## Critical Reviews in Plant Sciences

# Translational Genomics in Agriculture: Some Examples in Grain Legumes

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# Translational Genomics in Agriculture: Some Examples in Grain Legumes

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**Recent advances in genomics and associated disciplines like bioinformatics have made it possible to develop genomic resources,** such as large-scale sequence data for any crop species. While these datasets have been proven very useful for the understanding of genome architecture and dynamics as well as facilitating the discovery of genes, an obligation for, and challenge to the scientific community is to translate genome information to develop products, i.e. superior lines for trait(s) of interest. We call this approach, "translational genomics in agriculture" (TGA). TGA is currently in practice for cereal crops, such as maize (*Zea mays*) and rice (*Oryza sativa*), mainly in developed countries and by the private sector; progress has been slow for legume crops. Grown globally on 62.8 million ha with a production of 53.2 million tons and a value of nearly 24.2 billion dollars, the majority of these legumes have low crop productivity (<1 ton/ hectare) and are in the developing countries of sub Saharan Africa, Asia and South America. Interestingly, the last five years have seen enormous progress in genomics for these legume crops. Therefore, it is time to implement TGA in legume crops in order to enhance crop productivity

**and to ensure food security in developing countries. Prospects, as well as some success stories of TGA, in addition to advances in genomics, trait mapping and gene expression analysis are discussed for five leading legume crops, chickpea (*Cicer arietinum*), common bean (*Phaseolus vulgaris*), groundnut (*Arachis hypogaea*), pigeonpea (*Cajanus cajan*) and soybean (*Glycine max*). Some efforts have also been outlined to initiate/ accelerate TGA in three additional legume crops namely faba bean (*Vicia faba*), lentil (*Lens culinaris*) and pea (*Pisum sativum*).**

## I.   INTRODUCTION

The United Nations Department of Economic and Social Welfare in its demographic estimates and projections, predicts that the global human population will reach 9 billion by 2050. To feed this growing population, agricultural production must be 60% higher than current production. This will be a challenge in the face of climate changes such as higher temperatures, shifting seasons, more frequent and extreme weather events, flooding, and drought. The dramatic increases in food production and land productivity during 1960–1990s, due to the "green revolution", has reached a plateau (www.fao.org). Scientists have been striving to use conventional breeding approaches to enhance production and productivity of crop plants, thus emphasizing the need for new approaches to meet food and nutritional security for the future (Tester and Langridge, 2010).

With the advent of molecular markers and recent advances in genomics research, it has been possible to utilize genomics for enhancing the precision and efficiency of crop breeding. This process has been referred as "genomics-assisted breeding" (GAB; Varshney *et al.*, 2005). GAB includes deployment of structural, functional as well as comparative genomics to identify molecular markers including functional markers, candidate genes, and predictive markers for breeding. Several kinds of molecular markers such as simple sequence repeats (SSR) and single nucleotide polymorphism (SNP) markers have been used for trait dissection and for enhancing precision in selection in plant breeding programs (Xu *et al.*, 2012). Further, advanced research institutes (ARIs) and private sector organisations, mainly in developed countries, have made significant progress towards deploying GAB for enhancing yield under abiotic and biotic stresses (Varshney *et al.*, 2013a). For instance, downy mildew resistant pearl millet (HHB67-2 improved; http://www.icrisat.org/impacts/impact-stories/icrisat-is-hhb67.pdf), submergence tolerant rice (Swarna; Neeraja *et al.*, 2007), bacterial blight resistant rice (Triguna; Sundaram *et al.*, 2009) and quality protein maize (VivekQPM9; Gupta *et al.*, 2009; 2013) are some products of marker-assisted selection (MAS) or GAB in public sector. Improved lines have been developed, in fact, for many different crop plants (see Gupta *et al.*, 2009; Kulwal *et al.*, 2011).

Understanding the structure, organization and dynamics of genomes in plant species can provide insights into how genes have been adapted by natural and artificial selection to respond to environmental constraints and the potential for their manipulation for crop improvement. In pursuit of these goals, several plant genomes have been sequenced. Because of the high cost of Sanger sequencing and limited expertise in the plant science community, only a few plant species were initially selected as 'models' and targeted for both sequencing and the development of functional genomics resources. One purpose of generating genome sequences for model plant species was to better understand genome architecture and to create a 'parts list' for a plant. There were high hopes that much of this information could be transferred and utilized in crop species, generally referred as 'comparative genomics' (Ahn and Tanksley, 1993; Gale and Devos, 1998). The idea was prevalent that 'model to crop' translation would be a powerful tool for the application of genetics and genomics in crop plants; occasionally this approach was also referred to as 'translational genomics' (Elma *et al.*, 2007). In part the idea that 'model to crop translation' could solve the problems of agriculture was driven by an idea, prevalent in the 1990s, that transgenic solutions to the constrains that face crop species would be simple to find without the need for extensive genetic and genomic analyses of these target crop species. This was a seductive simplification with obvious attractions for lowered research costs.

As a result of emphasis on model plants, large-scale genome sequence information was first generated for *Arabidopsis thaliana* (The Arabidopsis Genome Initiative, 2000), followed by rice (*Oryza sativa*) both as model as well as crop (International Rice Genome Sequencing Project, 2005), poplar (*Populus trichophora*; Tuskan *et al.*, 2006), grape (*Vitis vinifera*; Jallion *et al.*, 2007), maize (*Zea mays*; Schnable *et al.*, 2009) and later the first legume genome sequence, of soybean (Schmutz *et al.*, 2010). Recent advances in next generation sequencing (NGS) technologies, with increased throughput and reduced sequencing costs, dramatically changed the sequencing scenarios for plant genomes (Deschamps and Campbell, 2010; Thudi *et al.*, 2012; Varshney *et al.*, 2009a). To date, the genome sequences for more than 55 plant species have been produced (Michael and Jackson, 2013) and many more are being sequenced (http://www.onekp.com/). The genome sequence information available has enabled the identification and development of genome-wide markers and a range of marker genotyping platforms including KASPar assays, Sequenom, BeadXpress System, GoldenGate assays, Infinium assays, genotyping-by-sequencing, etc. In addition, several organizations have started to re-sequence large-scale germplasm collections (Branca *et al.*, 2011; Lam *et al.*, 2010; Varshney *et al.*, 2013a; Xu *et al.*, 2011). It is important to mention that advances have not been limited to genome sequences; data at the transcriptome and epigenome level have also contributed greatly. NGS technology has become routine now for transcriptome sequence (Hiremath *et al.*, 2011), gene expression analysis (Hoen *et al.*, 2008; Wang *et al.*, 2012), and epigenetics (Jackson *et al.*, 2011), not only for model plants but in crop species too.

It is evident from the above that we are living in sequence-rich or genome information era. For the majority of crop species, this transition occured during the past 10 years. Before this transition, the breeding community could not initiate genomics-assisted breeding due to lack of genome information. Moreover, it is still difficult for the breeding community today to navigate and interpret sequence data in order to devise strategies for crop improvement. In our opinion, the plant science community has a challenge as well as an obligation to translate this genomic information for improved agriculture to feed the anticipated 9 billion people in the next 35 years. We propose to call the systematic application of genome wide sequence information in support of crop improvement as 'translational genomics for agriculture' (TGA). Because of its importance and the attention of global plant research community, including the private sector, TGA has been successfully applied in several cereals; maize and rice are the crop species where TGA is most advanced.

In addition to cereals, legumes play important roles both in food and nutritional security as well as in the sustainability of agricultural systems. Among legume species, major food legumes are chickpea (*Cicer arietinum*), common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), faba bean (*Vicia faba*), groundnut (*Arachis hypogaea*), lentil (*Lens culinaris*), pea (*Pisum sativum*), pigeonpea (*Cajanus cajan*) and soybean (*Glycine max*). Globally these legumes are grown on 62.8 million ha with a production of 53.2 million tons and fetch about 24.2 billion dollars (http://www.icrisat.org/crp/CRP3.5_Grain_Legumes_15Aug12.pdf). However, the crop productivity of these legumes crops in farmers' fields in developing countries is generally less than 1 ton per hectare. These statistics indicate that in parallel to improving agronomic practices, advancing genomics research as well as enhanced deployment of TGA in these legume crops is urgently needed.

This review discusses recent advances in genomics research as well as the prospects and potential of TGA in eight leading legume crops namely chickpea, common bean, faba bean, groundnut, lentil, pea, pigeonpea and soybean.

## II. NEXT GENERATION GENOMICS

With an objective to understand basic plant biology and use that information to understand and improve important crop species, a few plant species were considered as "model systems." Their ease of manipulation, simple genome organization, patterns of inheritance, rapid life cycle, desirable experimental properties etc., were important features for a model system (Koebner and Varshney, 2006). Model species were supposed to share reasonably good synteny and orthology with genomes of related crop species and help to facilitate discovery of genes and association of genes with phenotypes.

