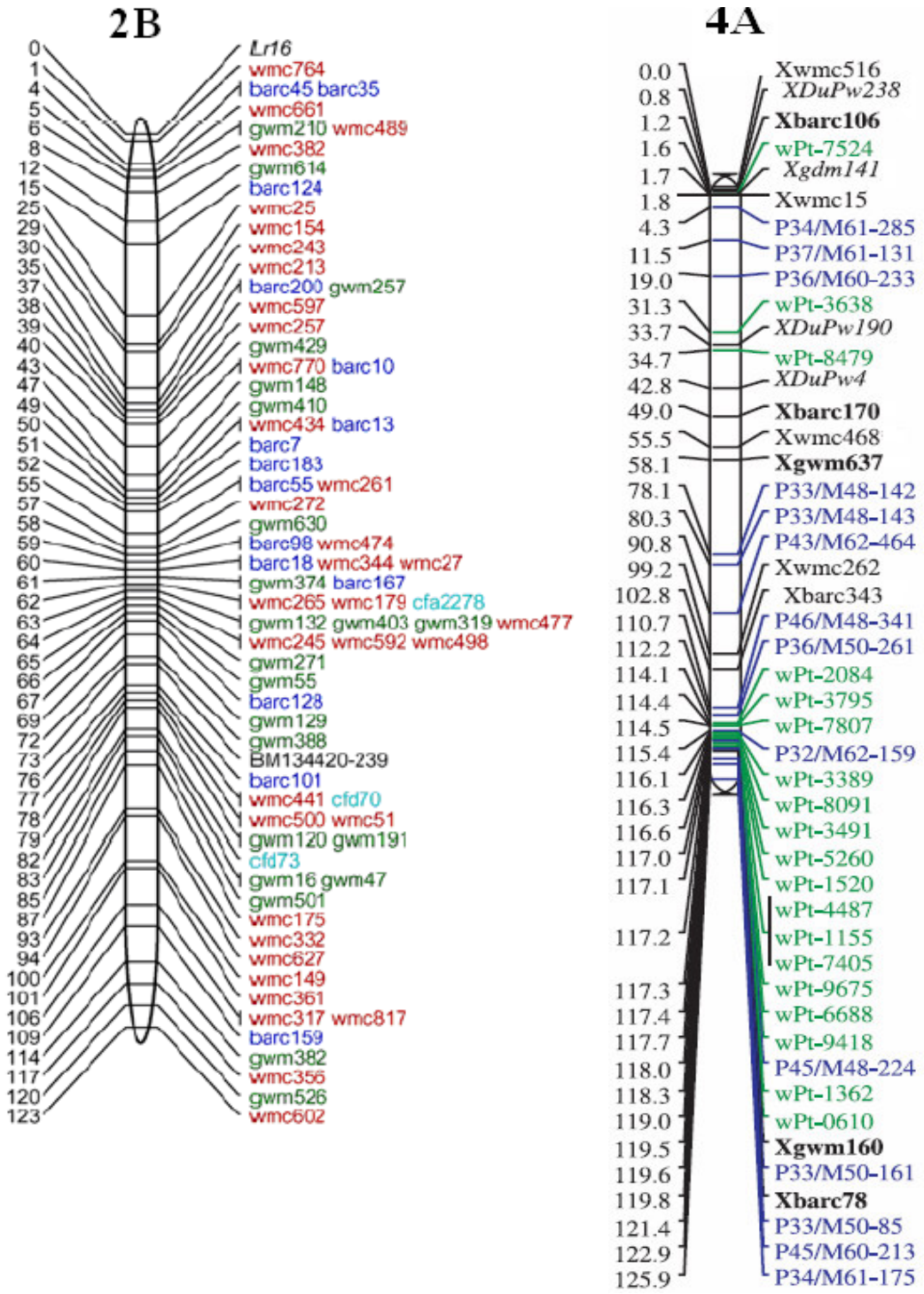


Figure 6. Map of chromosomes 2B (left) and 4A (right) in bread wheat (*Triticum aestivum*). Chromosome 2B is an example of a well saturated microsatellite consensus map. Expressed sequence tags (EST) markers are in black; the remainders loci are microsatellite markers and are color coded by microsatellite source (red -Wheat Microsatellite Consortium (WMC); green - GWM/GDM, cyan - CFA/CFD; blue - BARC). Loci that cosegregated are grouped beside a vertical line on the right side of the chromosome (Somers et al., 2004). Chromosome 4A shows high clustering of diversity arrays technology (DArT) markers (green) compared to amplified fragment length polymorphism (blue) and microsatellite (black) markers (Semagn et al., 2006). Numbers on the left shows map distances in centiMorgans (cM) from the top of each chromosome.

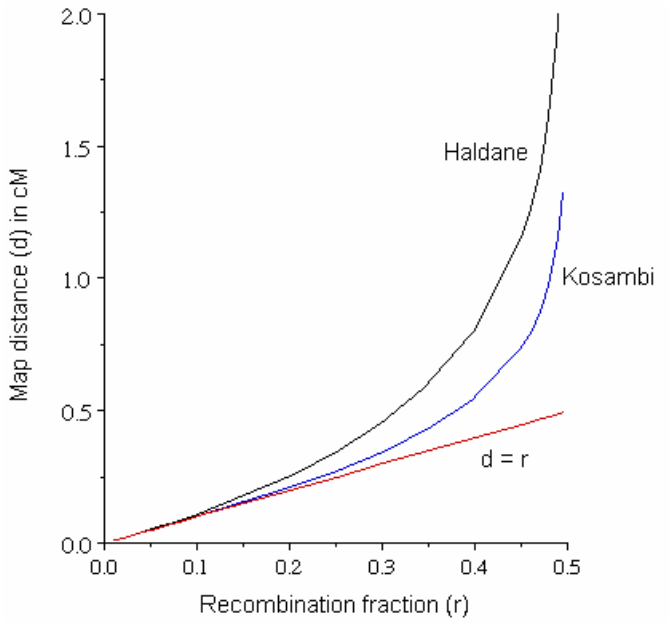


Figure 7. Comparison of Haldane's and Kosambi's mapping functions. Below a recombination frequency of 0.1 (10%), there is almost no difference between the two mapping functions (r = d). For recombination frequencies above 0.1 or 10%, Haldane mapping function gives higher map distance than Kosambi mapping function.

kb per cM (Kurata et al., 1994). In wheat, the variation is even more extreme, with 1 cM equivalent to 118 to 22,000 kb (Gill et al., 1996a, b). Therefore, genetically close markers may actually be far apart in terms of base pairs (or vice versa) due to differences in the frequency of recombination along the length of a chromosome (Figure 8). The non linear relationship between genetic and physical map distances can hinder the ability of geneticists to identify genes by map-based techniques. Understanding the rules that govern the distribution of recombination events will, therefore, be of great value to researchers who aim at identifying genes on the basis of their position in a genetic map.

