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REVIEW PAPER

Accelerating genetic gains in legumes for the development of prosperous smallholder agriculture: integrating genomics, phenotyping, systems modelling and agronomy

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Abstract

Grain legumes form an important component of the human diet, provide feed for livestock, and replenish soil fertility through biological nitrogen fixation. Globally, the demand for food legumes is increasing as they complement cereals in protein requirements and possess a high percentage of digestible protein. Climate change has enhanced the frequency and intensity of drought stress, posing serious production constraints, especially in rainfed regions where most legumes are produced. Genetic improvement of legumes, like other crops, is mostly based on pedigree and performance-based selection over the past half century. To achieve faster genetic gains in legumes in rainfed conditions, this review proposes the integration of modern genomics approaches, high throughput phenomics, and simulation modelling in support of crop improvement that leads to improved varieties that perform with appropriate agronomy. Selection intensity, generation interval, and improved operational efficiencies in breeding are expected to further enhance the genetic gain in experimental plots. Improved seed access to farmers, combined with appropriate agronomic packages in farmers' fields, will deliver higher genetic gains. Enhanced genetic gains, including not only productivity but also nutritional and market traits, will increase the profitability of farming and the availability of affordable nutritious food especially in developing countries.

Keywords: Drought stress, genetic gains, genomics-assisted breeding, legumes, nutrition, rainfed agriculture.

Introduction

Legumes are the third largest group among higher plants with more than 18 000 species in 650 genera. Grain legumes belong to subfamily Papilionoideae. Economically important food and feed legumes mostly fall in four clades of Papilionoideae: (i) genistoids, (ii) aeschynomenoids/dalbergioids, (iii) Hologalegina, and (iv) phaseoloids/millettioids.

Abbreviations: AGS, advanced generation selection; BLUP, best linear unbiased prediction; EGS, early generation selection; GAB, genomics-assisted breeding; GS, genomic selection; MABC, marker-assisted back crossing; MARS, marker-assisted recurrent selection; MAS, marker-assisted selection; QDS, quality declared seed; RCGS, rapid cycling genomic selection; SNP, single nucleotide polymorphism.

Recent molecular studies placed cool-season legumes in the inverted repeat loss clade of Hologalegina, while warm season legumes were included in the phaseoloid/millettioid clade (Wojciechowski *et al.*, 2004). Cool season legumes include chickpea (*Cicer arietinum*), faba bean (*Vicia faba*), lentil (*Lens culinaris*), and pea (*Pisum sativum*). Warm season legumes include common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), pigeonpea (*Cajanus cajan*), soybean (*Glycine max*), and groundnut (*Arachis hypogaea*) (Doyle and Luckow, 2003). Signature features of legumes include biological nitrogen fixation in symbiotic association with bacteria and mycorrhiza, geotropic peg and pod development in groundnut, and vernalization in chickpea, each of which is of economic and scientific interest. Legumes form an important component of the human diet, provide animal feed, and replenish soil fertility through biological nitrogen fixation. In addition, legumes can recover unavailable forms of soil phosphorus, possibly lower the emission of greenhouse gases, and are prospective assets in future cropping systems (Stagnari *et al.*, 2017). A recent review gives a good summary of the many virtues of food legumes and sets an agenda for their improvement in the decades to come (Sinclair and Vadez, 2012; Foyer *et al.*, 2016).

According to United States Census Bureau International Database, the global population is predicted to approach 9.8 billion by 2050. Further, the Global Alliance for Improved Nutrition, which works to strengthen the availability of nutritious and affordable foods for infants and women, estimated that 2 billion people across the world are undernourished and 2.6 million children die due to malnutrition (http://www.gainhealth.org/knowledge-centre/fast-facts-malnutrition/). The majority of crop improvement programs, however, have emphasized only crop productivity traits in the past including during the green revolution. As a result, despite the attaining of global food security, a continuous increase in micronutrient malnutrition has been recorded in most of the developing countries. Under such a scenario, the grain legumes are relevant in the fight against malnutrition and are considered to provide 'nutritious seeds for a sustainable future'. Therefore, a comprehensive strategy and dedicated effort are required to produce more and dense nutritious legume crops to ensure food and nutritional security.

Climate change has significant adverse impacts on all components of crop production—area, intensity, and yield— and hence producing more food to feed the growing population is a great challenge before agriculturists and other stakeholders. The World Resources Institute predicted that by 2040, the USA, China, and India are expected to face 40–70% more water stress. Globally the demand for food legumes is increasing as legumes may complement cereals in protein requirements and possess a high percentage of digestible protein. The majority of the area under legumes is in Asia (~76%), principally soybean, beans, groundnut, and chickpea. More recent studies indicate that between 1961 and 2014, 75% of the legume area in South America and 90% of that in North America are under soybean cultivation (FAOSTAT, 2016). In Sub-Saharan Africa, food legumes are cultivated on 20 million ha, and 44% of production comes from cowpea and 31% from dry beans. Sub-Saharan Africa alone contributes 54% of global cowpea production (Akibode, 2011).

High tolerance to environmental stresses of many rainfed legumes, when compared with soybean, is required for sustainable production in often harsh soil and climatic conditions in dryland agriculture (Foyer *et al.*, 2016; Sita *et al.*, 2017). Erratic rainfall increases the occurrence of drought stress necessitating drought-tolerant legume varieties that can produce in water-limited environments. Drought tolerance is a very complex trait and hence an in-depth understanding of the genomic control and molecular mechanism of drought tolerance is essential for effective deployment in breeding.

Genetic gain can be defined as the rate of increase in yield over a given time period—pure genetic gain is estimated against potential yield, but can also be assessed under defined stress conditions. Barker *et al.* (2010) reported a maize genetic gain of 211 kg ha^{-1} year^{-1} in favorable environments in Woodland, CA, USA. Further, the same study reported lower genetic gains under water limited environments, of 124 and 91 kg ha^{-1} year^{-1} expressed during flowering and mid-grain filling, respectively. Recently, by using marker-assisted recurrent selection (MARS) in maize, a 3% increase in yield per cycle under water stress conditions was reported (Bankole *et al.*, 2017). Among legumes, Koester *et al.*, (2014) reported a genetic gain of 26.5 kg ha^{-1} year^{-1} by studying the historical data of 80 years of soybean breeding at the Crop Research and Education Center in Urbana (IL, USA). This gain in grain yield is attributed to increases in light interception, energy conversion, and partitioning efficiencies.

A contemporary question in legume improvement is how to enhance the synergy among the different disciplines of genomics, phenomics, crop physiology, growth modelling, and agronomy. In this article, we discuss the technological advances in different disciplines and advocate their integrated use both to understand the genetics of traits and to deploy them in crop improvement programs of soybean, chickpea, pigeonpea, and groundnut. A special emphasis has been placed on deployment of genomic selection in breeding programs to attaining faster genetic gain.

Technological advances

Agricultural research has benefitted from new technologies that have helped in achieving current food sufficiency in many parts of the world. However, to realize future demands, researchers need to apply new tools, technologies, and partnerships to achieve even higher productivity and profitability of farming and better nutrition for all consumers. Emerging crop improvement technologies are outlined in the following sections.

Sequencing and genotyping

During the past two decades, advances in molecular marker technologies and next-generation sequencing technologies have enhanced our understanding of several traits in crop plants including food legumes (Varshney *et al.*, 2015). Genome sequences for most of the grain legumes are now

available, for instance soybean (Schmutz *et al.*, 2010), groundnut progenitors (Bertioli *et al.*, 2016; Chen *et al.*, 2016), chickpea (Varshney *et al.*, 2013*d*; Parween *et al.*, 2015), pigeonpea (Varshney *et al.*, 2012*a*), common bean (Schmutz *et al.*, 2014; Yang *et al.*, 2015), and adzuki bean (Kang *et al.*, 2015; Yang *et al.*, 2015) (Table 1). Efforts are underway to sequence the remaining legume genomes. The past decade has witnessed an exponential increase in availability of genomic resources and their deployment in trait discovery and breeding (see Bohra *et al.*, 2014; Varshney *et al.*, 2015; Pandey *et al.*, 2016). As a result, several of these legume crops have genomic resources and associated phenotypic data to support genomics-based discovery and breeding approaches to develop superior legume varieties.

