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CROPS AND SOILS REVIEW

Genomic resources for improving food legume crops

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SUMMARY

Food legumes are the main source of dietary protein for a large part of the world's population, and also play an important role in maintaining soil fertility through nitrogen fixation. However, legume yields and production are often limited by large genotype × environment (G × E) interactions that influence the expression of agronomically important, complex quantitative traits. Consequently, genetic improvement has been slower than expected. Molecular marker technology enables genetic dissection of such complex traits, allowing breeders to identify genomic regions on the chromosome that have main effects or interactive effects. A number of genomic resources have been developed in several legume species during the last two decades, and provide a platform for exploiting marker technology. The present paper reviews the available genomic resources in food legumes: linkage maps, high-throughput sequencing technologies, expression sequence tag (EST) databases, genome sequences, DNA chips, targeting induced local lesions in genomes (TILLING), bacterial artificial chromosome (BAC) libraries and others. It also describes how these resources are being used to tag and map genes/quantitative trait loci (QTLs) for domesticated and other agronomically important traits. This information is important to genetic improvement efforts aiming at improving food and nutrition security worldwide.

INTRODUCTION

Food legumes are important food and feed crops worldwide. Dry peas (*Pisum sativum*), soybean (*Glycine max*), dry beans (*Phaseolus vulgaris*), groundnut (*Arachis hypogaea*), chickpea (*Cicer arietinum*), pigeonpea (*Cajanus cajan*), lentil (*Lens culinaris*), mungbean (*Vigna radiata*), urdbean (*Vigna mungo*) and cowpea (*Vigna unguiculata*) are among the most important legume crops. Legumes are rich in protein (180–290 g/kg), complementing cereal staples in the human diet. They also play an important role, particularly in low-input farming systems, in maintaining soil fertility by fixing atmospheric nitrogen through symbiotic association with bacteria. Food legumes are grown mostly under rainfed conditions on marginal lands, resulting in poor yields. Global production, currently about 55·9 million metric tonnes, can easily be increased by 30–40% if losses caused by biotic and abiotic stresses (e.g. wilt, rust, ascochyta blight, drought, heat and cold) are prevented (Sharma *et al*. 2008; Canci & Toker 2009).

In the last five decades, global pulse production involving major grain legume crops except soybean and groundnut has increased only slightly, by 0·77% per year, with wide fluctuations in production (FAO 2010). In India, the world's largest producer, growth in terms of yield production was only 0·24% (AICRP on MULLaRP 2009–10). Per capita availability of pulses has declined. In India, which is predominantly vegetarian, per capita availability has fallen from 63 g/day in 1961 to 35·3 g/day in 2009 and is expected to drop to 27·3 g/day in 2010 (Commodity Online 2009). This decline is caused by a number of factors including biotic and abiotic stresses, diversion of cultivated land to other uses, rising temperature, frequent drought and declining factor productivity (Bellaloui *et al*. 2008; Koutroubas *et al*. 2009; Zheng *et al*. 2009).

Progress in genetic improvement and yield stability has been slow, partly due to large genotype × environment (G × E) interactions on the expression of

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quantitative traits (Imrie & Shanmugasundaram 1987; Malhotra & Singh 1991; Singh & Kumar 1994; Kumar *et al*. 1996; Kumar & Ali 2006; Phakamas *et al*. 2008). However, advances in molecular marker technology now offer opportunities for genetic dissection of complex quantitative traits such as grain yield: quantitative trait loci (QTLs) analysis can help identify QTLs providing stable responses across environments and interacting with specific environments. The molecular markers associated with the desirable QTLs that are identified can be used by plant breeders for more precise genetic manipulation of target traits. In the past two decades, a vast amount of genomic resources have been developed in legume crops. However, these resources are not yet routinely used in breeding programmes to improve productivity and grain quality. The present review focuses on the development, dynamics and utilization of genomic resources in major legume crops.

CHARACTERIZATION OF LEGUME SPECIES

There are about 20 000 species of legumes, belonging to three subfamilies: Mimosoideae, Caesalpinioideae and Papilionoideae. Most of the economically important food and feed legumes belong to Papilionoideae, which has four clades (Doyle & Luckow 2003; Gepts *et al*. 2005). Two clades, haseoloids/millettioid and galegoids/hologalegina, which have a common ancestor, comprise the world's most important tropical and temperate food legume species. Tropical or warm-season food legumes such as common bean (*P. vulgaris*), cowpea (*V. unguiculata*), soybean (*G. max*) and pigeonpea (*C. cajan*) fall into the haseoloids/ millettioid clade. Temperate or cool-season legumes are members of the galegoids/ hologalegina clade, which further splits into Loteae and inverted repeat-loss subclades. The latter is characterized on the basis of a lost copy of the inverted repeat found in the chloroplast genome of most angiosperms. The model legume species *Lotus japonicus* is the member of Loteae, while many cool-season legumes including alfalfa (*Medicago truncatula*), chickpea (*C. arietinum*), faba bean (*Vicia faba*), lentil (*L. culinaris*) and pea (*P. sativum*) belong to the inverted repeat-loss subclade. Chickpea, pea and lentil were among the earliest domesticates in the Fertile Crescent of the Near East during Neolithic times (Zohary & Hopf 2000). Peanut (*A. hypogaea* L.) and lupins (*Lupinus angustifolius*) are the two exceptions; they fall separately in the dalbergioid clade (which is more basal and mostly tropical) and the genistoid clade (Moretzsohn *et al*. 2007). Based on phylogenetic relationships, species from different clades show genetic proximity to each other due to extensive genome conservation (Weeden *et al*. 1992; Menancio-Hautea *et al*. 1993; Zhu *et al*. 2005), although crop legumes differ greatly in their genome size, base chromosome number, ploidy level and compatibility status (Table 1).

During the course of evolution, plant species retained different levels of conservation in their genomes depending on their phylogenetic separation. In several studies, these conserved or orthologous regions have been shown to have physical and genetic colinearity in gene order and contents among different taxa (Choi *et al*. 2004*a, b*; Wojciechowski *et al*. 2004; Gepts *et al*. 2005; Zhu *et al*. 2005; Phan *et al*. 2007). Several studies demonstrate that the *M. truncatula* genome has high-level synteny with *Medicago sativa* (Choi *et al*. 2004*a*), pea (Aubert *et al*. 2006), bean (Hougaard *et al*. 2008) and lentil (Phan *et al*. 2007). Conserved synteny has also been observed between lentil and pea (Weeden *et al*. 1992), common bean and soybean (Lee *et al*. 2001) and *Lotus* and bean (Hougaard *et al*. 2008). Limited synteny has been observed between cool-season and warm-season legume species (Choi *et al*. 2004*a*; Zhu *et al*. 2005).

GENOMICS IN LEGUMES

A broad range of genomic resources is available, and can be used to accelerate legume improvement. These include expression sequence tag (EST) database, genome sequences (whole or partial), physical maps, molecular maps, DNA chips and bacterial artificial chromosome (BAC) or similar genomic libraries.

Genome sequences

Progress in legume genome sequencing has been particularly encouraging in three model species: *Medicago, Lotus* and *Glycine*. In cool-season legumes, *M. truncatula* and *L. japonicus* have been chosen as model species due to their small diploid genomes (*c*. 500 and 471 Mbp in size), short life cycle and availability of supportive resources (Young *et al*. 2005). In *Medicago*, 0·6–0·7 of the estimated euchromatic genomic regions has been sequenced, capturing *c*. 0·60 of the genes. Sequencing is expected to be completed soon with an assembly of *c*. 300 Mbp, covering nearly all the euchromatin and capturing *c*. 0·90 of the genes (Young & Udvardi 2009).