Meiotic recombination occurs preferentially at defined sites, termed hot spots, along chromosomes of various eukaryotic organisms (Shiroishi et al., 1993; Smith, 1994; Lichten and Goldman, 1995). In all eukaryotic organisms that have been analyzed in detail, regions of high (hot spots) and low (cold spots) recombination have been reported (Lichten and Goldman, 1995; Wahls, 1998). In hexaploid wheat, more than 85% of the genes are present in gene-rich regions, physically spanning only 5–10% of the chromosomal region (Gill et al., 1996a,b). The gene-rich regions are interspersed with blocks of repetitive DNA sequences visualized as regions of low gene density. These gene-rich regions undergo recombination much more frequently than do gene-poor regions. Kilobase pair per cM estimates ranged from 118 kb for gene-rich regions to 22,000 kb for gene-poor regions (Gill et al., 1996a). Physical distribution of recombination events is non random in other plant species as well (Rick, 1971). Division of higher organism genomes into gene-rich and gene-poor compartments seems a common feature (Sumner et al., 1993). Regions corresponding to centromeres (Figure 9), and even some telomeres in tomato and potato, show a 10-fold decrease in recombination compared to other regions in the genome (Tanksley et al., 1992). Reduced recombination frequency in pericentric regions is also seen in many species including wheat (Dvorak and Chen, 1984; Snape et al., 1985; Curtis and Lukaszewski, 1991; Gill et al., 1993; Gill and Gill, 1994; Gill et al., 1996a,b), barley (Leitch and Heslop-Harrison, 1993; Pedersen et al., 1995; Kunzel et al., 2000), rye (Heslop-Harrison, 1991; Wang et al., 1992), and Lolium (Hayward et al., 1998 ; Bert et al., 1999). When considering the average length of DNA per unit of recombination, different segments of a chromosome should therefore be considered independently.

The genetic- and physical-map orders of markers are not without errors. Inaccuracies in genetic maps can result from genotyping errors, as well as from the use of a limited number of informative meioses to generate maps. Errors in the order of markers on physical maps can be due to problems with assembly or to incorrect identification of marker positions. Even when the order of markers is known to be without error, accurate estimates of recombination fractions will play an important role in linkage studies (Clerget-Darpoux et al., 1986; Risch and Giuffra, 1992; Goddard et al., 2000; Collins et al., 2001; Reich et al., 2001).

PROSPECTS OF GENETIC MAPPING

The development of genetic maps based on markers that are simple to generate, highly reproducible, codominant, and specific for known linkage groups are highly desirable for their application in breeding. The transferability of maps constructed using AFLPs, RAPDs, and ISSRs is limited between populations and pedigrees within a species (Chagne et al., 2003) because each marker is primarily defined by its length (i.e., sequence information may be limited). Moreover, the same size band amplified across populations/species does not necessarily mean that bands possess the same sequence, unless proven by hybridization studies (Thormann et al., 1994). In contrast, the development of high density maps that incorporate EST-derived RFLP, SSR and SNP markers will provide researchers with a greater arsenal of tools for identifying genes or QTLs associated with economically important traits. Furthermore, such EST-based markers mapped in one population can be used as probes and primers for characterizing other populations within the same species.

