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Legume Genomics and Breeding

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I. INTRODUCTION

Legumes account for 27% of the world's crop production, with grain legumes alone contributing 33% of the dietary protein nitrogen needs of humans (Vance et al. 2000). Grain and forage legumes are grown on some 190 million hectares, and their production is about 300 million metric tons across the world. Grain legumes are also a rich source of essential vitamins, minerals, and important amino acids (Duranti and Gius 1997; Grusak 2002). Moderate consumption of legumes helps to prevent cardiovascular diseases, stroke, Parkinson's disease, Alzheimer's disease, and even cancer (Singh 2007). Proteins of grain legumes are generally high in lysine but low in methionine and cysteine. However, combined with cereals, they result in a balanced diet of energy and protein. In fact, grain legumes are critical components in the diets of resource-poor people in the developing world, especially for vegetarian populations and those who cannot afford to supplement their diets with meat. Legume crops also garner higher market prices than other staple crops and are therefore attractive to farmers.

From an agronomic perspective, the ability of legumes to fix atmospheric nitrogen (N) in the soil through their symbiotic association with *Rhizobium* bacteria (Schultze and Kondorosi 1998; Serraj 2004), thereby reducing the need for fertilizers, and to serve as rotation crops is very important to current agricultural production systems. For instance, under nitrogen-limiting conditions, legume-*Rhizobium* symbiosis results in the formation of the root nodules. *Rhizobium* bacteria that harbors in the root nodules differentiate the nodules into symbiotic bacteroids that are the sites of catalysis of dinitrogen into ammonia by nitrogenase. As an energy source to achieve N fixation, the bacteria obtain dicarboxylic acids from the host plant. By a complex amino acid cycle, the reduced N is provided to the plant (Lodwig and Poole 2003), where it is accumulated into proteins. Thus legumes can also help replenish nutrient-depleted soil.

The leguminosae (*Fabaceae*), contain over 18,000 species divided into the three subfamilies Mimosoideae, Caesalpinoideae, and Papilionoideae. The majority of species of Papilionoideae are herbaceous, although some are trees and shrubs. By contrast, majority of Caesalpinoideae are tropical and subtropical trees, while Mimosoideae include trees and shrubs. It is an extraordinarily diverse family of worldwide distribution with representatives occurring from alpines, to arctic regions, to equatorial tropics. Major dietary legumes include soybean (*Glycine max,* the single major contributing species, which is used for multiple applications in the food and feed industries); peanut (*Arachis hypogaea*); cowpea (*Vigna unguiculata*); common bean (*Phaseolus vulgaris*); chickpea (*Cicer arietinum*); pigeonpea (*Cajanus cajan*); lentil (*Lens culinaris*); mung bean (*Vigna radiata*); and faba bean (*Vicia faba*); all that contribute significantly to the diets of large numbers of people in Asia, Africa, and South America (Table 6.1). As the majority of these legume crops are grown in marginal environments of Africa and Asia, their production is heavily challenged by a number of abiotic (drought, freezing, salinity, waterlogging) and biotic (fungi, bacteria, nematodes, viruses, insects, parasitic plants) stresses.

The unique nature of legume species, due to their symbiotic interactions with specific soil-borne bacteria, the rhizobia, to fix atmospheric N attracted the plant science community to undertake large-scale investigations in legume species. As a result, two species, *Medicago truncatula* (Cook 1999) and *Lotus japonicus* (Handberg and Stougaard 1992), emerged as model legumes to understand the genetics and molecular biology of nodulation (Stacey et al. 2006) and other important processes, such as resistance or tolerance to stresses (Dita et al. 2006). Their small diploid genomes, autogamous nature, short generation times, and prolific seed production made them ideal choices for undertaking genomics research, including genome sequencing. As a result, powerful genetic and genomic tools, such as establishment of genetic and physical maps (Pedrosa et al. 2002; Thoquet et al. 2002), expressed sequence tags (ESTs) (Asamizu et al. 2004; Kulikova et al. 2001), genome-wide sequence data (Young et al. 2005; Cannon et al. 2006), bioinformatics tools and databases (Town 2006), functional genomics, and metabolomics platforms, have been developed for these two legume species (see Varshney et al. 2009). Furthermore, due to unique importance of soybean in North America and its emergence as a bioenergy crop, the soybean genome was also targeted by Joint Genomics Institute of Department of Energy (JGI-DoE) of the United States for genome sequencing.

Due to the phylogenetic relationships within the legume family (Mahalakshmi et al. 2002; Wojciechowski et al. 2004), heavy investments in *Medicago, Lotus,* and soybean research fueled expectations that this genomic and biological knowledge information could be transferred from reference legumes to other food and feed legumes of major economic importance. Recent years, however, have witnessed significant

Table 6.1. Features of some important grain legumes.

Common name	Species	Chromosome no.	Genome size	Regions of diversity
Adzuki bean	*Vigna angularis* (Willd.) Ohwi and Ohashi	$2n = 2x = 22$	~600 Mb	Japan, China
Chickpea	*Cicer arietinum* L.	$2n = 2x = 16$	740 Mbp	South West Asia, Ethiopia, India
Common bean	*Phaseolus vulgaris* L.	$2n = 2x = 22$	~637 Mbp	Mexico, Guatemala
Cowpea	*Vigna unguiculata* (L.) Walp.	$2n = 2x = 22$	620 Mbp	West Africa, India
Faba bean	*Vicia faba* L.	$2n = 2x = 12$	446 Mb	Asia, Mediterranean
Lentil	*Lens culinaris* Medic.	$2n = 2x = 14$	4,063 Mbp	South West Asia, Mediterranean
Lima bean	*Phaseolus lunatus* L.	$2n = 2x = 22$	Info not available	Peru
Mung bean	*Vigna radiate* (L.) Wilczek	$2n = 2x = 22$	~520 Mb	India, South East Asia
Pea	*Pisum sativum* L.	$2n = 2x = 14$	5000 Mb	SW Asia, Mediterranean
Peanut	*Arachis hypogaea* L.	$2n = 2x = 20$ (AA and BB genome); $2n = 4x = 40$ (AABB genome)	$2n = 1260$ Mbp (*A. duranensis*-AA genome; *A. ipanensis*-BB genome), $4n = 2890$ Mbp	South America
Pigeonpea	*Cajanus cajan* (L.) Millsp.	$2n = 2x = 22$	858 Mbp	India
Soybean	*Glycine max* (L.) Merr.	$2n = 4x = 40$	1115 Mb	East Asia
Mung bean	*Vigna radiata* (L.) Wilczek	$2n = 2x = 22$	~520 Mb	India, South East Asia
Lima bean	*Phaseolus lunatus* L.	$2n = 2x = 22$	Info not available	Peru

progress towards developing genome-specific genomic resources in these food legume crops as well. This chapter provides an update on recent progress in the area of legume genomics and their applications in legume breeding.

II. CONSTRAINTS IN CROP PRODUCTION

Legumes are the second most important crop plants after the Gramineae in their importance to humans. Unfortunately, improvements in legume crop yields have not kept pace with those of cereals (Fig. 6.1). Several abiotic (drought, freezing, salinity, waterlogging) and biotic (fungi, bacteria, nematodes, viruses, parasitic plants, insects) factors are major constraints to sustainable legume production, especially in the tropical and subtropical regions of the world. In addition, nutrient depletion of soils is a particular problem for small landholders in developing countries, where much grain-legume production occurs, and many farmers cannot afford to use fertilizers. Progressive soil chemical and physical degradation and acid soil conditions may also limit legume productivity.