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Table 1. *Information on the prominent legumes*

Crop	Generic name	Chromosome no. (*n*)	Genome size (Mbp)	EST*	Molecular maps (cM)
Blackgram	*Vigna mungo*	11	574	49	783 (Chaitieng *et al.* 2006), 865 (Gupta *et al.* 2008)
Burclover	*Medicago truncatula*	8	500–550	285 252	513 (Choi *et al.* 2004*a*)
Chickpea	*Cicer arietinum*	8	740	35 422	2077 (Winter *et al.* 2000; Nayak *et al.* 2010)
Common bean	*Phaseolus vulgaris*	11	637	107 890	960 (Vallejos *et al.* 1992), 739·6 (Radhika *et al.* 2007)
Cowpea	*Vigna unguiculata*	11	620	187 660	684 (Menancio-Hautea *et al.* 1993), 972 (Menéndez *et al.* 1997), 669·8 (Ubi *et al.* 2000), 2670 (Ouedraogo *et al.* 2002*a*)
Field pea	*Pisum sativum*	7	4400	21 507	1700 (Ellis *et al.* 1992), 550 (Dirlewanger *et al.* 1994), 1330 (Gilpin *et al.* 1997), 1094 (Laucou *et al.* 1998)
Lotus	*Lotus japonicus*	6	472	242 984	367 (Sandal *et al.* 2002), 508·5 (Wang *et al.* 2008)
Mungbean	*Vigna radiata*	11	579	1576	1570 (Menancio-Hautea *et al.* 1993), 758·3 (Lambrides *et al.* 2000), 691·7 (Lambrides *et al.* 2000), 737·9 (Humphry *et al.* 2002)
Pigeonpea	*Cajanus cajan*	11	858	25 132	–
Soybean	*Glycine max*	20	1115	1 429 050	(Cregan *et al.* 1999*a*)
Lupin	*Lupinus polyphyllus*		468–1177	39	–
Lentil	*Lens culinaris*	7	4063	9516	1073 (Eujayl *et al.* 1998*a*), 784 (Rubeena *et al.* 2003), 2172 (Duran *et al.* 2004), (Hamwieh *et al.* 2005), 1868 (Tullu *et al.* 2008)
Alfalfa	*Medicago sativa*	8	800–900	13 358	–
Faba bean	*Vica faba*	7	13 000	60 181	300–350 (Torres *et al.* 1993), 1200 (Vaz Patto *et al.* 1999), 1445 (Roman *et al.* 2002)
Adzuki bean	*Vicia angularis*	11	540	25	1250 (Kaga *et al.* 1996), 1445 (Roman *et al.* 2002), 832·1 (Han *et al.* 2005)
Groundnut	*Arachis hypogaea*	10–20	1260–2890	87 170	1270·5 (Varshney *et al.* 2009*b*)
Red clover	*Trifolium pratense*	7	440	49	(Isobe *et al.* 2003)
White clover	*Trifolium repens*	8	956	285 252	(Zhang *et al.* 2007)

* http://www.ncbi.nlm.nih.gov/nucest (accessed 18 May 2010; verified 11 May 2011).

Similarly, gene space sequencing of the lotus genome is also nearly complete: 0·67 (315·1 Mbp out of 472 Mbp), probably covering 0·91 of the gene space, has been sequenced (Sato *et al.* 2008). Genome sequencing of these two species has provided a significant amount of information – available in the public domain – about their gene structure as well as physical and genetic maps. This has increased understanding of genetic network systems involved in biological functions of legume-specific phenomena (Stacey *et al.* 2006). Among Phaseoloid legumes, soybean has been chosen as a model genome for sequencing (Gepts *et al.* 2005) due to its economic importance (Nunberg *et al.* 2006), moderate genome size (*c.* 1115 Mbp), existing infrastructure (Jackson *et al.* 2006) and because it represents an excellent model for polyploid legume species (Jackson *et al.* 2006). Recently, it has been reported that the soybean

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whole-genome shotgun comprises 950 Mbp of assembled and anchored sequences representing about 0·85 of the predicted genome size. It has been predicted that the soybean genome has 46 430 protein-coded genes and nearly 0·75 of these genes are present in multiple copies (Schmutz *et al.* 2010). This complete draft assembly of the soybean genetic map is now available, with *c.* 5500 genetic markers (http://www.Soybase.org, verified 11 May 2011). Among diploid phaseoloid legumes, common bean has been selected as the best species for genome sequencing because of its medium-sized genome (588–637 Mbp) (Bennett & Leitch 2010), availability of BAC libraries, 9× physical map, 25 linkage maps and 83 530 ESTs and knowledge of the genic (0·29) and repetitive (*c.* 0·49) portions of genome. The extensive macrosynteny with soybean as well as other legume species has also favoured genome sequencing. Much less genomic information is available for other legumes, though some progress has been made in pea, alfalfa (lucerne, *M. sativa*), peanut (=groundnut) and cowpea (for review, see Timko *et al.* 2008). The gene-space sequence reads (GSRs) had homology to genes encoding transcription factors (TFs) that can be utilized in mapping and tagging the genes for agronomically important traits in cowpea (Timko *et al.* 2008).

BAC/binary bacterial artificial chromosome (BIBAC) and physical maps

BAC and BIBAC libraries help in genome sequencing, development of new molecular markers and physical maps, and map-based cloning of genes (Tao *et al.* 2001). Libraries of 100–150 kbp clone size have been developed in chickpea (23 780 clones with a coverage of 3·8 genome equivalents; Rajesh *et al.* 2004), soybean (>78 000 BAC clones, representing 9·6× genome; Wu *et al.* 2004), cowpea (60 000 BAC clones assembled into a 10× physical map), common bean (89 000 BAC ends sequencing yielded a 9× draft physical map or 0·09 of the common bean genome; Schlueter *et al.* 2008), pea (120 960 BAC clones; Coyne *et al.* 2007) and groundnut (84 096 clones from AA genome equivalent to 7·4× genome and 75 648 BAC clones from BB genome, representing 2·7–5·3 haploid genome equivalents; Varshney *et al.* 2009*b*). Using molecular markers, the physical map from BAC clones could also be related to the genetic map by locating existing genetic markers on the contigs (Lewers *et al.* 2002). This is a starting point for positional cloning of specific genes, and faster discovery of genes underlying phenotypes of agronomic interest (Liu *et al.* 2001; Xu *et al.* 2001). For example in soybean, a physical map has been developed from the gene-rich region of linkage group A2 near the black seed coat and *Rhg4* loci (Lewers *et al.* 2002). BAC libraries have also been used to generate simple sequence repeat (SSR) markers leading to identification of two genomic regions involved in resistance to the soybean cyst nematode (CSN; Cregan *et al.* 1996, 1999*b*). For fine mapping, BAC clones can provide large numbers of molecular markers from the genomic regions harbouring the QTL/genes.

Molecular maps

Molecular markers have been mapped in several legume species. These molecular maps have been prepared mostly using more than one type of marker, such as restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD) and SSR. Dense molecular maps consisting of more than 400 loci have been developed in a few legume crops including azuki bean (*Vigna angularis*; Han *et al.* 2005), blackgram (*V. mungo*; Gupta *et al.* 2008), common bean (Freyre *et al.* 1998) and cowpea (Ouedraogo *et al.* 2002), using different types of markers (Table 1). In legumes, both inter- and intra-specific mapping populations have been used for preparation of molecular maps: the former is more commonly used because of the low level of polymorphism in the cultivated gene pool. For example, in lentil, use of divergent parents (wild×cultivated) in development of molecular maps often results in lower recombination rates and smaller map sizes (Tadmor *et al.* 1987). As a result, molecular maps developed from these populations cannot be used as reference maps. Intervarietal maps, which have more practical utility in tagging desirable gene(s), have not yet been developed, mainly due to limited availability of polymorphic molecular markers. The first intra-specific linkage map based on SSRs and gene analogue markers has been developed in chickpea and used to map a major resistance QTL for ascochyta blight disease (Flandez-Galvez *et al.* 2003*a*, *b*). Recently, there have been efforts to develop dense intervarietal molecular maps based on highly polymorphic SSRs, single nucleotide polymorphism (SNP) and gene-based markers in soybean (Hwang *et al.* 2009), chickpea (Nayak *et al.* 2010) and common bean (Hanai *et al.* 2010).

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Functional genomics

EST databases

Extensive efforts have been made, in several legume species, to develop ESTs from genes expressing in different conditions and developmental stages (Table 1). The EST database can aid gene discovery, and generate raw material for production of cDNA arrays for transcriptome analysis (Coram & Pang 2005*a*). As a result, these easily accessible EST sequences have emerged as a valuable and cost-effective resource for *in silico* generation of markers. They assist in comparative mapping in species where limited or no sequence information is available (Table 1). EST databases provide insights into the genes and putative relationship between EST and proteins. They assist in identifying candidate genes, and in mining the alleles responsible for target traits (Buhariwalla *et al*. 2005). For example, EST libraries in chickpea have been generated and analysed for isolation of candidate genes controlling the defence mechanism against ascochyta blight (Coram & Pang 2005*b*), root development and abiotic stress tolerance (Jayashree *et al*. 2005).