Besides disclosing the blueprint of genomes of several legumes, different research groups also re-sequenced legume germplasm lines, which further increased our understanding of genome architecture, structural variations, genome evolution, and genome dynamics during domestication. Several million structural variations that aid in trait mapping and trait improvement were reported (Kumar *et al.*, 2016; Thudi *et al.*, 2016*b*). In addition, genome-wide single nucleotide polymorphisms (SNPs) were also used to identify significant marker trait associations for economically important traits (Zhou *et al.*, 2015*a*; Varshney *et al.*, 2017). Resequencing germplasm lines also enabled us to understand the spatial and temporal trends in diversity in released varieties of chickpea (Thudi *et al.*, 2016*a*), cultivated and wild accessions of soybean (Lam *et al.*, 2010; Zhou *et al.*, 2015*a*), and a reference set of pigeonpea (Varshney *et al.*, 2017; Table 1). Resequencing of 28 Brazilian soybean cultivars suggested that, despite the diversification of modern Brazilian cultivars, the soybean germplasm remains very narrow because of the large number of genome regions that exhibit low diversity (Maldonado dos Santos *et al.*, 2016). In recent years, genotyping by sequencing, skim sequencing, diversity array technology (DArT)-seq and restriction site associated DNA sequencing approaches were also employed for developing high density genetic maps, refining the QTL mapping and identifying trait linked markers in legumes (Jaganathan *et al.*, 2015; Kale *et al.*, 2015; Contreras-Soto *et al.*, 2017; Leamy *et al.*, 2017; Valdisser *et al.*, 2017). Nevertheless, the percentage of missing data points and the SNP calling rates greatly reduce the number of final SNPs for different studies and this has been a concern. To overcome these constraints several high-throughput SNP genotyping platforms, such as Veracode assays, Illumina GoldenGate assays, Infinium chips and Axiom arrays, are now available, which not only increase the precision of SNP calling but also enable genotyping of larger populations at reduced cost (Table 1). Axiom arrays with >50K SNPs with uniform genome coverage were developed and are being used for germplasm characterization, trait mapping and molecular breeding in chickpea (Roorkiwal *et al.*, 2017), pigeonpea (ICRISAT unpublished data), groundnut (Pandey *et al.*, 2017*a*) and soybean (Lee *et al.*, 2015; Table 1).

High-density and precise phenotyping

Understanding the complex relationships between genotype and phenotype is a major challenge in plant sciences in view of the multi-scale nature of phenotypes and of the large phenotypic plasticity displayed by plants subjected to varying environmental conditions that results in different values of phenotypic variables and different rankings of genotypes in different experiments. It requires (i) capturing information on physiological traits and performance of large numbers of plants, together with their environment, (ii) analysing and organizing the resulting datasets, and (iii) developing models able to disentangle and simulate plant behavior in a range of scenarios (Tardieu *et al.*, 2017). Good and relevant phenotyping starts with a detailed understanding of plant biological processes underlying tolerance/resistance to well-defined constraints. For instance, tolerance of chickpea to terminal drought in South Asia depends on plant traits that ensure the availability of water during the grain filling phase (Zaman-Allah *et al.*, 2011; Vadez *et al.*, 2013*a*; Vadez 2014). Therefore, phenotyping first needs to be well targeted and defined. Precise phenotyping is the next step and involves the design of protocols and approaches that ensure the assessment of key traits at the highest rate and the cheapest cost. The cost of phenotyping increases with increase in population size, especially in the case of deployment of genomic selection (see later), which requires a larger population for high prediction accuracy.

The availability of non-destructive root phenotyping methods has, in the past, limited our understanding of traits involved in drought tolerance of legumes such as stomatal control or root system architecture. Hence, genome-wide association studies of traits associated with drought tolerance, based on large-scale germplasm re-sequencing (Varshney *et al.*, 2017), require a suite of high-throughput and precise phenotyping technologies for capturing, analysing, and interpreting images in order to infer heritable traits that can be analysed genetically (Tardieu *et al.*, 2017).

Recognizing the importance of phenotyping, in recent years several large public, private and academic efforts have led to the establishment of state-of-the-art phenotyping facilities word-wide in an exponential phase of automated high-throughput phenotyping (Table 2). These include the German and French Plant Phenotyping Networks (http://www.dppn.de; https://www.phenome-fppn.fr/), European Plant Phenotyping Network (2020) (EPPN^{2020}; https://eppn2020.plant-phenotyping.eu), European Plant Phenotyping Infrastructure (EMPHASIS), and International Plant Phenotyping Network (IPPN; https://www.plant-phenotyping.org/). These infrastructure networks enable access to the necessary tools for phenotyping, in particular robot-assisted image capture (Cooper *et al.*, 2009; Fiorani and Schurr, 2013), statistical designs and models for extracting relevant physiological variables from raw data (Cabrera-Bosquet *et al.*, 2016), and specialized information systems managing large datasets originating from phenotyping experiments (Tardieu *et al.*, 2017). GrowScreen-PaGe is a non-invasive, high-throughput phenotyping system developed at the Institute of Biosciences

Table 1. *Summary of genome sequence, resequencing efforts and available high throughput genotyping platforms in important legumes*

Crop	Genome sequence	Germplasm lines resequenced	High throughput genotyping platforms
Soybean	• 85% of *Glycine max* var William 82 genome (1115 Mb); 46 430 protein coding genes (Schmutz *et al.*, 2010) • 915.4 Mb of *G. soja* var. IT182932 (Kim *et al.*, 2010)	• 106 (7 wild, 43 landraces and 56 elite; Valliyodan *et al.*, 2016) • 302 (62 wild, 130 landraces and 110 elite; Zhou *et al.*, 2015*a*) • 28 (commercial cultivars; Maldonado dos Santos *et al.*, 2016) • 89 lines (Lee *et al.*, 2015) • 286 (14 wild, 153 landraces and 119 elite; Zhou *et al.*, 2015*b*)	• Illumina 384 SNP VeraCode assays (Lee *et al.*, 2015) • NJAU 355 K SoySNP array (Wang *et al.*, 2016) • Illumina Infinium SoySNP6K BeadChip (Akond *et al.*, 2013) • SoySNP50K array (Song *et al.*, 2013) • 384 SNP GoldenGate assay (Hyten *et al.*, 2008) • SoyaSNP180K Axiom (Lee *et al.*, 2015)
Pigeonpea	• 72.7% of *Cajanus cajan* var Asha genome (833.07 Mb); 48 680 protein coding genes (Varshney *et al.*, 2012*a*)	• 292 lines (Varshney *et al.*, 2017) • 20 (crossing parentals of recombinant inbred lines, introgression lines, MAGIC and NAM population; Kumar *et al.*, 2016)	• 60K Axiom®Cajanus SNP array (Saxena *et al.*, 2017 and unpublished)
Chickpea	• 72.12% of *Cicer arietinum* var CDC Frontier genome (738 Mb); 28 269 protein coding genes (Varshney *et al.*, 2013*d*) • 416 Mb of *C. reticulatum* var PI 489777 genome; 25 680 protein coding genes (Gupta *et al.*, 2017)	• 35 (parental genotypes of mapping populations; Thudi *et al.*, 2016*a*) • 129 released varieties (Thudi *et al.*, 2016*b*) • 300 lines (ICRISAT, unpublished) • 3000 lines (ICRISAT, unpublished)	• GoldenGate assays based on VeraCode technology (Roorkiwal *et al.*, 2013) • 60K Axiom®Cicer SNP array (Roorkiwal *et al*., 2017) • GoldenGate assays based on VeraCode technology (Roorkiwal *et al.*, 2013)
Groundnut	• 1081 Mb of *Arachis duranensis* V14167 and 1371 Mb of *A. ipaensis* K30076 (Bertioli *et al.*, 2016) • *A. duranensis* var PI475845; 50 324 protein coding genes (Chen *et al.*, 2016)	• 11 genotypes including synthetics and their diploid parents (Chen *et al.*, 2016) • 41 diverse genotypes (30 tetraploids and 11 diploids) (Clevenger *et al.*, 2017; Pandey *et al.*, 2017*a*)	• 58K Axiom®Arachis SNP array (Pandey *et al.*, 2017*a*) •1536 SNP GoldenGate assay (Nagy *et al.*, 2012)
Common bean	• 80.57% of *Phaseolus vulgaris* var G19833 genome (587 Mb); 26 279 protein coding genes (Schmutz *et al.*, 2014)	• 17 varieties (Song *et al.*, 2015)	• BARCBean6K_1, BARCBean6K_2 chips, BARCBean6K_3 SNP chips (Song *et al.*, 2013, 2015)
Mung bean	• 84.48% of *Vigna radiata* var *radiata* VC1973A geome (548 Mb); 22 427 predicted genes (Kang *et al.*, 2014) • 84.48% of *Vigna radiata* var *sublobata* TC1966A geome (501 Mb); 22 834 predicted genes (Kang *et al.*, 2014) • 81.81% of *Vigna radiata* var *glabra* V1160 geome (968 Mb); 41 484 predicted genes (Kang *et al.*, 2014)	—	—
Adzuki bean	• 96.56% of *Vigna angularis* var Gyeongwon genome (612 Mb); 21 532 predicted genes (Kang *et al.*, 2015) • 83.02% of *Vigna angularis* var Jingnong geome (542 Mb); 34 183 predicted genes (Yang *et al.*, 2015)	—	—
Cowpea	• 323 Mb of *Phaseolus vulgaris* var IT97K genome (724 Mb) (Muñoz-Amatriaín *et al.*, 2017)	• 36 diverse accessions (Muñoz-Amatriaín *et al.*, 2017)	• Cowpea iSelect Consortium Array (Muñoz-Amatriaín *et al.*, 2017) • 1536 SNP GoldenGate assays (Muchero *et al.*, 2009)
Pea	https://www.france-genomique.org/spip/spip.php?article141&lang=fr	—	• GenoPea 13.2K SNP Array (Tayeh *et al.*, 2015*a*) • 384 SNP GoldenGate assays (Deulvot *et al.*, 2010)