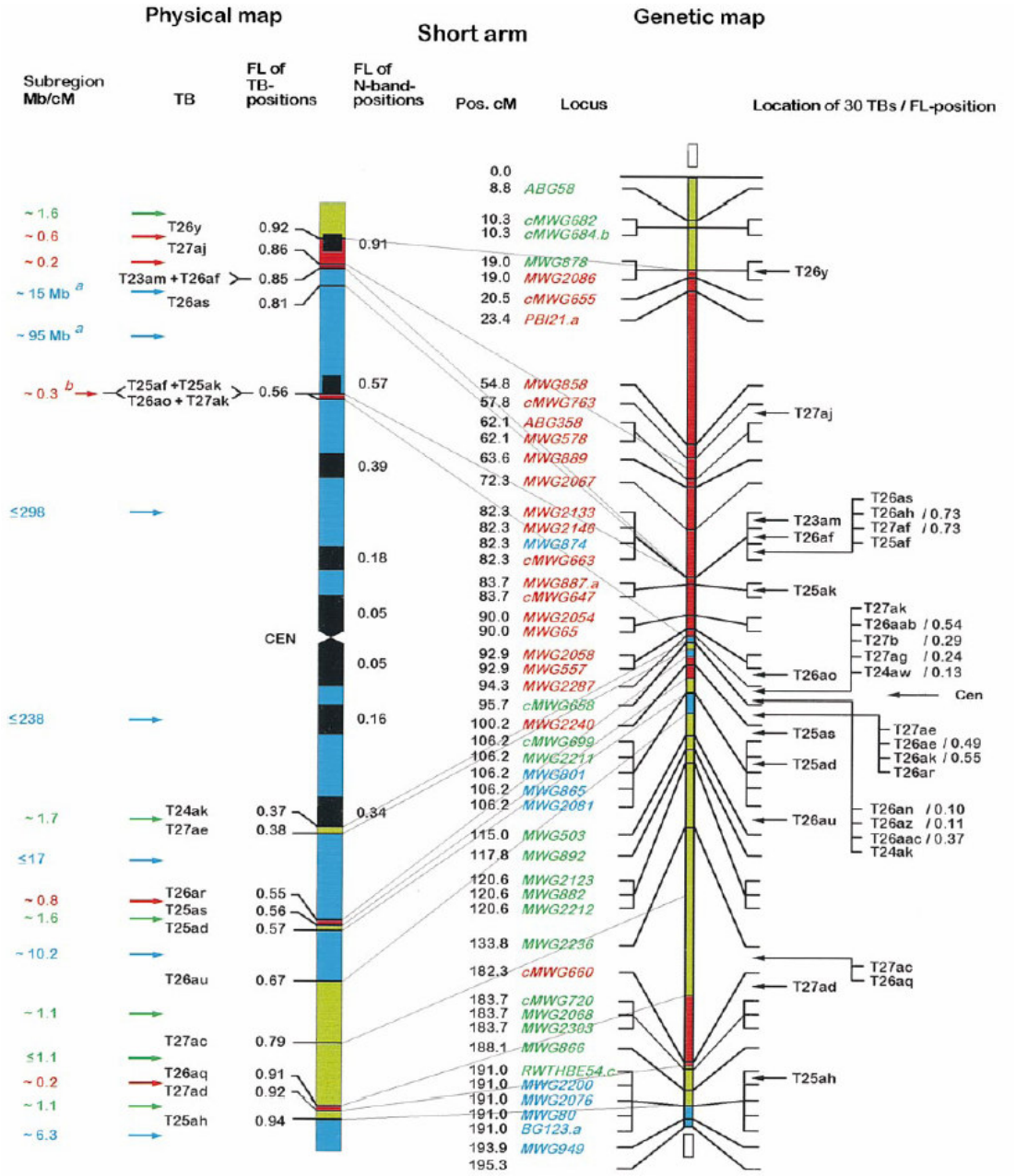


Figure 8. Comparison of physical and genetic map of barley chromosome 2H (Kunzel et al., 2000). The idiograms and RFLP maps are aligned at approximate centromere positions (CEN). Subregions of similar recombination rates are shown in the same color. As compared to the genome-wide average (4.4 Mb/cM), blue indicates suppressed (> 4.4 Mb/cM), green increased (1.0–4.4), and red strongly increased (≤ 1.0 Mb/cM) recombination. Black regions of the physical maps mark Giemsa N bands. Positions of N bands, nucleolus organizer regions (NOR) and translocation breakpoints (TB) are given in fraction-length (FL) estimates. If several TBs were mapped between the same loci, the Mb distance between the two physically most distant TBs was divided by the cM distance of the two flanking markers; such estimates are marked by the preceding symbol ≤. Special cases are denoted by superscript a–c. (a) Corresponding genetic distance is not definable since the TBs are located between cosegregating markers, as indicated to the right of the genetic maps. (b) Physical subregions are arbitrarily assigned to 0.01-FL intervals because TBs of the same FL estimate are located in different regions of the genetic map. (c) cM positions of both the NOR and CEN are included by inference on the basis of the Steptoe/Morex linkage map.

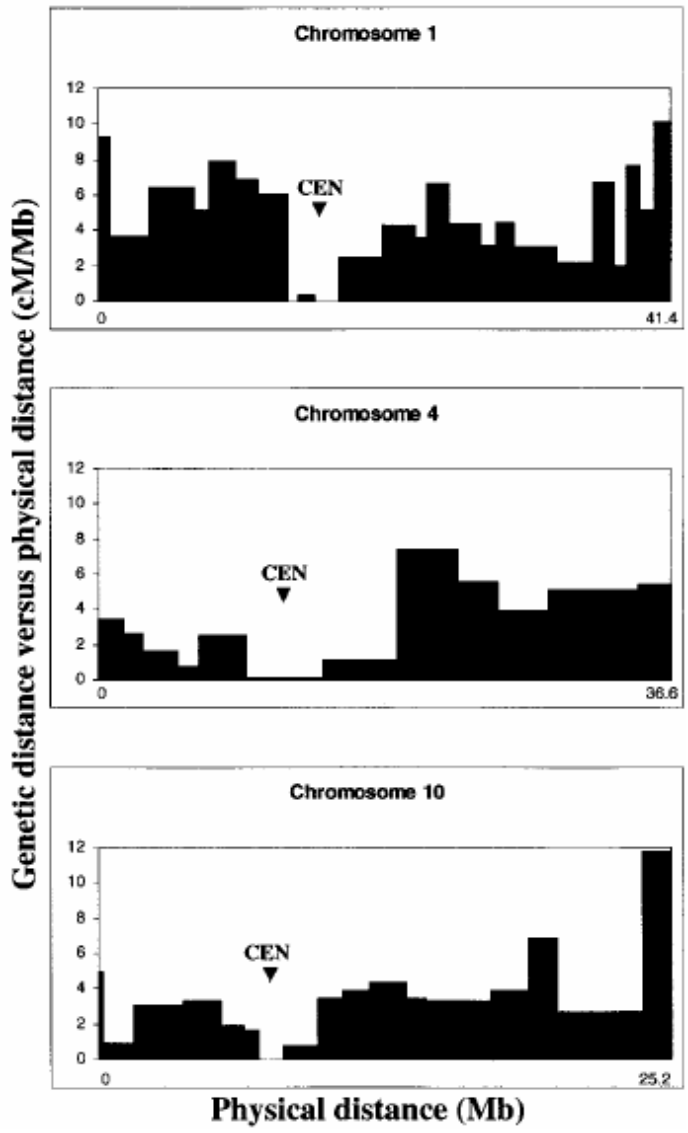


Figure 9. The relationship between genetic and physical distances on 3 rice chromosomes (Chen et al., 2002). Recom-bination is suppressed around centromere and the ratio of genetic/physical distances in this region is much lower than all other parts of the chromosomes. In contrast, there is often high rate of recombination in the telemore, which results to higher genetic/physical ratios.