Gene cloning

Classical genetic mapping identifies only the genes/QTL responsible for controlling the variation underlying the trait. However, what kind of function such genes/QTL performs at molecular and metabolic levels is not known. Using functional genomics, many genes expressing differentially in contrasting genotypes can be quickly identified. Genes that are functionally related to the target trait and are found within the genomic region where the QTL was mapped can be selected as candidates. These efforts have facilitated not only cloning of genes/QTL with major effects but also those with minor effects, helping to unlock gene networks underlying complex traits (Salvi & Tuberosa 2005). The knowledge of nucleotide sequence of genes cloned in several legume species (Table 2) has enabled the development of functional markers for marker-assisted selection (MAS) and also to introgress valuable alleles of a gene through genetic engineering. For example, the majority of disease and pest resistance genes (R genes) are members of large gene families that encode the nucleotide-binding site (NBS) and leucine-rich repeat (LRR) domains. Many functionally known resistance gene analogues (RGA) have been cloned and identified in several food legume species including *Lens* (Yaish *et al*. 2004). Transcription factors (TFs), which are proteins, play an important role in controlling the expression of genes in most biochemical pathways including the response to stress (Kasuga *et al*. 1999; Eulgem 2005). Recent studies have identified numerous genes encoding TFs in plants and paved the way for improving stress tolerance (Singh *et al*. 2002). TFs have been analysed on a large scale in *Arabidopsis* (Eulgem 2005). Because the distribution of TF genes across TF families between legume and non-legume plants does not have significant differences, several TF genes have been identified in legumes on the basis of sequence homology with *Arabidopsis* genes (see reviews: Dita *et al*. 2006; Libault *et al*. 2009).

Tools for functional genomics

Serial analysis of gene expression. Serial analysis of gene expression (SAGE) allows rapid and detailed analysis of thousands of transcripts. In chickpea, 80 238 26-bp tags representing 17 493 unique transcripts (UniTags) from drought-stressed and non-stressed control roots have been generated using SuperSAGE technology to analyse gene expression in chickpea roots in response to drought (Molina *et al*. 2008). Sanger sequencing has been used to a limited extent to access the chickpea and pigeonpea transcriptomes (27 000 and 13 000 ESTs, respectively).

Microarrays or DNA chips and transcriptome analysis. Microarrays or DNA chips are important tools for identifying the network of genes underlying the expression of an agronomically important trait (Meyers *et al*. 2004; Coram & Pang 2005*a*). These can be developed from hundreds of thousands of ESTs or cDNA libraries available in model legumes (Medicago, Lotus) and crop species (soybean, chickpea, pea, lentil, etc.). An open source platform, EMMA, has also been developed (Dondrup *et al*. 2003) for storage and analysis of large datasets from microarray experiments. Microarrays based on EST and other oligo sequences have been used to study the expression of genes involved in nodule formation during symbiotic association, and in flower, pod and seed development in *M. truncatula* (Barrel Medick or Barrel Clover; Liu *et al*. 2003; Yahyaoui *et al*. 2004; Firnhaber *et al*. 2005; Lohar *et al*. 2006). A commercial affymetrix chip with a 51 k GeneChip could also be useful for comparative analysis of gene expression in related grain and forage legumes resulting in

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Table 2. *List of some genes cloned in legume species*

Crop	Pathway	Gene (encoding enzyme/protein)	Function	References
Chickpea	Transcription factor	*CarNAC1* (NAC domain)	Plant development and stress responses	Peng *et al*. (2010)
Common bean	Phytic acid pathway	*PvMIPSs and PvMIPSv* (myo-inositol 1-phosphate synthase), *PvIMP* (inositol monophosphatase), *PvMIK* (myo-inositol kinase), *PvIPK2* (inositol 1,4,5-tris-phosphate kinase), *PvITPKa* and *PvITPKb* (inositol 1,3,4-triphosphate 5/6-kinase) and *PvIPK1* (inositol 1,3,4,5,6 pentakisphosphate 2-kinase)	Seed development	Fileppi *et al*. (2010)
	Biosynthesis of proline	*PvP5CS* and *PvP5CS2* (Δ-1-pyrroline-5-carboxylate synthetase)	Salt and drought tolerance	Chen *et al*. (2009, 2010)
Cowpea	Jasmonic acid, lipid signalling and abscisic acid pathways	CPRD12 (alcohol dehydrogenase), CPRD22 (dehydrin), CPRD14 (NADPH-dependent aldehyde reductase), CPRD8 (12-oxo-phytodienoic acid reductase), CPRD46 (lipoxygenase), VuNCED1 (9-*cis*-epoxycarotenoid), VuPLD1 (phospholipase D), VuPAT1 (a patatin-like galactolipid acyl hydrolase) , VuPI-PLC (hosphatidylinositol-specific phospholipase C), VuC (multicystanin), VuAPX (ascorbate peroxidase)	Controlling drought stress	Iuchi *et al*. (1996*a*, *b*, 2000), El-Maarouf *et al*. (1999, 2001), Matos *et al*. (2001), Diop *et al*. (2004), D'Arcy-Lameta *et al*. (2006), Contour-Ansel *et al*. (2006)
Pea, soybean, burclover and lotus	Photoresponsive pathway	MADS-box, *CONSTANS,* and *FLOWERING LOCUS T/TERMINAL FLOWER1*	Controlling flowering time	Hecht *et al*. (2005)
Soybean	Nodulation formation pathway	*Rj2* and *Rfg1*	Nodulation restriction in specific strain	Yang *et al*. (2010)

identification of thousands of genes that are induced or repressed during the development of nodules and symbiotic nitrogen fixation (Küster *et al*. 2004; Baier *et al*. 2007; Benedito *et al*. 2008; Jones *et al*. 2008). Several other studies have also investigated the transcriptional basis of seed development, differentiation, desiccation, plant responses to aluminium toxicity and changes in nitrogen nutrition using microarray chips (Buitink *et al*. 2006; Gallardo *et al*. 2007; Narasimhamoorthy *et al*. 2007; Chandran *et al*. 2008; Ruffel *et al*. 2008; Verdier *et al*. 2008). Long-oligo arrays of *M. truncatula* have also been used effectively to identify the transcripts upregulated in alfalfa trichomes secreting the molecules during insect defence (Aziz *et al*. 2005). For providing microarray data relating to abiotic stress resistance, an expression database called MtED has been developed that contains gene-expression profiles of the roots of *M. truncatula* based on time-course salt–stress experiments using the Affymetrix Medicago GeneChip (Li *et al*. 2009).

In peas, a microarray (Ps6kOLI1) consisting of 70-mer oligo probes targeting *c*. 5200 EST clusters, assembled predominantly from cotyledons under the Grain Legumes Integrated Project (GLIP) has been developed primarily for identifying genes relevant to seed formation. In soybean, high-density expression arrays containing 18 000 cDNAs (Shoemaker *et al*. 2003) and low redundancy unigene sets of 27 513 clones have been constructed from cDNA libraries made from a wide range of organs, developmental stages, disease-challenged tissues and various stress

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conditions. These microarrays have been used to examine tissue-specific gene expression and global expression in mutant iso-lines. This led to the identification of sets of candidate genes potentially encoded or modulated by the mutant phenotype (Vodkin *et al*. 2004). The micro-array tools developed in soybean have also been used successfully to identify genetic markers closely linked to soybean aphid (*Aphis glycines* Matsumura (Hemiptera: Aphididae)) resistance gene *Rag1* (Kaczorowski *et al*. 2008), and genes involved in iron deficiency chlorosis response in soybean under iron-deficient conditions (O'Rourke *et al*. 2007). In chickpea, microarray expression analysis of putative defence-related ESTs resulted in isolation and analysis of candidate ascochyta blight defence genes (Coram & Pang 2005*a*). In another study, 768-featured microarray comprising 559 chickpea cDNAs, 156 grasspea cDNAs, 41 lentil RGAs and 12 controls were used to study the transcriptional change in genes conferring tolerance to different abiotic stresses. This led to the identification of a number of genes differentiating tolerant and susceptible genotypes with respect to drought, cold and salinity (Mantri *et al*. 2007, 2010). These genes code for various functional and regulatory proteins and highlighted the complexity of abiotic stress-response mechanisms due to multiple gene control (Mantri *et al*. 2007). The expression of common genes indicated crosstalk in the genetic pathways involved in responses to stress (Mantri *et al*. 2010). Similarly, in lentil, a cDNA microarray approach has deciphered the ascochyta blight resistance genes (Mustafa *et al*. 2009).