Table 2. *A list of key high-throughput phenotyping platforms*

Phenotyping platform (and institute or company)	Salient features	Reference
LeasyScan phenotyping platform (ICRISAT, India)	• A novel 3D scanning technique to capture leaf area development continuously • Scanner-to-plant concept to increase imaging throughput and analytical scales to combine gravimetric transpiration measurements. • Combines 3D imaging and lysimetry for high-throughput phenotyping of traits controlling plant water budget	Vadez *et al.* (2015)
Semi-hydroponic phenotyping system (The University of Western Australia, Australia)	• Permits mapping and digital measurement of dynamic growth of taproot and lateral roots • Desirable tool for examining root architecture of deep root systems and large sets of plants in a relatively small space	Chen *et al.* (2011)
DEEPER: an integrated phenotyping platform for deeper roots (PennState Colleage of Agriculture, USA)	• A platform for identifying the traits of deeper rooted crops in non-destructive field phenotyping of rooting depth, root modeling, high-throughput 3D imaging of root architecture, and anatomy	http://plantscience.psu.edu/research/labs/roots/projects/deeper-an-integrated-phenotyping-platform-for-deeper-roots
GLO-Roots: luminescence-based imaging system (Dinnenylab, USA)	• Combines custom-made growth vessels and new image analysis algorithms to non-destructively monitor RSA development over space (2D) and time • Allows information on soil properties (e.g. moisture) to be integrated with root growth data • Makes use of luminescence imaging of roots expressing plant codon-optimize luciferase	Rellán-Álvarez *et al.* (2015)
X-Ray computed tomography (University of Nottingham, UK)	• Non-destructively visualizes opaque root structures by measuring the attenuation of ionizing radiation as it passes through the root • A series of projections are acquired and combined to reconstruct a 3D image of the root system	Mairhofer *et al.* (2012), Mooney *et al.* (2012)
Rhizophonics (University of Liège, Belgium)	• Combines hydroponics and rhizotrons • System is made of a nylon fabric supported by an aluminum frame • The set-up is immersed in a tank filled with liquid medium • Allows non-destructive, 2D imaging of root architecture while simultaneously sampling shoots	Mathieu *et al.* (2015)
Clear pot method (The University of Queensland, Australia)	• Uses transparent pots filled with soil or other p otting media • Seeds are planted close to the pot wall to enable high- throughput imaging of roots along the clear pot wall • To prevent light exposure, the clear pot is placed in black pots while roots are developing	Richard *et al.* (2015)
Rhizoslides (Institute of Agricultural Sciences, ETH Zurich, Switzerland)	• The set-up consists of a Plexiglas sheet covered with moistened germination paper. Seeds are planted on the slit of the Plexiglas • Allows separation of crown roots from embryonic roots	Le Marié *et al.* (2014)
Shovelomics (PennState Colleage of Agriculture, USA)	• Involves manual excavation of plants and separating roots from shoots • Washed roots are then placed on a phenotyping board for root trait quantification • New algorithms allow extraction of several root traits in a high throughput manner	Trachsel *et al.* (2011), Bucksch *et al.* (2014)

Table 2. *Continued*

Phenotyping platform (and institute or company)	Salient features	Reference
Soil coring (CSIRO and The University of Queensland, Australia)	• Uses a tractor-mounted, hydraulic soil corer to drive steel alloy sampling tubes into the soil • When combined with novel planting configurations (e.g. hill plots), this method allows for phenotyping deep rooted crop varieties	Wasson *et al.* (2014)
Rhizo-lysimetry (E. H. Graham Centre for Agricultural Innovation, Australia)	• Elaborate facility consisting of an underground corridor and concrete silos and pipes to house soil-containing soil cores for direct root observation	Eberbach *et al.* (2013)
Minirhizotrons	• A transparent observation tube permanently inserted in the soil. Images of roots growing along the minirhizotron wall at particular locations in the soil profile can be captured over time	Iversen *et al.* (2011), Maeght *et al.* (2013)
RhizoTube (INRA, France)	• Cylindrical rhizotrons that allow full 2D visualization of the root system of a single or up to six plants simultaneously • The RhizoCab is designed to take images of the entire root systems of plants growing in RhizoTubes, and also permits a focus on some parts of the root systems	Jeudy *et al.* (2016)
RADIX (Institute of Agricultural Sciences, ETH Zurich, Switzerland)	• Rhizoslide platform allowing high throughput digital image analysis of root system expansion	Le Marié *et al.* (2016)
Scanner bank (The James Hutton Institute, UK)	• Low-cost, high-resolution root phenotyping platform, requiring no sophisticated equipment and adaptable to most laboratory and glasshouse environments, and applied to quantify environmental and temporal variation in root traits	Adu *et al.* (2014)
The Plant Accelerator® (The University of Adelaide, Australia)	• The facility offers modern plant growth environments and state-of-the-art high-throughput automated imaging and computing technologies to monitor the performance of plants under different environmental conditions (e.g. which genotype performs best under drought stress) • Research projects facilitated by this technology vary from large scale screening of early growth, salinity tolerance to water and nutrient use efficiency	http://www.plantphenomics.org.au/services/accelerator/
DroughtSpotter (The University of Adelaide, Australia)	• A gravimetric platform with precision irrigation to assess transpiration dynamics of plants with a precision of up to 1 g • Integrated irrigation units allow precise and reproducible water application for drought stress or related experiments that require an accurate control of water volume to 1 ml	http://www.plantphenomics.org.au/services/droughtspotter/
Crop Plant Root Module (The University of Adelaide, Australia)	• Comprises destructive and non-destructive measurement of root growth, architecture, morphology, and water uptake in soil in controlled environments and in the field	http://www.plantphenomics.org.au/services/croproot/
Jülich Plant Phenotyping Centre (Jülich, Germany)	• Reproducibly quantifies growth and architecture of roots • Elucidates dynamic establishment of roots in space and time • Determines interaction of root responses with above ground plant part	http://www.fz-juelich.de/ibg/ibg-2/EN/organisation/JPPC/JPPC_node.html
PHENOPSIS (INRA, France)	• Automated platform for reproducible phenotyping of plant responses to soil water deficit	Granier *et al.* (2006), Bresson *et al.* (2015)
WIWAM (SMO and VIB, Belgium)	• Automated phenotyping platform for automated weighing, watering, and imaging of plants and, therefore, strictly controlling the applied watering regime	Skirycz *et al.* (2011), Clauw *et al.* (2015)

Table 2. *Continued*

Phenotyping platform (and institute or company)	Salient features	Reference
PHENOSCOPE (INRA, France)	• Automated large-scale phenotyping platform that automatically adjusts watering and is equipped with a zenithal imaging system to monitor rosette size and expansion rate during the vegetative stage, with automatic image analysis allowing manual correction	Tisné *et al.* (2013)
LemnaTec (LemnaTec, Germany)	• Versatile phenotyping system and analytics platform for diverse temporal responses to water availability	Chen *et al.* (2014), Neumann *et al.* (2015)
GlyPh (self-construction)	• Simple and low-cost automatic platform for high throughput measurement of plant water use and growth to assess drought tolerance	Pereyra-Irujo *et al.* (2012)

and Geosciences suitable for investigating root systems and root plasticity of large sets of both dicots and monocots (Gioia *et al.*, 2016). The LeasyScan platform developed at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) offers a novel 3D scanning technique that capture leaf area development continuously and phenotype traits controlling plant water budget (Vadez *et al.*, 2015). The University of Western Australia, Australia has developed a semi-hydroponic phenotyping system that examines architecture of deep root system and is amenable for phenotyping large sets of plants in a relatively small space (Chen *et al.*, 2011). The salient features of several high throughput phenotyping platforms, such as PHENOPSIS (Bresson *et al.*, 2015; Granier *et al.*, 2006), PhenoArch (Cabrera-Bosquet *et al.*, 2016), DEEPER PHENOSCOPE (Bresson *et al.*, 2015), and RADIX (Le Marié *et al.*, 2016), are summarized in Table 2.