A. Abiotic Stresses

Maintaining or improving crop productivity under conditions of abiotic constraints in the field is a major concern for farmers in many areas in the world where legumes are grown. The adaptability and productivity of legumes are limited by major abiotic stresses including drought, heat, frost, chilling, waterlogging, salinity, and mineral toxicities. Rainfed

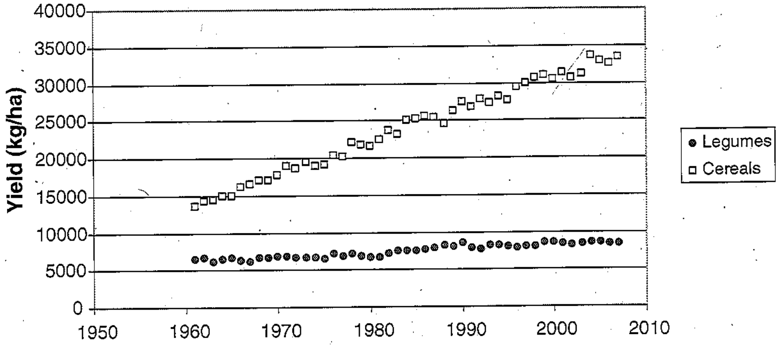

Fig. 6.1. Comparative trends in yield distribution of selected cereal and legume crops during last six decades. Comparison shows the continuous increase in total yield of cereals while stagnant or slow increase in the yield of legumes.

legumes are often exposed to terminal drought due to inadequate rains to meet the water requirements during pod filling. Cultivation of legumes under irrigated conditions for prolonged periods or use of ground water for irrigation, however, invariably leads to higher sodicity or salinity in the agricultural production systems. In fact, drought and salinity are considered among the most severe stresses for legume-growing areas.

1. Drought. Drought is one of the most severe stresses for the sustainable legume production especially in the semiarid tropics (SAT) where short and erratic rainfall is common. SAT legume crops are grown under rainfed conditions and suffer from both intermittent and terminal drought stress, thus incurring major yield losses. Worldwide, yield losses each year due to drought are estimated to be around US$500 million (Sharma and Lavanya 2002).

Water uptake and water-use efficiency of crop plants are two major factors that influence their yield. Hence, there is a greater need for a more comprehensive understanding of root biology in those crops where roots have already proved to be beneficial for yield under terminal drought (common bean, soybean, chickpea) and to explore these traits in those crops where there is little information on roots (e.g. peanut). Specifically, there is a need to understand the dynamics of roots, how roots contribute to the overall water budget, especially how they contribute at the time of grain filling. Recent studies at the International Crops Research Institute the Semi-Arid Tropics (ICRISAT, India) indicate that deeper rooting correlates with a higher harvest index (HI) in chickpea in conditions of more severe drought (Kashiwagi et al. 2005, 2006; Vadez et al. 2008). Transpiration efficiency (TE) is another trait that is being addressed in some legume crops such as peanut using different biotechnological, physiological, and breeding approaches (Krishnamurthy et al. 2007).

2. Salinity. Soil salinity is another important limiting factor for crop yield improvement; it affects 5% to 7% of arable lands (i.e., approximately 77 million ha worldwide) (Oldeman et al. 1991). Legumes, in general, are sensitive to salinity, and within legumes, chickpea, faba bean, and pigeonpea are more sensitive than other food legumes. The salinity problem is increasing, particularly in areas where irrigation is a common practice. Although management options exist to alleviate salt effects, these options often contradict the immediate economic choices of concerned farmers; thus, crop improvement for salt tolerance appears to be the only alternative.

The problem of salinity is basically two-fold. First, soil is saturated with sodium (Na) and soil pH remains within an optimal range for crop growth. This type of salinity refers to coastal or dryland salinity. These are soils that get saturated with sodium because an existing saline ground water table is rising (proximity to the sea or salt that has accumulated in the soil profile), bringing the salt to the surface. Second, soil is both saturated with Na (exchangeable sodium percentage, ESP > 6) and pH has reached levels above 8.5. This type of salinity is also called transient salinity and is hereafter referred to as *sodicity* or *sodic soils*. In this case, the sodium saturation brings about the same effect as salinity, but the high pH dramatically affects the availability of micronutrients (low availability/solubility of micronutrient salts at these pH levels), the soil structure, and porosity (poor drainage, tendency for waterlogging, little oxygenation because of saturation of the exchange complexes in the soil by sodium). In the past, most studies have focused on *salinity* and only a few on *sodicity*. Despite the importance of salinity in crop production worldwide and the abundant knowledge on the effect of salinity on plant growth and development, there has been surprisingly little effort to breed for improved salinity tolerance, with the exceptions of wheat, rice, barley, alfalfa, and soybean. Breeding tolerant legume crop varieties is therefore urgently needed.

Besides terminal drought and salinity, high or low temperature drastically affects the grain filling in legumes (e.g., chickpea, lentil, pea) (Croser et al. 2003; Singla and Garg 2005). Waterlogging is another serious constraint affecting yield adversely in some legume crops such as soybean (Linkemer et al. 1998) and pigeonpea (Kumutha et al. 2008). Nitrogen (N) and phosphorous (P) deficiencies are other common limiting factors for crop production in some legumes, especially in arable soils (Atkins et al. 1984; Schulze and Drevon 2005).

B. Biotic Stresses

The major biotic stresses affecting legumes are fungal diseases, although insects, nematodes, viruses, bacteria, and parasitic weeds can also drastically decrease legume production. Foliar diseases caused by biotrophic pathogens, such as rusts and downy and powdery mildews, are major limiting factors in legume production. The most important of these diseases are present in all areas where legumes are cultivated.

1. Fungal Diseases. Fusarium wilt, caused by *Fusarium oxysporum*, is one of the most serious fungal diseases, not only in legumes but also in many plant species (Beckmann 1987). The fungus infects through the roots and penetrates into the vascular system, with few symptoms on the root surface. The pathogen spreads throughout the plant, causing vascular discoloration, wilting, and death. This can result in substantial stand reduction and yield loss. In general, different *Forma specialis* of *F. oxysporum* are responsible for causing the Fusarium wilt in different legume crop species. For instance, *F. oxysporum* f. sp. *ciceri* causes wilt in chickpea, *F. oxysporum* f. sp. *pisi* in pea, *F. oxysporum* f. sp. *tracheiphilum* in cowpea and soybean, *F. oxysporum* f. sp. *phaseoli* in common bean, and *F. oxysporum* f. sp. lentis in lentil. *Fusarium udum* is responsible for causing Fusarium wilt in pigeonpea. Fusarium wilt causes severe yield losses in different legume species.

Ascochyta blight, caused by *Ascochyta* sp., is another yield-reducing fungal disease in several legumes (Tivoli et al. 2006). For instance, in case of chickpea, *Ascochyta rabiei* is able to grow from the pod wall into the seed while it is still immature. It can be found in the seed coat or even in the cotyledons. A study has shown that 50% to 80% of seeds collected from pods with *Ascochyta* lesions were infected, but seed collected from healthy pods on the same plants were not infected. Spores can also contaminate the seed surface during harvest operations. Both deep and superficial seed infections transmit the disease to seedlings. The fungus sporulates on seeds as soon as they are planted in moist soil. Similarly, *A. phaseolorum* causes infection in cowpea, common bean, and soybean. In case of field pea, three *Ascochyta* species are responsible for Ascochyta blight complex. *A. pisi* and *A. pinodes* both cause lesions on leaves, stems, and pods that are difficult to distinguish from one another. *Phoma medicaginis* var. *pinodella* (synonym *Ascochyta pinodella*) is more common on stem bases than on leaves and pods. Ascochyta blight of lentil is caused by the fungus *A. lentis*. The fungus has a narrow host range and cannot cause disease on other pulse crops. Similarly, *Ascochyta* blight of chickpea, pea, or cowpea does not infect lentil.

Several rust species also infect grain and forage legumes, most of them belonging to the genus *Uromyces*, such as *U. appendiculatus* on common bean; *U. ciceris-arietini* on chickpea; *U. pisi* on pea; *U. striatus* on alfalfa; *U. viciae-fabae* on faba bean, lentil, and common vetch; and *U. vignae* on cowpea (Sillero et al. 2006). Also, rust species belonging to other genera can be major problems on legumes, such as *Phakopsora pachyrhizi* and *P. meibomiae* on soybean or *Puccinia arachidis* on peanut (Rubiales et al. 2002). Asian rust (*Phakopsora pachyrhizi*) is a severe disease that causes important yield losses in soybean and is spreading rapidly around the world (Carmona et al. 2005; Pivonia and Yang 2004; Du-Preez et al. 2005). Powdery mildew of pea has a worldwide distribution, being particularly important in climates with warm, dry days and cool nights, adversely affecting yield and quality. Severe infection may cause 25% to 50% yield losses (Warkentin et al. 1996). Downy mildew, caused by *Peronospora viciae,* occurs in most places where the crops are grown but is most frequent and severe in cool, maritime climates (Sillero et al. 2006).