RNAi and targeting induced local lesions in genomes (TILLING) for reverse genetics. Forward genetics begins with specific phenotypes and eventually aims at identifying the responsible genes. This can be followed either through map-based cloning or T-DNA and transpose insertional or insertion mutagenesis for cloning the genes. For example, in *L. japonicus*, transposon tagging helped to isolate a *Sym* gene (*LjNin* or *LjSym20*). This was the first gene that was isolated by the group of Jens Stougaard (University of Aarhus, Denmark). In the same species, two new *Sym* genes (*LjSym1* and *LjSym2*) have been isolated through a map-based cloning approach. The *LjSym2* gene encodes a receptor-like kinase (hence its name was changed to *LjSymRK*) (Endre *et al*. 2002). The mutant population generated through T-DNA and retrotransposon insertions is also an important resource for reverse genetics, where gene sequences or a protein with unknown function is associated with the mutated phenotype. For example, screening of a tobacco retrotransposon, *Tnt1* mutagenized population by sequencing of tagged sites has led to the isolation of *M. truncatula 'Pim'* gene (Benlloch *et al*. 2006).

RNAi- and virus-induced gene silencing are other important approaches of reverse genetics to understand the function of genes. Both methods can block genes that belong to a gene family or are expressed across a number of tissues and developmental organs where antisense gene technology fails to perform similarly (Allen *et al*. 2004). Virus-induced gene silencing has been used in pea (Constantin *et al*. 2004) and soybean (Tuteja *et al*. 2004), and could potentially be used in many other legumes as well. RNAi-induced gene silencing is well established in soybean and other model legumes using stable transformation either through biolistics or *Agrobacterium tumefaciens* (Srinivasa Reddy *et al*. 2003; Ivashuta *et al*. 2005; Lim *et al*. 2005; Subramanian *et al*. 2005; Nunes *et al*. 2006), hairy root transformation (Jackson *et al*. 2006) and transposon mutagenesis (Jackson *et al*. 2006; Tadege *et al*. 2008). These methods will be greatly aided by knowledge of the genome and open reading frames (ORFeome) (Jackson *et al*. 2006). The above methods for reverse genetics require *Agrobacterium*-mediated transformation. Unfortunately, in legumes, functional gene validation by transformation is impractical due to the difficulty of transforming legume species using *Agrobacterium*. But at the same time, this situation makes legumes ideal candidates for use of TILLING or deletion-TILLING (de-TILLING) to study the function of gene sequence. In this case, an effective association can be worked out between gene repositories available in the public domain and the genetic variability available in natural germplasm or in induced mutant populations. Several ongoing projects are using TILLING or de-TILLING to study the system biology of legume plants (Cooper *et al*. 2008; Porch *et al*. 2009; Ramos *et al*. 2009). A recent review by Tadege *et al*. (2009) provides updated information on TILLING resources in food legumes including the ongoing projects on reverse genetics. In a TILLING-based high-throughput genotyping project in *M. truncatula,* 3840 individually curate germplasm lines are used for SNPs in five separate genes of relevance to plant–microbe interactions, which have yielded from 4 to 9 mutant alleles/gene, at an average recovery rate of 1 lesion/kbp/351 germplasm lines. These 3840 germplasm lines are

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Table 3. *List of website having databases of various legume species (URLs verified 11 May 2011)*

Crop	Website	Trait
Chickpea	http://www.icrisat.org/gt-bt/ICGGC/Transcriptomics.htm	Transcriptome analysis
Common bean	http://phaseolus.genomics.purdue.edu/ http://beangenes.cws.ndsu.nodak.edu/ http://www.ccg.unam.mx/phaseolusest/	Molecular biology of various traits, transcriptome analysis (ESTs)
Cowpea	http://cowpeagenomics.med.virginia.edu/CGKB/ http://harvest.ucr.edu/	Molecular biology of various traits
M. trunculata	http://www.noble.org/mediccyc/introduction.html/	Biochemical traits
Minor legumes	http://www.ecpgr.cgiar.org/	Morphological traits
Pea	http://urgv.evry.inra.fr/UTILLdb	Molecular biology of various traits
Peanut	http://peanutgenetics.tamu.edu/cmap	Linkage groups and marker-trait association
Soybean	http://soybase.org/ http://soybeangenome.siu.edu http://www.gmo-compass.org/eng/database/plants/67.soybean.html http://casp.rnet.missouri.edu/soydb/	Molecular biology of various traits

expected to yield 10–22 mutant alleles/gene, with additional alleles being recovered from more germplasm that is available but not included in initial screening (Tadege *et al*. 2009). Using the same procedure, *c*. 2000 individual germlines were generated in *M. truncatula* (VandenBosch & Stacey 2003), a species phylogenetically related to lentil. Similarly, a TILLING facility has also been set up in *L. japonicus*. For this purpose, a population of >40 000 mutants was developed through induced mutation by using ethyl methanesulfonate (EMS) comprising mutants defective in morphological, metabolic and nodule formation characters (Perry *et al*. 2003, 2009). Mutants with variant alleles of SYMRK and sucrose synthesis genes were also developed using TILLING (Stracke *et al*. 2002; Horst *et al*. 2007).

High throughput sequencing/genotyping platforms. For breeding applications, new generation sequencing and genotyping platforms such as Solexa 1 Gbp, 454/FLX sequencing and Illumina GoldenGate assay have revolutionized plant functional genomic research. These platforms, an alternative to DNA arrays, can generate millions of ESTs per run for whole-genome expression analysis, identification of SNPs, candidate gene discovery and development of molecular markers (Varshney *et al*. 2005). Using these methods, millions of EST and transcriptomes have been generated in several legume species including *M. truncatula* (Benedito *et al*. 2008; Young & Udvardi 2009), pigeonpea, chickpea and groundnut (Varshney *et al*. 2009*a*). These platforms are useful tools for discovery of SNPs with high sensitivity and capable of identifying >0·95 of variant sites (Harismendy *et al*. 2009), particularly in pulses which have a narrow genetic base. Several institutions are working to develop SNP markers in cowpea, pigeonpea, chickpea and groundnut using these tools (Varshney *et al*. 2009*a*).

Bioinformatics tools and websites for accessing the genomic resources. Information on legume genomic resources has been provided by various organizations as subsets within larger information resources. However, Beavis (2004) made an effort to organize legume information resources on one web-based platform and summarized them as multispecies and species-specific information resources, making legume genomic resources more easily available. A number of other websites also provide information on genomic resources available for different legumes species (Table 3). The Cowpea Genespace/Genomics Knowledge Base (CGKB) database was developed under the Cowpea Genomics Initiative (CGI) programme; it contains information derived from 298 848 cowpea genespace sequences (GSS) isolated by methylation filtering of genomic DNA (Chen *et al*. 2007*a*). *M. truncatula* databases have been developed in TRUNCATULIX, which integrates five public databases for gene sequences and gene annotations, as well as a database for microarray expression data covering raw data, normalized datasets and complete expression profiling experiments. This database is freely available online (http://lily.cebitec.uni-bielefeld.de/truncatulix/app, verified 11 May 2011). It can be

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accessed via an AJAX-based web interface using a standard web browser. For the first time, users can now search quickly for specific genes and gene-expression data in a huge database based on high-quality annotations. The results can be exported as Excel, HTML or as CSV files for further usage (Henckel *et al*. 2009). Software called as SeqTrim, has been developed, which can be used as a high-throughput pipeline for pre-processing any type of sequence read (Falgueras *et al*. 2010). BAC end sequences or low-pass shotgun sequencing provides a glimpse of local gene content. Here, bioinformatics tools are vital for gene prediction and annotation, and exploitation of syntenic relationships.