Genetic maps with good genome coverage and confidence in locus order requires not only large numbers of DNA markers, but also the analyses of large numbers of individuals. The requirement for a large number of markers or mapping populations to reduce the linkage group number to haploid chromosome numbers and increase map accuracy has been emphasized in mapping studies (e.g., Jeuken et al., 2001; Sharma et al., 2002; Crane and Crane, 2005). In a genome of 1 million kb and a total genetic map length of 1000 cM, for example, 1 cM is 1000 kb. To localize markers within distances of 100 kb or less means mapping to a resolution of 0.1 cM or less. This would require analysis of more than 3000 segregating progeny in the hope of obtaining those few individuals in which crossovers had occurred very close to the target gene (Tanksley et al., 1995). However, analyses of such large number of individuals require very high throughput techniques. The methods for detection and analysis of widely-used markers are automated and much faster than some years ago. One example of an improvement in the efficiency of marker analysis is multiplex PCR, which enables multiple marker loci to be tested simultaneously. PCR products up to 9 different primer pairs with non-overlapping ranges of allele sizes can be multiplexed and run on high throughput DNA sequencing machines. New types of high-throughput marker systems, such as SNPs, should play an important role in the construction of high density maps, provided that these methods are not too expensive. Due to the abundance of SNPs and development of sophisticated high-throughput SNP detection systems, it is expected that SNP markers will have a great influence on future mapping studies (Rafalski, 2002; Koebner and Summers, 2003). Comparison of sequences of the two rice cultivars 'Nipponbare' (*japonica*) and 'Kasalath' (*indica*) revealed a total of 80,127 polymorphic SNPs and 18,828 potentially polymorphic SSRs. This suggests the high potential of SNP and SSR markers for other species as well for the construction of highly saturated genetic maps.

Genetic maps based on DNA markers are available for several economically important plants, including arabidopsis, maize, rice, wheat, barley, tomato, potato, sunflower, pea, bean, rye, millet, cotton, soybean, sorghum, cowpea, tobacco, turnip rape, cauliflower, sunflower, alfalfa, carrot, sugarcane, sugar beet, coffee, and grape. In model species (such as arabidopsis and rice) and other extensively studied species, one can find several genetic maps developed by different researchers using different mapping populations, sample size, marker systems, and statistical programs. However, it is not always possible to get the same map length and marker order in these different genetic maps. Such type of problem can be solved with the development of a wide range of high throughput techniques for physical mapping of chromosomes. It is only with the availability of physical maps that one can be sure of the order of markers along chromosomes and their actual length in kilobase pairs. The ultimate physical map is the whole genome DNA sequence, which is available for a few species such as *Arabidopsis thaliana* (The Arabidopsis Genome Initiative, 2000) and rice (The Rice Genome Mapping Project, 2005).

REFERENCE

Ahn S, Tanksley SD (1993). Comparative linkage maps of the rice and maize genomes. Proc. Natl. Acad. Sci. USA 90: 7980-7984.

Akbari M, Wenzl P, Caig V, Carlig J, Xia L, Yang S, Uszynski G, Mohler V, ehmensiek A, Howes N, Sharp P, Huttner E, Kilian A (2006). Diversity arrays technology (DArT) for high throughput profiling of the hexaploid wheat genome. Theor. Appl. Genet.113:1409-1420.

Arcade A, Anselin F, Faivre Rampant P, Lesage MC, Paques LE, Prat D (2000). Application of AFLP, RAPD and ISSR markers to genetic mapping of European and Japanese larch. Theor. Appl. Genet. 100: 299–307.

Babu R, Nair SK, Prasanna BM, Gupta HS (2004). Integrating marker-assisted selection in crop breeding – Prospects and challenges. Curr. Sci. 87: 607-619.

Bailey NTJ (1949). The estimation of linkage with differential viability, II and III. Heredity 3: 220 228.

Barrett BA, Kidwell KK (1998). AFLP-based genetic diversity assessment among wheat cultivars from the Pacific North-west. Crop. Sci. 38: 261-1271.

Beavis WD, Grant D (1991) A linkage map based on information from four FP populations of maize (*Zea mays* L.). Theor. Appl. Genet. 82: 636-644.

Bennett MD, Smith JB (1976). Nuclear DNA amounts in angiosperms. Philos. Trans. R. Soc. Lond. Ser. B. Biol. Sci. 274: 227-274.

Bert PF, Charmet G, Sourdille P, Hayward MD, Balfourier F (1999). A high-density molecular map for ryegrass (*Lolium perenne*) using AFLP markers. Theor. Appl. Genet. 99: 445-452.

Bradshaw HD, Stettler RF (1994). Molecular genetics of growth and development in Populus. II Segregation distortion due to genetic load. Theor. Appl. Genet. 89: 551–558.

Burr B, Burr FA, Thompson KH, Albertson MC, Stuber CW (1988). Gene mapping with recombinant inbreds in maize. Genetics 118: 519-526.

Byrne M, Murrell JC, Allen B, Moran GF (1995). An integrated genetic linkage map for eucalypts using RFLP, RAPD and isozyme markers. Theor. Appl. Genet. 91: 869-875.

Cato S, Gardner R, Kent J, Richardson T (2001). A rapid PCR based method for genetically mapping ESTs. Theor. Appl. Genet. 102: 296–306.

Chagne D, Brown G, Lalanne C, Madur D, Pot D, Neale D, Plomion C (2003). Comparative genome and QTL mapping between maritime and loblolly pines. Mol. Breed. 12: 185-195.

Chalmers KJ, Cambell AW, Kretschmer J, Karakousis A, Henschke PH, Pierens S, Harker N, Pallotta M, Cornish GB, Shariflou MR, Rampling LR, McLauchlan A, Daggard G, Sharp PJ, Holton TA, Sutherland MW, Appels R, Langridge P (2001). Construction of three linkage maps in bread wheat, *Triticum aestivum*. Aus. J. Agr. Res. 52:1089–1119.

Chen M, Presting G, Barbazuk WB, Goicoechea JL, Blackmon B, Fang G, et al. (2002). An integrated physical and genetic map of the rice genome. Plant Cell 14: 537–545.

Cho YG, Ishii T, Temmykh S, Chen X, Lipovich L, McCouch SR, Park WD, Ayres N, Cartinhour S (2000). Diversity of microsatellites derived from genomic libraries and genebank sequences in rice (*Oryza sativa* L.). Theor. Appl. Genet. 100: 713–722.

Clerget-Darpoux F, Bonaiti-Pellie C, Hochez J (1986). Effects of misspecifying genetic parameters in LOD score analysis. Biometrics 42: 393–399.

Coe E, Hancock D, Kowalewski S, Polacco M (1995). Gene list and working maps. Maize Genet. Coop. Newslett. 69: 191-269.

Collard BCY, Jahufer MZZ, Brouwer JB, Pang ECK (2005). An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. Euphytica 142: 169-196.

Collins A, Ennis S, Taillon-Miller P, Kwok PY, Morton NE (2001). Allelic association with SNPs: metrics, populations, and the linkage disequilibrium map. Hum. Mutat. 17: 255–262.