Robotic-assisted imaging platforms and computer vision-assisted analysis tools have also been developed for precise phenotyping of physiological growth, development, and other phenotypic properties (Fahlgren *et al.*, 2015*a*,*b*). The data processing software that handles high throughput phenotyping for 2D, 3D, and anatomy cross sections of root have been extensively reviewed by Kuijken *et al.* (2015). The availability of automated high throughput phenotyping platforms enables testing of progenies from large germplasm populations across a range of target environments in terms of their impact on yield. The efficiency of these platforms, in this context, depends on the heritability and correlation of the traits with agronomically relevant breeding targets. Proper identification of the key constraints for a particular production ecology and an understanding of the biological processes can now be achieved with increasing scale and speed using existing platforms and designing new ones.

Multiple challenges lie ahead for high throughput phenotyping such as (i) targeting the development of phenotyping protocols and technology specifically for the target traits of their breeding product profiles; (ii) development of precise protocols amenable for high throughput phenotyping for agronomically important traits; (iii) developing appropriate technology for collecting, collating, and analysing data; (iv) storage and processing of huge datasets collected during high throughput phenotyping; and (v) integration and deployment of high throughput phenotyping in breeding pipelines. On top of that, the cost per sample, especially when dealing with large-scale populations, still remains an important challenge to the phenotyping community. One important aspect of better integration of genomics compared with crop physiology in breeding is the lower cost of genotyping per sample compared with field-based phenotyping. Another area that needs immediate attention is the automation of data collection, analysis and delivery of phenotypic data to support the breeding community in a cost-effective and timely manner. Addressing these challenges will accelerate the integration of modern phenotyping tools into breeding programs and accelerate the development of crop varieties with wider adaptation, resilience, and increased productivity and profitability.

Crop growth simulation and modelling approaches

In recent years, crop simulation and modelling approaches have challenged the idea of broad adaptation cultivars and have brought a new paradigm in breeding for target environments. Crop models, with general genetic inputs, suggest how a given combination of alleles confers a positive or negative effect on plant performance in different locations and seasons (Hammer *et al.*, 2002; Tardieu and Tuberosa, 2010; Messina *et al.*, 2011). Modelling enables us to predict the effect of a change in the biological architecture of a plant type (for instance having faster growing roots, Vadez *et al.*, 2012; for water use efficiency and stay green, Kholová *et al.*, 2014), or of a change in the agronomic management (for instance increasing planting density, Vadez *et al.*, 2017). As such, modelling should become an important resource-saving tool to guide the choice of breeding and agronomic management investment. Crop models have simulated the effect of crop management and climate on yield (Duncan *et al.*, 1967; de Wit *et al.*, 1970; de Wit, 1978; Kumar *et al.*, 2009; Kim *et al.*, 2010). Later, crop models were redesigned into farming systems models that could consider more broadly the effects of the management system including the carryover effects of rotations, planting density and intercropping. More broadly, systems models such as the Agricultural Production Systems sIMulator (APSIM) and the Decision Support System for Agrotechnology Transfer (DSSAT https://dssat.net/) simulate agricultural production systems (Keating *et al.*, 2003; Jones *et al.*, 2003; Holzworth *et al.*,

2014; Hoogenboom *et al.*, 2017), modelling interactions of plants, animals, climate, soil, and land management. Teixeira *et al.* (2015), using APSIM, demonstrated the importance of rotations for simulating climate impact assessments and Sennhenn *et al.* (2017) found new niches for short season legumes in Kenya. APSIM has been used in simulation studies for yield gap assessment in legumes such as soybean, groundnut, pigeonpea, and chickpea in India (Bhatia *et al.*, 2007; Chauhan *et al.*, 2008), in simulation of soil temperature in the podding zone of groundnut (Chauhan *et al.*, 2007), and in assessment of the impacts of fertilizers and legumes on N_2O and CO_2 emissions from soils in subtropical agricultural systems (Huth *et al.*, 2010).

With the availability of high throughput phenotyping platforms, the use of crop models in a genetic context has become possible. A conceptual framework was developed by Tardieu and Tuberosa (2010) with four modules that take into consideration phenotyping, genetics, climate, and crop models for estimating the effects of genetic diversity on crop performance. More recently Parent and Tardieu (2014) compared the algorithms involved in 19 crop models developed for predicting the effects of climate or cultivation techniques on a reference genotype. This study reported significant differences in combined effects of temperature and water deficit on plant development, but these differences have a low impact on the yield prediction of a reference genotype because errors in the effects of different traits compensate each other. The impact of climate on crop yield is assessed using two common approaches: (i) process-based simulation models, which attempt to represent key dynamic processes affecting crop yields, and (ii) statistical models, which estimate functional relationships between historical observations of weather and yields (Lobell and Asseng, 2017). The first approach is closer to physiological processes and can explicitly take into account the genetic variability of traits as measured in phenotyping platforms, for both main effects and genotype×environment interaction. However, it is often over-parametrized and can lead to inaccurate predictions in some cases because the model follows its own logic even if not applicable to the considered set of conditions (Tardieu *et al.*, 2017). The statistical approach is more conservative and safer, because predicted yields seldom depart from those observed experimentally. Both approaches are therefore complementary. The impact of drought on legume production is still not well understood in how it varies with legume species, region, agroecosystem, soil texture, and drought timing. For legumes specifically, a model has been developed (Simple Simulation Modelling; SSM) that uses the same model architecture across a range of grain legumes and is easy to use (Soltani and Sinclair, 2012). SSM has been used successfully to predict growth and yield in chickpea (Soltani and Sinclair, 2011; Vadez *et al.*, 2012, 2013*b*), lentil (Ghanem *et al.*, 2015*a*,*b*), common bean (Marrou *et al.*, 2014), soybean (Sinclair *et al.*, 2014), and groundnut (Vadez *et al.*, 2017). In the case of soybean, a recent modelling study indicated that a faster rate of root growth has a negative impact on yield as available soil moisture was depleted faster by more vigorous root growth (Sinclair *et al.*, 2010). While significant progress is being made in crop growth simulation and modelling, their integration with genetics and breeding is still in its infancy.

Genomics-assisted breeding

Most legume breeding programs focus on yield under drought stress. However, the pace of progress has been slow and the rate of yield gains has been minimal due to the complex nature of drought and non-availability of precise drought screening methods. As a result, the genetic gain achieved is about 1% per year in several species (Duvick, 2005; Cooper *et al.*, 2009; Brisson *et al.*, 2010; Lopes *et al.*, 2012; Aisawi *et al.*, 2015). The most promising option to design more drought resilient and sustainable production is to target the major traits of adaptation that include early flowering and seed set before the onset of terminal drought (Sennhenn *et al.*, 2017).

During the past two decades, the availability of molecular markers such as simple sequence repeats (Gupta and Varshney, 2000) and SNPs (Varshney *et al.*, 2010) facilitated dissecting complex traits that hamper crop production, using QTL mapping and genome wide association mapping approaches (Varshney *et al.*, 2015). Genome wide SNPs based on resequencing of several germplasm lines were also used to identify marker-trait associations in the cases of legumes such as pigeonpea (Varshney *et al.*, 2017) and soybean (Zhou *et al.*, 2015*a*).

Genomics-assisted breeding (GAB; Varshney *et al.*, 2005) was proposed to integrate genomics in breeding and it has been quite successful for several traits in cereals (Septiningsih *et al.*, 2013; Varshney *et al.*, 2006) and legumes (Varshney, 2016; Pratap *et al.*, 2017). Recently, Reynolds and Langridge (2016) have suggested crossing parents with different complex but complementary traits to achieve cumulative gene action for yield, while selecting progeny using remote sensing in combination with genomic selection. Genetic and genomics approaches and innovative tools have been made available during the past decade to breed climate-resilient legumes; for instance, root xylem plasticity and its role in improving water use efficiency in soybean (Prince *et al.*, 2017).