Development of random genomic and functional markers

Genomic resources developed allow legume breeders to develop both random genomic (SSR, inter simple sequence repeats (ISSR), AFLP and RFLP) and functional or perfect (EST-SSR) markers. Among these markers, polymerase chain reaction (PCR)-based SSR and SNP markers are considered more practical, i.e. easy to handle and do not require specific equipment or skilled technicians. These markers also have a high level of polymorphism and reproducibility. In legumes, these markers are in use in several crops including cowpea (768 BAC end sequence (BES)-SSRs), chickpea (510 genomic SSRs and 1655 BES-SSRs), pigeonpea (130 genomic SSRs), groundnut (700 genomic SSRs and >2000 EST-SSRs), lentil (*c*. 100 genomic SSRs) and common bean (*c*. 500 genomic and EST-SSRs) (Varshney *et al*. 2009*a*), and in soybean (6920 EST-SSRs; Hwang *et al*. 2009). But many more such markers need to be developed. For example, the Pigeonpea Genomics Initiative (PGI) was launched in November in 2006 by the Indian Council of Agricultural Research (ICAR) and the Government of India, under the umbrella of Indo-US Agricultural Knowledge Initiative (AKI). This programme led to the development of SSR (>3000), SNP and diversity array technology (DArT) (>15 000 features) markers (Varshney *et al*. 2010*a*). The progress has also been noted in other pulses (Torres *et al*. 2010).

The use of functional markers is of great interest to plant breeders as a huge amount of genomic sequences are junk DNA or repetitive sequences. Over the last few years, functionally characterized genes, ESTs and coding genome sequences have also become available to build molecular markers like SNP, SSR or conserved orthologous sets (COS) (Varshney *et al*. 2005). For example, use of the sequences of RGAs or resistance-gene candidates (RGACs) have been transformed into molecular markers including RGA polymorphism (Mutlu *et al*. 2006), NBS profiling (van der Linden *et al*. 2004), cleavage amplification polymorphism (CAP) (Quint *et al*. 2002) and derived CAPs (dCAPs) (Komori & Nitta 2005). RGAs belonging to NBS gene families were recently isolated and characterized in faba bean and chickpea (Palomino *et al*. 2006). dCAPs and CAPs developed from 10 RGA classes have been used to explore the presence of SNPs and map them into the available faba bean, pea and chickpea mapping populations (Palomino *et al*. 2009; Torres *et al*. 2010).

UTILIZATION OF GENOMICS IN LEGUME IMPROVEMENT

The use of genomics and functional genomics in lentil and chickpea breeding is reviewed in detail by Muehlbauer *et al*. (2006) and Coram *et al*. (2007). In other legumes, a vast amount of genomic resources are available in the public domain. Plant breeders can exploit these genomic resources along with the available genetic resources, using different approaches (Fig. 1).

Marker-assisted diversity analysis

Crop improvement requires the presence of genetic diversity within the cultivated gene-pool. Understanding of crop genetic diversity helps in selecting diverse parental lines for generating segregating populations with more variability, broaden the genetic base of germplasm by introgressing genes from wild relatives, and conservation of landraces. Different kinds of molecular markers have been used to study genetic diversity in a number of food legume crops involving a set of cultivated and wild accessions (Ford *et al*. 2002; Seehalak *et al*. 2006; Yang *et al*. 2006; Zong *et al*. 2009; Ahmad *et al*. 2010). Assessment of genetic diversity helps identify and rescue genetic resources at risk of extinction (Polegri & Negri 2010). For example, in cowpea, landraces from Umbria (Italy) were initially characterized for morphological, organoleptic and genetic traits and reintroduced among farmers. This led to an expansion of the area under land races and increased farmers' income. To further encourage cultivation of land races, a request for the Protected Designation of Origin (PDO) status was initiated and

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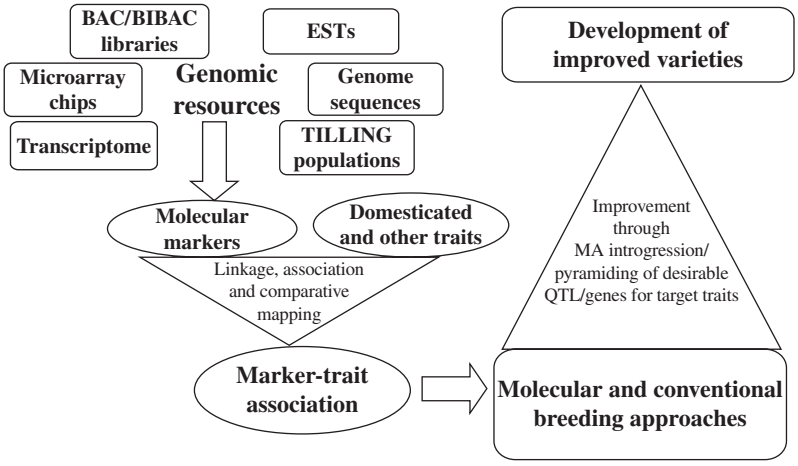


Fig. 1. Strategies to use legume genomic resources for improvement of food legumes.

studies conducted using AFLP markers with the aim of certifying that land races used in farmers' fields actually belonged to the local traditional agricultural and cultural context. The genetic diversity and phylogenetic analysis based on AFLP markers classified the local land races and others into two separate groups, suggesting that farmers conserved those land races (Polegri & Negri 2010). There is a general perception among the scientists that current genetic improvement methods lead to narrowing down of the cultivated gene-pool due to the limited use of diversity. However, genetic diversity estimates using molecular markers in different crops including pea as representative of pulse crops demonstrates that no gain or reduction of genetic diversity has occurred in the last five decades (van de Wouw *et al*. 2010).

Harnessing the desirable variability of wild relatives

Wild species/relatives are the reservoirs of genes conferring resistance to many biotic and abiotic stresses. However, their transfer from wild species to elite cultivars through conventional breeding has been limited, mainly due to the associated transfer of undesired alleles (linkage drag). It is now feasible to recover/transfer the favourable alleles in elite germplasm that were left behind by the domestication process more efficiently using molecular maps and integrative QTL analysis (for details, see Chamarthi *et al*. 2010). There are two approaches: the first is to construct introgression libraries that are made up of several introgression lines (ILs). These lines are developed by successive backcrossing (generally three to four generations) of F_1s derived from wild × cultivated lines. As a result, the donor genome (from the wild species) is distributed over the whole genome in the introgression lines and the impacts of these fragments on phenotypic expression can be studied. A few attempts to develop such libraries have been made in soybean using wild soybean species (*Glycine soja*) (Concibido *et al*. 2003) and in peanut from synthetic tetraploids (Foncéka *et al*. 2009). The second approach is to use advanced-backcross QTL (AB-QTL) analysis for detecting additive, dominant, partially dominant and over-dominant QTL (Tanksley & Nelson 1996). This approach also employs repeated backcrossing with the elite parent in wild × cultivated species crosses in order to decrease the number and size of the exotic introgressions. This reduces the burden of linkage drag and advanced backcrossed populations (BC_2F_2 or BC_2F_3) are used to identify desirable genes/QTL through QTL analysis. Thus, it leads to simultaneous discovery of QTL and generation of introgression lines. Once favourable QTL alleles are identified, only a few additional marker-assisted generations are required to develop full near-isogenic lines (NILs) that can be field-tested and used for varietal development. The AB-QTL approach has been used successfully in common bean and soybean (Blair *et al*. 2003; Chaky *et al*. 2003).

Testing the hybridity of F_1 plants

Making crosses between diverse parents is difficult in practice in food legume crops, especially lentil, where flower size is too small. As a result, it increases the chances of selfing. Moreover, differentiating F_1 plants from selfed ones also becomes difficult due to low

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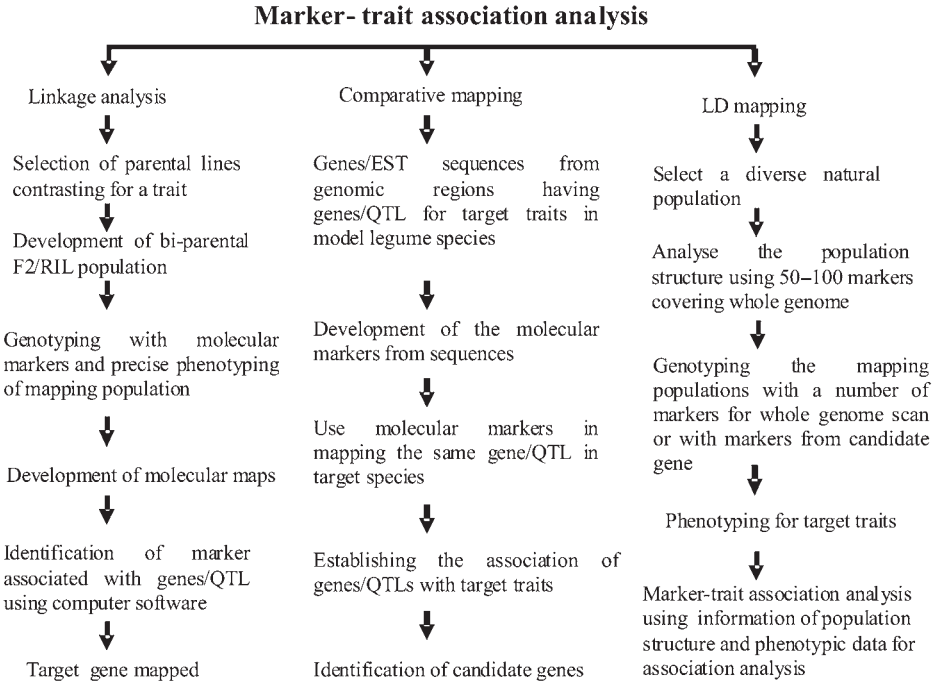