Anthracnose, caused by *Colletotrichum lindemuthianum,* is most common bean disease that attacks the foliage and fruit of beans and causes serious yield losses in several parts of world. The disease is most common and severe on common bean but may also affect cowpea, lima bean, and faba bean. The anthracnose fungus infects leaves, stems, and pods of common bean plants. The most characteristic symptom of the disease is the black-red sunken cankers or spots that develop on infected pods. As these spots become older, the edges develop a black ring with a red outer border and may show pink ooze in the center, which contains the spores of the fungus. Similar spots may develop on seeds. Red-brown spots and streaks also develop on stems, petioles, and leaves.

2. Viral Diseases. Virus diseases are among the important biotic constraints for the production of many legume crops. For example, bean common mosaic virus (BCMV) and its close relative, bean common mosaic necrotic virus (BCMNV), are the most widespread and frequent viruses of common bean leading to significant losses. In addition, over the past two decades, bean golden mosaic virus (BGMV) has been considered the most important yield-limiting disease for bean production in parts of Central America and the lowlands of the Caribbean, with yield losses between 10% and 100% (Coyne et al. 2003). Pea seed-borne mosaic virus chiefly infects lentil. Members of the family *Luteoviridae* (luteovirids) such as soybean dwarf virus (SbDV) and beet western yellows virus (BWYV) appear to be very common in both chickpea and lentil (Tadesse et al. 1999; Abraham et al. 2002). Sterility mosaic disease (SMD) is probably one of the most important yield-reducing factors in pigeonpea (Kulkarni et al. 2002). Of the important biotic constraints specific to sub-Saharan Africa (SSA), peanut rosette disease (GRD) is endemic to the African continent and epidemics occur often throughout SSA, reducing peanut production and crippling rural food security (Naidu et al. 1999).

3. Insect Pests and Nematode Diseases. More than 200 species of insects feed on several legumes, of which pod borer (*Helicoverpa armigera*), spotted pod borer (*Maruca vitrata*), pod fly (*Melanagromyza obtuse*), pod sucking bugs (*Clavigralla* spp., *Nezara viridula*) and the bruchid (*Callosobruchus* spp.) are most important economically. In addition to the huge economic losses caused directly by the pests, several indirect costs arise from the deleterious effects of pesticides on the environment and human health (Sharma 2001).

The insect pests of major concern in chickpea and pigeonpea are pod borers (*H. armigera* and *M. vitrata*) and podfly (*Melanagromyza* spp.). These insect pests feed on various plant parts, such as leaves, tender shoots, flower buds, and immature seeds. Few farmers in developing countries are able to spend precious income on chemical pest control. In these situations, there are serious concerns of the adverse effects of pesticides on the environment and all living organisms. It has been difficult to breed for *Helicoverpa* resistance in chickpea and pigeonpea because sources with a high level of resistance are not available in the cultivated species of these legumes (Sharma et al. 2005). Recent studies have shown the potential of utilizing the wild species for insect pest resistance breeding programs, as these species have shown higher levels of resistance (Sharma et al. 2005; Dwivedi et al. 2007; Mallikarjuna et al. 2007).

Cowpea is highly susceptible to flower thrip during budding and early flowering, when they can cause flower abortion and pod distortion (Frei et al. 2005). Flower thrip damage in cowpeas starts at preflowering, when nymphs and adults may attack the terminal leaf buds and bracts/stipules, causing the latter to become deformed with a mottled brownish-yellow appearance. However, the main attack is on the flower buds and flowers. Infested buds appear dried and brown and may eventually abort, leaving dark red scars. In case of common bean, leafhoppers, white flies, bean pod weevils, and bean beetles cause severe damage in the field, and bean weevils can be a problem during storage.

Plant parasitic nematodes are serious production in some legume crops. For instance, the soybean cyst nematode (SCN), *Heterodera glycines*, has long been recognized as a globally significant pest in nearly all soybean regions, including North America, Indonesia, Japan, Korea, China, and South America (Riggs and Niblack 1999). Soybean production losses due to SCN are significant and may be above 3 million metric tons globally (Wrather et al. 1997). Infection causes significant root damage and often can result in plant stunting and yellowing. Nematode cysts can remain in the soil for more than 10 years. Resistance to SCN is quantitative in nature (Mansur et al. 1993), making it difficult to assay in a field setting. Bioassays can be challenging and costly in greenhouse and growth chamber systems as well.

III. GENOMIC RESOURCES IN LEGUMES

Although several of the above-mentioned constraints that limit grain legume production or quality have been addressed by conventional breeding and enhanced management, the success has been variable. In such situations, there is a hope that the use of genomics tools will help to address these problems. Molecular markers and molecular genetic linkage maps are the prerequisites for genomics-enabled crop improvement (Dwivedi et al. 2003, 2006; Varshney et al. 2005). Among different legumes, *Medicago, Lotus,* and soybean have had significant investment toward developing genomic resources including genome sequencing. In case of other legumes, especially tropical legumes, the progress in the area of genomics has been very slow until recently. Even today some legume crops such as pigeonpea either do not have any appropriate marker repertoire or lack genetic maps. Nevertheless, as a result of advances in sequencing and genotyping technologies and also due to several international collaborations, this situation is changing in several legume crops (see Varshney et al. 2009b).

A. Genome Sequencing for Understanding Genome Architecture

There are more than 730 genera and 19,400 species in the Fabeaceae, of which only a handful have been domesticated as crops. Genome sequencing in the legumes has been in two relatively closely related groups of the Papillionoid legumes: soybean (*Glycine max*) in the Phaseoleae group and *Medicago truncatula* and *Lotus japonicus* in the Galegoid group (Doyle et al. 2000). These two groups, Phaseoloid and Galegoid, represent most of the crops species in the legumes except for peanut and a few others.

The sequencing of the *Lotus* and *Medicago* genomes began about the same time, and both were done as models for symbiosis and nitrogen fixation and because they both had relatively small nuclear genomes (Young et al. 2005). Although they began about the same time, the approaches for sequencing differed somewhat between these two genomes.

Lotus was sequenced initially by the Kazusa DNA Research Institute (Japan), using a modified bacterial artificial chromosome (BAC)-by-BAC approach followed by draft sequencing of selected regions of the *Lotus* genome, also via BACs (Sato et al. 2008). The sequencing project began using a BAC-by-BAC approach from seed points, often genes or genetic markers, from which the sequencing would walk out along a BAC tiling path. Later, to increase speed and cut costs, researchers switched to targeted sequencing of BAC pools combined with some reduced representation whole genome shotgun sequencing. This is a grossly simplified explanation of the approach employed, but the end result is that it is predict that they recovered nearly 91% of the gene space of *Lotus*.

Medicago genome sequencing has proceeded via a traditional BAC-by-BAC approach but focused solely on the euchromatic part of the genome, which should also be its gene-rich part. This portion of the genome was first determined cytologically (Kulikova et al. 2001), but due to the lack of precision in estimating DNA packaging and meiotic chromosome lengths, this number has increased over the course of the sequencing project. Initially, the BACs were sequenced to a level similar to rice and the human genome, but as the euchromatic genome size increased, the project switched to a level of draft of sequencing of individual BACs (http://medicago.org/genome/genome_stats.php). The end result of this project, which should be published in 2009, will be a genetically and physically integrated sequence map of most of the euchromatin of the *Medicago* genome and should capture greater than 90% of the genes.

Both *Medicago* and *Lotus* used some type of BAC-by-BAC approach, also called the traditional sequencing method, as was used for the human genome. Other sequencing approaches include whole genome shotgun (WGS) as was done for several species of Drosophila (Consortium 2007), a human genome (Venter et al. 2001), and many bacterial genomes. This approach is powerful and fast but has been problematic for larger, complex plant genomes, as repeated sequences in large genomes can complicate the correct assembly and ordering of the pieces. The soybean genome was recently sequenced using a shotgun approach (www.phytozome.net/soybean). Despite the concern over the large complex, duplicated genome (Schlueter et al. 2007), it appears to have assembled well. There are pseudomolecules representing each of the 20 linkage groups.