*Arabidopsis* was the first model plant species for which a genome sequence was produced (Arabidopsis Genome Initia-tive, 2000). However, with the argument that *Arabidopsis* may not be good model (Devos *et al.*, 1999) and, in particular, does not represent monocot plant species, rice was selected as a second model system for monocot plant species, especially cereals. As rice is also a crop species, the crop community got excited by the prospect of sequencing the rice genome so that rice genes, especially those involved contributing to yield, could be used for crop improvement in this and other plant species. As a result, two draft genomes, one each for *japonica* and *indica* rice, were released simultaneously (Goff *et al.*, 2002; Yu *et al.*, 2002).

Legumes are quite different from other plant species in certain features such as symbiotic nitrogen fixation, protein rich physiology and secondary metabolism. Therefore it was argued that the model systems, i.e. *Arabidopsis* and rice, did not serve as good models for legumes (Cook, 1999; Li *et al.*, 2012). Most notably because of the connection between mycorrhization and nodulation in legumes (Duc *et al.*, 1989), the former being of wide significance, but not accessible using *A. thaliana* as a model, and also for the understanding of plant architecture regulation by strigolactones (Gomez-Roldan *et al.*, 2008). For these reasons, two legume plant species, *Medicago truncatula* (Barker *et al.*, 1990) and *Lotus japonicus* (Handberg and Stougaard, 1992) were selected as model systems for legumes. Subsequently after spending several years time, and much money, genome sequences were assembled for *Lotus* (Sato *et al.*, 2008) and *Medicago* (Young *et al.*, 2011).

Although genome sequencing used to be restricted to model systems, the advent of NGS technologies and increased expertise in sequence assembly in the scientific community has led to genome projects for other crops. The main rationale behind targeting crop species for sequencing is the often complex genomic composition of crop species and past experience has shown that comparative genomics, epitomized by the 'model to crop translation' approach, was not very useful for crop improvement (Koebner and Varshney, 2006). An illustration of the sequencing of some key model and crop plant species is shown in Figure 1.

After work began on the model legumes *Medicago* and *Lotus* discussed above, soybean was the first crop legume for which reference genome was assembled (Schmutz *et al.*, 2010). Legumes like chickpea, common bean and pigeonpea, constitute an important dietary component for the vast majority of populations in many developing countries but did not immediately benefit from the genomic revolution (Varshney *et al.*, 2010a). However, as a result of community efforts, draft genome sequences have become available recently for pigeonpea (Varshney *et al.*, 2012a) and chickpea (Varshney *et al.*, 2013a). These legumes, once considered orphan crops, are no-longer so and now have joined the group of genome resource-rich species (Varshney *et al.*, 2010b). Recently the common bean community has developed genome assemblies for two accessions (Scott Jackson, personal communication). Significant efforts are underway in sequencing other important legume genomes such as peanut (http://www.peanutbioscience.com/),
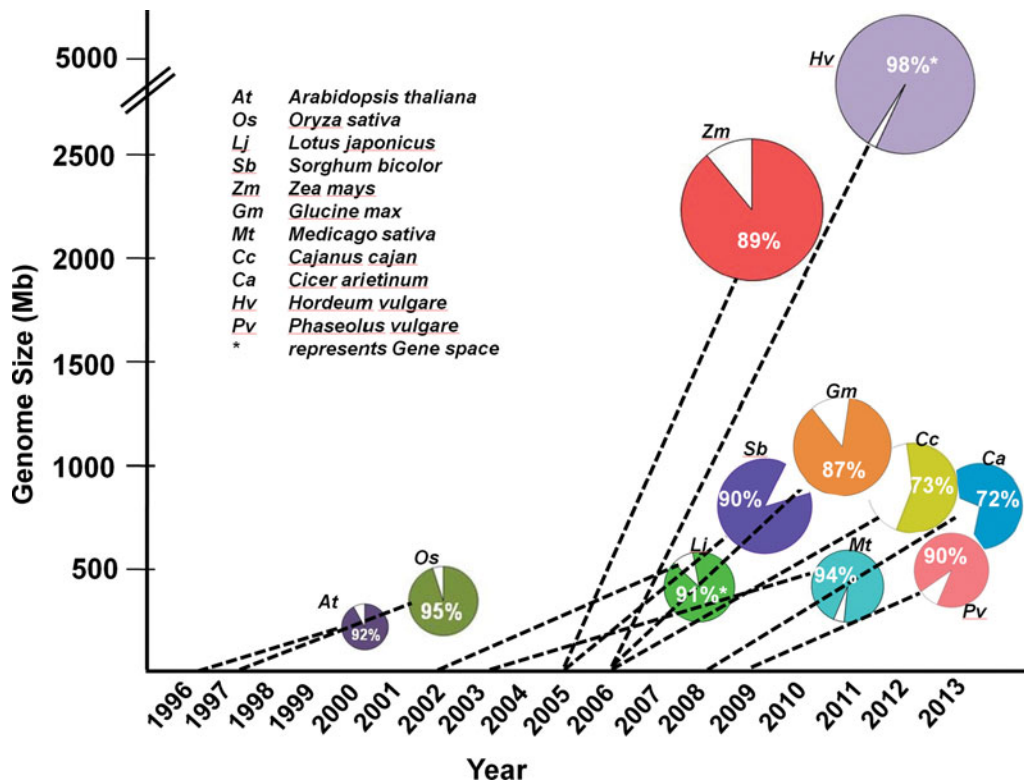
FIG. 1.    A snapshot on sequencing status of key model plant/ crop genomes. This figure shows sequencing status of some key model plant as well as crop species including legumes. Initiation of the sequencing project has been shown by dotted lines with the year and % genome assembled has been showed as filled circles.

pea  (http://www.coolseasonfoodlegume.org/pea_genome)  and lentil (Judith Burstin, Bert Vandenberg, personal communication). The genome sequences of model legumes, together with those of the above mentioned crops, serve as references to help assemble and organize sequence scaffolds from the related legume crop species (Cannon *et al.*, 2009).

In addition to the generation of reference genome sequences, NGS has facilitated re-sequencing of genomes of several varieties/ cultivars/ accessions in order to identify genomic variation, such as SNPs or structural variants, and to develop haplotype maps (Imelfort *et al.*, 2009; Lorenc *et al.*, 2012). For example in the model legume *Medicago*, 26 genomes from diverse accessions were sequenced and identified >3 million SNPs and characterized sequence polymorphisms and patterens of linkage disequilibria (LD) (Branca *et al.*, 2011). In the case of soybean, 17 wild and 14 cultivated soybean genomes were re-sequenced identifying 205,614 SNPs that revealed patterns of genetic variation between wild and cultivated soybeans (Lam *et al.*, 2010). Re-sequencing of 90 chickpea genomes revealed 4.4 million vari-ants (SNPs and INDELs) (Varshney *et al.*, 2013a). Re-sequencing enables rapid identification of SNP markers, development of high density genetic maps, and creation of haplotype maps (HapMap) for genome wide association studies (GWAS).

## III.    TRANSCRIPTOME ASSEMBLIES, FUNCTIONAL MARKERS AND GENE EXPRESSION ATLAS

Global gene expression studies provide insights into the transcriptome at the whole genome level in terms of the response to a particular biological conditions or constraints. These studies, even in the absence of a complete genome sequence, can help in understanding gene function, transcriptional programs, and the molecular basis of various cellular processes. Much work was undertaken in the area of transcriptome and gene expression analysis even before genome sequences became available. Initially, and for the majority of cases, either Sanger sequencing based ESTs or microarray based gene expression analysis was conducted. Using gene expression studies and gene cloning, a number of candidate genes for resistance/ tolerance to several biotic/ abiotic stresses have been isolated or cloned from several legume crops (Table 1). In recent years, due to the advent of the NGS technologies, it has become possible to develop *de novo* transcriptome assemblies with low cost and indeed NGS technologies are being used for gene expression analysis. Transcriptome assemblies developed using either Sanger sequencing or NGS technologies, or a combination of both, have been used for gene annotation for genome sequencing projects. These transcriptome assemblies provide a large number of functional markers (derived from genes/ transcripts) such as SSRs, SNPs,