Crane CF, Crane YM (2005). A nearest-neighboring-end algorithm for genetic mapping. Bioinformatics 21: 1579-1591.

Curtis CA, Lukaszewski AJ (1991). Genetic linkage between C-bands and storage protein genes in chromosome 1B of tetraploid wheat. Theor. Appl. Genet. 81: 245-252.

Davila JA, Loarce Y, Ferrer E (1999). Molecular characterization and genetic mapping of random amplified microsatellite polymorphism in barley. Theor. Appl. Genet. 98: 265–273.

Davis GL, McMullen MD, Baysdorfer C, Musket T, Grant D, Staebell M, Xu G, Polacco M, Koster L, Melia-Hancock S (1999). A maize map standard with sequenced core markers, grass genome reference points and 932 expressed sequence tagged sites (ESTs) in a 1,736-locus map. Genetics 152: 1137–1172.

Demeke T, Sasikumar B, Hucl P, Chibbar RN (1997). Random amplified polymorphic DNA (RAPD) in cereal improvement. Maydica 42: 133–142.

Dirlewanger E, Pronier V, Parvery C, Rothan C, Guye A, Monet R (1998). Genetic linkage map of peach (*Prunus persica* L. Batsch) using morphological and molecular markers. Theor. Appl. Genet. 97: 888–895.

Doerge R (2002). Mapping and analysis of quantitative trait loci in experimental populations. Nature Rev. 3: 43-52.

Dvorak J, Chen KC (1984). Distribution of nonstructural variation between wheat cultivars along chromosome arm 6Bp: evidence from the linkage map and the physical map of the arm. Genetics 106: 325-333.

Echt C, Knapp S, Liu BH (1992). Genome mapping with non-inbred crosses using Gmendel 2.0. Maize Genet. Coop. Newslett. 66: 27-29.

Eujayl I, Sledge MK, Wang L, May GD, Chekhovskiy K, Zwonitzer JC, Mian MAR (2004). *Medicago truncatula* EST-SSRs reveal cross-species genetic markers for *Medicago* spp. Theor. Appl. Genet. 108: 414–422.

Eujayl I, Sorrells ME, Wolters P, Baum M, Powell W (2002). Isolation of EST-derived microsatellite markers for genotyping the A and B genomes of wheat. Theor. Appl. Genet. 104: 399–407.

Fang DQ, Roose ML (1997). Identification of closely related citrus cultivars with inter-simple sequence repeat markers. Theor. Appl. Genet. 95: 408-417.

Ferreira A, da Silva MF, da Costa e Silva L, Cruz CD (2006). Estimating the effects of population size and type on the accuracy of genetic maps. Genet. Mol. Biol. 29: 182-192.

Fox SL, Jellen EN, Kianian SF, Rines HW, Phillips RL (2001). Assignment of RFLP linkage groups to chromosomes using monosomic F_1 analysis in hexaploid oat. Theor. Appl. Genet. 102: 320-326

Fulton TM, Van der Hoeven R, Eannetta NT, Tanksley SD (2002). Identification, analysis, and utilization of conserved ortholog set markers for comparative genomics in higher plants. Plant Cell 14: 1457-467.

Garcia-Dorado A, Gallego A (1992). On the use of the classical tests for detecting linkage. J. Hered. 83: 143 146.

Gardiner J, Coe E, Melia-Hancock S, Hoisington D, Chao S (1993). Development of a core RFLP map in maize using an immortalised F_2 population. Genetics 134: 917–930.

Gill KS, Gill BS (1994). Mapping in the realm of polyploidy: the wheat model. BioEssays 16: 841-846.

Gill KS, Gill BS, Endo TR (1993). A chromosome region specific mapping strategy reveals gene rich telomeric ends in wheat. Chromosoma 102: 374-381.

Gill KS, Gill BS, Endo TR, Boyko EV (1996a). Identification of high-density mapping of gene-rich regions in chromosome group 5 of wheat. Genetic 143: 1001-1012.

Gill KS, Gill BS, Endo TR, Taylor T (1996b). Identification and high-density mapping of gene-rich regions in chromosome group 1 of wheat. Genetics 144: 1883-1891.

Goddard KA, Hopkins PJ, Hall JM, Witte JS (2000). Linkage disequilibrium and allele-frequency distributions for 114 single-nucleotide polymorphisms in five populations. Am. J. Hum. Genet. 66: 216–234.

Gupta PK, Varshney RK, Sharma PC, Ramesh B (1999). Molecular markers and their application in wheat breeding: a review. Plant Breed. 118: 369-390.

Hackett CA, Broadfoot LB (2003). Effects of genotyping errors, missing values and segregation distortion in molecular marker data on the construction of linkage maps. Heredity 90: 33-38.

Haldane JBS (1931). The cytological basis of genetical interference.

