

Legume Genomics: From Genomic Resources to Molecular Breeding

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WITH an explosive growth rate, especially in developing countries, the world population of 7.2 billion is expected to reach 9.6 billion by 2050. There is a need to produce about 70% more food to feed this predicted population. Legumes form important constituents of a vegetarian diet and are rich sources of dietary protein (Duranti and Gius, 1997). Legumes comprise the third largest family of flowering plants and provide important sources of food, fodder, oil, and fiber products. Legume seeds typically contain 20 to 25% protein and are also a rich source of dietary fiber. In addition, legumes have the capability to fix atmospheric N₂ with the help of symbiotic nitrogen fixing bacteria in root nodules, thereby reducing fertilizer use in agriculture, and the cost of nitrogen inputs by smallholder farmers in developing countries. Due to their higher protein content and other nutrients, legumes are considered important to confront malnutrition among resource-poor people in developing countries. In brief, legumes including beans (*Phaseolus vulgaris*), chickpea (*Cicer arietinum*), cowpea (*Vigna unguiculata*), lentils (*Lens culinaris*), pea (*Pisum sativum*), peanut (*Arachis hypogaea*), and soybean (*Glycine max*), etc. play an important role in ensuring food security, reducing poverty, improving human health and nutrition, and enhancing ecosystem resilience, especially in developing countries.

Considering the importance of legumes for food and nutritional security, there have been sincere efforts

toward increasing legume production. However, average global yield for legumes (0.86 t/ha) is much less than the average yield of cereals (3.54 t/ha) (FAO, 2011). Despite continuous efforts to improve productivity, crop production has witnessed severe challenges and suffers with yield loss due to several biotic and abiotic factors. Biotic factors affecting yield include aphids (*Aphis craccivora*), flower thrips (*Megalurothrips sjostedti*), pod borer (*Maruca vitrata*), weevil (*Callosobruchus maculatus*) in cowpea, rust (*Phakopsora pachyrhizi*), stem rot (*Sclerotinia sclerotiorum*), red leaf blotch (*Phoma glycinicola*), cyst (*Heterodera glycines*) in soybean, rust (*Puccinia arachidis*), late leaf spot (*Cercosporidium personatum*), early leaf spot (*Cercospora arachidicola*) in peanut, ascochyta blight (*Ascochyta rabiei*), fusarium wilt (*Fusarium oxysporum*), botrytis gray mold (*Botrytis cinerea*), dry root rot (*Rhizoctonia bataticola*), and pod borer (*Helicoverpa armigera*) in chickpea (Dauost et al., 1985; Pandey et al., 2012; Varshney et al., 2013a). Among abiotic stress drought, salinity and temperature are major yield constraints. In addition, climate changes have had a tremendous influence on crop production and productivity (Varshney et al., 2011; Lake et al., 2012).

To meet food requirements and increase legume production to combat malnutrition, it is essential to develop the crop with a higher yield. However, efforts to increase legume production using conventional approaches have been happening for some time, but global production has only increased marginally during the past 50 yr (FAO, 2011). This suggests a need to develop crop varieties with a higher yield that also include environment-specific responses to stress. In this scenario, genomics-assisted breeding (GAB), that integrates the use of genomic tools