TABLE 1
Some candidate genes identified in five legume crops

| Crop | Candidate gene(s) | Stress/trait(s) | Approach | Reference |
|---|---|---|---|---|
| Chickpea | *CarNAC3* | Drought and developmental processes | cDNA library | (Peng *et al.*, 2009) |
| | *CarF -box1* | Drought, salinity and developmental processes | Molecular cloning | (Jia *et al.*, 2012) |
| Common bean | *αAI-Pv* | Bruchid beetles | Overexpression | (Shade *et al.*, 1994) |
| Groundnut | *AhLPAT* | Triacylglycerol biosynthesis | Homology based | (Chen *et al.*, 2009) |
| Pigeonpea | *CcHyPRP* | Drought | Overexpression | (Priyanka *et al.*, 2010) |
| | *CcCYP* | Drought, salinity and extreme temperatures | Overexpression | (Sekhar *et al.*, 2010) |
| | *CcMT1* | Heavy metal stress | Overexpression | (Sekhar *et al.*, 2010) |
| Soybean | *GmRPS1, GmRPS6, GmRPL37* | Cold stress | Suppression Subtractive Hybridization | (Kim *et al.*, 2004) |
| | *P5CR* | Drought and heat | Overexpression | (de Ronde *et al.*, 2004) |
| | *GmDREBa, GmDREBb, GmDREBc* | Salinity, drought and cold | Expression analysis | (Li *et al.*, 2005a) |
| | *GmMIPS1* | Seed development | RNAi-mediated silencing | (Nunes *et al.*, 2006) |
| | *GmNAC* | Cold and developmental processes | Molecular cloning | (Meng *et al.*, 2007) |
| | *GmEREBP1* | Defense response | Overexpression | (Mazarei *et al.*, 2007) |
| | *GmbZIP44, GmbZIP62 or GmbZIP78* | Salt and freezing tolerance | Overexpression | (Liao *et al.*, 2008) |
| | *GS52* | Nodulation | RNAi-mediated silencing | (Govindarajulu *et al.*, 2009) |
| | *Rpp4C4* | Asian soybean rust | virus-induced gene silencing | (Meyer *et al.*, 2009) |
| | *GmDREB3* | Cold, drought and salt | Overexpression | (Chen *et al.*, 2009) |
| | *GmOLPb, P21e* | Salinity, methyl jasmonate and salicylic acid | Expression analysis | (Tachi *et al.*, 2009) |
| | *Glyma14g38510, 38560 and 38580* | Soybean mosaic virus | Homology based | (Wang *et al.*, 2011) |
| | *Glyma03g28610/ Glyma03g 28630* | Iron deficiency chlorosis | Transcriptome sequencing | (Pieffer *et al.*, 2012) |
| | *Glyma07g05410/ Glyma16g01980* | Flowering time/maturation | Homology based | (Kim *et al.*, 2012) |
| | *GmDGAT2C/ GmDGAR1B* | Seed yield | Homology based | (Eskandari *et al.*, 2013) |

conserved orthologous sequence (COS) and intron spanning region (ISR) markers (Dubey *et al.*, 2011; Hiremath *et al.*, 2011; Jhanwar *et al.*, 2012; Kudapa *et al.*, 2012).

Using the Roche 454-FLX platform, a transcriptome assembly in *M. truncatula* was generated with a total of 184,599 contigs (Cheung *et al.*, 2006) and this assembly was found to contain 610 SSRs. In the case of *Lotus*, a tissue-specific transcriptome analysis containing 21,495 transcripts was generated (Takanashi *et al.*, 2012). Among legume crop species, several versions of transcriptome assemblies were generated by different research groups (Table 2). For instance, in the case of chickpea, several transcriptome assemblies based on different sequencing platforms have been developed (Garg *et al.*, 2011a; 2011b; Hiremath *et al.*, 2011). These assemblies together with unpublished data from the University of Saskatchewan have been used for defining a comprehensive trasncriptome assembly

TABLE 2
NGS-based transcriptome assemblies and genomic resources

| Crops | Platform | Unigenes/ transcripts | SSRs | SNPs | Reference |
|---|---|---|---|---|---|
| Chickpea | Illumina | 53,409 | 4,816 | - | (Garg *et al.*, 2011a) |
| | 454FLX | 34,760 | 4,111 | 495 | (Garg *et al.*, 2011b) |
| | 454FLX and Illumina | 1,03,215 | 26,252 | 26,082 | (Hiremath *et al.*, 2011) |
| | 454FLX | 1,60,883 | - | 1,022 | (Gaur *et al.*, 2012a) |
| | 454FLX and Illumina | - | - | 14,454 | (Hiremath *et al.*, 2012) |
| | 454FLX | 37,265 | 4,072 | 36,446 | (Jhanwar *et al.*, 2012) |
| | 454FLX and Illumina | 43,389 | 5,409 | 39,940 | (Agarwal *et al.*, 2012) |
| Common bean | 454FLX and Illumina | 1,60,036 | - | 3,487 | (Hyten *et al.*, 2010) |
| | 454FLX | 59,295 | 1,516 | - | (Kalavacharla *et al.*, 2011) |
| Groundnut | 454FLX | 7,43,232 | 2,884 | - | (Guimarães *et al.*, 2012) |
| | Illumina | 59,077 | 5,883 | - | (Zhang *et al.*, 2012) |
| Pigeonpea | 454FLX | 43,324 | 3,771 | - | (Dutta *et al.*, 2011) |
| | 454FLX and Illumina | 127,754 | 50,566 | 12,141 | (Dubey *et al.*, 2011) |
| | Illumina | - | - | 17,113 | (Saxena *et al.*, 2012) |
| Soybean | Illumina | 5,02,020 | - | 1,682 | (Deschamps *et al.*, 2010) |
| | Illumina | - | - | 205,614 | (Lam *et al.*, 2010) |

comprising of 46,369 contigs with an average N50 of 1,726 bp (Kudapa *et al.*, 2014). Details of some key transcriptome assemblies based on NGS technology or combination of NGS technologies with Sanger ESTs in select legume species have been given in Table 2. The Legume Information System (LIS, http://www.comparative-legumes.org/) hosts transcriptome assemblies for several legume species.

Mining of transcriptome assemblies with SSR search tools has provided large numbers of SSR markers and these may be validated as genetic markers in wet lab experiments. For example, 250,393 SSRs were identified from 247 faba bean accessions (Yang *et al.*, 2012) using 454/FLX sequencing technology. Beyond providing SSR markers, these transcriptome assemblies have been used for identification of SNPs from NGS datasets generated from two or more genotypes (Table 2). For instance, in the case of soybean, a total of 1,682 SNPs were identified by deep re-sequencing of the reduced representation libraries using Illumina Genome Analyzer (GA) (Deschamps and Campbell, 2010). Similarly, 26,082 SNPs were discovered from two contrasting drought responsive genotypes in chickpea (Hiremath *et al.*, 2011), 36,188 SNPs for two contrasting salinity genotypes in pea (Leonforte *et al.*, 2013) and 12,141 SNPs from 10 pigeonpea genotypes representing five mapping populations segregating for Fusarium wilt and sterility mosaic disease (Dubey *et al.*, 2011) were identified. In addition, COS markers have found wide application in cross-genome comparative studies in legume species. For example, 387 COS markers were developed in chickpea from the transcriptome dataset (Hiremath *et al.*, 2011). In some cases, transcriptome assemblies were analyzed for the identification of flanking intron junctions based on alignment to cognate or related genome sequences. As a result many

ISR markers have been identified in legumes; for example, 2,088 and 10,009 ISRs were identified in chickpea (Hiremath *et al.*, 2011) and pigeonpea (Kudapa *et al.*, 2012), respectively and approximately 1,000 have been identified for pea using a comparative genomics approach (http://bioweb.abc.hu/mt/pisprim) and about 5,500 unigenes have been used to generate a consencus genetic map for pea (Bordat *et al.*, 2011).

Although vast genomic resources have been developed rapidly in recent years for legumes, gene expression profiling data is insufficient to correlate the developmental processes to transcriptomes, leaving a large gap to associate the phenotype and genome/gene sequence. However, systematic mutant populations have been developed in several species in order to address this issue. TILLING populations are available for *L. japonicus,* pea, *M. truncatula* and chickpea (Dalmais *et al.*, 2008; Le-Signor *et al.*, 2009; Perry *et al.*, 2003; Varshney *et al.*, unpublished), Fast Neutron generated deletion mutant populations for *M. truncatula*, pea and soybean (Bolon *et al.*, 2011; Hofer *et al.*, 2009; Rogers *et al.*, 2009; Smykal *et al.*, 2012) and insertion mutant populations generated using exogeneous (*Medicago*, d'Erfurth *et al.*, 2003) and endogeneous retrotransposons (*Lotus,* Urbański *et al.*, 2012) have been generated and have contributed to gene discovery in these species (see Domoney *et al.*, 2013; Domonkos *et al.*, 2013; Urbański *et al.*, 2013).

