

## Next generation breeding in pulses: Present status and future directions

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**Abstract:** Human population growth in combination with changing patterns of global food consumption under climate change is posing formidable challenge to attaining sustainable global food security. Besides being economically viable sources of plant based protein for human consumption, pulses are also beneficial for the environment owing to their inherent capacity of nitrogen fixation. Hence, further development of pulses has become imperative in the vigorously transitional global scenario where flourishing anthropogenic activities are triggering irreplaceable depletion of natural resources. During past years, considerable attention has been given on the use of next generation sequencing for enriching the genomic resources in pulse crops including high-throughput DNA markers, candidate gene(s) and QTLs for predicting plant phenotypes, and whole genome sequences. With refinements in DNA sequencing technologies and computational analytical tools, the rapidly grown numbers of sequenced pulse genomes offer novel insights on crop evolution and breeding history. Integration of new-generation genomic and phenomic tools with generation acceleration procedures like genomic selection and speed breeding could greatly accelerate progress in pulses genetic improvement. The present review discusses current status and future scope of using next-generation breeding approaches in pulses that will cause not only an increase in the rate of developing climate-resilient superior cultivars but also help to reach to goal of global food security.

**Keywords:** Pulses, DNA marker, genome, gene, QTL, haplotype, genetic gain


### INTRODUCTION

Pulses, defined as legumes that yield dry seed for human use, are agronomically valuable plants, both in the food system and in the field. Grain legumes used for human consumption especially pulses have witnessed a reinvigoration in the last decade as a way to tackle agricultural issues all around the world (Bohra et al. 2015, Varshney et al. 2015). Pulses are among the best plant-based sources of dietary protein and other nutrients such as iron, zinc, magnesium and of dietary fibre (Bohra et al. 2014, Kouris-Blazos and Belski 2016, Maphosa and Jideani 2017). A plant-based agrarian diet which is rich in fruit or legume fibre assists to enhance microbial diversity and exerts a positively influence in the levels of short-chain fatty acids, which are important for maintaining a good intestinal health (Simpson and Campbell 2015). Apart from providing nutritional health benefits, legumes also augment the soil's fertility owing to their characteristic feature of symbiotic



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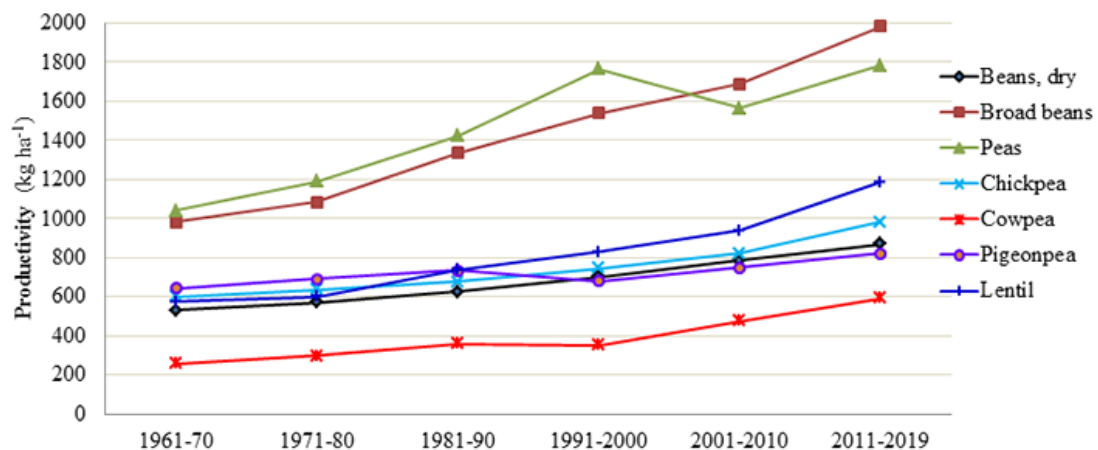
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nitrogen fixation with the help of *Rhizobium* spp. in their root nodules (Graham and Vance 2003, Stagnari et al. 2017).