Other types of genome sequence information are beginning to emerge for other legume crops. This sequence information is often not complete but rather snapshots or pieces of the genome. For example, the cowpea genome has been sequenced using an approach that samples the hypomethylated portion of the genome by methylation filtration (MF), providing over 250,000 gene-space sequence reads (GSRs) with an average length of 610 basis points (bp) representing about 160 Mb of sequence information (Timko et al. 2008). This type of approach can enrich gene sequences rather than sampling everything in the genome randomly but does not result in a sequence that can be assembled.

B. Species-Specific Genomic Resources

Advances in genomics research of *Medicago*, *Lotus*, and soybean opened the doors for comparative genomics to use the maker or sequence information from these species to other temperate and tropical legume species, and comparative maps were developed (Choi et al. 2004b; Zhu et al. 2005). However, as the majority of the food legume crops suffer from a low level of diversity, especially in the cultivated gene pools, markers coming from other legume species could were not very useful for assaying the polymorphism, developing dense genetic maps, or mapping the traits. Therefore, there is a need for developing species-specific genomic resources in several grain legume crops at international level.

1. **Molecular Markers.** Among the different marker systems currently available, simple sequence repeats (SSR) and single nucleotide polymorphism (SNP) marker systems have emerged as markers of choice for plant breeding applications (Gupta and Varshney 2000; Varshney et al. 2007). While SSR markers can be assayed in low-tech laboratories, SNP assays need sophisticated genotyping platforms or can be outsourced (Varshney et al. 2009b). Therefore, availability of SSR markers for a legume species will be very useful for the breeding community for wider applications.

For development of SSR markers, three approaches are being used:

1. Isolation of SSRs from genomic DNA libraries (Gupta and Varshney 2000)
2. Mining ESTs or gene sequence data (Varshney et al. 2005)
3. Mining the BAC-end sequences (discussed later)

Until recently, SSR markers were developed using the genomic DNA library approach. As a result, only a few hundred SSR markers were available in these legume species (Varshney et al. 2007). As these legume crops have low levels of polymorphisms, the SSR markers available were not sufficient to develop good genetic maps. However, due to recent advances in sequencing technologies (Gupta 2008; Hudson 2008), a larger number of ESTs have become available (Varshney et al. 2009b), and these are being used to mine for SSRs (Varshney et al. 2005). Similarly, a large number of BAC-end sequences have been generated for several legume species (see Varshney et al. 2009b) that have also been useful for mining the SSRs (Mun et al. 2006; Shultz et al. 2007). Isolated or identified SSRs are being used to converting them into markers at several labs (e.g., ICRISAT for chickpea, pigeonpea, and peanut; University of California-Davis for cowpea, pigeonpea, and chickpea; University of Georgia, Catholic University (Brazil), and Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA, Brazil) for peanut; Centro Internacional de Agricultura Tropical (CIAT, Colombia), and Purdue University for common bean). As a result, several thousand SSR markers have become available for several of these legume species (see Varshney et al. 2009b). Some legume crops such as lentil and faba bean, however, still lag in developing SSR markers.

As SNP markers have become more popular due to their high-throughput in a cost-effective way for using them in association genetics, several research groups are actively engaged in developing high-throughput SNP genotyping platform. For instance, a custom 384-SNP GoldenGate assay has been designed in soybean using SNPs that had been discovered through the resequencing of five diverse accessions that are the parents of three recombinant inbred line (RIL) mapping populations (Hyten et al. 2008). Very recently, the University of California-Riverside developed a GoldenGate assay for genotyping 1,536 SNPs in case of cowpea (T.J. Close, pers. commun). Significant efforts have been invested at the University of California-Davis to develop assays for genotyping 768 SNPs to 1536 SNPs in four tropical legumes (chickpea, pigeonpea, common bean, and cowpea (Doug Cook, pers. commun). Similar efforts are under way as collaborative efforts of the University of Georgia, University of California-Davis (both U.S.) and Catholic University (Brazil) to develop SNP assays for AA and BB genome species of peanut. It is expected that soon the majority of these legume species will have larger number of SSR markers and high-throughput SNP assays that will overcome the problem of identifying a sufficient number of polymorphic marker loci required for genome mapping and trait association studies.

2. Genetic Maps. Although development and/or use of molecular markers started in many of these legume species sometime in the 1990s (Keim et al. 1990; Fatokun et al. 1992; Nadimpalli et al. 1994), progress in developing genetic maps in the majority of these legume species has been very slow. As mentioned earlier, narrow genetic diversity in gene pools of these legume species in general and paucity of polymorphic markers in particular have been main constraints. Due to availability of larger number of markers in these legume species during last two to three years, progress has accelerated in developing genetic maps for several legume species, such as peanut (Varshney et al. 2009a) and chickpea (Nayak et al. unpublished). A few important genetic mapping studies in legumes are listed in Table 6.2.

3. BAC Libraries and Physical Maps. Large insert libraries, such as bacterial artificial chromosome libraries, are very important for developing the local/genome-wide physical maps for cloning the gene(s)/quantitative trait loci (QTL) of interest (Salvi and Tuberosa 2005) or undertaking genome sequencing (Jackson et al. 2006). Although BAC libraries were available only for few legume crops until recently, the University of California-Davis has developed deep coverage (ca. 10

Table 6.2. Details on some genetic maps in selected legume crop species.

Crop marker loci	Mapping population	Reference
Chickpea		
Interspecific		
29 marker loci (morphological and isozyme)	*C. arietinum* × *C. reticulatum* (F2)	Gaur and Slinkard 1990a,b
28 marker loci (morphological and isozyme)	*C. arietinum* × *C. reticulatum* (F2), *C. arietinum* × *C. echinospermum* (F2)	Kazan et al. 1993
91 marker loci (morphological, isozyme, RFLPs and RAPDs)	*C. arietinum* × *C. reticulatum* (F2), *C. arietinum* × *C. echinospermum* (F2)	Simon and Muehlbauer 1997
120 STMS loci	*C. arietinum* × *C. reticulatum* (F2)	Winter et al. 1999
354 marker loci (SSRs, DAF, AFLPs, ISSRs, RAPDs, isozyme, cDNA, SCAR and morphological)	*C. arietinum* × *C. reticulatum* (F2)	Winter et al. 2000
116 marker loci (RAPDs, ISSRs, isozyme, and morphological)	*C. arietinum* × *C. reticulatum* (F2)	Santra et al. 2000
144 marker loci (1 morphological, 11 isozyme, 111 RAPDs, 21 ISSRs)	FLIP84–92C × PI 599072 (RIL)	Santra et al. 2000
56 marker loci (55 SSRs and 1 RGA)	*C. arietinum* ICC4958 × *C. reticulatum* PI489777 (RIL)	Tekeoglu et al. 2002
117 marker loci [addition of RGA Potkin 1–2 171 to linkage group 5 of Santra et al. (2000)]	*C. arietinum* × *C. reticulatum* (F2)	Rajesh et al. 2002
83 loci (SSRs, RAPDs, ISSRs and RGA)	*C. arietinum* × *C. echinospermum* (F2)	Collard et al. 2003
296 marker loci (47 defense response gene markers to the map of Winter et al. 2000)	*C. arietinum* × *C. reticulatum* (F2)	Pfaff and Kahl 2003
83 marker loci (54 RAPDs, 14 SSRs, 9 ISSRs, 6 RGA)	*C. arietinum* 'Lasseter' × *C. echinospermum* 'PI527930' (F2)	Collard et al. 2003
93 marker loci (91 SSRs, 2 CytP450 markers)	*C. arietinum* 'Hadas' × *C. reticulatum* 'Cr205' (RIL)	Abbo et al. 2005

(*continued*)

Table 6.2 (*Continued*)

