EUROPEAN ACADEMIC RESEARCH
Vol. II, Issue 3/ June 2014

Impact Factor: 3.1 (UIF)
DRJI Value: 5.9 (B+)

ISSN 2286-4822
www.euacademic.org

Molecular Markers and their Application in Genetic Mapping

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Abstract:

The development of molecular techniques in the past few decades has led to increase the vast knowledge of plant genomics research. DNA based Molecular markers, like RAPD, RFLP, ISSR, Microsatellite, EST-SSR and SNPs are useful for plant genome analysis, have now become an important tool in crop breeding. Several major traits targeted for improvement in cereals, legumes and horticultural plants breeding programs are disease resistance, abiotic stress resistant, fruit quality and quantity, secondary metabolites etc. In this review we attempt to include most of the available traditional and Insilco based DNA markers that were successfully employed in various proposes of plant genome analysis such as germplasm characterization, genetic diversity, transferability, genome mapping, QTL analysis, marker assisted breeding, genome wide analysis and population genetics.

Key words: Legumes, Molecular marker, Mapping, Marker assisted breeding

Introduction

Molecular markers are considered to be the most reliable tools to identification of germplasm, to estimate the relationships

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between genotypes at the DNA level and also for marker assisted selection (Tams et al. 2004; Raddova et al. 2003). Molecular markers can be biochemical or DNA markers. When proteins and isozymes are taken as biochemical markers, they reveal polymorphism at protein level. The most common protein markers are isozymes, which are variant forms of the same enzyme (Vodenicharova 1989). Protein markers reveal differences in gene sequences and functions and are co-dominant in nature. DNA markers reveal polymorphism at DNA level. DNA markers are promising tools to evaluate genetic diversity among germplasm (Chao-Zhi et al. 2003). These can be categorized as hybridization based and PCR based. Hybridization based polymorphisms include RFLP (Restriction Fragment Length Polymorphism) (Sambrooke et al. 1989) and VNTR (Variable Number of Tandem Repeats) loci (Rogstad 1993, 1996; Weising et al. 1992, 1998), where probes such as random genomic clones, cDNA clones, and probes for microsatellite and minisatellite sequence are hybridized to filters containing DNA which has been digested with restriction enzymes (Kumar 1999). PCR based DNA markers are RAPD, ISSR, EST-SSR, Microsatellite, CAPS etc. The molecular marker has been used previously for construction of genetic maps in many plants species. The molecular markers have been used to be very effective for mapping in many plant species (Table 1).

The review below comprises of two sections, section A deals with aspects of methodology of genetic map construction, and section B includes the progress made in the construction of genetic map in pea.

Section A- Methodological aspects of genetic map construction

The genetical review given below pertains to methodologies used in map making, the nature of mapping populations that

are used in segregational analysis of markers and types of molecular markers that are currently available for genetic mapping purposes.

Genetic linkage map construction

The basic genetic mapping and linkage analysis techniques were developed in 1911 by D.H. Morgan. The distance between any two markers/loci is measured in terms of recombination frequency between them. The development of DNA molecular markers has increased reliability and resolution of mapping. A linkage map is the graphical representation of genes, in which genes are positioned linkage group-wise on the basis of distance between them and total length of linkage groups. In the advanced genetic maps a linkage group represents a chromosome thus number of linkage groups is equal to haploid chromosome number. Each linkage group has on it morphological, molecular and biochemical markers and the distance between any two markers is indicated in centimorgan cM (Kosambi 1944). A number of softwares with different capacity of work are available (Mapmaker, Mapmanager, and Join map), which prepare the genetic maps and determine genetic distances based on recombination frequencies. Mapmaker software does not have graphical capacity and it is window based programme. Join map software now is frequently used for genetic mapping and QTLs analyses. Following steps are necessary for construction of genetic linkage map: (1) Identification of the polymorphic parents; (2) Generation of mapping population; (3) Screening of different kinds of DNA primers with parents to identify markers Polymorphic DNA for mapping population; (4) Segregational scoring of polymorphic markers in mapping population; (5) Statistical analysis for recombination frequency estimations; (5) Applications of software based programme for construction of linkage map; (6)

Identification of linkage groups; and (6) Assigning of linkage groups to chromosomes.