Pulses provide a sustainable option by plummeting the demand of chemical fertilization and several high protein containing pulses can be explored as a substitute of meat around the world (Maphosa and Jideani 2017). Food and nutritional security is a global issue, as indicated by nearly 800 million people suffering from chronic malnutrition worldwide (<http://faostat.fao.org/>). With the world's population expected to reach 9-10 billion people, the growing quest for sustainable food systems caused a paradigm shift in nutritious global diets (Godfray et al. 2010, Massawe et al. 2016, Varshney et al. 2021). Land-use alterations, which are one of the key forces affecting soil sustainability and biodiversity, will be exacerbated by global warming and anthropogenic campaign especially in agriculture (Houghton et al. 2012). In view of above, economically nutritious foods need to be introduced or created in order to eliminate all types of hunger and malnutrition, as stated by the United Nations (UN) Sustainable Development Goals (United Nations 2015). Pulses are harvested primarily for their dry grains resulting in a total of 11 pulse crops (<http://faostat.fao.org/>) (Cheng et al. 2019).

Leguminosae or Fabaceae, comprising 750 genera and 20,000 species (Polhill 1981), constitutes the third largest family of flowering plants after the orchid (Orchidaceae) and sunflower (Asteraceae) families (Walters 1960). Globally, a total of 93.23 million tons (m t) of pulses are harvested from 91.77 million (m) ha of land, with a productivity of 1016 kg ha<sup>-1</sup> (<http://faostat.fao.org/>). In total, 92.82 % of the global pulse production (86.53 m t) with an acreage of 91.58% (84.05 million ha) is shared by major pulse crops, viz. dry beans (mainly common bean), chickpea, dry peas (pea), cowpea, pigeonpea, lentil and faba bean with cumulative average productivity of 1030 kg ha<sup>-1</sup> (<http://faostat.fao.org/>).

Pulse crops are broadly categorized into two distinct groups based on their adaptability to tropical and temperate agro-climatic conditions, viz. 1) warm season crops (common bean, pigeonpea and cowpea), and 2) cool season crops (pea, chickpea, lentil and faba bean) (Cannon et al. 2009, Young et al. 2003, Zhu et al. 2005). Owing to domestication early in pre-history (c. 11,000 years ago), chickpea, pea and lentil are not only considered among the founder grain crops but also paved the way for establishment of modern agriculture (Zohary and Hopf 2000). Due to their high agricultural value, extensive research has been conducted on pulse improvement through conventional breeding, resulting in the development and release of several high-yielding varieties (Singh 2005, Saxena 2008, Pérez de la Vega et al. 2011, Torres et al. 2011, Gaur et al. 2012), as well as an increase in the global area under pulses from 64 to 91.77 million hectares over the last 60 years (<http://faostat.fao.org/>). However, productivity aspects of the above mentioned seven major pulse crops is still lacking and needs to be addressed in order to meet the growing protein calorie demand of the world (Figure 1). Factors like cultivation in risk prone environments, erratic rainfall, prolonged dry spells, vulnerability to variety of pest and disease limit pulse production and make them lag behind the other crops especially cereals (Borlaug 1973, Varshney et al. 2011, Varshney et al. 2013a). Concerted efforts are required to overcome the biotic and abiotic barriers hampering the yield of pulse crops (Table 1). This herculean task can be achieved by dynamic fusion of genomic tools with conventional breeding methods to augment the crop improvement progress.



**Figure 1.** Global trends in productivity of seven major pulse crops. The Figure illustrates trends in productivity of major pulse crops witnessed over last six decades.