Fig. 2. Flow diagram of different methods of marker-trait association analysis.

phenotypic diversity between the crossed plants. In this situation, molecular markers can be used to identify F_1 plants and generate a true segregating F_2 population for selection of desirable plants and avoiding segregation distortion. Recently, this has been applied successfully in lentil: 0·21 F_1 plants were identified as true F_1 plants, with the remainder being either selfed or admixtures (Solanki *et al.* 2010). These results suggest that molecular markers can reduce the time and money required to grow a population from selfed or admixed plants and increase the efficiency of plant breeders in selection of recombinant plants (Solanki *et al.* 2010).

Genetic dissection of network of genes underlying the complex traits (QTL analysis)

Markers can be used to decipher the network of genes underlying a complex trait. For this purpose, molecular maps developed in a number of legume species can be utilized as a reference map. Plant breeders can use the mapped markers to develop the framework linkage map from a trait-specific mapping population. This will help to identify markers associated with genomic regions contributing as major loci or interacting with environments (Kulwal *et al.* 2004). Individual QTL is designated as major or minor or environment-responsive QTL if it expresses in a particular environment. Major QTL generally account for a relatively larger phenotypic variation ($R^2 > 0{\cdot}20$) and minor for a small ($R^2 < 0{\cdot}20$) variation. In general, traditional linkage mapping, association mapping and comparative genomics are routinely used methods for establishing the marker-trait association in food legume crops (Fig. 2). The traditional linkage mapping has been used to map a number of genes/QTL controlling both quantitative and qualitative traits (see Table 4 for references). It involved the use of biparental mapping population and focused to map the major genes controlling resistance to diseases and insect-pests. Among food legumes, it was first used in pea and cowpea (Adam-Blondon *et al.* 1994; Dirlewanger *et al.* 1994; Timmerman *et al.* 1994). In order to identify a network of genes controlling a trait of interest, there is a need to prepare dense molecular maps and hence the efforts are now focused on development of such maps in soybean (Hwang *et al.* 2009), common bean (Hanai *et al.* 2010) and chickpea (Nayak *et al.* 2010).

During mapping, it becomes important to identify the closely linked markers so that these can be utilized in breeding programmes; therefore a distance of <5 cM between marker and target gene/QTL has been suggested as useful (Michlmore 1995). Traditional linkage mapping usually localized a QTL within a 10–20 cM interval due to the use of a bi-parental mapping population that involves few recombination

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Table 4. *Molecular markers linked to desirable genes/QTL for MAS in legumes*

Crops	Traits	QTL/genes	Type of markers	References
Alfalfa	Aluminium toxicity	–	RFLP	Sledge *et al.* (2002)
Blackgram	Yellow mosaic virus resistance	Monogenic	STS-RGA	Basak *et al.* (2004)
			ISSR, SCAR	Souframanien & Gopalakrishna (2006)
Blue lupin	*Diaporthe toxica* resistance	*Phr1*	SCAR	Yang *et al.* (2002)
	Colletotrichum gloeosporiodes resistance	*Lanr1*	SCAR	Yang *et al.* (2004*a*, *b*)
Chickpea	*Ascochyta* blight resistance	QTL	RAPD	Millan *et al.* (2003), Cobos *et al.* (2005)
		Ar19	RAPD	Rakshit *et al.* (2003)
		QTL_{AR3}	SSR	Cho *et al.* (2004), Iruela *et al.* (2007)
		QTL	SSR	Flandez-Galvez *et al.* (2003*b*), Anbessa *et al.* (2009)
		QTL	SSR, RGA	Flandez-Galvez *et al.* (2003*a*)
	Fusarium wilt resistance	*foc-0*	RAPD, SSR	Cobos *et al.* (2005)
		foc-3	SSR, STS	Sharma *et al.* (2004)
		foc-4	SSR	Cho *et al.* (2004)
		foc-5	SSR	Iruela *et al.* (2007)
	Double podding, seeds/pod, mean seed weight	*Sfl, Spp,* QTL	RAPD, ISSR, RGA, SSR, ASAP	Radhika *et al.* (2007)
	Seed shape and size, stem colour, flowering time	QTL	SSR	Hossain *et al.* (2010)
Common bean	Common bacterial blight	QTL	RAPD, SCAR, STS, SSR, RFLP	Jung *et al.* (1997), Yu *et al.* (2000), Miklas *et al.* (2006*a*), Tar'an *et al.* (2001), Kelly *et al.* (2003), Miklas *et al.* (2003*a*), Yu *et al.* (2004), Liu *et al.* (2008)
	Bean common mosaic virus	*I*	SCAR	Melotto *et al.* (1996)
		bc-3	RAPD	Johnson *et al.* (1997)
		bc-1, bc-2, bc-3	RAPD, SCAR	Miklas *et al.* (2006*a*)
	Anthracnose resistance	*Are*	RAPD, SCAR	Adam-Blondon *et al.* (1994)
	Bean gold mosaic virus	*Bgm-1*	RAPD, SCAR	Urrea *et al.* (1996), Blair *et al.* (2007)
	Anthracnose	*Co-4*	SCAR	Melotto & Kelly (2001)
	White mold resistance	QTL	AFLP, SCAR	Miklas *et al.* (2001), Kolkman & Kelly (2003), Ender *et al.* (2008)
	Leaf hopper resistance	QTL	PV-atcc 003	Murray *et al.* (2004)
	Fusarium wilt resistance	*PvPR1, PvPR2*	RAPD	Schneider *et al.* (2001)
Cowpea	Anthracnose resistance	*Are*	RAPD, SCAR	Adam-Blondon *et al.* (1994)
	Striga gesneriodes resistance	*Rsg1*	SCAR	Boukar *et al.* (2004)
		Rsg3, 994-Rsg	AFLP	Ouedraogo *et al.* (2002*a*)
	Aphid resistance	*Rac1*	RFLP	Myers *et al.* (1996)
Faba bean	Broomrape resistance	*Oc1, Oc2, Oc3*	RAPD	Roman *et al.* (2002)
	Ascochyta blight resistance	*Af-1, Af-2*	RAPD	Roman *et al.* (2003)
	Rust resistance	*Uvf-1*	RAPD	Avila *et al.* (2003)
Mungbean	Powdery mildew resistance	QTL	AFLP, RFLP	Young *et al.* (1993), Chaitieng *et al.* (2002), Humphry *et al.* (2003)

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Table 4. (*Cont.*)