The QTLs/genomic regions and markers associated with traits are used to breed for stress resilience using marker-assisted selection (MAS), marker-assisted back crossing (MABC), and MARS approaches (Varshney *et al.*, 2012*b*). The legume community has been successful in developing several molecular breeding products despite the late arrival of genomic resources and trait-associated markers (Varshney *et al.*, 2013*a*,*b*; Pandey *et al.*, 2016; Varshney, 2016). Some key examples include resistance to Fusarium wilt and ascochyta blight (Varshney *et al.*, 2013*b*) and improved drought tolerance (Varshney *et al.*, 2013*a*) in chickpea; resistance to nematode and high oleic acid (Chu *et al.*, 2011), resistance to leaf rust (Varshney *et al.*, 2014), and resistance to high oleic acid (Janila *et al.*, 2016) in groundnut; resistance to rust disease (Khanh *et al.*, 2013), soybean mosaic virus (Saghai-Maroof *et al.*, 2008; Shi *et al.*, 2009; Parhe *et al.*, 2017), and low phytate (Landau-Ellis and Pantalone, 2009) in soybean; *Striga* resistance and seed size in cowpea (Lucas *et al.*, 2015; see Boukar *et al.*, 2016); pyramid genes for resistance to

ascochyta blight and anthracnose in lentil (Taran *et al.*, 2003); powdery mildew resistance (Ghafoor and McPhee 2012), lodging resistance (Zhang *et al.*, 2006), frost tolerance (see Tayeh *et al.*, 2015*b*), and *Aphanomyces* root rot resistance (Lavaud *et al.*, 2015) in pea; and resistance to common bacterial blight disease (Miklas *et al.*, 2000, 2006; Mutlu *et al.*, 2005; O'Boyle and Kelly, 2007), rust and viruses (Stavely, 2000), rust, anthracnose, and angular leaf spot (Oliveira *et al.*, 2008), rust (Feleiro *et al.*, 2001), and anthracnose (Alzate-Marin *et al.*, 1999) in common bean. Several of these improved lines have either been released or are in the release pipeline in different countries. In addition to the above, the gene/QTL pyramiding efforts are at an advanced stage for several legume traits such as in groundnut (leaf rust resistance+late leaf spot+high oleic acid), chickpea (fusarium wilt resistance+ascochyta blight resistance+drought tolerance; see Pandey *et al.*, 2016), and cowpea (resistance to *Striga*+aphid+macrophomina root rot; see Boukar *et al.*, 2016). The majority of the legume crops now enjoy the availability of genomic resources and such examples are seen more frequently in grain legumes. The MARS approach was deployed in cowpea successfully for improving grain yield, drought tolerance, *Striga* resistance and *Macrophomina* resistance (see Boukar *et al.*, 2016), but this approach did not work in the case of chickpea (see Varshney *et al.*, 2013*c*).

Next generation GAB approaches

While some examples, as mentioned above, are available for the use of molecular breeding, they include introgression of one to a few traits with higher heritability through MABC. Due to advances in low-cost genotyping/sequencing and availability of diagnostic markers, we expect use of early generation selection, genomic selection, and genome editing technologies in future GAB approaches.

Early generation selection

Early generation selection (EGS) is performed in highly segregating populations (mostly F_2) while advanced generation selection (AGS) begins with F_4 onwards followed by assessment of yield performance and other important agronomically superior traits in subsequent generations. Both EGS and AGS can be used to breed improved lines followed by evaluating these lines in target populations of environment (i.e. the set of conditions under which the set of considered varieties has been bred) to select promising lines with wider adaptation and higher yield under water limited environments. The success of EGS depends on (i) efficiency and accuracy of phenotyping a selected trait in a segregating population of single plants, for instance phenotyping for leaf wilting and selection for root depth in tubes, and (ii) genetic makeup of the population; for instance, drought tolerance has been introgressed from the wild species resulting in the appearance of undesirable and agronomically segregating populations. EGS will be highly desirable only when F_2s are from agronomically superior elite lines. In the case of soybean, EGS for pods per plant proved to be the most effective for enhancing the yield (Singh and Sharma, 2016). AGS holds considerable promise for traits that are best expressed in homozygous progeny.

While EGS and AGS have been earlier practised based on phenotypic selection, diagnostic markers are now being integrated for traits, for both EGS and AGS. A high-throughput genotyping project (HTPG; http://cegsb.icrisat.org/high-throughput-genotyping-project-htpg/), an initiative led by ICRISAT in collaboration with the International Maize and Wheat Improvement Center (CIMMYT) and the International Rice Research Institute (IRRI) and funded by the Bill & Melinda Gates Foundation, is expected to accelerate the deployment of EGS/AGS. It is important to note that the HTPG project has made it possible to screen populations at a 2017 cost of US$ 1.5 per sample for 10 SNP markers including DNA extraction. While several institutes such as CIMMYT, ICRISAT and IRRI have started to deploy EGS at a large scale in maize, rice, wheat, and groundnut, the genomics community needs to work on developing additional diagnostic markers for more traits especially nutrition traits across all legume crops.

Genomic selection

Genomic selection (GS), proposed by Meuwissen *et al.* (2001), is a promising breeding approach for simultaneous improvement of complex traits, especially those with low heritability. GS uses genomic signatures or dense marker profiles of individuals as well as parents for predicting the breeding values. The use of GS for accelerating genetic gains, based on genomic-estimated breeding values predicted using genome-wide dense markers, has been deployed extensively in dairy cattle (Van Raden *et al.*, 2009). García-Ruiz *et al.* (2016) reported a positive impact of GS on cattle breeding through drastic reduction of generation interval and increased selection intensity for low heritable traits. Initially, computer simulations and parametric and non-parametric statistical models were used on maize and wheat datasets to study the prediction accuracies in real plant breeding scenarios (Bernardo and Yu, 2007; de los Campos *et al.*, 2009; Crossa *et al.*, 2010, 2011). Promising results in major cereals provided a kick start for deploying GS in a few legume crops, such as pea, soybean, chickpea, groundnut, and pigeonpea (Varshney, 2016). GS in crop plants including legumes has been extensively reviewed recently elsewhere (Crossa *et al.*, 2017).

In GS, in brief, a training population (genotyped with genome wide markers and extensively phenotyped over years and in several locations) is trained with appropriate models to estimate the genomic-estimated breeding values in a breeding population (genotyped with genome wide markers) and validated in a validation population. Hickey *et al.* (2017) compared both plant and animal breeding approaches to make a case for bringing the two together through the application of GS. In recent years, the GS approach has been deployed in different types of populations, for instance bi-parental, multi-parental (Beyene *et al.*, 2015), and synthetic populations (Schopp *et al.*, 2017) and diverse panel of inbred lines, which basically differ in the pedigree, number of founders used to develop the population, linkage disequilibrium decay, and population structure.

The genetic advance achieved through selection depends on the total variation (σ^2), the repeatability of the trait (h^2)

and the selection pressure (S) imposed. The selection pressure implies the proportion of the population selected. Even if the repeatability is high the genetic advance (genetic gain, R) would be small without a large genetic variation. With selection, the genetic variation and consequently the repeatability and thus the advance from one to the next generation decline while the mean value of the trait increases (or decreases, depending on the trait).

Genotyping platforms, training populations and statistical models

Although the availability of genome wide markers and cost of genotyping were two major factors that restricted implementation of GS in crop breeding, they are no longer constraints as most of the legume communities are now equipped with genome sequence information as well as high density SNP arrays. For instance, high density SNP arrays have become available in case of chickpea (Roorkiwal *et al.*, 2017), groundnut (Pandey *et al.*, 2017*a*), and pigeonpea (Saxena *et al.*, 2017 and unpublished). In addition, the efficiency and accuracy with which superior lines can be predicted also depend on the size of the reference population (Jannink *et al.*, 2010; Lorenz *et al.*, 2011). The genetic relatedness or population structure (Saatchi *et al.*, 2011; Riedelsheimer *et al.*, 2013; Wray *et al.*, 2013) may result in overestimating the heritability of the traits (Price *et al.*, 2010; Visscher *et al.*, 2012; Wray *et al.*, 2013). The population structure of the training population can be determined with greater accuracy using genome wide SNPs compared with the simple sequence repeats and SNP arrays (Isidro *et al.*, 2015). Accuracy of estimating breeding values is important in GS. For instance, Jarquín *et al.* (2014) obtained a high prediction accuracy of 0.64 by deploying GS for improving yield and agronomic traits using genotyping-by-sequencing in a breeding program. In addition, GS for yield ridge regression best linear unbiased prediction (BLUP) coupled with fivefold cross-validations and marker preselection based on haplotype blocks is an interesting option for a cost-efficient implementation of genomic selection for grain yield in soybean breeding (Ma *et al.*, 2016). In the case of pea, using GS, Tayeh *et al.* (2015*c*) reported mean cross-environment prediction accuracies of 0.83 for thousand-seed weight, 0.68 for number of seeds per plant, and 0.65 for date of flowering. Population structure did not impact the prediction accuracy, and modelling genotype by environment by management (G×E×M) indicated improved prediction efficiency in chickpea (Roorkiwal *et al.*, 2016). Further, Roorkiwal *et al.* (2016) used statistical models such as RR-BLUP, Kinship GAUSS, Bayes Cπ, Bayes B, Baysian LASSO, and random forest regression and reported high prediction accuracies for days to maturity, days to flowering, and seed dry weight. The development and deployment of improved and more precise statistical models will eventually enhance further the prediction accuracy leading to enhanced GS efficiency in legume crops. Development of models that use deep machine-learning methods and multi-trait and multi-environment information is essential to realize the potential of GS in legume breeding and to enhance the prediction accuracies (Crossa *et al.*, 2017).