Cytologia 3:54–65.
Haley CS, Andersson L (1997). Linkage mapping of quantitative trait loci in plants and animals. In: Dear PH (ed) Genome mapping: a practical approach. Oxford University Press, New York, pp 49-71.
Hartl DL (1988). *A primer of population genetics*. 2nd edition, Sinauer Associates, Inc., Sunderland, USA.
Harushima Y, Kurata N, Yano M, Nagamura Y, Sasaki T (1996). Detection of segregation distortions in an indica-japonica rice cross using a high-resolution molecular map. Theor. Appl. Genet. 92: 145–150.
Harushima Y, Yano M, Shomura A, Sato M, Shimano T, Kuboki Y, et al. (1998) A high-density rice genetic linkage map with 2275 markers using a single F_2 population. Genetics 148: 479–494.
Hayward MD, Forster JW, Jones JG, Dolstra O, Evans C, McAdam NJ (1998). Genetic analysis of *Lolium*. I. Identification of linkage groups and the establishment of a genetic map. Plant Breed. 117: 451-455.
He P, Li JZ, Zheng XW, Shen LS, Lu CF, Chen Y, Zhu LH (2001). Comparison of molecular linkage maps and agronomic trait loci between DH and RIL populations derived from the same rice cross. Crop Sci. 41: 1240-1246.
Helentjaris T, Slocum M, Wright S, Schaefer A, Nienhuis J (1986). Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphisms. Theor. Appl. Genet. 72: 761-769.
Helentjaris T, Weber D, Wright S (1988). Identification of the genomic locations of duplicate nucleotide sequences in maize by analysis of restriction fragment length polymorphisms. Genetics 118: 356-363.
Heslop-Harrison JS (1991). The molecular cytogenetics of plants. J. Cell Sci. 100: 15-21.
Huang X, Zeller FJ, Hsam SLK, Wenze, G, Mohler V (2000). Chromosomal location of AFLP markers in common wheat utilizing nulli-tetrasomic stocks. Genome 43: 298-305.
Iwata H, Ujino-Ihara T, Yoshimura K, Nagasaka K, Mukai Y, Tsumura Y (2001). Cleaved amplified polymorphic sequence markers in sugi, *Cryptomeria japonica* D. Don, and their location on a linkage map. Theor. Appl. Genet. 103: 881–895.
Jeuken M, van Wijk R, Peleman J, Lindhout P (2001). An integrated interspecific AFLP map of lettuce (*Lactuca*) based on two *L. sativa* × *L. saligna* F_2 populations. Theor. Appl. Genet. 103: 638–647.
King J, Armstead IP, Donnison LS, Thomas HM, Jones RN, Kearsey MJ, Roberts LA, Thomas A, Morgan WG, King IP (2002). Physical and genetic mapping in the grasses *Lolium perenne* and *Festuca pratensis*. Genetics 161: 315-324.
Koebner RMD, Summers W (2003). 21st century wheat breeding: Plot selection or plate detection? Trends Biotechnol. 21: 59–63.
Kojima T, Nagaoka T, Noda K, Ogihara Y (1998). Genetic linkage map of ISSR and RAPD markers in Einkorn wheat in relation to that of RFLP markers. Theor. Appl. Genet. 96: 37-45
Kosambi DD (1944). The estimation of map distances from recombination values. Ann. Eugen. 12:172-175.
Kunzel G, Korzun L, Meister A (2000). Cytologically integrated physical restriction fragment length polymorphism maps for the barley genome based on translocation breakpoints. Genetics 154: 397-412.
Kurata N, Nagamura Y, Yamamoto K, Harushima Y, Sue N, Wu J (1994). A 300 kilobase interval genetic map of rice including 883 expressed sequences. Nat. Genet. 8: 365-372.
Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987). MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1: 174–181.
Lefebvre V, Palloix A, Caranta C, Pochard E (1995). Construction of an intraspecific integrated linkage map of pepper using molecular markers and doubled-haploid progenies. Genome 38: 112–121.
Leitch IJ, Heslop-Harrison JS (1993). Physical mapping of 4 sites of 5s rRNA sequences and one site of the α-*amylase-2* gene in barley (*Hordeum vulgare*). Genome 36: 517-523.
Lichten M, Goldman ASH (1995). Meiotic recombination hotspots. Annu. Rev. Genet. 29: 423-444.
Liu HB (1998). Statistical genomics, linkage, mapping and QTL analysis. CRC, Boca Raton, Florida, 611 pp.
Lorieux M, Goffinet B, Perrier X, González de León D, Lanaud C (1995a). Maximum-likelihood models for mapping genetic markers showing segregation distortion. 1. Backcross populations. Theor. Appl. Genet. 90: 73–80.
Lorieux M, Ndjiondjop MN, Ghesquière A (2000). A first interspecific *Oryza sativa* x *Oryza glaberrima* microsatellite-based genetic linkage map. Theor. Appl. Genet. 100: 593–601.
Lorieux M, Perrier X, Goffinet B, Lanaud C, Gonzalez D de L (1995b). Maximum-likelihood models for mapping genetic markers showing segregation distortion. 2. F_2 populations. Theor. Appl. Genet. 90: 81-89.
Lu H, Romero-Severson J, Bernardo R (2002). Chromosomal regions associated with segregation distortion in maize. Theor. Appl. Genet. 105: 622-628.
Lyttle TW (1991). Segregation distorters. Annu. Rev. Genet. 25: 511-557.
Manly KF, Cudmore Jr RH, Meer JM (2001). Map Manager QTX, cross-platform software for genetic mapping. Mamm. Genome 12: 930–932.
Marino CL, Nelson JC, Lu YH, Sorrells ME, Leroy P, Tuleen NA, Lopes CR, Hart GE (1996). Molecular genetic maps of the group 6 chromosomes of hexaploid wheat (*Triticum aestivum* L. em. Thell). Genome 39: 359-366.
Markert CL, Moller F (1959). Multiple forms of enzymes: Tissue, ontogenetic and species specific patterns. Proc. Natl. Acad. Sci. USA 45: 753-763.
Matsumoto A, Tsumura Y (2004). Evaluation of cleaved amplified polymorphic sequence markers. Theor. Appl. Genet. 110: 80–91.
Matsushita S, Iseki T, Fukuta Y, Araki E, Kobayashi S, Osaki M, Yamagishi M (2003). Characterization of segregation distortion on chromosome 3 induced in wide hybridization between indica and japonica type rice varieties. Euphytica 134: 27-32.
McCouch SR, Doerge RW (1995). QTL mapping in rice. Trends Genet. 11: 482–487.
Mohan M, Nair S, Bhagwat A, Krishna TG, Yano M (1997). Genome mapping, molecular markers and marker-assisted selection in crop plants. Mol. Breed. 3: 87-103.
Moreno S, Martin JP, Ortiz JM (1998). Inter-simple sequence PCR for characterization of closely related grapevine germplasm. Euphytica 101: 117–125.
Nelson JC, Sorrells ME, van Deynze AE, Lu YH, Atinkson M, Bernard M, Leroy P , Faris JD, Anderson JA (1995c). Molecular mapping of wheat. Major genes and rearrangements in homoeologous groups 4, 5, and 7. Genetics 141: 721 731.
Nelson JC, van Deynze AE, Autrique E, Sorrells ME, Lu YH, Merlino M, Atinkson M, Leroy P (1995a). Molecular mapping of wheat. Homoeologous group 2. Genome 38: 516 524.
Nelson JC, van Deynze AE, Autrique E, Sorrells ME, Lu YH, Negre S, Atinkson M, Leroy M (1995b). Molecular mapping of wheat. Homoeologous group 3. Genome 38: 525 533.
O'Donoughue LS, Kianian SF, Rayapati PJ, Penner GA, Sorrells ME, Tanksley SD (1995). A molecular linkage map of cultivated oat. Genome 38: 368–380.
Ortiz JPA, Pessino SC, Bhat V, Hayward MD, Quarin CL (2001). A genetic linkage map of diploid *Paspalum notatum*. Crop Sci. 41: 823-830.
Parker GD, Chalmers KJ, Rathjen AJ, Langridge P (1998). Mapping loci associated with flour colour in wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 96: 238–245.
Paterson AH (1996). Making genetic maps. In: Paterson AH (ed.) Genome mapping in plants, San Diego, California: Academic Press, Austin, Texas, pp. 23–39.
Paterson AH, Bowers JE, Burow MD, Draye X, Elsik CG, Jiang C-X, Katsar CS, Lan TH, Lin YR, Ming R, Wright RJ (2000). Comparative genomics of plant chromosomes. Plant Cell 12: 1523-1539.
Pedersen C, Giese H, Linde-Laursen I (1995). Towards an integration of the physical and the genetic chromosome map of barley by *in situ* hybridisation. Hereditas (Lund) 123: 77-88.
Peters JL, Cnops G, Neyt P, Zethof J, Cornelis K, Lijsebettens MV, Gerats T (2004). An AFLP-based genome-wide mapping strategy.