Crops	Traits	QTL/genes	Type of markers	References
	Bruchid resistance	*Br*	RFLP RAPD, CAP, AFLP	Kaga & Ishimoto (1998) Chen *et al.* (2007*b*)
Lentil	*Ascochyta* blight resistance	*QTL*	RAPD	Ford *et al.* (1999)
		Ra/2	RAPD, SCAR	Chowdhery *et al.* (2001), Tar'an *et al.* (2003*a*)
		QTL	AFLP	Rubeena *et al.* (2006)
	Anthracnose resistance	*LCt-2*	AFLP, RAPD	Tullu *et al.* (2003), Tar'an *et al.* (2003*a*)
	Fusarium wilt resistance	*Fw*	RAPD, SSR	Eujayl *et al.* (1998*b*), Hamwieh *et al.* (2005)
	Cold Winter hardiness	*Frt*	RAPD, SSR RAPD, SSR, AFLP	Eujayl *et al.* (1999) Kahraman *et al.* (2004)
	Earliness and plant height	QTL	RAPD, SSR, AFLP	Tullu *et al.* 2008
	Plant structure, growth habit and yield	QTL	RAPDs, ISSRs, AFLPs, SSRs	Fratini *et al.* 2007
	Stemphylium blight resistance	QTLs	SSRs, SRAPs, RAPDs	Saha *et al.* (2010*a*)
	Rust resistance	*R*	STS, SSRs, RFPLs, RAPDs, CAPS, dCAPS	Saha *et al.* (2010*b*)
Pea	Powdery mildew Erysiphe resistance (pisi)	*er-1*	SCAR, RFLP	Dirlewanger *et al.* (1994), Timmerman *et al.* (1994), Janila & Sharma (2004)
	Ascochyta blight resistance	QTL	SSR, RFLP	Dirlewanger *et al.* (1994), Tar'an *et al.* (2003*b*)
	Pea seed borne mosaic virus resistance	*Sbm-1, Sbm-1, Sbm-2*	RAPD, STS, cDNA-AFLP	Frew *et al.* (2002), Gao *et al.* (2004)
	Orobonche crenata	*Ocp1, Ocp2*	STS, RAPD	Valderrama *et al.* (2004)
Rice bean	Domestication-related trait	QTL	SSR	Isemura *et al.* (2010)
Soybean	Soybean cyst nematode	*rhg-1, rhg-t1*	SSR	Cregan *et al.* (1996), Mudge *et al.* (1997), Ferdous *et al.* (2006)
	Soybean mosaic virus resistance	*Rsv 3,Rsv4*	SSR, SNP, AFLP	Hayes *et al.* (2000), Jeong *et al.* (2002, 2004), Hwang *et al.* (2006)
	Forgeye leaf spot resistance	*Rcs3*	SSR	Mian *et al.* (1999)
	SDS	QTL	SSR	Njiti & Lightfoot (2006)
	Root and stem rot resistance	*Rps8, Rps3*	SSR	Sandhu *et al.* (2005)
	Brown stem rot resistance	*Rbs1;Rbs2*	SSR	Bachman *et al.* (2001)
	Soybean rust resistance	*Rpp1*	SSR	Hyten *et al.* (2007)
	Soybean aphid resistance	*Rag1*	SSR	Li *et al.* (2007)
	Protein	Glycinin (11S, G4); beta-conglycinin (7S)	SSR	Panthee *et al.* (2004)
	Isoflavones	QTL	SSR	Primono *et al.* (2005)
	Palmitate acid	*fap(nc)*	EST	Cardinal *et al.* (2007)
	Linolenic acid	QTL	SSR	Spencer *et al.* (2004)
	Alpha-tocophenol	QTL	SSR	Dwiyanti *et al.* (2007)
	Iron-deficiency chlorosis	–	SSR	Charlson *et al.* (2005)

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Table 4. (*Cont.*)

Crops	Traits	QTL/genes	Type of markers	References
	Salt tolerance	–	SSR	Lee *et al.* (2004)
	Manganese toxicity	–	SSR, RAPD	Kassem *et al.* (2004)
	Salt stress	–	SSR	Lee *et al.* (2004)
	Water logging	–	SSR	Van Toai *et al.* (2001)
	Phosphorous deficiency	*fsw1, fsw2, fsw3 and rp1*	SSR, RFLP, EST	Van Toai *et al.* (2001)
		rp2, lp1, lp2	SSR	Li *et al.* (2005)
	Phytophthora root rot resistance	8 QTLs	SSR	Li *et al.* (2010)

STS = sequence-tagged site.
SRAP = sequence-related amplified polymorphism.

events occurring during their construction (Doerge 2002; Holland 2007). Therefore, further fine mapping is required to identify the tightly linked markers for MAS and cloning of gene (Price 2006). Association mapping or linkage disequilibrium (LD) mapping provides high-resolution mapping between the marker and QTL-controlling target traits (i.e. within 1–2 cM intervals or within gene) due to the use of a natural population, which is developed after several rounds of recombination events occurring over a period of years (Risch & Merikangas 1996; Nordborg & Tavare 2002). Moreover, its use also reduces the time required for development of biparental mapping population and identifies greater numbers of alleles (Yu & Buckler 2006). This can be performed as (i) candidate-gene association mapping where the associations between selected candidate genes and target traits are studied and (ii) genome-wide association mapping or genome scan where genetic variation in the whole genome is surveyed and associated with complex traits (Risch & Merikangas 1996). For this purpose, only a few markers (50–100) distributed on the whole genome are utilized first for analysis of population structure of a diverse natural population comprising 100–500 individuals. The information obtained from population structure analysis and precise phenotypic data on target traits obtained over the environments are used to analyse the marker–trait association (for details, see Rafalski 2010). In association mapping, diverse recombinant inbred lines (RILs) derived from several high-resolution biparental populations having one parent common can be used to afford very high resolution and power to detect those kinds of associations involving epistatic interactions. This approach, often known as nested association mapping, reduces the linkage disequilibrium (LD) and avoids population structure. Another advantage of this approach is that it allows a new trait to be mapped immediately by taking the new phenotype measurements, because very high-density genotypic data are already available on each biparental population (McMullen *et al.* 2009). Thus, a new allele of QTL can be mined for complex traits through association mapping (Zhu *et al.* 2008). Despite this, little effort has been made to deploy it in legume species except for a few studies (Huh & Huh 2001; Smýkal *et al.* 2008; Kwak & Gepts 2009; Vir *et al.* 2009). A candidate gene-based approach has been used successfully to map different loci for iron deficiency chlorosis (Wang *et al.* 2008), and several candidate genes implicated in oleate biosynthesis have been mapped and their co-segregation with oleate and linoleate QTL investigated in soybean (Bachlava *et al.* 2009). Association mapping undoubtedly has great potential for legumes because large collections of global germplasm accessions are available for several grain legumes (Varshney *et al.* 2009*a*). Fortunately, candidate-gene sequences for various complex traits are now available in several model species, which can be used to develop functional markers for association mapping of specific traits (Palomino *et al.* 2009; Torres *et al.* 2010). The high throughput next generation sequencing and genotyping technologies markedly reduced the cost of SNPs (Hirschhorn & Daly 2005; Syvanen 2005) and DArT markers (used in pigeonpea for diversity analysis; Yang *et al.* 2006), leading to the possibility of genome-wide association mapping for complex traits in chickpea, common bean and soybean.

In legumes, the close phylogenetic relationship has also paved the way for cross-species mapping of genes/QTL for complex domesticated traits such as pod dehiscence, stem height, root mass, harvest index,

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seed dormancy, seed size and seed-quality characters. At least 15 qualitative and quantitative genes are known to control such traits (Weeden 2007). QTL analysis studies also demonstrate that a few QTLs control a large proportion of the phenotypic variability seen in domesticated traits. This is seen in, e.g. common bean, where three different QTLs collectively explain 0·36–0·48 of variation for seed weight and length (Park *et al.* 2000) and the contribution of the environment was observed to be relatively small. For seed size, a major gene distinguished wild progenitor and cultivated descendant in cowpea and mungbean (Fatokun *et al.* 1992). The genes controlling different traits of domestication syndrome are shown to be frequently clustered or linked within the genome in legumes and several other crops. In common bean, the genes responsible for domestication syndrome were clustered in only three genomic locations that separately control growth habit and flowering time, seed dispersal and dormancy, and pod and seed size (Koinange *et al.* 1996). At the same time, for some traits, apparent clustering may be the result of a single gene with pleiotropic effects (Johnson *et al.* 1996; Koinange *et al.* 1996; Xiong *et al.* 1999; Poncet *et al.* 2000). However, with the increasing number of examples of linked domestication traits, it is unlikely that pleiotropy is the sole explanation for clustering of domestication syndrome loci (Park *et al.* 2000). It has been shown that loci controlling the domesticated traits are conserved because they are involved in adaptation and hence are favoured during selection. For example, a seed weight QTL mapped in cowpea was found apparently conserved in cowpea and mungbean on similar locations (Fatokun *et al.* 1992). A comparative study between common bean, cowpea and mungbean suggested that a seed weight QTL associated with *Phs* locus coding the most abundant seed storage protein (phaseolin) in common bean has a putative orthologue in mungbean (Johnson *et al.* 1996). Interestingly, a similar candidate for orthology was not identified in cowpea. Maughan *et al.* (1996) identified a different soybean seed weight locus with a potential counterpart in cowpea. Moreover, comparative genomics using molecular markers linked with QTL for domesticated traits reveal whether two crops have same or different pattern of genes/QTL. In pea, a different set of genes was used to produce the same or similar phenotypic changes when compared with common bean, which demonstrate that relatively few genes appear to have been modified during its domestication (Weeden 2007). Comparative genomics has also helped to develop a QTL conditioning resistance to *Ascochyta rabiei* in chickpea (Bian *et al.* 2007). Thus, similar gene patterns for trait(s) among different species can facilitate the use of marker-trait association from one species to other related crop species in marker-assisted breeding or cloning of the economically important genes.