Selection intensity and generation interval

The selection differential (S) is defined as the difference of base population mean and the mean of the selected parents

$$R = h^2 S$$

where h^2 is the narrow-sense heritability (Arruda *et al.*, 2016).

The selection intensity depends on how different the selected parents are from the overall population average. The closer the selected parents to the population average, the smaller the selection intensity and vice versa. The impact of GS and generation intervals in cattle breeding was first systematically studied by de Roos *et al.* (2010). Recently, García-Ruiz *et al.* (2016) reported that decreased generation interval and increased selection intensity for low heritable traits is as a result of the positive impact of GS on the US cattle industry. Genomic selection in combination with a reduced generation interval may double the rate of genetic gain while keeping the rate of inbreeding per generation constant.

Rapid cycling

The usefulness of rapid cycling genomic selection (RCGS) was first reported in a bi-parental mapping population derived from B73 and Mo17. Massman *et al.* (2013) reported that RCGS had a superior response for stover yield, as well as stover and grain yield indices that were 14–50% higher than those of MARS. Recently, in tropical maize, by employing RCGS on eight bi-parental populations evaluated under drought stress environments, Beyene *et al.* (2015) reported an average gain of 0.086 ton ha^{-1} per cycle, and hybrids derived from cycle 3 produced 7.3% (0.176 ton ha^{-1}) higher grain yield than those from cycle 0 and conventional pedigree breeding methods. Further, Zhang *et al.* (2017) using RCGS in a tropical maize multi-parental population reported a genetic gain for grain yield from cycle 1 to cycle 4 reached 0.225 ton ha^{-1} per cycle, which is equivalent to 0.100 ton ha^{-1} year^{-1} over a 4.5 year breeding period from the initial cross to the last cycle. While similar rates of gain have not been reported in legumes, recent reports on over three generations per year in traditional breeding for pigeonpea (Saxena *et al.*, 2017) offer new opportunities to apply RCGS to accelerate rates of genetic gain in grain legumes.

Genome editing

The sequencing-based trait dissection and gene discovery are enabling the functional characterization of genes. An alternative approach for modifying targeted genomic regions, genome editing, may be better suited for improving the deficiency of one or two traits within popular varieties that have suitable production and market traits. Enhancing the performance of market-preferred varieties offers the advantage of higher productivity and higher replacement rates by farmers (Dar *et al.*, 2013). Genome editing harnesses the strength of programmable nucleases in cutting and pasting the specific genetic information in living cells (Kim, 2016). The availability of more and more information on functionality of genes or haplotypes for economically important traits will facilitate

modification of multiple SNPs through genome editing without leading to a deterioration in the original behavior of a popular cultivar. In several of the legume crop species, with genetic barriers such as ploidy differences, the exchange of genetic material through natural process is restricted and therefore the huge genetic variation lying within crop's wild relatives remains untapped and unutilized. In this context, if the function of the specific genome variations in wild relatives can be assigned, genome editing can enable targeted editing of a popular cultivar without fear of linkage drag.

The recently developed targeted genome-editing technologies such as zinc finger nucleases, RNA-guided endonucleases, transcription-activator-like effector nucleases, and CRISPR (cluster of regularly interspaced palindromic repeats) have undergone tremendous improvement over the past couple of years (Wang *et al.*, 2017). Of the several approaches, CRISPR received wider acceptance among researchers due to its huge potential role in crop improvement in coming years (Kim, 2016). This technology has already been optimized in three model legume crops, soybean (Sun *et al.*, 2015; Li *et al.*, 2015), *Lotus japonicas* (Wang *et al.*, 2016) and *Medicago truncatula* (Meng *et al.*, 2017). The efficiency of genome editing using various endogenous and exogenous RNA polymerase III promoters has been compared (Sun *et al.*, 2015; Du *et al.*, 2016) and in soybean the Cas9–single guide RNA together with donor DNA fragments was successfully transformed into soybean using the particle bombardment method (Li *et al.*, 2015). *Medicago* and *Lotus*, having smaller diploid genomes, are the model legume crops for conducting research in several areas including symbiotic nitrogen fixation. The efficacy of the CRISPR system has been assessed in these two crops by modifying the multiple genes related to symbiotic nitrogen fixation (Michno *et al.*, 2015; Wang *et al.*, 2016; Meng *et al.*, 2017). Recently, Benson Hill Biosystems, an agricultural technology company based in the UK, launched a commercial service for genome editing for crop improvement (https://www.prnewswire.com/news/benson-hill-biosystems). These developments will further accelerate the deployment of this promising technology in improving desired traits in legume crops.

Genome editing is considered to be a safe technology for developing improved crop plants by US regulators, who indicated that genome editing products developed using oligonucleotide-directed mutagenesis or site-directed nucleases should not be subjected to regulation as these technologies are similar to mutagenesis (see Sprink *et al.*, 2016). There are multiple examples of development of improved plant varieties using genome editing technology and 37 such examples in Arabidopsis, tobacco, maize, rice, wheat, canola, soybean, camelina, tomato, and cucumber have been well documented recently (see Kamburova *et al.*, 2017). Of these successful efforts, several of these products have been approved in different countries for cultivation, such as herbicide-tolerant SU Canola (Cibus 5715) in Canada in 2014 (https://cen.acs.org/articles/95/i24/CRISPR-new-toolbox-better-crops.html), browning-resistant Arctic apples in the USA and Canada in 2015 (Smyth, 2017), and less-acrylamide-producing potatoes for chip processing in Canada in 2016 (Smyth, 2017), while tomato with a greater number of fruits and soybean with high oleic acid are near to reaching approval. Expected products in Canada and the USA in the coming years include glyphosate-tolerant flax in 2019. Products expected for 2020 include late-blight-resistant potato, herbicide-tolerant rice, and starchy or 'waxy' corn.

Improving the operational efficiency in breeding programs

Improvement in operational efficiency in the breeding programs will help in conducting precise and well-documented research experiments. Currently, the majority of breeding programs still record data on paper. The digitalization of breeding programs and improved operational efficiency will reduce the chance of error, which in turn will allow breeders to assess the potential of improved breeding procedures (Varshney *et al.*, 2016). In this context, digitalization, automation, and mechanization in breeding procedures need to be adopted during the breeding process. More emphasis is required on uniform ontology, digitalized pedigree information, appropriate experimental design, barcoding of breeding material, digital data recording in the field, data management systems, and quality control. Integrated Breeding Platform (http://www.integratedbreeding.net) is one such initiative that is helping breeding programs to modernize and improving their breeding efficiency. For instance, the Breeding Management System of Integrated Breeding Platform is being used extensively at ICRISAT and its partner breeding programs. Similarly, B4R (http://bbi.irri.org/home) is a program for managing breeding data that has been developed and is being used by IRRI. The volume of data generated throughout the breeding process has increased significantly due to the involvement of high throughput genotyping and phenotyping technologies. Data volume now poses a significant challenge in compilation, processing, and interpretation. Available tools engaged today may no longer be suitable for handling high volume data in the future, thereby necessitating development of improved tools/software that can drive science-based breeding at a faster pace with user-friendly tools and databases. The Genomic Open-source Breeding Informatics Initiative is one such endeavor (http://gobiiproject.org/) targeting deployment of high density genotyping information in public sector breeding programs for more precise selection to achieve higher genetic gains. Further, the Excellence in Breeding (EiB; http://excellenceinbreeding.org/) platform came into existence very recently to bring all the components of CGIAR crop improvement under a single platform to focus on better integration and modernizing of breeding programs in developing countries. The above efforts will help in improving the efficiency and resilience of agricultural systems to achieve more sustainable food production for increased profitability of farming, greater resilience and nutrition of global agrifood systems.