Plant growth and development are controlled by the programmed (by time, tissue and abundance) expression of suites of genes in response to exogeneous or endogeneous queues. Hence, there is a need to generate genome-wide expression data from a range of tissues/ developmental stages in order to understand gene expression profiles in order to relate phenotypes and genotypes in legumes. A gene expression atlas was developed

from a comprehensive set of developmental stages and tissues for some important crops such as rice (Wang *et al.*, 2010) and maize (Sekhon *et al.*, 2011).

In the case of legumes, the *M. truncatula* Gene Expression Atlas (MtGEA) was developed covering a range of tissues such as roots, nodules, stems, petioles, leaves, vegetative buds, flowers, seeds and seed pods with detailed developmental time-series for nodules and seeds, using the Affymetrix GeneChip Medicago Genome Arrays (Benedito *et al.*, 2008). It has also incorporated the transcriptome data from plants subjected to various kinds of abiotic and biotic stresses and data from specific cell and tissue types. These data are useful for gene function determination, biological discovery, and molecular breeding efforts (http://mtgea.noble.org/v3/). Similarly, gene expression atlases have been developed in *Lotus* (http://ljgea.noble.org/) and soybean (Libault *et al.*, 2010; Severin *et al.*, 2010) from diverse tissues and developmental time series. Similar kinds of efforts have been initiated in chickpea, pigeonpea and groundnut at ICRISAT. These gene expression atlases are a powerful resource for legume genomics research, which can be used for understanding the regulatory network of developmental processes, tracing the expression profiles of stress responsive candidate genes etc.

In addition to gene expression atlases, efforts have been started to compile protein sequence information for different plant species. For example, all proteins identified for legumes (*Medicago*, *Lotus* and soybean) are available at http://bioinfoserver.rsbs.anu.edu.au/utils/PathExpress4legumes/. This database is a valuable resource for comparative seed proteomics and pathway analysis within and beyond the legume family, and protein sequences are exceptionally useful for genome annotation and determining the nature of genes for which only distant relatives are known. Similarly, another legume protein database (LegProt) has been created containing sequences from seven legume species, i.e., *M. sativa, M. truncatula, L. japonicas, G. max, P. vulgaris, P. sativum* and *L. albus* (Lei *et al.*, 2011; http://bioinfo.noble.org/manuscript-support/legumedb). In addition the Soybean Proteome Database has been generated exclusively for soybean (http://proteome.dc.affrc.go.jp/Soybean/).

## IV. COMPREHENSIVE GENETIC MAPS AND PREDICTIVE MARKERS

As previously mentioned, the availability of large-scale genomic resources has led to development of large numbers of molecular markers, particularly SNPs that can be assayed on a range of genotyping platforms. For instance, a variety of SNP genotyping platforms including GoldenGate (Kassa *et al.*, 2012), VeraCode (Roorkiwal *et al.*, 2013) and Competitive Allele Specific PCR (KASPar) assays (Saxena *et al.*, 2012) have been developed for pigeonpea. Such genotyping platforms in combination with classical SSR genotyping platforms have been used to generate large-scale marker segregation data on mapping populations and have led to comprehensive genetic maps

(Saxena *et al.*, 2012). Several legume crop species did not have good genetic maps until recently. For example, the first SSR-based genetic linkage map for cultivated groundnut was recently developed for the mapping population, TAG 24 × ICGV 86031 (Varshney *et al.*, 2009b). Subsequently five more genetic maps were developed based on mapping populations segregating for drought and foliar diseases (Gautami *et al.*, 2012a; Ravi *et al.*, 2011; Sujay *et al.*, 2012). A consensus map for drought tolerance related traits with 293 SSR loci (Gautami *et al.*, 2012a) and foliar disease resistance with 225 SSR loci (Sujay *et al.*, 2012), respectively have been developed. Furthermore, international collaborative efforts have resulted in the construction of consensus map with 897 SSR marker loci using genotyping data from 11 mapping populations. This consensus map was upgraded with maps for two more populations and the updated version map covers 2,651 cM with 3,693 marker loci anchored to 20 consensus linkage groups (LG) corresponding to the A and B genomes (Shirasawa *et al.*, 2013). Another example of development of comprehensive genetic maps is in cowpea, where a 1,536-SNP GoldenGate genotyping array was developed and applied to 741 recombinant inbred lines from six mapping populations. 1,375 out of 1,536 SNPs provided dependable markers and a subset of 928 were incorporated to develop a consensus genetic map spanning 680 cM with 11 linkage groups and an average marker distance of 0.73 cM (Muchero *et al.*, 2009). This map has been further updated and the consensus map has 1,107 SNP loci (Lucas *et al.*, 2011).

Details on genetic maps in selected legume crops are listed in Table 3. These dense consensus genetic maps are useful resources for the identification of highly informative and well distributed markers to be used for background selection in breeding schemes, the construction of new genetic maps or analysis of genetic diversity. Analysis of genetic maps, together with trait phenotyping on the respective segregating populations provides predictive markers for traits of interest. Both biotic and abiotic stresses are complex in nature, so trait dissection is important for improving component traits through breeding. Often agronomical traits are composites of many underlying phenotypes, but their dissection into component, genetically determined, contributions represent the underlying biology and can be used for marker-based breeding. Both bulked segregant analysis (BSA) as well as quantitative trait loci (QTL) mapping based marker analysis, have been used to identify markers linked to these genetic determinants of traits. In fact, quantitative traits have been studied in legumes since Mendel. In his 1866 paper he commented on the near continuous variation of flower colour in *Phaseolus* crosses: "Even these enigmatical results, however, might probably be explained by the law governing *Pisum* if we might assume that the color of the flowers and seeds of *Ph. multiflorus* is a combination of two or more entirely independent colors, which individually act like any other constant character in the plant" [http://www.mendelweb.org/]

For simple inherited traits, BSA has been used in several plant species including the legumes discussed in this article.

TABLE 3
List of some comprehensive genetic maps for selected legumes

| Name of population | Type | Number of loci | References |
|---|---|---|---|
| Chickpea | | | |
| ICC 4958 × PI 489777 | RIL | 406 | (Choudhary *et al.*, 2012) |
| ICC 4958 × PI 489777 | RIL | 1,063 | (Gaur *et al.*, 2012b) |
| ICC 4958 × PI 489777 | RIL | 1,328 | (Hiremath *et al.*, 2012) |
| ICC 4958 × PI 489777 | RIL | 1,291 | (Thudi *et al.*, 2011) |
| ICC 4958 × PI 489777 | RIL | 300 | (Gujaria *et al.*, 2011) |
| ICC 4958 × PI 489777 | RIL | 521 | (Nayak *et al.*, 2010) |
| Common Bean | | | |
| DOR3646 × BAT477 | RIL | 291 | (Galeano *et al.*, 2011) |
| BAT93 × Jalo EEP558 | RIL | 275 | (McConnell *et al.*, 2010) |
| BAT93 × Jalo EEP558 | RIL | 413 | (Hanai *et al.*, 2010) |
| BAT93 × Jalo EEP558 | RIL | 275 | (McConnell *et al.*, 2010) |
| DOR364 × G19833 | RIL | 215 | (Córdoba *et al.*, 2010) |
| Xana × Cornell 49242 | RIL | 294 | (Pérez-Vega *et al.*, 2010) |
| Faba bean | | | |
| Vf 6 × Vf 136 | RIL | 277 | (Díaz-Ruiz *et al.*, 2009a) |
| Vf 6 × Vf 27 | RIL | 258 | (Cruz-Izquierdo *et al.*, 2012) |
| Groundnut | | | |
| *A-genome genetic maps* | | | |
| *A. duranensis* × *A. duranensis* | $F_2$ | 2,319 | (Nagy *et al.*, 2010) |
| *A. duranensis* × *A. stenosperma* | $F_2$ | 369 | (Leal-Bertioli *et al.*, 2009) |
| *B-genome genetic maps* | | | |
| *A. batizocoi* PI 298639 × *A. batizocoi* PI 468327 | $F_2$ | 449 | (Guo *et al.*, 2010) |
| *AB genome genetic maps* | | | |
| Tifrunner × GT-C20 | $F_2$ | 381 | (Wang *et al.*, 2013; 2012) |
| Satonoka × Kintoki | $F_2$ | 516 | (Shirasawa *et al.*, 2013; 2012) |
| Nakateyutaka × YI-0311 | $F_2$ | 293 | (Shirasawa *et al.*, 2013; 2012) |
| Tifrunner × GT-C20 | RIL | 239 | (Qin *et al.*, 2012) |
| *A. duranensis* × (*A. ipäensis* × *A. duranensis*) | $BC_1F_1$ | 298 | (Foncéka *et al.*, 2009) |
| ICP 28 × ICPW 94 | $F_2$ | 239 | (Bohra *et al.*, 2011) |
| ICP 28 × ICPW 94 | $F_2$ | 910 | (Saxena *et al.*, 2012) |
| Pusa Dwarf × HDM04-1 | $F_2$ | 296 | (Kumawat *et al.*, 2012) |
| Lentil | | | |
| ILL 5588 × L 692-16-1(s) | RIL | 283 | (Hamwieh *et al.*, 2005) |
| Eston × PI 320937 | RIL | 207 | (Tullu *et al.* 2006; 2008) |
| Digger (ILL 5722) × NorthWeld (ILL 5588) | RIL | 211 | (Gupta *et al.*, 2012a) |
| CDC Robin × 964a-46 | RIL | 543 | (Sharpe *et al.*, 2013) |
| CDC Robin × 964a-46 | RIL | 577 | (Fedoruk *et al.*, 2013) |
| Pea | | | |
| Puget × 90-2079 | RIL | 324 | (Pilet-Nayel *et al.*, 2002) |
| Wt 10245 × Wt 11238 | $F_2$ | 204 | (Irzykowska and Wolko, 2004) |
| Carneval × MP 1401 | RIL | 207 | (Tar'an *et al.*, 2003a; 2004) |
| DP × JI 296 | RIL | 206 | (Prioul *et al.*, 2004) |
| Shawnee × Bohatyr | RIL | 302 | (Loridon *et al.*, 2005) |
| Orb × CDC Striker | RIL | 224 | (Ubayasena *et al.*, 2010) |
| P665 × Messire | RIL | 246 | (Fondevilla *et al.*, 2008; 2010) |
| Orb × CDC Striker | RIL | 255 | (Sindhu *et al.*, 2013) |
| Soybean | | | |
| Essex × Forrest | RIL | 959 | (Xia *et al.*, 2007) |
| Essex × Forrest | RIL | 237 | (Kassem *et al.*, 2006) |