Theor. Appl. Genet. 108: 321–327.
Plomion C, O'Malley DM, Durel CE (1995). Genomic analysis in maritime pine (*Pinus pinaster*): comparison of two RAPD maps using selfed and open-pollinated seeds of the same individual. Theor. Appl. Genet. 90: 1028–1034.
Powell W, Machray GC, Provan J (1996). Polymorphism revealed by simple sequence repeats. Trends Plant Sci. 7: 215–222.
Rafalski A (2002). Applications of single nucleotide polymorphisms in crop genetics. Curr. Opin. Plant Biol. 5: 94–100.
Reich DE, Cargill M, Bolk S, Ireland J, Sabeti PC, Richter DJ, Lavery T, Kouyoumjian R, Farhadian SF, Ward R, Lander ES (2001). Linkage disequilibrium in the human genome. Nature 411:199–204.
Reiter RS, Williams JGK, Feldman KA, Rafalski A, Tingey SV, Scolnik PA (1992). Global and local genome mapping in *Arabidopsis thaliana* by using recombinant inbred lines and random amplified polymorphic DNAs. Proc. Natl. Acad. Sci. USA 89: 1477-1481.
Rick CM (1971). Some cytological features of the genome in diploid plant species. Stadler Genet. Symp. 1: 153-174.
Risch N (1992). Genetic linkage: Interpreting LOD scores. Science 255: 803–804.
Risch N, Giuffra L (1992). Model misspecification and multipoint linkage analysis. Hum. Hered. 42: 77–92.
Roder MS, Korzun V, Wendehake K, Plaschke J, Tixier MH, Leroy P, Ganal MW (1998). A microsatellite map of wheat. Genetics 149: 2007–2023.
Sandler L, Golic K (1985). Segregation distortion in Drosophila. Trends Genet. 1: 181-185.
Sandler L, Novitski E (1957). Meiotic drive as an evolutionary force. Amer. Naturalist 41: 105-110.
Schmidt R, West J, Love K, Lenehan Z, Lister C, Thompson H, Bouchez D, Dean C (1995). Physical map and organisation of *Arabidopsis thaliana* chromosome 4. Science 270: 480-483.
Schon CG, Hayes PM, Blake TK, Knapp SJ (1991). Gametophytic selection in a winter x spring barley cross. Genome 34: 918-922.
Schwarz G, Herz M, Huang XQ, Michalek W, Jahoor J, Wenzel G, Mohler V (2000). Application of fluorescent-based semi-automated AFLP analysis in barley and wheat. Theor. Appl. Genet. 100: 545-551.
Semagn K, Bjørnstad Å, Ndjiondjop MN (2006). An overview of molecular marker methods for plant. Afr. J. Biotechnol. 25:2540-2569.
Semagn K, Bjørnstad Å, Skinnes H, Marøy AG, Tarkegne T, William M (2006). Distribution of DArT, AFLP, and SSR markers in a genetic linkage map of a doubled-haploid hexaploid wheat population. Genome 49: 545–555.
Sharma R, Aggarwal RAK, Kumar R, Mohapatra T, Sharma RP (2002). Construction of RAPD linkage map and localization of QTLs for oleic acid level using recombinant inbreds in mustard (*Brassica juncea*). Genome 45: 467–472.
Shields DC, Collins AK, Buetow H, Morton NE (1991). Error filtration, interference, and the human linkage map. Proc. Natl. Acad. Sci. USA 88: 6501–6505.
Shiroishi T, Sagai T, Moriwaki K (1993). Hotspots of meiotic recombination in the mouse major histocompatibility complex. Genetica 88: 187-196.
Shoemaker J, Zaitlin D, Horn J, De Mars S, Kirshman J, Pitas J (1992). A comparison of three agrigenetics maize RFLP linkage maps. Maize Genet. Coop. Newsl. 66: 65-69.
Sibov ST, de Souza Jr CL, Garcia AAF, Garcia AF, Silva AR, Mangolin CA, Benchimol LL, de Souza AP (2003). Molecular mapping in tropical maize (*Zea mays* L.) using microsatellite markers. 1. Map construction and localization of loci showing distorted segregation. Hereditas (Lund) 139: 96-106.
Smith GR (1994). Hot spots of homologous recombination. Experientia 50: 234-242.
Snape JW, Flavell RB, O'dell M, Hughes WG, Payne PI (1985). Intrachromosomal mapping of the nucleolar organiser region relative to three marker loci on chromosome 1B of wheat (*Triticum aestivum*). Theor. Appl. Genet. 69: 263-270.
Somers DJ, Isaac P, Edwards K (2004). A high-density microsatellite consensus map for bread wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 109: 1105-1114.
Song QJ, Shi JR, Singh S, Fickus EW, Costa JM, Lewis J, Gill BS, Ward R, Cregan PB (2005). Development and mapping of microsatellite (SSR) markers in wheat. Theor. Appl. Genet. 110: 550-560.
Squirrell J, Hollingsworth PM, Woodhead M, Russell J, Lowe AJ, Gibby M, Powell W (2003). How much effort is required to isolate nuclear microsatellites from plants? Mol. Ecol. 12: 1339-1348.
Stam P (1993a). Construction of integrated genetic linkage maps by means of a new computer package: JoinMap. Plant J. 3: 739-744.
Stam P (1993b). JoinMap Version 1.4: A computer program to generate genetic linkage maps. CPRO-DLO, Wageningen. Centre for Plant Breeding and Reproduction Research CPRO-DLO, Wageningen, The Netherlands.
Staub JE, Serquen FC (1996). Genetic markers, map construction, and their application in plant breeding. HortScience 31: 729-740.
Strauss SH, Conkle MT (1986). Segregation, linkage, and diversity of allozymes in knobcone pine. Theor. Appl. Genet. 72: 483–493.
Suiter KA, Wendel JF, Case JS (1983). Linkage-I: A pascal computer program for the detection and analysis of genetic linkage. J. Hered. 74: 203-204.
Sumner AT, Torre JDL, Stuppia L (1993). The distribution of genes on chromosomes: a cytological approach. J. Mol. Evol. 37: 117-122.
Tani N, Takahashi T, Iwata H, Mukai Y, Ujino-Ihara T, Matsumoto A, Yoshimura K, Yoshimaru H, Murai M, Nagasaka K, Tsumura Y (2003). A consensus linkage map for sugi (*Cryptomeria japonica*) from two pedigrees, based on microsatellites and expressed sequence tags. Genetics 165: 1551–1568.
Tanksley SD, Ganal MW, Martin GB (1995). Chromosome landing: a paradigm for map-based gene cloning in plants with large genomes. Trends Genet. 11: 63-68.
Tanksley SD, Ganal MW, Prince JP, de-Vicente MC, Bonierbale MW, Broun P (1992). High density linkage maps of the tomato and potato genomes. Genetics 132: 1141-1160.
Tanksley SD, Young ND, Patterson AH, Bonierbale MW (1989). RFLP mapping in plant breeding: New tools for an old science. Bio/Technology 7: 257–263.
The Arabidopsis Genome Initiative (2000). Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. Nature 408: 796-815.
The Rice Genome Sequencing Project (2005). The map-based sequence of the rice genome. Nature 436: 793-800.
Thormann CE, Ferreira ME, Camargo LEA, Tivang JG, Osborn TC (1994). Comparison of RFLP and RAPD markers to estimating genetic relationships within and among cruciferous species. Theor. Appl. Genet. 88: 973-980.
Torres AM, Mau-Lastovicka T, Williams TE, Soost RK (1985). Segregation distortion and linkage of Citrus and Poncirus isozyme genes. J. Hered. 76: 289-294.
Van Deynze AE, Dubcovsky J, Gill KS, Nelson JC, Sorrells ME, Dvorak J, Gill BS, Lagudah ES, McCouch SR, Appels R (1995). Molecular-genetic maps for group 1 chromosomes of Triticeae species and their relation to chromosomes in rice and oat. Genome 38: 45-59.
Van Ooijen JW, Voorrips RE (2001). JoinMap® 3.0, Software for the calculation of genetic linkage maps. Plant Research International, Wageningen, the Netherlands.
Vision TJ, Brown DG, Shmoys DB, Durrett RT, Tanksley SD (2000). Selective mapping: a strategy for optimizing the construction of high-density linkage maps. Genetics 155: 407–420.
Vuysteke M, Mank R, Antonise R, Bastiaans E, Senior ML, Stuber CW (1999). Two high density AFLP linkage maps of *Zea mays* L.: analysis of distribution of AFLP markers. Theor. Appl. Genet. 99: 921–935.
Wahls WP (1998). Meiotic recombination hot spots: shaping the genome and insights into hypervariable minisatellite DNA change. Curr. Top. Dev. Biol. 37: 37–75.
Wang ML, Atkinson MD, Chinoy CN, Devos KM, Gale MD (1992). Comparative RFLP-based genetic maps of barley chromosome 5 (1H) and rye chromosome 1R. Theor. Appl. Genet. 84: 339-344.
Wendel JF, Parks CR (1984). Distorted segregation and linkage of alcohol dehydrogenase ec-1.1.1.1 genes in camellia-japonica thec-