**Table 1.** Genome organization, productions areas, major constraints and anti-nutritional factors in key pulse crops

Pulse crop	Scientific name	Ploidy level/ chromosome count	Genome size [1C (Mbp)] <sup>a</sup>	Major growing areas	Production constraints		Major anti-nutritional factors
					Biotic	Abiotic	
Adzuki bean (Red bean)	<i>Vigna angu- laris</i>	2n = 22	490	Japan, Korean peninsula, and China, Nepal and Bhutan (Vaughan et al. 2005)	Brown stem rot ( <i>Phi- alophora gregata</i> ), phytophthora stem rot ( <i>Phytophthora vignae</i> f.sp. <i>adzukicola</i> ), wilt ( <i>Fusarium oxysporum</i> f. sp. <i>adzukico- la</i> ), and bruchids (Vaughan et al. 2005)	Low tempera- ture	Trypsin inhibitors, phylates and galacto- sides (Yoshida et al. 2010)
Bambara bean (Earth pea, ground- bean)	<i>Vigna sub- terranea</i>	2n = 22	882	Mali, Burkina Faso, Cameroon, Niger, Togo and the Demo- cratic Republic of Congo (Majola et al. 2021)	Cercospora leaf spot ( <i>Cercospora canescens</i> ), powdery mildew ( <i>Erysiphe polygani</i> ), Fusarium wilt ( <i>Fusarium oxysporum</i> f. sp. <i>voandzeia</i> ), rust ( <i>Puccinia graminis</i> f.sp. <i>tritici</i> ), leaf blight ( <i>Colletotrichum graminicola</i> ), cowpea aphid-borne mosaic virus (CABMV), black-eye cowpea mosaic virus (BECMV), peanut mottle potyvirus (PMV), cowpea mottle comovirus (CMV), cowpea yellow mo- saic virus (CYMV), cowpea weevil, bruchids, root-knot nematode ( <i>Meloidogyne javanica</i> ) (Majola et al. 2021)	Drought (Majola et al. 2021)	Condensed tannins (CTs), phytic acid phosphate (PAP), poly- phenol, and trypsin inhibitor (Unigwe et al. 2018)
Chickpea (Gram)	<i>Cicer arietini- um</i>	2n = 16	749.7	India, Australia, Pakistan, Myanmar, Turkey, Ethiopia, Iran, Mexico, Canada and USA ( <a href="http://faostat.fao.org/">http://faostat.fao.org/</a> )	Dry root rot ( <i>Rhizoctonia bataticola</i> ), Fusarium wilt ( <i>Fusarium oxysporum</i> f. sp. <i>ciceris</i> ), collar rot ( <i>Sclero- tium rolfsii</i> ), wet root rot ( <i>Rhizoctonia solani</i> ) and black root rot ( <i>Fusarium solani</i> ), Ascochyta blight ( <i>Ascochyta rabiei</i> ), Botrytis gray mold ( <i>Bot- rytis cinerea</i> ), Stemphyli- um blight ( <i>Stemphylium sarciniforme</i> ), Bacte- rial blight ( <i>Xanthomonas campestris</i> pv. <i>cassiae</i> ) Beet armyworm ( <i>Spodop- tera exigua</i> ), leafminer ( <i>Liriomyza cicerina</i> ), black aphid ( <i>Aphis craccivora</i> ), Pod borers ( <i>Helicoverpa armigera</i> ) (Nene et al. 2012)	Drought, heat and cold stress	Protease inhibitors, amylase inhibitors, phytolectins, polyphe- nols, and oligosac- charides
Common bean	<i>Phaseolus vulgaris</i>	2n = 22	588	Nigeria, Myanmar, India, Brazil, Niger, USA, Tanzania, Mex- ico, China, Uganda (FAOSTAT, 2019)	Web blight ( <i>Thanatepho- rus cucumeris</i> ), Cercospora leaf spot ( <i>Cercospora cru- enta</i> ), Anthracnose ( <i>Colle- totrichum lindemuthi- anum</i> ), rust ( <i>Uromyces appendiculatus</i> ), Angular leaf spot ( <i>Pseudocercos- pora griseola</i> ), Bacte- rial blight ( <i>Xanthomonas axonopodis</i> pv. <i>phaseoli</i> ), Halo blight ( <i>Pseudomonas syringae</i> pv. <i>phaseolicola</i> ), Bean common mosaic virus (BCMV), Aphids, Ar- myworms, Corn earworm , Cutworms, Leafminers, Mexican bean beetle, Stinkbugs (Degu et al. 2020, OECD 2016)	Low soil phosphorus (Beebe et al. 2014)	lectin, saponin, trypsin inhibitor and phytic acid (Rui et al. 2016)