Seed systems

Once superior varieties are developed, they should reach farmers' fields as early as possible such that the average age of the varieties in the farmers' fields are not more than 10 years.

Cultivar replacement is indeed one of the basic undertakings in the EiB platform. In the past, however, most released varieties of legumes have not enjoyed high rates of adoption (Atlin *et al.*, 2017). One reason could be low performance of new varieties under farmers' field management and conditions. The second reason is limited multi-location testing of public sector varieties due to limited funds. As a result, seed companies do not know the level of superiority of a new variety for a certain production ecology and are reluctant to invest in producing and promoting a new seed product.

Our experience from the Tropical Legumes project (http://tropicallegumes.icrisat.org/) shows that adoption of new varieties requires promotion just like with new products in the manufacturing sector. As compared with hybrid maize, where the private sector invests heavily in thousands of demonstration plots to create awareness and popularize new varieties, only very limited demonstration plots of new legume varieties and accompanying agronomic practices are conducted. Farmers' awareness of improved varieties has been reported to be strongly correlated with higher adoption rates for pigeonpea in Tanzania (Amare *et al.*, 2012) and for chickpea in Ethiopia (Abate *et al.*, 2012).

However, unlike the private manufacturing sector where a new product is promoted and new demand can be met quickly, seed is the vehicle through which genetic gains are realized in farmers' fields, especially with small-scale farmers in the case of legumes. Production of seed takes time through cycles of breeding, foundation and certified seed, each stage taking at least one cropping season. Compared with cereals and canola, legumes generally have a lower seed multiplication rate, thereby requiring extra space, labor, time, effort, and more generations to produce sufficient quantities of certified seed. This increases the cost of seed production to seed producers, which must be paid for by farmers, many of whom find the costs prohibitive compared with non-authentic sources. In addition, virtually all legumes are self-pollinated (pigeonpea is an exception) and farmers usually recycle their own seeds. Therefore, the incentive to develop a business around seed production in most grain legumes is low.

Some legumes have relatively large seed rate requirements, sometimes more than 100 kg ha^{-1}, meaning farmers have to buy large quantities to plant a relatively smaller area compared with cereals. This has additional implications in terms of requirement of seed storage space and packaging material, further increasing the cost of seed. In addition, transportation of the seed to remote areas is both cumbersome and expensive due to the bulky nature of grain legumes. Legume seeds also suffer from loss of germination faster than cereals, especially in hot, humid environments. Seed producers and traders must meet these challenges by investing in proper storage, thereby increasing the willingness of farmers to buy seed regularly off-farm with an assurance of better quality than farm-save seed (Sperling and McGuire, 2010). Besides these challenges, legumes are highly self-pollinated and it is assumed that farmers save their own seed for several seasons and do not need to buy new seed each season, which makes it difficult for seed companies to predict demand for seed. It was, however, reported in 2016 that a significant fraction of legume farmers (64.4%) actually do buy 'seed' or rather grain from local markets (McGuire and Sperling, 2016). However, due to high cost, limited availability, and access, farmers do not buy legume seed from the formal seed sector (seed companies and agrodealers).

Innovative approaches are therefore necessary to tackle the challenge of legume seed supply to ensure availability, accessibility, affordability, and sustainability for the varieties to replace older varieties. This requires an integrated approach to seed production and delivery systems that includes formal public–private sector partnerships and a variety of farmer-based seed production and supply initiatives (Siddique *et al.*, 2012; Johansen and Siddique 2017). One of the approaches used to increase total seed production and availability, particularly of early generation seed, is through licensing of public varieties for decentralized production. An example of this is in seed production and distribution of improved varieties of common bean in Ethiopia. Well-established innovation platforms along the bean value chain contributed to sustaining a decentralized seed production system (Rubyogo *et al.*, 2010). Seed certification, normally by public agencies, is an important quality control step but it also increases the cost of seed significantly. Kenya and Zambia are examples of countries where certification is licensed to private institutions and individuals. Quality declared seed (QDS) is an approach to producing seed by competent seed producers and suppliers that accommodates the diversity of farming systems, particularly in the more difficult areas where highly organized seed systems do not function well (Plant Production and Protection Division, 2006). QDS standards and monitoring procedures are slightly less demanding, allowing for less expensive seed and more decentralized producers. The quality and performance of QDS seed on farmers' fields is comparable—but the seed is less expensive (Granqvist, 2006).

Innovative approaches are also needed for increasing availability, supply and access to high quality seed of improved varieties (e.g. through small packs, financial support, better coordination with extension or development programs). A small seed pack approach was pioneered by Pan-African Bean Research Alliance two decades ago to encourage informal varietal diffusion and adoption of new varieties (Grisley, 1993) and gained popularity as an efficient and cost effective means of reaching more farmers with bean seed of improved varieties (Maereka and Rubyogo, 2015). It has been adopted and popularized in the Tropical Legumes II/III project (Monyo and Varshney 2016), involving national programs and the private sector (Rubyogo *et al.*, 2016). Demand creation for quality seed includes working with off-takers like grain exporters, demonstration plots of better varieties, post-harvest handling, and market linkages. Good examples of the role of off-takers can be cited with the Raphael Group Ltd in southern Tanzania that has promoted the adoption of the 'Uyole 03' sugar bean variety and ACOS Ltd in Ethiopia that has promoted market-orientated production of various varieties of white pea bean and kabuli chickpea. Reaching farmers 'at the last mile' by bundling seed with other products, piggybacking on existing product supply channels such as fertilizers and pesticides, and strengthening community seed

production approaches are all critically important areas for innovation.

Agronomy packages

Improved seeds alone do not guarantee improved yields. Soil fertility is often a big constraint for smallholder farmers in the semi-arid tropics (Kamanga *et al.*, 2013). Deployment of improved varieties should be accompanied by integrated crop management practices, underscoring the prevailing cropping practices. In fact, consideration of agronomic practices should be considered early in the development of product profiles so that breeding populations are developed accordingly and selection pressure integrates prevailing agronomic practices (e.g. soil fertility, crop density). Combining organic and mineral fertilizer is a sound management principle for smallholder farmers when combined with techniques such as crop rotations to improve soil fertility and nutrient availability. Two examples clearly illustrate the integration of integrated soil fertility management principles: (i) dual purpose grain legume–maize rotations with P fertilizer targeted at the legume phase and N fertilizer targeted at the cereal phase in the moist savanna agro-ecozone (Sanginga *et al.*, 2003), and (ii) micro-dose fertilizer applications in legume–sorghum or legume–millet rotations with retention of crop residues and water harvesting techniques in semi-arid agro-ecozones (Bationo *et al.*, 1998). In trials in West Africa, control of early season insect pests and diseases increased crop vigor, and greater yields have been reported in legumes such as cowpea (Tekwa *et al.*, 2010) and groundnut (Yakubu *et al.*, 2011) with ApronStar, a seed treatment fungicide–insecticide mixture for controlling downy mildew, damping-off diseases, as well as for protection of seeds and seedlings against early season insect pests and soil-borne diseases. Therefore, there is a need in the future to breed cultivars in a system perspective, i.e. to breed crops considering elements of the agro-ecosystem in which these will be deployed.

Understanding abiotic and biotic stresses is important in designing breeding programs. For example, planting groundnuts early in the season when aphid populations are still low coupled with maintaining a good plant density can reduce aphids that are the vector for rosette disease, which in turn reduces disease incidence (Waliyar *et al.*, 2007). This in turn would ensure optimum yield and that varieties developed for other traits, such as oil quality, early maturity, drought tolerance, and foliar disease resistance, are not lost due to rosette disease. Sowing time is also particularly important in pigeonpea, where there are different maturity groups. Early maturing varieties can compete with the cereals in intercropping systems but would be the best suited as a sole crop in places prone to short rainfall periods. Medium maturing varieties are planted after the main cereals and remain in the field when the main cereal is harvested. Similarly, proper timing is critical in chickpea to ensure the crop does not suffer from terminal drought (if planted too late) or seedling fungal diseases if planted too early during the rainy period.