Crop marker loci	Mapping population	Reference
89 marker loci (RAPDs, ISSRs, STS)	*C. arietinum* (ILC72) × *C. reticulatum* (Cr5–10) (RIL)	Cobos et al. 2006
Intraspecific		
103 marker loci (68 SSRs, 34 RAPDs, 4 ISSRs, and 5 morphological)	ICCV2 × JG62 (RIL)	Cho et al. 2002
55 marker loci (SSRs and Ascochyta blight resistance loci)	ILC1272 × ILC3279 (RIL)	Udupa and Baum 2003
69 marker loci (54 SSRs, 3 ISSRs, 12 RGAs)	ICC12004 × Lasseter (F2)	Flandez-Galvez et al. 2003a
138 marker loci (118 RAPDs, 13 SSRs, 4 morphological and 3 ISSRs)	CA2139 × JG62 (RIL), CA2156 × JG62 (RIL)	Cobos et al. 2005
273 marker loci (RAPD and ISSRs)	JG62 × Vijay (RIL), Vijay × ICC4958 (RIL)	Radhika et al. 2007
84 marker loci (82 SSRs and 2 ESTs)	ICC 4991 × ICCV 04516 (F2)	Kottapalli et al. 2009
Common bean		
244 marker loci (224 RFLPs, 9 isozyme and 9 seed protein, 2 morphological)	XR-235–1–1 × Calima (BC)	Vallejos et al. 1992
152 marker loci (112 RFLPs, 15 known genes, 8 RAPDs and 7 isozyme)	BAT93 × Jalo EEP558 (F2)	Nodari et al. 1993a
157 marker loci (51RFLP, 100 RAPD, 2 SCAR and 4 morphological)	Ms8EO2 × Corel (BC1)	Adam-Blondon et al. 1994
168 RAPDs	BAC 6 × HT 7719 (RIL)	Jung et al. 1996
563 marker loci (120 RFLPs, 430 RAPDs, few isozyme/morphological)	BAT93 × Jalo EEP558 (RIL)	Freyre et al. 1998
246 marker loci (102 RAPDs, 78 SSRs, 48 RFLPs and 18 AFLPs)	Consensus map of DOR364 × G 19833; BAT93 × Jalo EEP558 (all RILs)	Blair et al. 2003
235 marker loci	DOR364 × G19833 (RIL)	Hong et al. 2004
74 marker loci (50 RFLPs, 24 AFLPs)	DOR364 × G19833 (RIL)	Yan et al. 2004
115 marker loci (89 RAPDs and 26 SSRs)	BAT 881 × G 21212 (RIL)	Frei et al. 2005

85 TRAP marker loci	BAT 93 × Jalo EEP 558 (RIL)	Miklas et al. 2006a
31 marker loci (29 RAPD, 2 SCAR)	Jamapa × J-117, DOR364 × G19833 and BAT93 × JaloEEP558	Blair et al. 2006
113 SSR loci	BAT93 × Jalo EEP558 (RIL)	Grisi et al. 2007
97 marker loci (52 RAPDs, 32 RFLPs, 12 SCARs, and 1 morphological)	Andecha × A252	Rodríguez-Suárez et al. 2007
Cowpea		
197 marker loci (133 RAPDs, 39 RFLPs, and 25 AFLPs)	IT84S-2049 × 524B (RIL)	Menéndez et al. 1997
80 marker loci (77 RAPDs and 3 morphological)	IT84S-2246–4 × TVNu 110–3A (RIL)	Ubi et al. 2000
97 RFLP loci	IT2246 × TVN1963 (RIL)	Menancio-Hautea et al. 1993
77 RAPD loci	IT84S-2246–4 × TVNu110–3A (RIL)	Ewa et al. 2000
70 RAPD loci	GSC01 × GSC02 (F2)	Shim et al. 2001
423 marker loci (242 AFLPs, 181 previously mapped RAPDs, RFLPs, AFLPs, and biochemical)	IT84S-2049 × 524B (RIL)	Ouédraogo et al. 2002b
260 marker loci (242 AFLPs, 18 disease or pest resistance-related markers)	IT84S-2049 × 524B (RIL)	Ouédraogo et al. 2002a
171 marker loci (RAPDs, SSRs, AFLPs, and morphological)	cowpea cultivar × wild relative	Ortiz 2003
137 marker loci (134 AFLPs and 5 SSRs)	Sanzi × VITA7 (RIL)	Omo-Ikerodah et al. 2008
Fava bean		
17 marker loci (7 RFLPs, 4 morphological, 3 isozyme, 3 RAPDs)	var. paucijuga line 172 × cv. Optica × var. paucijuga line 172 (BC)	van de Ven etal.1991
51 maker loci (7 isozymes, 43 RAPDs, 1 RFLPs)	Vf6 × Vf35 (F2); Vf6 × Vf173 (F2)	Torres etal.1993
23 marker loci (8 morphological, 7 RFLPs, 4 isozyme, 4 RAPDs)	var. paucijuga line 172 × cv. Optica × var. paucijuga line 172 (BC)	Ramsay etal.1995
157 marker loci (147 RAPDs, 9 isozyme, 1 morphological)	Vf6 × Vf2 T5,Vf6 × Vf2 T6,Vf6 × Vf2 T3,Vf6 × Vf2 T4,Vf6 × Vf2 T4,Vf6 × Vf2 T5,Vf6 × Vf2 T6 (all F2s)	Satovic etal.1996

(continued)

Table 6.2 (*Continued*)

Crop marker loci	Mapping population	Reference
116 marker loci (105RAPDs, 7 isozyme, 1 morphological, 3 seed protein genes)	Vf6 × Vf2 T4,Vf6 × Vf2,Vf6 × Vf2 T6 (all F2s)	Vaz-Patto etal.1999
121 marker loci (117 RAPDs, 2 isozyme, 2 seed protein genes)	Vf 6 × Vf 136 (F2)	Roman etal.2002
191 marker loci (176 RAPDs, 6 isozyme, 4 seed protein genes, 4 SSRs and 2 morphological)	Composite map based on 11 F2 populations	Roman etal.2004
103 marker loci (94 RAPDs, 4 isozyme, 3 SSRs, 2 seed protein genes)	29H × Vf136 (F2)	A'vila etal. 2004
130 marker loci (130 AFLPs) and the Hg-cm-1 locus	TN16 × TN20 (F2)	Atibalentja etal.2005
151 intron-targeted amplified polymorphic marker (ITAPs) loci	Vf6 × Vf27 (RIL)	Ellwood etal.2008
Lentil		
34 marker loci (RFLP, isozyme and morphological)	*Lens culinaris* × *L. orientalis*	Havey and Muehlbauer 1989
177 marker loci (89 RAPDs, 79 AFLPs, 6 RFLPs, 3 morphological)	ILL 5588 × L692–16–1 (s) (RIL)	Eujayl et al. 1998a
114 marker loci (RAPD, ISSR and RGA)	ILL5588 × ILL7537 (F2)	Rubeena et al. 2003
200 marker loci (83 AFLPs, 71 RAPDs, 39 ISSRs, 5 morphological and 2 SSRs)	*L. culinaris* ssp. *culinaris* × *L. culinaris* ssp *orientalis* (F2)	Duran et al. 2004
283 marker loci (SSRs and AFLPs)	ILL 5588 × L 692–16–1(s)	Hamwieh et al. 2005
158 marker loci (83 AFLPs, 71 RAPDs, 39 ISSRs and 2 SSRs)	*Lens culinaris* ssp. *culinaris* Medik. cv. 'Lupa' × *L. culinaris*. ssp. *orientalis* (F2)	Fratini et al. 2007
207 marker loci (RFLPs, SSRs and RAPDs)	Eston × PI320937 (RIL)	Tullu et al. 2008
Pea		
355 RFLP marker loci	JI 281 × JI 399 (RIL)	Ellis et al. 1992