For instance, BSA was used for mapping of Fusarium wilt (FW) resistance with RAPD markers in the case of pigeonpea (Kotresh *et al.*, 2006). On the other hand, in order to understand the complex nature of drought tolerance in chickpea, precise phenotypic data for 20 different root traits was analyzed using a QTL mapping approach. As a result, nine QTL clusters containing QTLs for several drought tolerance traits have been identified that are being targeted for chickpea molecular breeding program. Among these QTL clusters, one QTL cluster corresponding to QTLs for 12 traits and explaining about 60% phenotypic variation has been identified on CaLG04, referred to as a "*QTL-hotspot*" (Varshney *et al.*, 2013b). Similar mapping efforts have been undertaken for important the biotic stresses like FW (Benko-Iseppon *et al.*, 2003; Cobos *et al.*, 2005; Sabbavarapu *et al.*, 2013), and Aschochyta blight (Anbessa *et al.*, 2009; Aryamanesh *et al.*, 2010; Kottapalli *et al.*, 2009).

One agronomic trait under complex genetic control (Buckler *et al.*, 2009; Mouradoy *et al.*, 2002) that has received much attention is flowering time. This was studied as a quantitative trait in rice and pea at the beginning of the 20th century (Hoshino, 1915), and the physiological genetics of flowering time in pea was a model for this that was eclipsed by the rise of *Arabidopsis* as an experimental system. The various lineages of angiosperm families diverged about 100 to 150 million years ago (Bell *et al.*, 2010), so it is not surprising that many structural genes that regulate this pathway are common to different families, but that their regulatory circuitry differs. In the legumes (that diversified 55 – 60 million years ago) the study of the regulation of flowering time is a resurgent and the novelty of the genetic control of flowering time in legumes is being revealed (Hecht *et al.*, 2011; Mach, 2011; Weller *et al.*, 2012) with strong indications that floral induction in pea may involve the action of several members of the *FT* family with distinct modes of action (Hecht *et al.*, 2011). Thus some major determinants of flowering time are known, so the underlying genes can be used (if necessary) to follow this trait. However the Buckler *et al.* (2009) analysis of the control of flowering time in maize suggests that there may also be many loci of small effect that together contribute greatly to the genetic variation of this trait. Some key studies on identification of QTLs and predictive markers associated with agronomically important traits in addition to tolerance/ resistance to abiotic and biotic stresses in select legumes are summarized in Table 4.

## V. SUCCESS STORIES OF TGA IN LEGUMES

Molecular breeding is a direct strategy to translate genome information for developing products i.e. superior lines for traits of interest. In general, in addition to MAS, three main approaches namely marker-assisted backcrossing (MABC), marker-assisted recurrent selection (MARS) and genomic selection (GS) can be used in molecular breeding. Several success stories utilizing molecular breeding have been reported in crop species such as rice, maize, wheat (see Kulwal *et al.*, 2011). With the notable
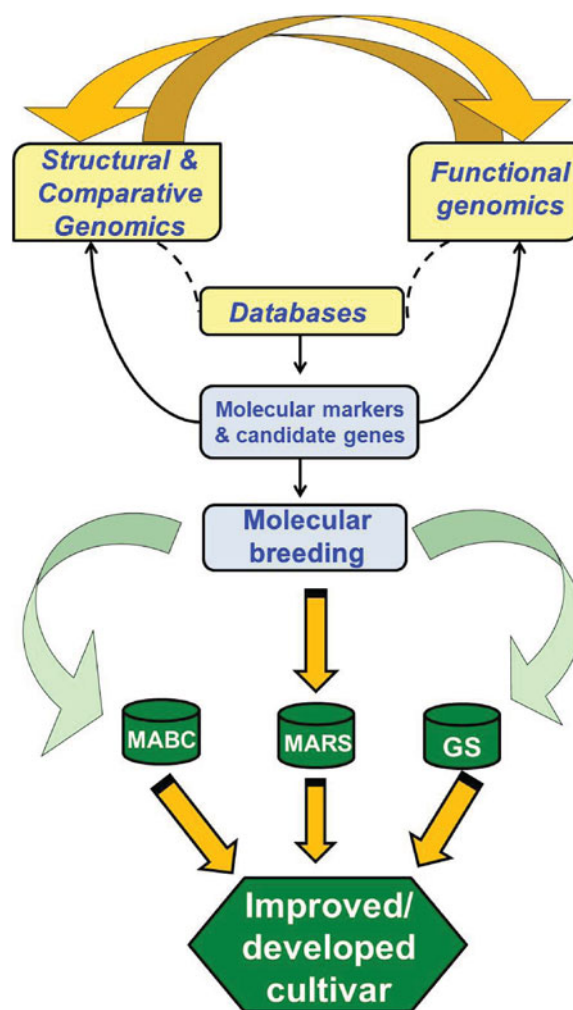


FIG. 2. Integrative genomics for accelerated crop improvement. The figure depicts the use of genomic resources for identification of marker /candidate gene. Subsequently the markers/genes identified may be used to detect gene-trait associations thus by enhancing molecular breeding program by deploying different approaches like MABC, MARS and GS. Ultimately integrating genomic resources through translational genomics would result in improved lines or developed cultivars.

exception of soybean in the commercial sector, for legumes, in general, molecular breeding has been delayed due to limited availability of genomic resources. However, recent advances in genomics especially in the legumes discussed here have opened the avenues for accelerating practicing of TGA. An overview of integrative genomics for accelerated crop improvement is illustrated in Figure 2.

MAS has been extensively deployed for development and release of improved lines/varieties in legumes, some key examples are summarized in Table 5. In the case of soybean, in addition to developing improved lines or varieties for resistance to different biotic stresses like soybean cyst nematode (SCN) races (Cahill and Schmidt, 2004; Concibido *et al.*, 1996), phytophthora root rot and brown stem rot