Development of mapping populations

Mapping population is the key requirement for construction of genetic linkage map. Selection of appropriate parents for developing mapping population is the most important step. Usually parents that are widely different in their genetic make up are chosen for crossing. The F_1 is variously advanced to raise mapping populations. The preferred types of mapping populations include F_2, $F_{2:5\text{-}7}$, back cross (BC), double haploid (DHs) and recombinant inbred lines (RILs). Sometimes near isogenic lines (NILs) are also used in genome mapping. For the preparation of linkage map, F_2 mapping population is the best population; it can be produced by selfing or sib mating the individuals in F_1 generation. Recombinant inbred lines (RIL) mapping population is developed by continous selfing of the F_2 individuals till F_6-F_7 generation. When the RILs reach acceptable level of phenotypic uniformity with respect to 50% flowering, day to maturity, plant height and other morphological traits then the lines can be genotyped using polymorphic markers identified based on the parental polymorphism. The double haploids are produced by culturing anthers from F_1 plants. The isogenic lines are either derived as mutants or by repeated backcrossing programme.

Bulk segregant analysis

The bulk segregant analysis method (BSA) was developed by Michelmore et al. in 1991. It is a very useful technique to identify markers linked to gene of interest and its molecular position on a genetic linkage group. The BSA method has been proved to be very effective for mapping when coupled with RAPD, ISSR, EST-SSR, Microsatellite, AFLP techniques for

identification of DNA markers linked with genes in many plant species. When a RAPD marker is found associated with a trait of interest it can be converted into a more reproducible marker such as SCAR marker (Sequence Characterized Amplified Region). Prevoiusly BSA had been frequently used for linkage mapping of different gene which were responsible for disease resistant as well as leaf development in pea (Schneider et al. 2002; Prioul et al. 2007; von Stackelberg et al. 2003).

Genetic markers

Locus which shows experimental (polymorphism) variation between the parents and the individuals of the mapping population is considered as a genetic marker. The genetic markers linked to agronomic traits are most important for accelerating traditional breeding programmes. This process is known as marker-assisted selection (Zheng et al. 1995). The most important properties for good quality of a genetic marker are: (a) highly polymorphic nature; (b) co-dominant inheritance; (c) frequent occurrence in genome; (d) selective neutral behavior; (e) easy and fast assay; (f) high reproducibility; and (g) low or null interaction with other markers allowing the use of many markers at the same time in a segregating population. Three types of markers have been used in genome analysis: (1) morphological, (2) isozyme/protein based and (3) DNA based.

Morphological markers

Morphological trait that is controlled by a single locus can be used as a genetic marker. The expression of morphological markers should be reproducible over a range of environments (Kumar 1999). Morphological markers are used by breeders when an important trait that is difficult to assess is tightly bound to a trait. Morphological markers are usually highly dependent on environmental and physical factors. For breeding

experiments, these markers are time consuming, labour intensive and large numbers of plants are required, needing huge plots or green house space. However, they are most important in investigation, concerning the yield and plant development.

Molecular markers

Random Amplified Polymorphic DNA (RAPD)

RAPD is a PCR based technique which does not require any prior information of cloning or sequencing of DNA. This technique was developed by Welsh and McClelland 1990; and Williams 1990. It has been proven valuable in the construction of genetic maps in several species and in the production of genetic markers linked to specific phenotypic traits in particular using bulked segregant pools. RAPD technology became popular because of its simplicity and ease of use in a modestly equipped laboratory in contrast to Restriction Fragment Length Polymorphism (RFLP) technology which is time consuming and labour intensive and not in much use in recent years. The RAPD can generate large number of markers which can complement traditional morphological markers, which may be limited in availability. Thus, this method provides a valuable new resource for phylogenetic studies. The RAPD technique has been used for analysis of genetic polymorphism in different pea cultivars, lines and mutants.