Common vetch	<i>Vicia sativa</i>	2n = 12	2254	Turkey, Albania, Lebanon, India, China, North America, Spain, Australia (Ennenking and Tate 2006, Firincioglu et al. 2010)	Powdery mildew ( <i>Erysiphe pisi</i> ), pea aphid ( <i>Acyrtosiphon pisum</i> )	Frost (Chung et al. 2013)	beta cyano L alanine and its derivatives (Tate and Ennenking 2006)
Cowpea (black eye bean)	<i>Vigna unguiculata</i>	2n = 22	1176	Nigeria, Niger, Burkina Faso, Tanzania, Cameroon, Mali, Myanmar, Kenya, Mozambique, Democratic Republic of the Congo ( <a href="http://faostat.fao.org/">http://faostat.fao.org/</a> )	Leaf smut or false smut ( <i>Protomyces phaseoli</i> ), Bacterial blight ( <i>Xanthomonas campestris</i> pv <i>vignicola</i> ), bacterial pustule ( <i>Xanthomonas campestris</i> pv. <i>vigna-unguiculatae</i> ), cowpea aphid borne mosaic (CABMV), cucumber mosaic virus (CMV), cowpea mild mottle virus (CPMMV) and cowpea severe mosaic virus (CPSMV), Root-knot nematodes ( <i>Meloidogyne incognita</i> and <i>M. javanica</i> ), Koch ( <i>Aphis craccivora</i> ), bruchids ( <i>Callosobruchus maculatus</i> (Fabricius)), beetles ( <i>Ootheca mutabilis</i> ), maruca ( <i>Maruca vitrata</i> ), leafhoppers and foliage beetles, Parasitic weeds: <i>Striga gesnerioides</i> (Willd.) Vatke and <i>Alectra vogelii</i> Benth (Horn and Shimelis 2020)	Drought and heat stresses and poor soil fertility (Horn and Shimelis 2020)	Phytate, polphenols, enzyme inhibitors (trypsin, chymotrypsin) (Frias et al. 1995)
Faba bean (Broad bean, horsebean)	<i>Vicia faba</i>	2n = 12	13034	China, Europe, Northern Africa, West Asia and Australia ( <a href="http://faostat.fao.org/">http://faostat.fao.org/</a> )	Ascochyta blight ( <i>Ascochyta fabae</i> ), chocolate spot ( <i>Botrytis fabae</i> ) rust ( <i>Uromyces viciae-fabae</i> ), faba bean necrotic yellows virus (FBNYV), bean yellow mosaic virus (BYMV), black root rot ( <i>Fusarium solani</i> ), faba bean root rot ( <i>Aphanomyces euteiches</i> ), powdery mildew ( <i>Erysiphe pisi</i> var. <i>pisii</i> ), stem rot ( <i>Sclerotinia trifoliorum</i> ), black bean aphid ( <i>Aphis fabae</i> ), pea leaf weevil ( <i>Sitona lineatus</i> ), broad bean weevil ( <i>Bruchus rufimanus</i> ) (Karkanis et al. 2018)	Drought and heat stress (Katerji et al. 2011)	phenol and condensed tannin/proanthocyanidin (Kumar et al. 2015)
Grass pea	<i>Lathyrus sativus</i>	2n = 14	8330	India, Pakistan, Bangladesh, Nepal, Ethiopia (Vaz Patto et al. 2006)	Powdery mildew ( <i>Erysiphe pisi</i> ), downy mildew ( <i>Peronospora</i> spp), rust ( <i>Uromyces</i> spp.), blight ( <i>Mycosphaerella pinodes</i> ), orobanche, root knot nematode ( <i>Meloidogyne artiella</i> ) and cyst nematode ( <i>Heterodera ciceri</i> ) (Vaz Patto et al. 2006)	-	ODAP, nitriles (Vaz Patto and Rubiales 2014)
Hyacinth bean (Lablab)	<i>Lablab purpureus</i>	2n = 22	367 (Iwata et al. 2013)	India, Nepal, China, Bagladesh, Thailand, Australia and Eastern Africa (Maass et al. 2010)	Bruchid ( <i>Callosobruchus</i> spp.), pod borer ( <i>Adisura atkinsoni</i> ), anthracnose ( <i>Colletotrichum lindemuthianum</i> ), leaf spot ( <i>Cercospora dolichi</i> ) and powdery mildew ( <i>Leveillula taurica</i> )	Drought (Maass et al. 2010)	Tannins, phylates and trypsin inhibitors (Murphy and Colucci 1999)