eae Biochem. Genet. 22: 739-748.
Wenzl P, Carling J, Kudrna D, Jaccoud D, Huttner E, Kleinhofs A, Kilian A (2004). Diversity Arrays Technology (DArT) for whole-genome profiling of barley. Proc. Natl. Acad. Sci. USA 101: 9915-9920.
Wight CP, Tinker NA, Kianian SF, Sorrells ME, O'Donoughue LS, Hoffman DL (2003). A molecular marker map in 'Kanota' × 'Ogle' hexaploid oat (Avena spp.) enhanced by additional markers and a robust framework. Genome 46: 28–47.
Wittenberg AHJ, van der Lee T, Cayla C, Kilian A, Visser RGF, Schouten HJ (2005). Validation of the high-throughput marker technology DArT using the model plant *Arabidopsis thaliana*. Mol. Genet. Genomics 274: 30-39.
Yang W, de Oliveira AC, Goodwin I, Schertz K, Bennetzen JL (1996). Comparison of DNA marker technologies in characterizing plant genome diversity: variability in Chinese sorghums. Crop Sci. 36: 1669–1676.
Yim YS, Davis GL, Duru NA, Musket TA, Linton EW, Messing JW, et al. (2002). Characterization of three maize bacterial artificial chromosome libraries toward anchoring of the physical map to the genetic map using high-density bacterial artificial chromosome filter hybridization. Plant Physiol. 130: 1686–1696.
Young ND (1994). Constructing a plant genetic linkage map with DNA markers In: Ronald IKV, Phillips L (eds) DNA-based markers in plants. Kluwer, Dordrecht/Boston/London, p. 39–57.
Yun SJ, Gyenis L, Hayes PM, Matus I, Smith KP, Steffenson BJ, Muehlbauer GJ (2005). Quantitative trait loci for multiple disease resistance in wild barley. Crop Sci. 45: 2563-2572.
Zivy M, Devaux P, Blaisonneaux J, Jean R, Thiellement H (1992). Segregation distortion and linkage studies in microspore-derived double haploid lines of *Hordeum vulgare* L. Theor. Appl. Genet. 83: 919-924.