This procedure generates nucleotide sequence polymorphisms in DNA by using a arbitrary nucleotide sequence primer of 10 bp frgamnet of size which are highly polymorphic and can be easily detected on ethidium bromide-stained agarose gels. In this reaction, a single primer (8-10 bp) anneals to the genomic DNA at two different sites on complementary strands of DNA template. However, due to the stochastic behaviour of DNA amplification with arbitrary sequence primers, it is important to optimize and strictly

maintain consistent reaction conditions for reproducible DNA amplification. They are dominant in nature and hence have limitations in their use as markers for mapping purpose. RAPD assay had been used by several groups as efficient tool for identification of markers linked to agronomically important traits, disease resistant and morphologically important traits in bulk segregant analysis. The importance of RAPD markers increased after development of SCAR marker from the cloning and sequencing of RAPD products of specific bands. Application of RAPD markers in genetic mapping, linkage analysis and individual-specific genotyping has largely been carried out, but is less popular due to problems such as poor reproducibility, faint or fuzzy products, and difficulty in bands scoring, which lead to inappropriate inferences. When properly used, RAPD markers are highly useful.

Microsatellites

The microsatellite term is given by Jeffery et al. (1985). Microsatellite primers are short tandem repeats (STRs), or simple sequence repeats (SSRs), which consist of one to six base pair long sequences that are repeated several times. The number of repeats for the microsatellites is usually less than 100. The length variation for SSRs is based on the differences in the number of repeats. Amplifying the tandem arrays and then visualizing them on a gel can detect variation in DNA length.

Microsatellite primers are mainly designed directly from the searching through the DNA sequence data bases for sequences containing simple repeats. Hybridization and sequencing are required for generating suitable microsatellites primers, to study the mapping and linkage analysis in animals and plants. Hybridization using simple repeats as probes to screen genomic clones can be used to identify the microsatellites. The flanking sequence can be obtained by sequencing the cloned fragments containing microsatellites.

Once the microsatellite markers are found, the utility of markers is high.

DNA sequences flanking SSRs are known to be conserved in the same manner as those flanking misisatellites (VNTRs). These unique sequences have been used for designing suitable primers which are polymorphic and specific for the SSR loci. When such type of primer pairs are used to amplify, they will reveal polymorphism in the form of length variation of the amplified product. This polymorphism is based on differences in repeats of simple sequences; polymorphism revealed by SSRs is also termed as simple sequence length polymorphism or SSLP. Further, these microsatellite markers use long PCR primers which are specific to a single genetic locus, they are codominant and, most importantly, they are multiallelic and detect a much higher level of DNA polymorphism than any other marker system. Such simple sequence length polymorphisms occur very frequently in a genome, and have proven to be extremely useful as DNA markers.

These properties make microsatellite primers a rich source for DNA markers, which provide specific tools for collaborative research acting as universal genetic mapping markers, and for characterization of accessions in plant germplasm collection. The presence of SSR in plants was first reported by Condit and Hubbel (1991), suggesting their abundance in plant systems. Later Akkaya et al. (1992) reported length polymorphism of SSR in soybean, which opened a new source of PCR-based molecular markers for other plant genomes. Additionally, it has also been demonstrated that SSRs are highly informative and locus specific markers in many species (Song et al. 2002). A well developed microsatellite based genetic map of pea was produced by Loridon et al. 2005, and various linkage analyses had been done by using of microsatellites primers in pea. Presently these primers have

become important tools for genomic study of plant as well as animal because their high reproducibility and polymorphism.