TABLE 4
Summary of some trait mapping studies in select legumes

| Trait | Gene/ QTL | *PVE (%) | Reference |
|---|---|---|---|
| **Chickpea** | | | |
| *Resistance to biotic stresss* | | | |
| Fusarium wilt | *foc-0, foc-1, foc-2, foc-3, foc-4, foc-5* | 15 | (Cobos *et al.*, 2005; Iruela *et al.*, 2007) |
| | QTL | | (Gowda *et al.*, 2009) |
| Ascochyta blight | QTL | 14–56 | (Anbessa *et al.*, 2009; Cobos *et al.*, 2006; Irula *et al.*, 2006; Kottapalli *et al.*, 2009; Lichtenzveig *et al.*, 2006; Tar'an *et al.*, 2007) |
| | BSA | - | (Rajesh *et al.*, 2002) |
| | *AR2, ar1, ar1a, ar1b, ar2a, ar2b, Ar19* | 28 | (Cho *et al.*, 200) |
| Botrytis gray mold | QTL | 44 | (Anuradha *et al.*, 2011) |
| Rust | QTL | 31 | (Madrid *et al.*, 2008) |
| *Agronomic and yield related traits* | | | |
| Agronomic and yield related traits | QTL | 19 | (Gowda *et al.*, 201) |
| Days to flower | QTL | 26–56 | (Cobos *et al.*, 2007; 2009; Lichtenzveig *et al.*, 2006) |
| Double podding | QTL | - | (Cobos *et al.*, 2005; Cho *et al.*, 2002; Rajesh *et al.*, 2002) |
| 100-seed weight | QTL | 52 | (Cho *et al.*, 2002) |
| Flower colour | B/b | | (Gowda *et al.*, 2009) |
| Seed coat colour, thickness, size weight | QTL | 49–73 | (Cobos *et al.*, 2005; 2009; 2007; Gowda *et al.*, 2011; Hossain *et al.*, 2011; Lichtenzveig *et al.*, 2006) |
| **Common bean** | | | |
| *Resistance to biotic stresses* | | | |
| Angular leaf spot | QTL | 22–64 | (López *et al.*, 2003; Oblessuc *et al.*, 2012; Teixeira *et al.*, 2005) |
| Anthracnose | *Co-genes* | - | (Rodriguez-Suarez *et al.*, 2007) |
| Ashy stem blight | QTL | 16–29 | (Miklas *et al.*, 2006b) |
| Bean common mosaic necrosis virus | BSA | - | Strausbaugh *et al.*, 1999) |
| | *bc-3; I* | 4 | (Johnson *et al.*, 1997) |
| Bean golden yellow mosaic virus | QTL | 15 | (Miklas *et al.*, 2006) |
| | *bgm* | 1 | (Blair *et al.*, 2007) |
| Bean pod weevil | QTL | 22 | (Blair *et al.*, 2006) |
| Bruchids | *Arc gene* | | (Blair *et al.*, 2010) |
| Bean rust resistance | BSA | - | (Correa *et al.*, 2000; Johnson *et al.*, 1995; Mienie *et al.*, 2005; Miklas *et al.*, 1993; Park *et al.*, 2008) |
| Bacterial brown spot | QTL | | (Jung *et al.*, 2003) |
| Beet curly top virus | BSA | - | (Larsen and Miklas, 2004) |
| Climbing ability and component traits | QTL | 25 | (Checa and Blair, 2008) |
| Common bacterial blight (CBB) resistance | QTL | 30–73 | (Liu *et al.*, 2005; Miklas *et al.*, 2006; Vandemark *et al.*, 2008) |
| Charcoal rot | QTL | 1 | (Hernandez-Delgado *et al.*, 2009) |

*(Continued on next page)*

TABLE 4
Summary of some trait mapping studies in select legumes *(Continued)*

| Trait | Gene/ QTL | *PVE (%) | Reference |
|---|---|---|---|
| Fusarium wilt | QTL | 63 | (Fall *et al.*, 2001) |
|  | *PvPR2, PvPR1* | 3 | (Schneider *et al.*, 2001) |
| Halo blight | QTL | - | (Miklas *et al.*, 2011) |
|  | *Pse* | 1 | (Miklas *et al.*, 2009) |
| Thrips | *Tpr6.1* |  | (Frei *et al.*, 2005) |
| White mold | QTL | 39–52 | (Park *et al.*, 2001; Soule *et al.*, 2011) |
| Phosphorus uptake | *Pup4.1, 10.1 and 2.1* |  | (Beebe *et al.*, 2006) |
| Rust | *UR-6, UR-13* | 19 | (Mienie *et al.*, 2005) |
| Seed chemical content | QTL | 51 | (Casanas *et al.*, 2013) |
| **Faba Bean** |  |  |  |
| Ascochyta blight | *QTL* | 24–45 | (Avila *et al.*, 2004; Díaz-Ruiz *et al.*, 2009b; Roman *et al.*, 2003) |
| Broomrape resistance | *QTL* | 33–43 | (Díaz-Ruiz *et al.*, 2009a; Gutiérrez *et al.*, 2013; Román *et al.*, 2002) |
| Rust | *Uvf1* |  | (Avila *et al.*, 2003) |
| Floral characters | *QTL* | 20 | (Avila *et al.*, 2005) |
| Days to flowering | *QTL* | 28 | (Cruz-Izquierdo *et al.*, 2012) |
| Flowering length | *QTL* | 31 | (Cruz-Izquierdo *et al.*, 2012) |
| Pod length | *QTL* | 25 | (Cruz-Izquierdo *et al.*, 2012) |
| Number of ovules per pod | *QTL* | 27 | (Cruz-Izquierdo *et al.*, 2012) |
| Number of seeds per pod | *QTL* | 26 | (Cruz-Izquierdo *et al.*, 2012) |
| Yield characters | *QTL* | 58 | (Avila *et al.*, 2005) |
| Frost tolerance | *QTL* | 40 | (Arbaoui *et al.*, 2008) |
| Fatty acid content | *QTL* | 63 | (Arbaoui *et al.*, 2008) |
| **Groundnut** |  |  |  |
| *Resistance to biotic stresses* |  |  |  |
| Late leaf spot, Leaf rust, *Aspergillus flavus* invasion, groundnut rosette disease, Tomato Spotted Wilt Virus | QTL | 1.70–82.96 | (Khedikar *et al.*, 2010; Liang *et al.*, 2009a; Qin *et al.*, 2012; Sujay *et al.*, 2012; Wang *et al.*, 2013) |
| *Drought tolerance related traits* |  |  |  |
| Transpiration,Transpiration efficiency, Specific leaf area, Leaf area, SPAD chlorophyll meter reading (SCMR), Biomass, Canopy conductance, Total dry matter | QTL | 3.48–22.39 | (Gautami *et al.*, 2012b; Ravi *et al.*, 2011; Varshney *et al.*, 2009b) |
| *Morphological and yield related traits* |  |  |  |
| Shoot dry weight, Pod weight, Seed weight, Haulm weight, Harvest index, Pod mass/plant, Mature pods/plant, Number of branches, Height of main axis, Stem diameter, Leaf length, width and length /width ratio, Length of main stem, Length of the longest branch, Number of branches, Weight of plant, Weight of mature pod per plant, Thickness of pod, Width of pod, Shape of tip of pods, Number of seeds per a plant, Yield parameters | QTL | 3.78–40.10 | (Gautami *et al.*, 2012a; Liang *et al.*, 2009; Ravi *et al.*, 2011; Selvaraj *et al.*, 2009; Shirasawa *et al.*, 2012; Varshney *et al.*, 2009b) |