69 marker loci (3 morphological, 4 RGA, 56 RFLPs, SSRs, 2 RAPDs)	Erygel × 661 (F2)	Dirlewanger et al. 1994
209 marker loci (RFLPs, RAPDs, AFLPs, RGA)	Prima × OSU442–15 (F2)	Gilpin et al. 1997
240 RAPD marker loci	Terese × K 586 (RILs)	Laucou et al. 1998
240 marker loci (164 AFLPs, 33 RAPDs, 14 morphological, 12 ISSRs, 11 isozymes, 5 CAPS)	Wt 10245 × Wt 11238 (RIL)	Irzykowska et al. 2001
324 marker loci(AFLP, RAPD, SSR, ISSR and STS)	Puget × 90- 2079 (RIL)	Pilet-Nayel et al. 2002
96 loci (28 RFLPs, 22 AFLPs, 43 RAPDs, and 3 SCARs)	3148-A88 × Rovar (F2:3 and F2:4 families)	Timmerman-Vaughan et al. 2002
206 marker loci (192 AFLPs, 13 RAPDs, 1 STS)	Carneval × MP 1401 (RIL)	Tar'an et al. 2003
204 marker loci (140 AFLPs, 24 RAPDs, 10 ISSRs, 5 CAPSs, 1 STS, 11 isozymes and 13 morphological)	Wt10245 × Wt11238 (F2)	Irzykowska and Wolko 2004
906 marker loci (146 RFLPs, 760 AFLPs)	BSR 101 × PI 437.654 (RIL)	Lewers et al. 1999
206 marker loci (RAPD, SSR and STS)	DP × J1296	Prioul et al. 2004
246 marker loci (230 RAPDs, 6 STSs and 6 ESTs, 3 morphological, 1 isozyme)	P665 × Messire (RIL)	Fondevilla et al. 2008
239 SSR loci	Terese × K 856; Champagne × Terese; Shawnee × Bohatyr (all RILs)	Loridon et al. 2005
Peanut		
117 RFLP loci	AA genome (2*x*)- *A. stenosperma* × *A. cardenassi* (F2)	Halward et al. 1993
167 RAPD loci	AA genome (2*x*) - *A. stenosperma* × *A. stenosperma* × *A. cardenassi* (BC)	Garcia et al. 1995
370 RFLP loci	AA × BB genome - *A. batizocoi* × (*A. cardenasii* × *A. diogoi*) (BC)	Burow et al. 2000
370 RFLP loci	Synthetic (4*x*)- TxAG 6 × Florunner (BC1)	Burow et al. 2001
102 AFLP loci	AA genome (2*x*)- *A. kuhlmannii* × *A. diogoi* (F2)	Milla 2003
308 AFLP loci	ICG 12991 × ICGVSM 93541 (F2)	Herselman et al. 2004

(*continued*)

Table 6.2 (*Continued*)

Crop marker loci	Mapping population	Reference
204 SSR loci	AA Genome (2x) - *A. duranensis* × *A. stenosperma* (F2)	Moretzsohn et al. 2005
94 SSR loci	BB Genome (2x) - *A. ipaensis* × *A. magna* (F2)	Gobbi et al. 2006
135 SSR loci	Cultivated (4x)- TAG 24 × ICGV 86031	Varshney et al. 2008
56 SSR loci	Cultivated (4x)- TAG 24 × GPBD 4	Khedikar et al. 2009
Soybean		
153 RFLP loci	PI 97100 × Coker 237 (F4)	Lee et al. 1996
155 RFLP loci	Young × PI 416 937 (F4)	Lee et al. 1996
840 marker loci (650 AFLPs, 165 RFLPs, 25 RAPDs)	BSR101 × P1437.654 (RIL)	Keim et al. 1997
155 RFLP loci	Young × PI416937 (RIL)	Mian et al. 1998
606 SSR loci	*G. max* × *G. soja* (F2), Minsoy × Noir 1 (RIL), Clark × Harosoy (F2)	Cregan et al. 1999
507 SSR loci	Williams 82 × Corsoy 79, Williams 82 × Dassel Williams 82 × DSR173, Williams 82 × S19–90, Williams 82 × Vinton 81 (all RILs)	Venancio et al. 2001
~500 marker loci (401 RFLPs, 96 SSRs, 5 phenotypic trait, 1 RAPD)	Misuzudaizu × Moshidou Gong (F2)	Yamanaka et al. 2001
120 marker loci (113 SSRs, 6 RAPDs and 1 RFLP)	Ma.Belle × Proto (F2)	Csanádi et al. 2001
104 SSR loci	Minsoy × Noir 1 (RIL)	Specht et al. 2001
436 marker loci (329 RAPDs, 103 SSRs, 4 other)	PI 437088A × Asgrow A3733 (RIL)	Chung et al. 2003
1849 marker loci (1,015 SSRs, 709 RFLPs, 73 RAPDs, 24 classical traits, 10 isozymes, 6 AFLPs)	integrated map based on 5 RILs (Minsoy × Noir 1, Minsoy × Archer, Archer × Noir 1, Clark × Harosoy, and A81–356022 × PI468916)	Song et al. 2004

452 marker loci (219 SSRs, 189 RFLPs, 40 ESTs, 3 R gene loci and 1 phenotype)	Kefeng No. 1 × Nanong 1138–2 (RIL)	Zhang et al. 2004
100 SSR loci	Essex × Williams (RIL)	Hyten et al. 2004
360 marker loci (177 RFLPs, 150 SSRs, 28 AFLPs and 5 phenotypic)	Misuzudaizu × Moshidou Gong 503 (RIL)	Watanabe et al. 2004
99 SSR loci	AC756 × RCAT Angora (RIL)	Primomo et al. 2005
21 SSR loci	Embrapa 20 × BRS 133 (F2)	Nicolas et al. 2006
237 SSR loci	Essex × Forrest (RIL)	Kassem et al. 2006
20 marker loci (5 BARC-SSRs, 11 SIUC-SSRs and 4 AFLP derived SCAR)	Essex × Forrest (NIL)	Ruben et al. 2006
94 SSR loci	N87–984–16 × TN93–99	Panthee et al. 2006
164 SSR loci	Charleston × Dongnong 594 (RIL)	Chen et al. 2007
128 marker loci (89 SSRs and 39 RAPDs)	OX760–6–1 × Conrad (RIL)	Han et al. 2007
959 marker loci (509 RFLPs, 318 SSRs, 318 AFLPs, 97 AFLPs-derived STS, 29 BAC-end or EST-derived STS, 5 morphological and 1 RAPD)	Essex × Forrest (RIL)	Xia et al. 2007
342 SNP loci	Minsoy × Noir 1; Minsoy × Archer; Evans × Peking (all RILs)	Hyten et al. 2008

times) BAC libraries in several legumes (chickpea, pigeonpea, cowpea, and peanut). Furthermore, BAC-end sequences have been generated for 25,000 to 50,000 BACs in these legume species (D.R. Cook, pers. commun). The BAC-end sequence data are being analyzed for getting the insights of genomes of these legume species (Foster-Hartnett et al. 2001; Schlueter et al. 2008) and for developing markers, such as SSRs, that would be very helpful to link the genetic and physical maps (Shultz et al. 2007).

In some legumes such as common bean and cowpea (excluding *Medicago*, *Lotus* and soybean), genome-wide physical maps also have been developed. For instance, fingerprinting of 41,717 BACs of common bean provided a draft physical map consisting of 1,183 clone contigs and 6,385 singletons with about 9 times coverage of the genome of common bean (Schuleter et al. 2008). Similarly in case of cowpea, based on high information content fingerprinting (HICF) of 60,000 BAC clones, a 10 times physical map of cowpea has been developed at the University of California—Riverside (T.J. Close, pers. commun). It is planned to anchor the cowpea physical map to the SNP-based genetic linkage map. Local physical maps for resistance gene homologs are also being developed in cowpea, pigeonpea, chickpea, and common bean at the University of California -Davis (see Varshney et al. 2009). It is anticipated that these physical maps will lead to sequencing of gene space or regions of interest very soon.

4. Transcriptome Resources. Recent years have witnessed significant progress in the area of transcriptomics in legumes other than *Medicago, Lotus,* and soybean. Until recently, it was difficult to imagine undertaking functional genomics in these legume species except model legume species and soybean. Nevertheless, the availability of genomic resources and recent technology advances have made it possible in a practical sense in several other legume species (Coram et al. 2007).