Inter Simple Sequence Repeat markers (ISSR)

Zietkiewicz et al. (1994) reported ISSR or universal marker and describe it is a PCR based technique. The ISSR primers based on microsatellites are utilized to amplify inter-SSR DNA sequences. It is a simple and quick method that combines most of the advantages of microsatellites (SSRs) and amplified fragment length polymorphism (AFLP) to the universality of random amplified polymorphic DNA (RAPD). ISSR markers are mostly dominant in nature and behave like a RAPD markers, though occasionally a few of them exhibit co-dominance. ISSR primers can be used variously because they can be synthesized in large number of combinations of di-, tri-, tetra- and penta-nucleotides [(4) 3 = 64, (4) 4 = 256] etc.

Cleaved Amplified Polymorphic Sequences (CAPS)

CAPS markers technique is based on digestion of monomorphic PCR product to generate polymorphism. Such digestion products are compared for their differential migration during electrophoresis (Jarvis 1994). CAPS primer can be synthesized based on the available sequence information from the databank of genomic or cDNA sequences or cloned RAPD bands. These markers are co-dominant in nature. This technique is similar to RFLP and known as PCR-RFLP (RFPL is based on hybridization). Konieczny and Ausubel (1993) described the use of CAPS marker procedure for genetic mapping.

Expressed Sequence Tags (ESTs)

EST markers are obtained by partial sequencing of random cDNA clones. EST markers which are synthesized from cDNA sequences are valuable source of molecular markers and presently being used extensively. EST analysis is a simple and quick strategy to study the transcribed parts of various

genomes. There are a number of advantages using expressed genes compared with anonymous sequences as genetic markers. They are useful in cloning of specific gene of interest and mapping of functional genes in various related organisms. ESTs are mainly used in full genome sequencing and identifying active genes which are associated with a trait of interest (Chen et al. 2001; Thiel et al. 2003). Therefore, EST-derived markers can provide opportunities for finding a unique gene and they can enhance the role of genetic markers by assaying variation in transcribed and known-function genes. EST derived markers are more highly conserved and more transferable between species (Corderio et al. 2001; Varshney et al. 2005). Several genetic maps of different plant systems were constructed by using EST derived markers. Recently EST derived markers based genetic map was developed by Fondervilla et al. 2008 in pea. EST-SSR markers are also proving highly useful in mapping of expressed genes and map making.

Table 1: Molecular markers commonly used for tagging and mapping genes of agronomic importance

Marker	Technique	Reference
RFLP	Restriction fragment length polymorphism	Botsteuin et al. 1980
SSCP	Single strand conformation polymorphism	Orita et al. 1989
AP-PCR	Arbitarily-primed PCR	Welsh et al. 1990
AS-PCR	Allele-specific PCR	Sarkar et al. 1990
RAPD	Random amplified polymorphic DNA	Williams et al. 1990
DAF	DNA amplification fingerprinting	Caetano et al. 1991
SAP	Specific amplicon polymophism	Williams et al. 1991
SCAR	Sequence characterized amplified region	Williams et al. 1991
SSR	Simple sequence repeats	Hearne et al. 1992
ISSR	Inter-SSR amplification	Zietkiewicz et al. 1994
SSLP	Simple sequence length polymorphism	Saghai Maroof et al. 1994
STS	Sequence tagged site	Fukuoka et al. 1994
CAPS	Cleaved amplified polymorphic sequences	Laurie et al. 1995
AFLP	Amplified fragment length polymorphism	Vos et al. 1995
ALP	Amplicon length polymorphism	Ghareyazie et al. 1995
SNAP	Single nucleotide amplified polymorphisms	Drenkard et al. 2000

Table 2: Comparison of RFLP, RAPD, ISSR and SSR marker

Particulars	RFLP	RAPD	ISSR	SSR
Principle	Restriction, Southern blot, hybridization	DNA amplification with random primers	Amplification with ISSR primers	PCR of simple sequence repeat
Type of polymorphism	Single base changes (Insertions/Deletions)	Single base changes (Insertions/Deletions)	Base changes (Insertions/Deletions) in SSR repeat length /no. of motifs	Variations in repeat length/no. of motifs
Level of polymorphism	High	Medium	High/Medium	High/very high
Inheritance mode	Co dominant	Dominant	Dominant/ Co-dominant	Co-dominant
Sequence information required	No	No	No	Yes
Reproducibility	Very high	Low	High/Medium	High
DNA required per assay	2-10µg	20ng	50ng	50ng
Development cost	High	Low	Low	Medium
Main application	Restriction site analysis, phylogenetic studies, linkage analysis	Fingerprinting studies, phylogenetic studies, polymorphic studies, marker identification	Identification of cultivars, phylogenetic studies	Linkage mapping, studies on genetic diversity, gene tagging
Labor	Labor intensive	Easy	Easy	High