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in conventional breeding, has the potential to develop superior crop varieties and offers new perspectives to counter the production constraints (Varshney et al., 2005). Genomic resources including molecular markers, genetic maps, and QTLs, however, are the prerequisite for undertaking GAB (Varshney et al., 2009a). Until recently, except soybean and common bean, most of the food legume crops were considered orphan crops as there were not many genetic and genomic resources available (Varshney et al., 2009a; Tuberosa et al., 2011). The lack of sufficient genomic resources had been one of the major hurdles in undertaking GAB approaches such as marker-assisted selection (MAS) for crop improvement in legumes. The last two decades have witnessed the advent of several high-throughput sequencing and genotyping technologies which have significantly reduced cost, time, and effort (Varshney et al., 2009b). For instance, as a result of the implementation of next generation sequencing (NGS) technologies, large-scale genomic resources such as molecular markers, transcript reads, BAC-end sequences (BESs), comprehensive genetic maps, and physical maps have been developed in several legume crops (Kelly et al., 2003; Muehlbauer et al., 2006; Gepts et al., 2008; Varshney et al., 2010; Rubiales et al., 2011; Gaur et al., 2012). Not only this, NGS technologies have facilitated genome sequencing in many crop species, including several legume crops (Michael and Jackson, 2013). Though until few years ago, *Medicago truncatula* and *Lotus japonicus*, model legume plant species, were the only legume species that were targeted for genome sequencing (Sato et al., 2008; Young et al., 2011), genome sequences have become available for soybean (Schmutz et al., 2010), pigeonpea (Varshney et al., 2012), and chickpea (Varshney et al., 2013b). Similar efforts are underway in other legume crops such as peanut (<http://www.peanut-bioscience.com>), lentil, pea, and mungbean. As a result of the availability of such genomic resources, marker-trait associations have also been established in several legume crops. Such trait-associated markers, after validation in different genetic backgrounds, can be implemented in GAB. Although several success stories of GAB are available in many crops, mainly cereals (Sundaram et al., 2008; Ceballos et al., 2012; Miedaner and Korzun, 2012; Singh et al., 2012), some examples have become available in some legume crops, e.g., soybean, peanut, chickpea, etc. (Tar'an et al., 2003; Miklas et al., 2006; Muehlbauer et al., 2006; Timko et al., 2011).

The VI International Congress on Legume Genetics and Genomics (ICLGG) with a mission to bring together scientists who work on research aspects of legume biology in model species using genetic and genomic tools, with those working on applied aspects and breeding of crop and pasture species, was successfully held in Hyderabad (India) from 2–7 Oct. 2012 (<http://www.icrisat.org/gt-bt/vi-iclgg/homepage.htm>). VI ICLGG focused on different disciplines of legumes ranging from very basic to applied aspects of science like symbiosis and development, evolution and diversity, nutrition and quality, next

generation genomics, abiotic stress, pathogenesis and disease resistance, genomic resources and trait mapping, genomics assisted breeding, and translational genomics. More than 500 scientists representing different countries, disciplines, and crops attended and discussed their experience in legumes. Selected high quality papers from the conference with a focus on legume genomics have been included in this special issue “Legume Genomics”. This special issue covers the genomic aspects of seven legumes including chickpea, cowpea, lentil, lotus, peanut, pongamia, and soybean (Table 1). In parallel, papers related to plant biology themes presented at the VI ICLGG have been included in another special issue entitled “Legume Biology” in *Functional Plant Biology*.

In total, this issue brings together 13 high quality papers including seven research and six review papers covering four different themes, namely, Genomic Resources, Diversity and Domestication, Functional Genomics, and Applied Genomics.

Genomic Resources

Genomic resources provide the starting point for understanding the unique traits present in the given crop and also tools for implementation of molecular breeding for the development of improved varieties. The first article in this section from Biswas et al. (2013) is a review article that highlights the importance of *Pongamia pinnata* as a candidate legume species for development as a feedstock for biodiesel and aviation fuel. The demand for food, fuel, and fiber continues to increase in parallel with an increasing world population. *P. pinnata* is a medium-sized tree legume which produces about 30 kg per tree per year of seeds and contains on average 40 to 50% oil (v/v). *P. pinnata* has a long history of use for fuel, green manure, insecticides, and traditional medicines in India and Southeast Asia. In addition, *Pongamia* due to its drought and salinity tolerance capability can grow on marginal land, which makes it more suitable in comparison to first generation biofuel feedstock plants such as corn, soybean, wheat, sugarcane, and rapeseed. The authors have emphasized the need to characterize the extent of genetic diversity amongst the wild populations using molecular markers and identify markers associated with oil content and composition.

The second article by Iwata et al. (2013) is another review that focuses on the need to unravel the complex genomic organization of crop species to use genomics more efficiently in breeding strategies. Genomic resources along with molecular cytogenetics may help to facilitate a better understanding of legume genomes and chromosomes. In this review, the authors have summarized the achievements of cytogenetic studies in legumes in the Phaseoloid clade and reported the stable karyotypes in the case of common bean, cowpea, soybean, and pigeonpea. The authors have highlighted the importance of cytogenetics in combination with genomic resources to understand the influence of repetitive sequences on the structure and function of legume genomes. The

Table 1. List of major legumes covered in the special issue.