Among plant species, much work has been done in the development of functional genomics resources such as ESTs and array development has been done in cereal crops and model legumes. For instance, hundreds of thousands ESTs are available in model and major legume species (see Varshney et al. 2009b). Due to the availability of next-generation sequencing technologies such as 454/FLX and Solexa 1 Gb Sequencing, large numbers of ESTs have been developed very recently. For instance, using 454/FLX sequencing on the normalized complementary deoxyribonucleic acid (cDNA) pools collected from more than 20 different tissues representing a variety of plant developmental stages of chickpea and pigeonpea provided 435,184 and 496,705 sequence reads for each, respectively. The average length of sequence reads in chickpea is 236.4 bp and 200.3 bp in pigeonpea. Analysis of these sequence data should provide good transcriptome assemblies for chickpea and pigeonpea that can be used to analyze the gene contents as well as marker discovery.

Although several transcript profiling studies have been undertaken in *Medicago, Lotus,* and soybean with an aim at identifying genes involved in nodule and seed development (Thibaud-Nissen et al. 2003; Benedito et al. 2008; Combier et al. 2008), a few studies have been targeted in some other legume species to identify genes involved in resistance/tolerance to biotic and abiotic stresses (e.g., Irsigler et al. 2007). For instance, a small array with 768 features has been developed in chickpea (Coram and Pang 2005a). This array has been used to identify genes involved in Ascochyta blight resistance (Coram and Pang 2005b, 2006) and tolerance to drought, cold, and salinity (Mantri et al. 2007). In the case of cowpea, by using RNA as a surrogate for DNA of cowpea with a readily available soybean genome array, 11% to 14.7% of all probe sets on the array showed "present" calls (Das et al. 2008). These researchers enumerated 1,058 potential single-feature polymorphisms (SFPs) between two parents of a RIL population segregating for several important traits. Sequencing of 25 putative polymorphism-containing amplicons yielded a SFP probe set validation rate of 68%. This study provides an example of extension of genomic resources from a well-supported species like soybean to orphan crops such as cowpea and pigeonpea.

IV. TRAIT MAPPING AND MARKER-ASSISTED SELECTION

Molecular markers are powerful diagnostics tools used to detect DNA polymorphism both at the level of specific loci and at the whole genome level (Azhaguvel et al. 2006). As compared to morphological traits or markers, molecular markers have several advantages as they are phenotypically neutral and are influenced neither by environments nor by pleiotropic and epistatic interactions, and their expression is not dependent on plant age or part (Jones et al. 1997). In fact, the use of molecular markers in improving efficiency in plant breeding was suggested as early as in 1989 (Tanksley et al. 1989; Melchinger 1990). In this regard, once linkage between a gene for the agronomic trait of interest and marker locus is established, DNA diagnostic tests can be used to guide plant breeding (Morgante and Salamini 2003; Gupta and Varshney 2004). The selection of useful lines for breeding with the help of linked molecular markers is called marker-assisted selection (MAS). Use of MAS is especially advantageous for traits with low heritability where traditional selection is difficult, expensive, or lacks accuracy or precision.

The use of MAS in plant breeding has revolutionized the improvement of temperate field crops (Koebner and Richard 2002; Varshney et al. 2006) and will have similar impacts on breeding of legume crops, particularly for traits where phenotyping is possible only late in the season and where screening of traits is difficult or prohibitively expensive. Among different legumes, soybean was the first legume crop where MAS was used for breeding for soybean cyst nematode. Two SSR markers (BARC-Satt309 and BARC-Sat_168) identified by Cregan et al. (1999) have proven highly effective in identifying lines carrying SCN resistance from those carrying the allele for SCN susceptibility at the *rhg1* locus.

Although a number of genes and QTL have been tagged using different kinds of molecular markers in several legume crops (Table 6.3), only a few markers have been validated and deployed in breeding programs (mainly in soybean and common bean). Indeed, soybean is the first legume crop where markers associated with several traits have been in use in MAS for a long time in both the public sector (Saghai Maroof et al. 2008) and the private sector (Cahill and Schmidt 2004). Because of the importance of soybean for the private sector, significant progress has been made in MAS in soybean breeding in the public sector. This is reflected in a press release of Pioneer Hi-Bred International Inc. in 2005: "Pioneer has led the development of patented processes for using MAS in soybeans," said John Soper, director of soybean research of this seed company (www.pioneer.com/web/site/portal/menuitem.f644671720b94a9724d533d0d10093a0/). "The technology has allowed researchers to see things that were not possible to see and capitalize on a decade ago. Before MAS, breeders were limited to using visual observations and yield data to evaluate varieties and make selections. With MAS, Pioneer scientists now are able to understand the genetic basis for what they are seeing and use this knowledge to design and select better varieties." MAS has been applied in some soybean breeding programs of the public sector as well. For instance, Saghai Maroof et al. (2008) have pyramided respective *Rsv* genes for soybean mosaic virus (SMV) from different loci (*Rsv1*, *Rsv3*, and *Rsv4*) in a susceptible cultivar 'Essex' through MAS. They found two-gene and three-gene isolines of *Rsv1Rsv3*, *Rsv1Rsv4*, and *Rsv1Rsv3Rsv4* acted in a complementary manner, conferring

Table 6.3. Some examples of mapping of QTLs/genes for agronomic traits and resistance/tolerance to biotic/abiotic stress tolerance.

Crop	Trait	No. QTL/markers associated with gene identified	Reference
I. Agronomic traits and tolerance to abiotic stress			
Chickpea	Single pod/double pod	Tagged with maker TA80	Rajesh et al. 2002; Cobos et al. 2005
	Flower color	Tagged with maker GAA47	Cobos et al. 2005
	Beta- carotene, leutin, seed weight, beta-carotene concentration and seed weight	15 QTLs	Abbo et al. 2005
	Time to flowering	R maker	Lichtenzveig et al. 2006
Common bean	Nodulation and common bean blight resistance (CBB)	4–8 QTLs	Nodari et al. 1993b; Tsai et al. 1998
	Drought	2 QTLs	Schneider et al. 1997
	Seed mass	4 QTLs	Guzman-Maldonado et al. 2003
	Calcium, iron, zinc	3- 26 QTLs	Guzman-Maldonado et al. 2003
	Plant height, climbing ability, internode length and branch number	1–9 QTLs	Checa and Blair 2008
	Phosphorus uptake efficiency related root traits	6–26 QTLs	Hong et al. 2004; Yan et al. 2004; Beebe et al. 2006
	Frost tolerance	3 QTLs	Link et al. 2008
Lentil	Cold	Gene	Eujayl et al. 1999
	Winter hardiness	Gene	Eujayl et al. 1999; Kahraman et al. 2004
Pea	Various agronomic traits	37 QTLs	Irzykowska and Wolko 2004
	Grain yield, seed protein concentration, and maturity	7 QTLs	Tar'an et al. 2004

(continued)

Table 6.3 (*Continued*)

Crop	Trait	No. QTL/markers associated with gene identified	Reference
	Seed weight, seed number and harvest index, plant maturity	~19 QTLs	Timmerman-Vaughan et al. 2004
Peanut	Transpiration, transpiration efficiency, specific leaf area and SPAD chlorophyll	2–5 QTLs	Varshney et al. 2009a
Pigeonpea	Cytoplasmic male sterility	RAPD marker	Souframanien et al. 2003
Soybean	Seed protien oil content	1- 11 QTLs	Lee et al. 1996; Hyten et al. 2004; Jun et al. 2008
	Water use efficiency	5 QTLs	Mian et al. 1996, 1998; Specht et al. 2001
	Specific leaf weight and leaf size	3–6 QTLs	Mian et al. 1998
	Seed weight	15 QTLs	Csanádi et al. 2001
	Flowering time	4 QTLs	Yamanaka et al. 2001
	Yield, maturity	3 QTLs	Specht et al. 2001
	Sprout yield	4 QTLs	Lee et al. 2001
	Seed isoflavone	6 QTLs	Meksem et al. 2001; Kassem et al. 2004; Primomo et al. 2005
	Various agronomic traits	63 QTLs	Zhang et al. 2004; Reinprecht et al. 2006
	Seed size	7 QTLs	Hyten et al. 2004
	Flowering time, maturity, reproductive period, seed hardness, viability of seed, germination rate of seed, water absorbability of seed and seed weight	39 QTLs	Watanabe et al. 2004
	Nodule number and nodule dry weight	2 QTLs	Nicolas et al. 2006
	Oligosachharides and sucrose	6 QTLs	Kim et al. 2006