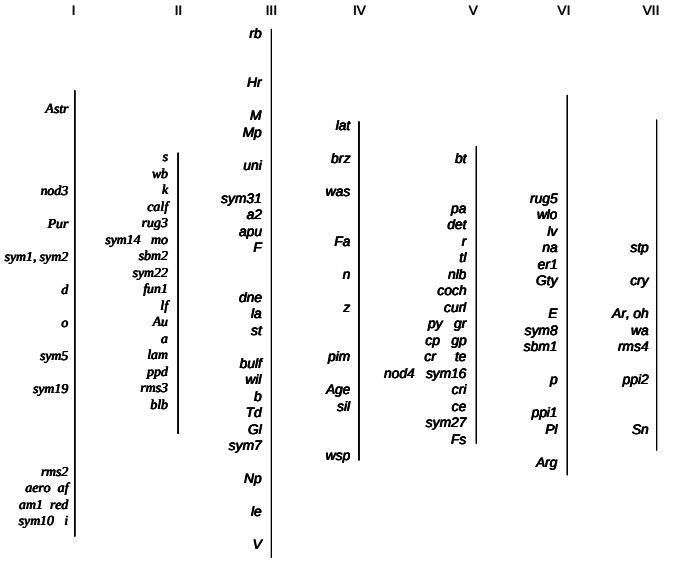
Section B- Progress in genetic map construction of pea

Several genetic maps of pea have been constructed with varieties of molecular-morphological- and isozyme- markers. The pea genetic map has been developing gradually during the past 60 years. The most recent map given by Fondevilla et al. 2008 has been developed through many changes over the years from the initial version given by Lamprecht in 1948. It was constructed using morphological markers, the number of which was rather limited. The molecular markers have tremendously increased the availability of markers for genetic mapping. As a

result the present day map of pea which is based upon both molecular and morphological marker is highly detailed and refined (Fondevilla et al. 2008).

The genetic map of pea based on morphological markers includes loci for characters such as round versus (vs) wrinkled (r) cotyledons, yellow (I) vs green (I) cotyledons, colored (A) vs white flowers, parchmented (V) vs parchmentless (v) pod wall, green (Gp) vs yellow (gp) color of unripe pods, non fascinated (Fa) vs fascinated (fa) apical flower position and long (Le) vs short (le) internode. A large list of such characters was provided by Blixt in his 1972 paper. The map of these characters has been elegantly described by Ellis and Poyser 2001 shown in figure 1.

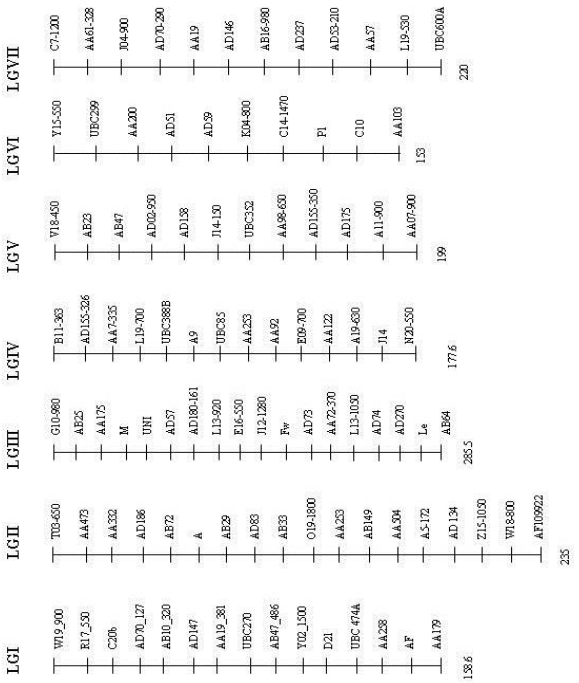
Figure 1: Morphological markers based linkage map of pea given by Ellis and Poyser (2002).