Crop	Chromosome number (n), ploidy level (x)	Genome size (Mbp)	Status of genome sequence	Covered theme
Chickpea (<i>Cicer arietinum</i> L.)	2n = 2x = 16	740	Draft assembly (Varshney et al. 2013b; Jain et al. 2013)	Diversity and Domestication (Gowda et al. 2013) Applied Genomics (Varshney et al. 2013c)
Cowpea (<i>Vigna unguiculata</i>)	2n = 2x = 22	620	Not available	Diversity and Domestication (Huynh et al. 2013)
Lentil (<i>Lens culinaris</i>)	2n = 2x = 14	4063	Not available	Applied Genomics (Fedoruk et al. 2013)
Lotus (<i>Lotus japonicus</i>)	2n = 2x = 12	472	Draft assembly (Sato et al. 2008)	Functional Genomics (Fukai et al. 2013)
Peanut (<i>Arachis hypogaea</i>)	2n = 4x = 40	2890	Underway (http://www.peanutbioscience.com)	Diversity and Domestication (Gowda et al. 2013) Applied Genomics (Khera et al. 2013; Wang et al. 2013)
Pongamia (<i>Pongamia pinnata</i>)	2n = 2x = 22	–	Not available	Genomic Resources (Biswas et al. 2013)
Soybean (<i>Glycine max</i>)	2n = 2x = 20	1115	Draft assembly (Schmutz et al. 2010)	Applied Genomics (Liu et al. 2013)

authors also discuss the future applications of molecular cytogenetics to better understand chromosome and genome structure and evolution in legumes.

Apart from crop yield (seed, grain, etc.), flowering and maturation time also have significance, as these characteristics are important for adaptation to different environments and regions. Flowering time is one of the most important parts of the plant life cycle, as this is highly associated with seed production. In the third article of this section, Kim et al. (2013) used approximately 200 flowering time controlling *Arabidopsis* genes to identify copies of these genes in three legume species, namely, *Lotus*, *Medicago*, and soybean. As a result, several homologs of flowering genes were identified in *Lotus* (96), *Medicago* (98) and soybean (304). The authors have categorized these genes into seven different flowering pathways covering photoperiod, vernalization, gibberellins, autonomous pathways, floral pathway integrators (FPIs), and floral meristem identity. The authors have shown significant variation in evolutionary processes like whole genome duplication in soybean, tandem duplication in *Medicago*, and ectopic duplication in *Lotus* that affect flowering genes in legumes. The authors have emphasized the need to understand the molecular basis of flowering networks to facilitate the development of improved varieties in response to environmental changes.

Diversity and Domestication

Genetic diversity is an important aspect and provides the basic resource in the form of genetic variation as molecular markers for breeding. Genetic diversity stored in germplasm banks must be utilized in a much broader way (McCouch et al., 2013). Plant genetic resources (PGRs) present in the genebank provide the starting point to understanding genetic diversity that can be used in modern breeding to develop high yielding and climate resilient cultivars. The first article in this section is a review by Gowda et al. (2013), who highlight

the importance of genomic resources in the conservation and use of legume plant genetic resources for crop improvement. The authors reported that out of a total of 1.1 million grain legume accessions in global genebanks, ICRISAT genebank holds 50,000 accessions of cultivated and wild relatives of chickpea, pigeonpea, and groundnut collected from 133 countries. Chickpea, pigeonpea, and groundnut have been suffering a narrow genetic base due to bottlenecks associated with the origin and domestication of these crops. The authors have emphasized the use of core and mini core collections in chickpea, pigeonpea, and groundnut to identify trait-specific diverse germplasm for use in breeding and genomic studies. The authors have also reported the successful use of wild accessions to bring resilience to some pests and diseases into cultivated accessions.