TABLE 4
Summary of some trait mapping studies in select legumes *(Continued)*

| Trait | Gene/ QTL | *PVE (%) | Reference |
|-------|-----------|----------|-----------|
| *Seed and oil quality* | | | |
| Oil content, Oil quality, Protein content, High oleate trait | QTL | 1.4–74.03 | (Liang *et al.*, 2009; Pandey *et al.*, 2012c; Sarvamangala *et al.*, 2011; Selvaraj *et al.*, 2009; Shirasawa *et al.*, 2012) |
| **Pea** | | | |
| Plant height | *QTL* | 19–65 | (Tullu *et al.*, 2008; Tar'an *et al.*, 2003b; Dirlewanger *et al.*, 1994) |
| Days to 50% flowering | *QTL* | 35 | (Fedoruk *et al.*, 2013) |
| Days to maturity (DM) | *QTL* | 34 | (Tar'an *et al.*, 2004) |
| Plant Maturity | *QTL* | 27 | (Timmerman-Vaughan *et al.*, 2004) |
| Earliness | *QTL* | 46 | (Tullu *et al.*, 2008) |
| Powdery mildew | genes | | (Fondevilla *et al.*, 2011) |
| *Fusarium* wilt (FW) resistance | *QTL* | - | (Hamwieh *et al.*, 2005) |
| *Stemphylium* blight (SB) resistance | *QTL* | 46 | (Saha *et al.*, 2010) |
| Rust | *QTL* | 63 | (Barilli *et al.*, 2010) |
| *Aphanomyces* root rot | *QTL* | 21–60 | (Hamon *et al.*, 2011, 2013; Pilet-Nayel *et al.*, 2002) |
| *Ascochyta* blight (AB) resistance | *QTL* | 35–75 | (Fondevilla *et al.*, 2008; Gupta *et al.*, 2012b; Prioul *et al.*, 2004; Rubeena *et al.*, 2006; 2003; Tar'an *et al.*, 2003b; Timmerman-Vaughan *et al.*, 2002; Tullu *et al.*, 2006) |
| Orobanche | *QTL* | 8–36 | (Fondevilla *et al.*, 2010) |
| Frost resistance/damage | *QTL* | 61 | (Dumont *et al.*, 2009; Klein *et al.*, 2014) |
| Winter hardiness | *QTL* | 43 | (Kahraman *et al.*, 2010) |
| Seed thickness | *QTL* | 38 | (Fedoruk *et al.*, 2013) |
| Seed plumpness | *QTL* | 40 | (Fedoruk *et al.*, 2013) |
| Grain yield | *QTL* | 38 | (Tar'an *et al.*, 2004) |
| Lodging resistance | *QTL* | 58 | (Tar'an *et al.*, 2003b) |
| Seed protein concentration/content | *QTL* | 59 | (Tar'an *et al.*, 2004; Burstin *et al.*, 2007) |
| Yield component and developmental traits | *QTL* | 62 | (Timmerman-Vaughan *et al.*, 2005) |
| Yield-related traits and seed protein content | *QTL* | 56 | (Irzykowska and Wolko, 2004) |
| **Pigeonpea** | | | |
| Fertility restoration | QTL | 15–24 | (Bohra *et al.*, 2012) |
| Fusarium wilt | BSA | | (Kotresh *et al.*, 2006) |
| Number of pods per plant | QTL | 19 | (Kumawat *et al.*, 2012) |
| Plant height | QTL | 28 | (Kumawat *et al.*, 2012) |
| Plant type | BSA | | (Dhanasekar *et al.*, 2010) |
| Primary branches per plant | QTL | 20 | (Kumawat *et al.*, 2012) |
| SMD resistance | QTL | 25 | (Gnanesh *et al.*, 2011) |
| | BSA | | (Ganapathy *et al.*, 2009) |
| **Soybean** | | | |
| *Resistance to biotic stresses* | | | |
| Cyst nematode, Corn earworm, Brown stem rot, Sclerotinia stem rot, Phytophora root rot, Sclerotinia stem rot, Soybean mosaic virus, Asian rust, Brown stem rot, Sudden death syndrome | QTL | 2–28 | (Atibalentja *et al.*, 2005; Guo *et al.*, 2006; Guo *et al.*, 2008; Han *et al.*, 2008; Huynh *et al.*, 2010; Kazi *et al.*, 2008; Li *et al.*, 2010; Ruben *et al.*, 2006; Shi *et al.*, 2008; Silva and Danielle, 2008; Vuong *et al.*, 2008; Wang *et al.*, 2010; Winter *et al.*, 2007) |

*(Continued on next page)*

TABLE 4
Summary of some trait mapping studies in select legumes *(Continued)*

| Trait | Gene/ QTL | *PVE (%) | Reference |
|---|---|---|---|
| Soybean mosaic virus | *Rsv, Rsv* | 1 to 3 | (Shi *et al.*, 2008) |
| Cyst nematode | *rhg1, Rhg4* | 5 | (Guo *et al.*, 2005; Ruben *et al.*, 2006; Vuong *et al.*, 2010; Winter *et al.*, 2007; Wu *et al.*, 2009) |
| *Agronomic and yield related traits* | | | |
| Seed protein oil content, Water use efficiency, Specific leaf weight and leaf size, Seed weight, Flowering time, Yield, maturity, Sprout yield, Seed isoflavone, Seed size, viability of seed, germination rate of seed, water absorbability of seed, ability, frequency, and efficiency of somatic embryogenesis, Vitamin E content, Chlorophyll a fluorescence parameter, Developmental behavior, Browning in soybean seed coats, Domestication, Seed composition, Seed shape, Photoperiod insensitivity, Net-like cracking in seed coats, Cleistogamy, Nodule number and nodule dry weight, Water logging, Oligosaccharide and sucrose | QTL | 3–63 | (Choi *et al.*, 2010; Funatsuki *et al.*, 2005; Githiri *et al.*, 2006; Githiri *et al.*, 2007; Khan *et al.*, 2008; Kim *et al.*, 2006; Lee *et al.*, 2009; Li-H. *et al.*, 2010; Liu *et al.*, 2007; Liu and Abe, 2010; Nicolas *et al.*, 2006; Oyoo *et al.*, 2010; Panthee *et al.*, 2006; Qi *et al.*, 2008; Reinprecht *et al.*, 2009; Salas *et al.*, 2006; Song *et al.*, 2010; Sun *et al.*, 2006; Tuyen *et al.*, 2010; Yin *et al.*, 2010) |
| Early maturity | *E8* | 8 | (Cober *et al.*, 2010) |
| Phosphorus deficiency | *fsw1, fsw2, rp1, fsw3, rp2, lp1, lp2* | 12 | (Li *et al.*, 2005) |

(Cahill and Schmidt, 2004), insect resistance (Narvel *et al.*, 2001; Walker *et al.*, 2002; Warrington *et al.*, 2008), mosaic virus (Saghai-Maroof *et al.*, 2008; Shi *et al.*, 2009), MAS products were also developed for low linolenic acid content (Sauer *et al.*, 2008) and yield (Concibido *et al.*, 2003). Furthermore, SNP markers tightly linked to soybean root-knot nematode resistance QTL have enhanced the efficiency of MAS (http://www.plantmanagementnetwork.org/pub/php/news/2007/Shortcut/). Similarly, in case of common bean, efforts at CIAT focused mainly in deploying single genes for enhancing resistance to viral diseases. As a result, the cultivar Perola with enhanced resistance bean Anthrocnose in Brazil (Raganin *et al.*, 2003), pinto beans in the United States (Miklas *et al.*, 2003) and Andean climbing bean in Mexico / Colombia (Garzon *et al.*, 2008) have been developed. In cowpea, SCAR markers have been used in discriminating *Striga* resistant and susceptible lines (Omoigui *et al.*, 2012).

MABC is the simplest way to develop superior lines by transfering QTLs with large phenotypic effect using tightly linked molecular markers to a given trait for foreground selection and genome-wide unlinked markers for background selection or recovery of the recurrent parent genome. In particular MABC is useful to capture major QTL(s)/gene(s) with a strong association to the given trait of interest. For example in groundnut, MABC has been used to develop and release an improved variety; markers linked with root-knot nematode (*Meloidogyne arenaria*) resistance were used for introgression through the amphidiploid pathway into cultivated groundnut (Simpson *et al.*, 2001). Identification of linked markers due to sequence divergence between diploid and tetraploid genomes (Chu *et al.*, 2007; Nagy *et al.*, 2010) was relatively easy in groundnut. The simultaneous introgression of nematode resistance and oil quality was achieved using a recessive *AhFAD2B* allele (which controls high ratio of oleic: linoleic acid (O/L)) and linked markers for foreground selection. These efforts led to the release of the improved Tiftguard variety "Tiftguard High O/L" (Chu *et al.*, 2011). The MABC approach has been initiated to introgress a major QTL contributing ca. 80% of the phenotypic variation for leaf rust into the genetic background of three elite cultivars namely ICGV 91114, JL 24 and TAG 24. By using 2–3 rounds of backcrossing and selfing, $BC_2F_3$ and $BC_3F_2$ homozygous lines have been developed at ICRISAT.

TABLE 5
Key success stories of TGA in legume crops

| Crop | Trait | Progenies developed/ cultivars released | Reference/source |
|---|---|---|---|
| Chickpea | Fusarium wilt resistance | Back cross progenies from (C 214 × WR 315) | (Varshney *et al.*, 2013c) |
| | Aschochyta blight resistance | Back cross progenies from (C 214 × ILC 3279) | (Varshney *et al.*, 2013c) |
| | Drought tolerance | Back cross progenies from (JG 11 × ICC 4958) | (Varshney *et al.*, 2013b) |
| | | Back cross progenies from (Chefe × ICC 8261), (KAK2 × ICC 8261), (ICCV 10 × ICC 4958) | (ICRISAT, India) |
| | | Back cross progenies from (Ejere × ICC 4958), (Arerti × ICC 4958) | (EIAR, Ethiopia) |
| | | Back cross progenies from (ICCV 97105 × ICC 4958), (ICCV 95423 × ICC 4958) | (EU, Kenya) |
| Common bean | Disease resistance | USPT-ANT-1, ABCP-8, ABC-Weihing | (Miklas *et al.*, 2003; Mutlu *et al.*, 2005, 2008) |
| | Resistance to white mold | Back cross lines | (Carneiro *et al.*, 2010) |
| Groundnut | Nematode resistance | COAN cultivar, NemaTam | (Simpson *et al.*, 2003) |
| | Nematode resistance and High O/L ratio | Tifguard High O/L | (Chu *et al.*, 2011) |
| | Rust resistance | Back cross progenies from (JL 24 × GPBD 4), (TAG24 × GPBD 4), (ICGV 91114 × GPBD 4) | (Varshney *et al.*, 2014) |
| | High O/L ratio | Back cross lines | (Koilkonda *et al.*, 2012) |
| Soybean | Disease resistance | JTN-5503, JTN-5303 | (Arelli *et al.*, 2006; 2007) |
| | Soybean mosaic virus | F$_{4:5}$ lines, Near Isogenic Line (NILs) | (Saghai-Maroof *et al.*, 2008; Shi *et al.*, 2008) |
| | Low phytate | Back cross lines | (Landau-Ellis and Pantalone, 2009) |
| | Soybean cyst nematode resistance | JTN-5109, DS-880 | (Smith et al., 2010) |
| | Rust resistance | Back cross lines | (Khanh *et al.*, 2013) |