The first rather detailed genetic map of pea was based on RAPD molecular markers. It was given by Laucou et al. in

1998. A total of 355 markers were placed on this map among seven linkage group covering a distance of 1881 cM. This map was incrementally improved in several studies. One of these contributions was of Pilet-Nayel et al. 2000. In this study Quantative Trait Loci (QTLs) related to resistance to the disease *Aphanomyces* root rot were mapped with relation to 324 AFLP, RAPD, SSRs, ISSRs, STS, isozyme and morphological markers. Tar'an et al. 2003 mapped QTLs related to plant height and resistance to *Mycospaerella* blight disease with reference 192 AFLP markers, 13 RAPD markers and one STS marker covering 1274 cM distance of the genome. Irzykowska et al. 2004 mapped QTLs controlling several morphological trait with reference to 204 isozyme, AFLP, ISSR, STS, CAPS and RAPD markers. Prioul et al. 2004 mapped the QTLs concerning to *Ascochyta* blight with reference to 206 RAPD, SSR and STS markers. A highly detailed microsatellite marker based map was constructed by Loridon et al. 2005. This covers 1430 cM distance and was based on 246 SSR markers evenly distributed on 7 linkage groups. In the most recent map developed by Fondevilla et al. 2008 QTLs for resistance to *Ascochyta* blight were mapped using a total 246 molecular markers, including RAPD, isozyme, STS, EST markers. Altogether a highly detailed integrated genetic map of pea is now in existence which is serving as the refernce point for further genetical analyses of pea. An abridged version of the current map is shown in Figure 2.

Figure 2: Present abridged genetic map of *P. sativum* (after Loridon et al. 2005).



Conclusion:

During last decades many molecular marker tools have been developed and successfully employed in several plant systems. However these marker systems have some limitations in mapping and breeding. Because of these limitations, marker assisted selection, QTLs analysis in crop breeding still not achieved in all plant systems. The main reason of this delay is insufficient availability of markers, low amplification, low transferability and high cost in developments.

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Table 3: Modified table of published map in which different types of mapping populations and different types of DNA markers specially RAPD and Microsatellite markers were used for mapping (Sarika 2008).