Integrated and coordinated approach

Legumes are nutrient-rich crops with high levels of protein and other important nutritional components that offer great support in fighting malnutrition across the world. Genetic improvement for legumes needs to accommodate traditional yield-improvement priorities alongside nutritional characteristics. A single technology or process cannot be singled out to achieve higher yields in farmers' fields with high consistency (Siddique *et al* 2012; Johansen and Siddique, 2017). Participatory feedback from different stakeholders along commodity value chains is required to develop appropriate product profiles so farmers can be more productive and profitable by accessing markets with surplus production. In this context, a holistic approach is required to realize higher genetic gains in less time and with more precision in the legume crops. We have proposed this strategy in Fig. 1.

Our crop improvement programs, which include not just breeding but all other disciplines, need to start with demand and feedback from the stakeholders including farmers, consumers, and markets. Based on these demands, crop improvement programs prioritize traits (including nutrition) and define a product profile of the varieties to be developed. Subsequently, genebank, pre-breeding and trait discovery groups together with breeders and biometricians formulate a list of suitable genotypes with desired traits, and high breeding values are identified after a comprehensive genome characterization using sequencing and genotyping platforms and phenotypic characterization in target environments. In parallel, we need to have diagnostic markers with higher prediction accuracy and candidate genes with causal effect for a given trait. For trait discovery, instead of using a traditional mapping approach, it is possible now to use sequencing-based trait mapping approaches such as QTL-Seq, Bulk-Seq and Indel-Seq (Singh *et al.*, 2016, 2017; Pandey *et al.*, 2017*b*). Similarly, recent advances in functional genomics such as gene expression atlases (Pazhamala *et al.*, 2017) and use of near-isogenic lines for transcriptomics approaches can identify the candidate genes for the target traits.

In order to increase selection intensity, it is essential to increase the number of crosses and the population of each cross in public sector breeding programs. In our opinion, each breeding program should make at least 100 crosses every year and each cross should have at least 500–1000 F_2s using the most appropriate parental combinations. Of course, the size of the population would also need to be adjusted to the genetics of the target trait. Early generation screening with the diagnostic markers or candidate genes for must-have traits can dramatically reduce early generation populations as a 'forward breeding' process. After selecting a small numbers of lines, genomic prediction can be undertaken and selected lines with higher breeding values can be targeted for testing in target population of environments. Subsequently, the selected lines can go to a national program for further multi-location and multi-year testing for possible release of improved varieties or can be included in the pool of parental selections in the new crossing schemes. We believe that such an approach will accelerate the development of superior grain legume varieties.

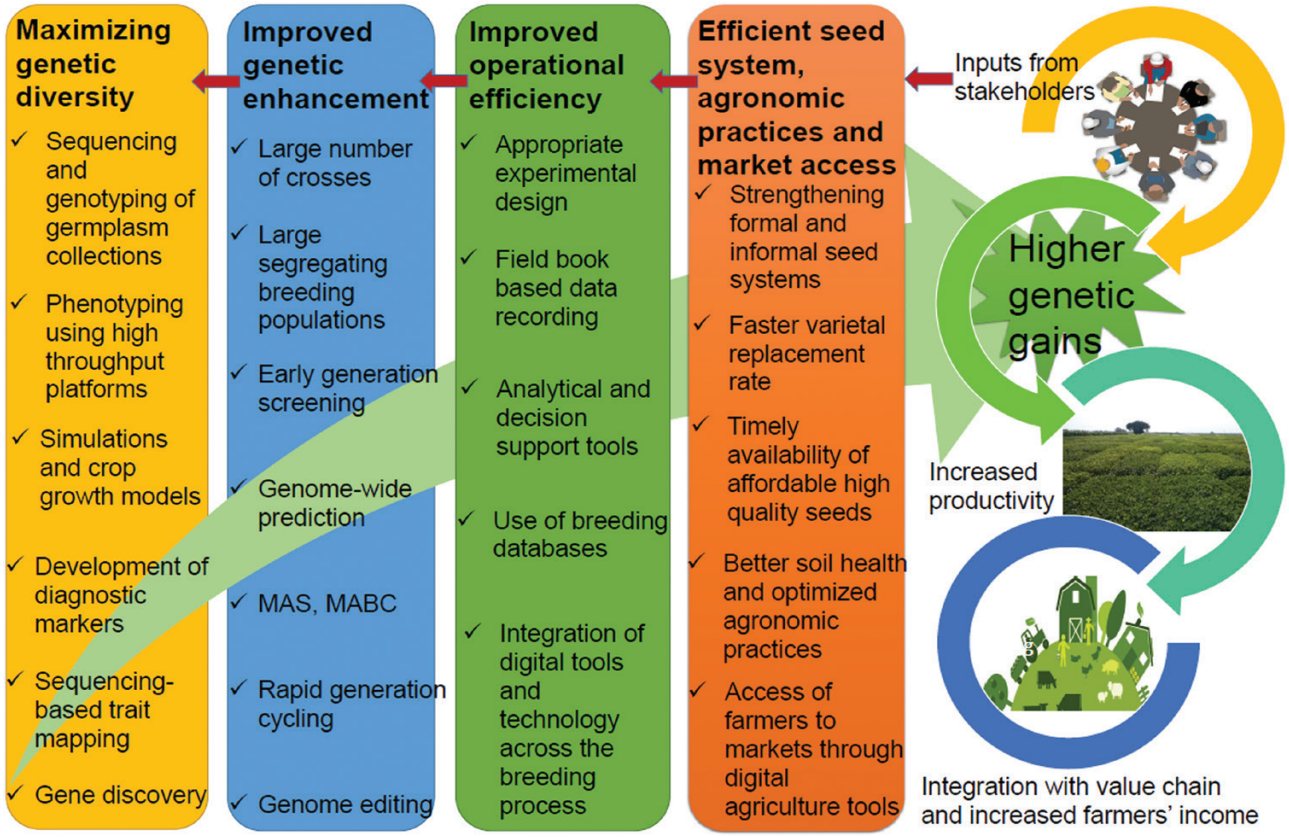

Fig. 1. Strategy for strengthening the breeding process and adopting improved technologies for achieving higher genetic gains in farmers' field. Low-cost sequencing and genotyping technology will eventually help in molecular characterization of entire diverse germplasms. High density genotyping data together with phenotyping data on entire germplasm will help filter the most useful germplasm lines for use in breeding programs. Low-cost sequencing and genotyping data will also facilitate dissection of multiple traits even in complex genetic populations and faster and precise gene discovery. Improved and modern approaches need to be integrated in trait mapping and trait improvement pipeline in addition to adoption of improved breeding operational efficiency. Higher genetic gains achieved with improvement of desired traits, key to major stakeholders, will eventually help not only in attaining higher productivity but also in increasing the profitability of farming.

In parallel, it is also possible to continue to undertake MAS or MABC in the ruling varieties for introgressing major genes/QTLs that have become deficient during their long-term cultivation in farmers' fields. While undertaking GAB approaches, it is also essential that we improve our operational efficiency with appropriate analytical and decision support tools. For instance, appropriate experimental design for testing a segregating population/germplasm collection is very important. Similarly, having phenotypic data for different breeding populations/germplasm collections in databases and using these databases for planning a new set of experiments is critical. Deployment of breeding databases such as BMS and B4R in breeding programs needs to be accelerated. Use of tablets and mobile-based 'Field Book' programs will reduce error and turnaround time for data-driven breeding decisions. While using the GAB strategies, EGS, GS, MABC or MAS, it is important that breeding programs use the appropriate decision support tools to select the superior lines instead of using spreadsheets or stand-alone programs. All these efforts and good breeding practices together offer operational efficiency in the breeding programs.

While use of GAB approaches together with operational efficiency methods can help in developing better varieties faster, the full genetic potential of these varieties can only be realized once they have been adopted and grown in farmers' fields. It is essential to work with government agencies together with informal seed system actors in different developing countries to accelerate varietal replacement. We need to start using 'digital seed road maps' (http://seedsystems.icrisat.org/) that can help different stakeholders of the seed value chain to assess the need and make different kinds of seeds (breeders' seed, foundation seeds, certified/truthfully labeled seeds) available to farmers. Finally, digital agriculture tools, for example, sowing apps (http://www.icrisat.org/tag/sowing-app/), plantix (http://www.icrisat.org/tag/plantix/), should be deployed to provide increased access to equitable markets by farmers to increase profitability.

We believe that use of such a holistic approach will not just deliver higher genetic gains in research plots of scientists but also in farmers' field. By using the entire approach from science of discovery to science of delivery, the scientific community will be able to contribute to both enhancing crop productivity and increasing farm profitability. Furthermore, it will also help to make cheap raw material available to industry, and finally, availability of

affordable nutritious food to the poorest of the poor in society.

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