Two major MABC projects are underway in chickpea at ICRISAT and its partner organizations. Under the Tropical Legume-I initiative of CGIAR Generation Challenge Programme in collaboration with Bill & Melinda Gates Foundation, significant efforts have been made to develop drought tolerant progenies (BC$_3$F$_{3:4}$) in the genetic background of JG11, a leading variety in India, by transferring a genomic region, "*QTL-hotspot,*" that contains several QTLs for drought tolerance traits (Varshney *et al.*, 2013b). Detailed phenotypic evaluation of these lines is underway in India, Kenya and Ethiopia and preliminary results are promising (unpublished). The second initiative is part of the Accelerated Crop Improvement Programme (ACIP) of Department of Biotechnology, Government of India. In this initiative, efforts are being made to introgress resistance to different races independently as well as pyramiding of resistance to two races for FW in some elite varieties in India. ICRISAT (India) is pyramiding resistances for *Foc1* and *Foc*3 from WR 315 and 2 QTLs for Ascochyta blight (AB) resistance from ILC 3279 line into C 214 (Varshney *et al.*, 2013c).

However, the majority of traits targeted by breeders e.g. drought tolerance or durable resistance to multiple races of pathogens are controlled by multiple QTLs or genes. In such cases, retaining desirable gene combinations or pyramiding of several QTLs through the MABC approach is a challenging task (Peleman and Voort, 2003). Hence, marker assisted recurrent selection (MARS), has been introduced as an alternative approach and demonstrated experimentally to be more effective in accumulating a large number of smaller effect QTLs (Ribaut *et al.*, 2010; Ribaut and Ragot, 2007). MARS, on the other hand, aims to take advantage of QTL information generated on breeding

populations to develop superior lines with an optimum combination of favourable alleles originating from both the parents. QTL alleles are accumulated through successive intercrossing using only genotypic selection. Recombined lines are then subjected to a final phenotypic screening to select the best varieties to release. MARS can be initiated without any prior knowledge of QTLs with the objective of discovering and harnessing the superior QTLs/alleles during the scheme itself, which is not possible in MABC. However, it is observed that existing marker-trait associations enhance the quantum of genetic gains in MARS scheme (Bernardo and Charcosset, 2006). The recurrent-selection method is routinely used mainly in cross-pollinated crops like maize and, this process can be improved with the help of molecular markers, which is why the process is called marker-assisted recurrent selection (MARS). While several multinational companies have been using MARS in crops like maize and soybean, only a few public sector institutes have used MARS in crops likes wheat (Charmet *et al.*, 2001), sorghum (Abdallah *et al.*, 2009) and rice (Grenier *et al.*, 2012). MARS based programs have been initiated in cowpea (see Ribaut *et al.*, 2012) targeting improvement in drought tolerance. Some efforts have been initiated to use MARS in the case of chickpea, for assembling favorable alleles for drought tolerance using ICCV 04112 × ICCV 93954 and ICCV 05107 × ICCV 94954.

Genomic selection (GS) is a novel approach in which genetic markers covering the whole genome are used so that all (QTL) are in linkage disequilibrium with at least one marker. GS focuses on the selection of desirable genotypes on the basis of an *index* derived from genome-wide DNA marker information. The index is designated as genomic estimated breeding values (GEBVs) and the phenomenon of selecting individuals on GEBV basis is referred as genomic selection (GS) (Heffner *et al.*, 2009). Genotyping and phenotyping of a 'training population' is required to train the GS models or extensively calculate GEBV estimates (Nakaya and Isobe, 2012). The GEBV estimates thus obtained are subsequently used for selection of genotypes from 'breeding population.' In GS, no phenotyping is required for the 'breeding population', however all the individuals are genotyped thoroughly. GS efficiently exploits the high density marker data available at reasonable cost and can also reduce the selection cycle length of a breeding program where it could take several seasons to develop reliable phenotypic data. In brief, GS as an approach relies on cycles of prediction and testing by phenotyping the training population as the process proceeds and this constant checking of the selection index vs the training population overcomes type I errors associated with multiple loci contributing small effects to many quantitative traits.

For estimating the GEBVs with high precision, an important component of GS, use of an appropriate statistical model is very critical. Among different models of GS, GEBVs predicted using either best linear unbiased prediction (BLUP) or Bayesian methods are effective according to simulation studies (Bernardo and Yu, 2007). In addition to a Bayesian method,

Bayes B, another method called wBSR (weighed Bayesian Shrinkage Regression) which reduces the computational burden on MCMC-based Bayesian methods is considered to be a method of choice for genomic selection (Takeshi and Hiroyoshi, 2010). Cornell University (Jannink *et al.*, 2010), the University of Minnesotta (Bernardo and Yu, 2007) and Hohenheim University (Piepho, 2009) also developed statistical models and/or pursued applications of GS in breeding of some major crops like maize, wheat. Though GS has not been used in any legume species at present, mostly due to lack of: (i) historical phenotyping data on several breeding lines (that can be used for the training population), (ii) big linkage disequilibrium (LD) blocks in breeding populations, and (iii) genome wide marker genotyping system like DArT or SNP markers, ICRISAT has initiated the efforts to deploy GS in chickpea and groundnut.

## VI.   CHALLENGES AND OPPORTUNITIES

Whole genome sequences of both model and crop legumes are expected to offer new perspectives for TGA in legume species. From the examples presented above it is evident that ongoing genomics research could accelerate crop improvement programs in legume crops. In the pre-genomics era, comparative genomics approach was successful for identifying homologues/orthologues or cloning genes in several legumes by using information from model plant systems. For example, conservation of *Arabidopsis* flowering time genes was studied in legumes and preliminary survey revealed that legume flowering-related genes (*LFY* and *TFL1*) identified significant differences in function to *Arabidopsis* counterparts (Hecht *et al.*, 2005). However, this approach was not very successful for developing superior varieties in legume crops. In the post-genomics era, availability of genome sequence information as well as species specific genomic resources offer greater opportunities for TGA even in the crops like lentil, pea and fababean where limited information is available. However, so far, success stories of TGA are limited in the targeted legume crops. In this context, there is a series of challenges that include: (i) availability of limited predictive molecular markers for target traits, (ii) limited access to marker technologies, (iii) limited availability of high-throughput, cost-effective and precise phenotyping platforms, (iv) lack of capacity both human as well as infrastructure and (v) absence of suitable data management systems (Varshney *et al.*, 2012b). High-throughput sequencing and genotyping facilities available in different countries could benefit from economies of scale. Although sample shipment across national borders sometimes poses logistic and quarantine challenges, especially in the developing world, access to those centers could facilitate deployment of molecular breeding in the legume crops. For modernization of the breeding programs, it is important to deploy decision support tools (computational tools) in every step of the process of breeding. The Integrated Breeding Platform initiative (www.integratedbreeding.net), houses a range of

decision support tools that can be used in a distributed way for example by National Agricultural Research Systems (NARS) in their breeding programs.

Although conventional breeding based exclusively on phenotypic selection remains the mainstay for most breeding programs in these legumes, adoption of TGA is increasing and in some cases is superseding conventional approaches. With advances in genomics, the ultimate aim is to increase the rate of genetic gain across target environments, in less time and at lower cost compared to conventional selection. Nonetheless, it is also important to mention the role of quality phenotypic data. Efforts need to be initiated to establish field based high throughput and cost effective phenotyping platforms. As plants are exposed to range of stresses, breeders in general perform selection based on the plant's overall performance and not just for a single trait. Therefore GS seems to be an ideal approach because it involves selection of the plants based not on just one trait but for overall performance of the plant based on whole genome marker profiling data. We believe that centralized genotyping service facilities, together with access to genomics and breeding analytical tools (decision support tools), should enhance implementation of TGA in these legume crops. Furthermore web accessible mutant populations are available for *Medicago*, *Lotus* and soybean. Developing such collections in other crop legumes may fasten the breeding programs. It is also important to continue the training of breeders and geneticists in integrated genomics and molecular breeding. Effective implementation of TGA in the legume crops will lead to crop improvement programs for ensuring food security in developing countries.

## FUNDING

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