Common name/Botanical name	Population used	Marker type	No. of mapped loci	Map length (cM)	Reference
Pea (*Pizum sattvum*)	Primo x OSU442-15	RAPD, RFLP, AFLP, STS	209	1330	B.J. Gilpin etal. 1997
	Terese x K586, Champagne x Terese, Shawnee x Bohatyr	Microsatellite, RAPD	239	1430	Loridon etal. 2005
	Terese x K586	RAPD	240	1139	Lacou etal. 1998
	JI 281 X JI399	RAPD, AFLP	355	1881	Ellis etal. 1992
	Wtl 0245 x Wtl 1238	AFLP, ISSR, Isozyme, STS, CAPS, Morphological	204	2416	Irzykowska etal. 2001
	Wtl 0245 x Wtl 1238	AFLP, ISSR, Isozyme, STS, CAPS, Morphological	204	2416	Irzykowska etal. 2002
	Wtl 0245 x Wtl 1238	AFLP, ISSR, Isozyme, STS, CAPS, Morphological	-	-	Irzykowska and Wolko 2004
	Terese x K586	RAPD, SCAR	-	-	Rameau etal. 1998
	Puget (susceptible) x 90-2079 (partially resistant	AFLP, ISSR, Isozyme, STS, CAPS, Morphological	324	1094	Pilet-Nayel etal. 2002
	DGV (def wild-type) x PF (def mutant)	RAPD, ISSR, SCAR AFLP, RAPD, SSR, ISSR, STS, Isozyme,	-	-	von Stackelberg et al. 2003
	Carneval x MP1401	morphological,	206	1274	Tar'an et al 2003
	DP (Partially resistant) x JI296 (Susceptible)	RAPD, AFLP, ISSR, CAPS, STS, Isozyme,	206	1061	Prioul etal. 2004
	JI296 x DP RIL	morphological, RAPD, SSR, STS	-	-	Prioul etal. 2007
	P665 x Messire (susceptible pea cultivar)	EST	246	1214	Fondevilla etal. 2008
Alfalfa (Medicago sativa L.)	**F2 (MqK93 x McW2)**	**RFLP, RAPD, isozyme, morphology**	**89**	**659**	**Kiss et al. 1993**
	F2 (W2xisco x USDAP1440501	**RFLP (cDNA)**	**108**	**467.5**	**Brummer et al. 1993**
	BC1(Noninbred parents)	**RFLP, RAPD**	**153**	**659**	**Eeh et al. 1994**
	F1 (consensus map of 2 BC population)	**RFLP, SDRFs**	**88**	**443**	**Brouwer & Osbom 1999**
	F2 (spp. Quasifalcafa x spp. Coreulea)	**RFLP, RAPD, isozyme, morphology, seed protein**	**868**	**754**	**Kalo el al. 2000**
Medicago truncatula L.)	2 F1 (Mercedes 4.11 & Magali 2)	AFLP, SSR	339,350	3045, 2649	Julier et al. 2003
	F2 (Jemalong x DZA315)	RAPD, AFLP, genes, isozyme	289	1225	Thoquet et al. 2002
	F2 (ecotypes A17 x A 20)	EST, BAC, RGA	288	513	Choi et al. 2004
	F1 (M. sativa subsp. Falcate x M. sativa subsp. Sativa)	SDA, BAC, SSR	286	624	Sledge et al. 2005
Barley (Hordeum vulgare L)	DH (Proctor x Nudinka)	AFLP	511	2673	Castiglioni et al. 1998
	DH (H vulgare var. Lina x H. spontaneum Canada Park)	SSR	242	1173	Ramsay et al. 2000
	F2 (Lerche x BGRC41936), DH (Igri x Franka)	SSR	57	840	Pillen et al. 2000
	F2 (H. Chilense)	RAPD, SSR, RFLP, SCAR, STS	123	694	Hernandez et al. 2001
	DH (OWB Dom x OWB Rec)	RAPD, SSR, RFLP	120	1387	Costa et al. 2001
	RI (Azumamugi x Kato Natate Gold)	AFLP, STS	272	926	Mano et al. 2001
	DH (H vulgare var. Lina x H. spontanwum Canada park)	IMP	88	-	Chang et al. 2001
	3DH- Consensus (Igri x Franka; Steptoe x Morex; OWB Dom x OWB Rec)	SSR	76	-	Thiel et al. 2003
	2DH- Consensus (Igri x Franka; Steptoe x Morex)	SSR	127	-	Li et al. 2003