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Lentil	<i>Lens culinaris</i>	2n = 14	4125.8	Canada, India, Turkey, Australia, Nepal, USA, China, Ethiopia, Bagladesh, Syrian Arab Republic ( <a href="http://faostat.fao.org/">http://faostat.fao.org/</a> )	Wilt ( <i>Fusarium oxysporum</i> f. sp. <i>lentis</i> ), Rust ( <i>Uromyces viciae-fabae</i> ), Ascochyta blight ( <i>Ascochyta fabae</i> f.sp. <i>lentis</i> ) Sitona weevil/bruchids, Aphids (Agrawal et al. 2013)	Drought, heat, cold and frost (Agrawal et al. 2013)	oligosaccharides, α-galactosides, trypsin inhibitors (Vidal-Valverde et al. 1994)
Lupins							
White	<i>Lupinus albus</i>	2n = 50	568.4	Australia, Poland, Ukraine ( <a href="http://faostat.fao.org/">http://faostat.fao.org/</a> )	Anthracnose ( <i>Colletotrichum lupini</i> ), Phomopsis stem blight ( <i>Diaporthe toxica</i> ), rust ( <i>Uromyces lupinicolus</i> ), gray mold ( <i>Botrytis cinerea</i> ),, cucumber mosaic virus (CMV), bean common mosaic virus (BYMV) (Clements et al. 2005)	Alkaline soil, frost	Alkaloids (Quinolizidine)
Yellow	<i>L. luteus</i>	2n = 52	980				
Narro-leafed	<i>L. angustifolius</i>	2n = 40	926.1				
Moth bean (Mat bean)	<i>Vigna acornitifolia</i>	2n = 22	1078				
Mungbean (Green gram)	<i>Vigna radiata</i>	2n = 22	588	India, Pakistan, China, Myanmar and Thailand (Isemura et al. 2012)	Leaf spot ( <i>Cercospora canesens</i> ), Powdery mildew ( <i>Erysiphe polygoni</i> ), anthracnose ( <i>Colletotrichum</i> spp.), mungbean yellow mosaic virus (MYMV), bruchids, white fly ( <i>Bemisia tabaci</i> ), thrips ( <i>Megalurothrips distalis</i> ) (Nair et al. 2019)	Alkaline soil, iron deficiency chlorosis (Prathet et al. 2012)	Trypsin inhibitors, haemagglutinins and phylates (Lambrides and Godwin 2007, Sompong et al. 2012)
Pigeonpea	<i>Cajanus cajan</i>	2n = 22	784	Asia, Eastern and Southern Africa, Latin America and Caribbean countries (Choudhary et al. 2011)	Fusarium wilt ( <i>Fusarium udum</i> ), sterility mosaic (Pigeonpea Sterility Mosaic Virus) and phytophthora blight ( <i>Phytophthora drechslei</i> sp. <i>cajani</i> ). Pod-bug ( <i>Calvigralla gibbosa</i> , <i>C. scutellarius</i> ), Pod borer ( <i>H. Armigera</i> ), leaf webbers, cutworms ( <i>Agratis ipsilon</i> and <i>Ochropleura flammata</i> ) and hairy caterpillars ( <i>Amsacta moorei</i> , <i>A. albistriga</i> and <i>Spilosoma obliqua</i> ) (Sharma et al. 2010)	Waterlogging, Drought, Low temperature, photoperiod, soil salinity, Al toxicity (Choudhary et al. 2011)	Protease inhibitors, amylase inhibitors, phytolectins, polyphenols, and oligosaccharides
Rice bean	<i>Vigna umbellata</i>	2n = 22	588	Eastern India, Myanmar, Thailand, Nepal and Southern China (Isemura et al. 2010)	Rust ( <i>Uromyces appendiculatus</i> ), cercospora leaf spot and web blight ( <i>Rhizoctonia solani</i> ) (Khadka and Acharya 2009)	-	Trypsin inhibitors and Phylates
Urd bean	<i>Vigna mungo</i>	2n = 22	588	India, Myanmar, Thailand, Philippines and Pakistan (Gupta et al. 2013a)	Leaf crinkle virus, MYMV and bruchids (Sharma et al. 2011)	Salinity and drought	Trypsin inhibitors and Phylates