The second article under the section “Diversity and Domestication,” authored by Huynh et al. (2013), reports the genotyping of a cowpea collection of landraces and African ancestral wild species genotypes with single nucleotide polymorphism (SNP) markers using the GoldenGate genotyping assay. In total, 1133 (74%) markers were reported polymorphic out of a total of 1536 used for genotyping. Gene pool structure analysis using polymorphic SNP markers revealed two major gene pools in cultivated cowpea from Africa. Landraces from western Africa and eastern Africa were distributed separately in these two groups and were reported closely related to wild from the same geographic region. The authors have suggested divergent domestication processes leading to the formation of two gene pools. The authors have suggested that the genetic relatedness may guide introgression efforts in breeding programs and for improving the efficiency of germplasm management.

Functional Genomics

Functional genomics plays a significant role in the identification of genes and determining the mechanisms

conferring resistance and/or tolerance to biotic and abiotic stresses of legumes. Functional genomics uses genomic data to describe gene functions and interactions by utilizing large-scale assays to measure and track many genes or proteins in parallel under different environmental conditions. All three articles in this section are reviews that represent the current scenario of functional genomics studies in legumes. Fukai et al. (2013) review the role of endogenous retrotransposon in epigenetic changes in *Lotus*. The authors have suggested that despite retrotransposons occupying a large portion of genomes in flowering plants, the majority of them remained silent or rarely transpose. The authors have used *Lotus Retrotransposon 1 (LORE1)* as an example to describe evolutionary genomics and for the use of *LORE1* as a genetic tool for understanding characteristics. Based on the *LORE1* study, the authors have suggested that epigenetic activation of transposable elements can be induced by tissue culture and the active state can be maintained in the regenerated plants.

The next article by Garg and Jain (2013) covers transcriptome analysis in legumes. The transcriptome serves as starting point to measure the activity of genes and understand gene regulation in different biological contexts. In this review, the authors have suggested the role of genome sequencing in boosting genomics research of legumes and also suggest the importance of the transcriptome to understand gene space, gene function, transcriptional programs, and the molecular basis of various cellular processes in legumes. To gain insights into the possible function of genes in a plant species, the authors have suggested the need for comparative transcriptome analysis. Transcriptomics in combination with proteomics and metabolomics can be more accurate to understand the global molecular changes occurring during development and legume biology.

The last article in this section by Mantri et al. (2013) discusses the role of miRNAs in response to abiotic stresses in legumes. Micro-RNAs (miRNAs) and small-interfering RNAs (siRNAs) are the two major classes of small RNA, which play important roles in plant growth and development and thus it is essential to understand their role in legumes. miRNAs target messenger RNAs (mRNAs) through translational repression to regulate gene expression in plants and have given a new direction to better detect and understand complex regulatory systems in plants in response to abiotic stress. This review summarizes recent developments in legume miRNAs and their roles in various stress responses. The authors have highlighted the need for comprehensive and targeted studies to understand the role of miRNAs in controlling the expression of important genes associated with abiotic stress tolerances.

Applied Genomics

Significant progress has been made over the past years in the development and exploratory application of genomic tools for marker-assisted breeding. This section includes five research articles that describe the diversity, QTL

analysis, and also the practical use of molecular breeding by introgression of QTL using MABC. The first article by Khera et al. (2013) reports the development of Kompetitive allele-specific polymerase chain reaction (KASP) assays in groundnut and their utility to understand diversity features and elucidating genetic relationships in the groundnut reference set. In the case of GAB where only a few SNPs are required for genotyping a varying number of samples, the KASP assay seems to be the most cost effective in comparison to GoldenGate assays. In this context, the authors reported the development of 96 cost effective and flexible KASP assays of which only 90 assays were validated. The authors used 94 genotypes including parental lines mapping populations and wild as a validation set. Validated groundnut KASP assay markers (GKAMs) were used for estimating genetic diversity across 280 diverse genotypes of the reference set. The authors have provided a new type of SNP marker system which is cost effective and highly flexible. This useful resource of validated and highly informative GKAMs can be used for genetics and breeding applications in *Arachis* species.