	3DH- Consensus transcript map (Igri x Franka; Steptoe x Morex; OWB Dom x OWB Rec)	SSR	185	1109	Varshney et al. 2006
	Consensus map (Igri x Franka, steptoe x morex , OWB $_{REC}$ x OWB $_{Dom}$, Lina x Canada Park, L94 x Vada and SusPtrit x vada)	SSR	775	1068	Varshney et al. 2007
Bean (Phaseolus vulgaris L.)	BC XR-235-1-1 x (Calima x XR-235-1-1)	RFLP, isozyme, seed protein, flower colour	244	1200	Vallejos et al. 1992
	F2 (BAT93 x Jalo EEP558)	RFLP, RAPD, isozyme, morphology	152	827	Nodari et al. 1993
	BC1 (Ms8E02 x Corel) x Corel)	RFLP, RAPD, SCAR, morphology	157	567.5	Adam-Blodon et al 1994
	RI (PC-50 x XAN-159)	RAPD, morphology	181	426	Jung et al. 1997
	Consensus map-RI (BAT93 x Jalo EEP558 (BJ)	RFLP, RAPD, isozyme, morphology	563	1226	Freyre et al. 1998
	F2:4 (OAC Seaforth x OAC 95-4)	RFLP, RAPD, SSR, AFLP	114	-	Tar'an et al. 2002
	2RI population (DOR 364 x G19833) (BAT93 x JaloEEP558)	SSR	100	1720	Blair et al
Cotton (Gossypium spp.)	F2 (G.hirusutum L. x G. barbadense L.)	RFLP,RAPD	355	4766	Kohel et al. 2001
	RIL (G. hirustum L.cv. TM1 x G. barbadense L. Pima 3-79)	SRAP, SSR, RAPD	193	1277	Park et al. 2005
Cotton (Gossypium spp.)	BC1 (G. hirustum L. x G. barbadense L.)	EST-SSR	442	4331	Song et al. 2005
	DH (G.hirusutum L. x G. barbadense L.)	SSR,	444	3263	Song et al. 2005
	BC1 (G. hirustum L. x G. barbadense L.)	SSR	907	5060	Han et al. 2006
	RIL (G. hirustum L. x G. barbadense L.)	SSR	433	2126	Frelichowski et al. 2006
	F2 (G. arboretum x G. herbaceum)	SSR	275	1147	Desai et al. 2006
	BC1 (G. hirustum L. x G. barbadense L.)	SRAP, SSR, RAPD,REMAP	1790	3426	Guo et al. 2007
Maize (Zea mays L.)	F2 (T x 303 x CO159)	ESTs, RFLP, SSR	1736	1727	Davis et al. 1999
	RI (B73 x Mo17)	AFLP	1539	1178	Vuylsteke et al. 1999
	F2 (D32 x D145)	AFLP	1355	1376	Vuylsteke et al. 1999
	F2 (B73 x A7)	AFLP	246	2057	Castiglioni et al. 1999
	RI (B73 x Mo17)	MITE-HBr	213	1092	Casa et al. 2000
	F2 (T1 x T2)	SSR	310	-	Maran et al. 2001
	RI (B73 x Mo17)	SSR	978	4906	Sharopova et al. 2002
Oat (Avena sativa L.)	RIL –consensus (Kanota x Ogle; Clintland64 x IL86-5698)	AFLP, RFLP	300	2351	Jin et al. 2000
(2x)	RIL (Kanota x Marion)	AFLP, RFLP	178	736	Groh et al. 2001
(2x)	RIL-consensus (Ogle x TAM O-301)	RFLP, AFLP, RAPD, STS	441	2049	Portyanko et al. 2001
(6x)	RIL (Ogle-C19401 x MAM17-5)	RFLP, AFLP, SSR	510	1396.7	Zhu & Kaeppler 2003
(6x)	RIL-consensus (Kanota x Ogle; Clintland64 x IL86-5698)	RFLP, AFLP, RAPD, SSR, isozyme	1166	1890	Wight et al. 2003
(6x)	RIL (MN841801 x Noble-2)	RFLP, AFLP, SSR, SCAR	230	1509	Portyanko et al. 2005
Rye (Scale cereale L.)	F2 (Synthetic 10.1 lines1-lines x genebank acc.)	RFLP, RAPD	92	760	Senft & Wricke 1996
	F2 (P87 x P105)	RFLP, RAPD	88	660	Korzun et al. 1998
	F2 (P87 x P105)	RFLP,isozyme, gene loci	183	1063	Korzun et al. 2001
	F2 (UC-90 x E-line) (King II x Imperial)	RFLP, SSR,	184	727	Ma et al. 2001
	F2 (DS2 x RXL10)	RFLP, SSR	282	1140	Masoje' et al. 2001
	F2 (synthetic10.1 lines)	RFLP, RAPD	71	215	Saal & Wricke 2002