Deployment of marker-trait association in breeding programmes (MAS)

Gene pyramiding is a pragmatic approach to achieving multiple and durable resistance (Shi *et al.* 2009). It is often cited that genetic markers can be deployed to identify and select specific genes or combine multiple-resistance genes (Gupta *et al.* 2010). It has been successfully demonstrated in soybean for stacking the genes controlling resistance to CSN (Concibido *et al.* 2004). Its use in this crop has been shown to be cost-effective compared to greenhouse screening, and has increased the efficiency and speed of developing cultivars resistant to CSN (Concibido *et al.* 2004). Also QTL/genes controlling tolerance to *Phytophthora* root rot and resistance to soybean mosaic virus have been pyramided in this crop (Shi *et al.* 2009; Li *et al.* 2010). More efforts are required to use marker-assisted pyramiding in other food legumes as well. Marker-assisted backcrossing and marker-assisted recurrent selection are being utilized for introgressing/pyramiding QTL/genes for drought-related traits and resistance to diseases (*Fusarium* wilt and *Ascochyta* blight) in elite lines of chickpea at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and Indian Institute of Pulses Research (IIPR) in collaboration with other partners (Chamarthi *et al.* 2010).

Increased knowledge about marker-trait association is useful to conventional plant breeders for developing improved cultivars through MAS. The direct manipulation of the genomic regions having positive additive effects on traits of interest can lead to maximum potential genetic gains through MAS for traits having low heritability and difficulties in scoring. In common bean, several lines have been developed using MAS for resistance to rust (Stavely 2000; Faleiro *et al.* 2001), anthracnose (Alzate-Marin *et al.* 1999) and bean golden yellow mosaic virus (Miklas 2002). Similarly, MAS for angular leaf-spot resistance was found to be effective when three genes were introgressed using RAPD and sequence characterized amplified region (SCAR) markers in this crop (de Oliveira *et al.* 2005). In addition, MAS for two QTLs residing on separate

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Table 5. *Improved line/cultivars of soybean and common bean developed and released in USA using molecular breeding approaches*

Crop	Trait	Cultivar/breeding line	References
Soybean	Disease resistance	JTN-5503, JTN-5303	Arelli *et al*. (2006, 2007)
	Soybean cyst nematode resistance	JTN-5109, DS-880	Arelli &Young (2009), Smith (2010)
Common bean	Disease resistance	USPT-ANT-1, ABCP-8, ABC-Weihing	Miklas *et al*. (2003*b*), Mutlu *et al*. (2005, 2008)

linkage groups in common bean have been shown to be effective in enhancing white mould resistance (Ender *et al*. 2008). In another study, MAS for a major QTL associated with root–rot resistance was found to be effective and it has given realized gain in plant biomass and vigour traits associated with root–rot complex in snap bean (Navarro *et al*. 2009). In soybean, MAS has proven effective for major genes controlling four-seeded pods (Zhu & Sun 2006). However, no significant improvement has been observed through marker-assisted introgression of QTL for multiple branching in common bean (Fazio *et al*. 2003) and for complex traits such as yield in soybean (Reyna & Sneller 2001), probably due to epistatic interactions. At present, both the public and private sectors are actively involved in development of improved cultivars using MAS, the prime objective of molecular breeding. Consequently, in common bean, an improved line USPT-ANT-1 carrying *Co-42* gene has been registered as resistant to all the known North American races of anthracnose (Miklas *et al*. 2003*a*). Similarly, the SCAR markers SAP6 (Miklas *et al*. 2003*b*) and SU91 (Pedraza *et al*. 1997), tightly linked with QTL controlling bacterial blight resistance, have been used to develop a germplasm line, USDK-CBB-15, through MAS. This line possesses the two major QTLs mentioned above, which enabled combat of this severe disease problem in the U.S. (Miklas *et al*. 2006*b*). Successful utilization of MAS has also resulted in development of improved cultivars in soybean and common bean, although trait mapping using molecular markers has been done in different legume species. In these crops, a number of cultivars developed through MAS have been released in the recent past (Table 5; Chamarthi *et al*. 2010).

FUTURE DIRECTIONS

Significant progress has been made in recent years in developing genomic resources in model (*L. japonicus* and *M. truncatula*) and other major food legumes. However, more genomic resources will be required in the less-studied food legume crops (Varshney *et al*. 2010*b*). Many biotic and biotic stresses can result from overexpression of gene(s) in a specific genetic context. More studies are needed, using microarray chips, transcriptome analysis and differential display, to explore gene overexpression systematically. The tools and techniques of functional genomics are valuable for isolation and identification of genes controlling traits of interest, and there is a need to promote widespread use in food-legume breeding. Microarrays can help answer the questions related to overexpression of genes of interest in different experimental conditions and to study their level of expression on large scale, but require highly skilled manpower and a well-established laboratory. To answer these questions, quantitative real-time-PCR (qRT-PCR) is the current method of choice and is also used to confirm microarray results (Mustafa *et al*. 2009). Use of RNAi and virus induce gene silencing (VIGS) for suppression of the gene function and overexpression of desirable genes requires development of transgenic plants. Application of these functional genomic tools for testing the functionality of candidate genes or other genes having unknown function will be greatly accelerated once it becomes routinely possible to regenerate transgenic plants in food legume crops. This will also help to generate transgenic populations created by insertion of T-DNA and transposable elements, which will serve as reverse-genetic resources for TILLING. In future, more efforts are needed to develop genetic-transformation protocols in legume crops. Induced mutation has been used to develop mutant populations in a few legumes. There is a need to develop such populations in other food legumes, and to use these populations as reverse-genetic resources for TILLING. These efforts should target a range of legume crops other than soybean, chickpea, cowpea, common bean and pigeonpea.

Plant breeders in association with molecular biologists can use these genomic resources to develop

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molecular markers. High-throughput sequencing can accelerate the development of polymorphic markers in legumes with a narrow genetic base. A wider range of dense maps with well-distributed molecular markers needs to be developed as a first step in identifying marker-trait associations. Candidate genes or tightly linked markers for resistance/tolerance to biotic and abiotic stresses can be identified through freely accessible germplasm collections capturing natural variability in different crop species, availability of gene sequences having unknown functions and availability of advanced molecular tools and techniques in the public domain, using association mapping and Eco-TILLING approaches.

Plant breeders are often concerned with the improvement of complex traits. A new approach called 'genome-wide selection' (GWS) or 'genomic selection' (GS), based on genome-wide marker profiling, can accelerate the genetic improvement of such traits. In this approach, superior progeny lines are selected for advancement in the breeding cycle on the basis of breeding values of progenies estimated using both genotypic and phenotypic data (Heffner *et al*. 2009; Jannink *et al*. 2010). Thus, QTL analysis for working out marker-trait associations is not needed (Bernardo 2010*a*, *b*; Tester & Langridge 2010).

The availability of high-throughput and cost-effective genotyping platforms, combined with automation in phenotyping methodologies, will increase the use of genomic tools in breeding programmes. There is a need to strengthen infrastructure and facilities for MAS that are still lacking. Development of highly polymorphic and reproducible markers such as SSR and SNP in marker-trait association analysis is a prerequisite for routine use of MAS. Interaction between biotechnologists and plant breeders should be enhanced in order to use MAS more systematically and efficiently. Overcoming these barriers may facilitate the use and handling of complex genomic datasets and the development of improved cultivars. Training for the next generation of scientists can span the 'gap' between genomics and breeding. Such training efforts are underway at several centres including ICRISAT and IIPR in India, Saskatoon Canada, the French National Institute for Agricultural Research (INRA), the International Center for Agricultural Research in the Dry Areas (ICARDA) in Syria and the US Department of Agriculture (USDA) in the USA: MAS has been included in breeding programmes despite several difficulties such as underestimation of QTL effects, genetic background effects and interactions on introgression of gene/QTL in diverse germplasm. However, young plant breeders and biotechnologists are aware of the power of MAS as a tool; and this bodes well for the future.

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