	Developmental behavior	15 QTLs	Sun et al. 2006
	Browning in soybean seed coats	5 QTLs	Githiri et al. 2007
	Domestication	2 QTLs	Liu et al. 2007
	Seed composition	52 QTLs	Li et al. 2007
	Sudden death syndrome	4 QTLs	Kazi et al. 2008
	Iron deficiency chlorosis (in nutrient solution)	3–19 QTLs	Lin et al. 2000
	Aluminum tolerance	11 QTLs	Bianchi-Hall et al. 2000; Qi et al. 2008
	Salt tolerance	1 QTL	Lee et al. 2004
	Phosporus deficiency	5 QTLs	Li et al. 2005
	Chilling tolerance in seed yield	3 QTLs	Funatsuki et al. 2005
	Seed shape	19 QTLs	Salas et al. 2006
	Cyst nematode	3 QTLs	Guo et al. 2005; Ferdous et al. 2006
	Sulfur-containing amino acids	4 markers (Satt235, Satt252, Satt427 and Satt436)	Panthee et al. 2006
	Cleistogamy	4 QTLs	Khan et al. 2008
	Maturity gene	AFLP marker	Matsumura et al. 2008
	II. Resistance to biotic stresses		
Chickpea	Aschochyta blight (different races)	>20 markers/loci	Santra et al. 1998, 2000; Tekeoglu et al. 2002; Collard et al. 2003; Flandez-Galvez et al. 2003a,b; Millan et al. 2003; Rakshit et al. 2003; Udupa and Baum, 2003; Cho et al. 2004; Rubeena et al. 2006; Cobos et al. 2006; Kottapalli et al. 2009
	Fusarium wilt resistance (different races)	>20 markers/loci	Ratnaparhke et al. 1998; Rubio et al. 2003; Millan et al. 2003; Benko-Iseppon et al. 2003; Cobos et al. 2005

(*continued*)

Table 6.3 (*Continued*)

Crop	Trait	No. QTL/markers associated with gene identified	Reference
Common bean	Anthracnose	14 RAPD and 4 AFLP markers	Adam-Blondon et al. 1994; Young and Kelly 1997; Geffroy et al. 1998; Young et al. 1998; Mendoza et al. 2001; Alzate-Marin et al. 2003; Rodríguez-Suárez et al. 2008
	Bean common mosic virus	SW13 ROC11/350/420, ROC20/460	Melotto et al. 1996; Johnson et al. 1997
	No. of root nodules and resistance to *Xanthomonas*	4 QTLs	Souza et al. 2000
	Fusarium wilt resistance	RAPD markers; $P7_{700}$, $G6_{1100}$ $S8_{500}$, $I1_{1700}$	Winter et al. 2000; Rajesh et al. 2004
	Thrips	1 QTL	Frei et al. 2005
	Bacterial brown spot	1 QTL	Jung et al. 2003
	White mold	2 QTL	Kolkman and Kelly 2003; Miklas et al. 2003
	Rust	5 SCAR	Park et al. 2004; Mienie et al. 2005
	Bacterial blight	6 QTL/SCAR	Yu et al. 2004; Liu et al. 2008; Vandemark et al. 2008
	Leaf hopper resistance	PV-atcc003	Murray et al. 2004
	Bean golden yellow mosaic geminivirus	1 SCAR marker	Blair et al. 2007
Cowpea	Aphid resistance	Bg4D9b	Myers et al. 1996
	Fusarium wilt resistance for race 1	1 locus	Simon and Muehlbauer 1997
	Anthracnose	6 RAPD markers	de Arruda et al. 2000
	Striga resistance	~9 RFLP and 20 AFLP markers	Ouédraogo et al. 2001; Ouédraogo et al. 2002a; Boukar et al. 2004
	Pod weevil	2 SCAR markers	Blair et al. 2006
	Flower bud thrips	1 locus	Omo-Ikerodah et al. 2008

	Bruchids	1 locus	Somta et al. 2008
Lentil	Fusarium wilt	RAPD marker	Eujayl et al. 1998b
	Anthracnose	2 RAPD and 3 AFLP markers	Tullu et al. 2003
	Aschochyta blight	RAPD, AFLP markers	Chowdhaury et al. 2001; Rubeena et al. 2006
Pea	*Erysiphe pisi*	Gene	Dirlewanger et al. 1994; Timmerman et al. 1994; Janila and Sharma 2004
	Ascochyta blight	6–25 markers/loci	Timmerman-Vaughan et al. 2002, 2004; Fondevilla et al. 2008
	Pea seed-borne mosaic virus (PSbMV)	Gene	Gao et al. 2004
	Mycosphaerella pinodes	RAPD, STS and EST markers	Tar'an et al. 2003; Fondevilla et al. 2007
Peanut	Rosette virus	1 locus	Herselman et al. 2004
	Ascochyta blight	6 loci	Avila et al. 2004
	Rust	13 QTLs	Khedikar et al. 2009
Pigeonpea	Fusarium wilt	2 RAPD markers	Kotresh et al. 2005
	Late leaf spot	5QTLs	Leal-Bertioli et al. 2009
Soybean	Cyst nematode	1–2 (16 AFLP markers; 5 BARC-SSRs, 11 SIUC-SSRs and 4 AFLP derived SCAR)	Tamulonis et al. 1997; Concibido et al. 2004; Atibalentja et al. 2005; Guo et al. 2006a,b; Ruben et al. 2006; Winter et al. 2006
	Corn earworm	3 loci	Rector et al. 1998
	Brown stem rot	2 loci	Lewers et al. 1999
	Sclerotinia stem rot	28 loci	Venancio et al. 2001
	Phytophora root rot	3 loci	Han et al. 2007
	Sclerotinia stem rot	4 loci	Guo et al. 2008
	Soybean mosaic virus	3 SSR	Shi et al. 2008
	Asian rust	SSR markers	Garcia et al. 2008; Silva et al. 2008

resistance against all strains of SMV, whereas isolines of *Rsv3Rsv4* displayed a late susceptible reaction to selected SMV strains. In the case of common bean, a few reports are available on MAS deployment (see Miklas et al. 2006a,b). For example, MAS has been used successfully to breed for enhanced resistance to anthracnose in the cultivar 'Perola' in Brazil (Raganin et al. 2003), pinto beans in the United States (Miklas et al. 2003), and Andean climbing beans in Mexico/Colombia (Garzón et al. 2008). Although efforts for validating and deploying markers in MAS are under way for root traits in chickpea at ICRISAT or for host plant resistance to striga in cowpea at the International Institute of Tropical Agriculture (IITA, Nigeria), there is a need to speed up marker validation and deployment in breeding programs in different legumes.

V. SUMMARY AND PROSPECTS

During last five years or so, significant progress has been made in developing genomic resources in model species (*Medicago, Lotus*), major legumes (soybean, common bean, peanut), and so-called orphan (cowpea, chickpea, pigeonpea) legume crops. For instance, legume crops now enjoy the availability of reference/draft genome sequences (soybean, *Medicago, Lotus*) and dense genetic as well as physical maps. Availability of an appropriate amount of molecular markers is also no longer a bottleneck in many legume species. Nevertheless, there is still a need to develop critical mass of molecular markers and good genetic maps in some minor but locally very important legume species (e.g., pigeonpea, lentil, faba bean, etc.). It is anticipated that reduced cost of sequencing technologies will change the situation soon in these minor legume species.

As large amounts of genome and transcript sequence data are available for many legume crops—amounts expected to expand several-fold in coming years due to heavy use of next-generation sequencing technologies—analysis, and use of genomic information for applied aspects is going to be challenging. It is anticipated that genomic information will enhance understanding of biological mechanisms, leading to new or improved screening methods for selecting superior genotypes more efficiently, and will improve the decision-making process for more efficient breeding strategies. Adoption of genomic information or markers associated with trait by the breeding community is another area that needs to be strengthened in the legume community.

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