The following article by Fedoruk et al. (2013) reports QTL analysis for seed quality in lentil using SNP markers. With an objective to determine the heritability of seed dimensions, identify genomic regions controlling these dimensions, and map seed coat and cotyledon colour genes, the authors have phenotyped 139 F₇-derived RILs at two locations for two seasons and genotyped using SNP Illumina GoldenGate assay, KASP assay, and SSR markers. The authors developed a genetic linkage map with 561 markers covering a total length of 697 cM in seven linkage groups (LGs). The authors were able to map loci for seed coat color and pattern mapped to LG 2 (*Ggc*), 3 (*Tgc*), and 6 (*Scp*) while the cotyledon color locus (*Yc*) was mapped to LG 1. Phenotypic data analysis estimated higher broad sense heritability for seed diameter (0.92) and seed plumpness (0.94), while moderate for seed thickness (0.60) and days to flowering (0.45). Significant QTLs for seed dimension were reported on six LGs and QTL for diameter and plumpness was found at the cotyledon color locus (*Yc*). The authors reported the important markers which can be used to enhance efficiency in the lentil breeding program for desired seed quality characteristics.

The next article by Liu et al. (2013) reports QTL analysis for plant height and seed weight in soybean. A bi-parental population derived from a cross between Chinese elite line Zhongpin03-5373 and cultivar Zhonghuang13 which comprise 254 RILs was used and evaluated for plant height and seed weight in multi-location field trials and genotyped with 508 molecular markers. The authors were able to map QTLs controlling plant height and seed weight and also evaluated the contributions of epistasis effects to plant height and seed weight variance. In total, 11 QTLs for plant height and 18 QTLs for seed weight across six diverse environments were reported, of which three pairs of QTLs for plant height,

vs. seed weight, were located in close proximity. Two QTLs for plant height and five for seed weight were stable across environments. Phenotypic variation explained varied from 2.02 to 47.60% in plant height and 2.13 to 14.35% in seed weight. The authors have reported four QTLs with no epistatic interaction, namely, *qPH-13*, *qSW-11*, *qSW-12-2*, and *qSW-18*, and thus can be implemented in MAS.

The following article by Wang et al. (2013) discusses genetic mapping and QTL analysis for disease in peanut. Early leaf spot (ELS), late leaf spot (LLS), and tomato spotted wilt virus (TSWV) are the major biotic factors affecting yield in the case of peanut. This article reports the QTL analysis for thrips, TSWV, and leaf spot (LS) including ELS and LLS using genotyping data generated at the F₂ and F₅ generation and phenotyping data generated at higher generations. QTL analysis based on a biparental mapping population using multi-environment phenotyping data for disease resistance resulted in identification of 54 QTLs in the F₂ map and 23 QTLs in the F₅ map. The article reports higher phenotypic variance for consistent QTL identified than non-consistent QTLs and lower phenotypic variation is reported in the F₅ map. The authors report the novel QTLs for thrips, TSWV, and LS in peanut (*Arachis hypogaea* L.), and emphasize the need to refine these QTLs in the future.

The last article of this special issue by Varshney et al. (2013c) reports the first ever report of deployment of molecular breeding for drought tolerance in chickpea. Terminal drought is the major constraint for chickpea production which alone causes 40 to 50% of yield losses. A genomic region, referred as “QTL-hotspot” on linkage group 4 (CaLG04) that harbors several drought-related trait QTL inclusive of root traits, contributing up to 58.20%, was identified by other study (Varshney et al., 2013d), which was used for introgression from ICC 4958 into an Indian leading chickpea variety JG 11, by a marker-assisted backcrossing (MABC) approach. Based on foreground and background selection, 29 BC₃F₂ plants generated after three backcrosses and selfing were selected and used for root trait screening. Higher root length density (RLD), and root dry weight (RDW) was observed in all and/or most of the introgression lines as compared to the recurrent parent, JG 11 as well as donor parent ICC 4958. The authors reported that introgression lines developed in just 3 yr may be released as an improved variety after multi-location field trials.

In summary, this issue provides a comprehensive collection of articles on a range of topics, including genome resources for legumes, understanding the diversity and domestication in legumes, utilization of genomic resources to discover novel genes, and understanding the mechanism and practical implementation of genomic resources for crop improvement. We hope that this special issue “Legume Genomics” will provide a better understanding of the potential of legume genomics and will encourage researchers to work in this exciting area of crop improvement.

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