\*Information used from <http://data.kew.org/cvalues/>.

Availability of economically viable next generation sequencing (NGS) technologies has led to remarkable advances in genomic resources of pulses including the whole genome sequencing (Varshney et al. 2013b, Varshney et al. 2017). NGS based protocols such as genotyping by sequencing (GBS) have been implemented for discovering and genotyping SNPs in large populations and germplasm collections (Bohra et al. 2020a, Jaganathan et al. 2020). Stupendous scope has been generated for forward genetics approaches like QTL mapping intending to decipher the gene(s)/QTLs underlying a particular phenotype. Further, exciting opportunities like marker development, trait mapping and molecular mapping have knocked on the door with the advent of application of genome-wide strategies like restriction-site associated DNA sequencing (RADSeq) in pulses (Yang et al. 2012, Yang et al. 2013a, Yang et al. 2013b). In consideration of the above, this review summarizes the production scenario and constraints, the available genomic resources and their downstream applications as well as prospects for genomics-assisted breeding (GAB) in selected pulse crops.

## **MOLECULAR MARKERS AND GENOTYPING ASSAYS IN PULSES**

Since its discovery in 1980s, the DNA marker system has revolutionized the science of plant breeding. The molecular marker technology evolved remarkably since the discovery of first molecular marker system restriction fragment length polymorphism (RFLP). Several classifications have been proposed to classify DNA based molecular markers. For instance, classification based on their generation of development (First generation vs 2<sup>nd</sup> generation vs 3<sup>rd</sup> generation vs 4<sup>th</sup> generation vs 5<sup>th</sup> generation), hybridization vs non-hybridization, array based vs non-array based, sequence based vs non-sequence based, low-throughput vs high-throughput vs ultra-high throughput, past vs present vs future molecular markers (Mir et al. 2013a, Mir and Varshney 2013, Gupta et al. 2013, Kumar et al. 2021). The recent advances in genomics tools and techniques have helped in the development of variety of molecular markers in crop plants including legume crops. Legume crops like chickpea, pigeonpea, groundnut, lentil, etc. were once considered as “orphan crops” due to lack of sufficient or availability of insufficient genomic resources in these legume crops. However, in the last decade, tremendous progress was made and large repertoire of molecular markers has been developed in these important legume crops. The success in development of these markers could be attributed to the evolution of new sequencing technologies that led to the reduction in cost of DNA sequencing (Varshney et al. 2019). A number of marker types that are available include thousands of SSRs, diversity arrays technology (DArT) markers, single nucleotide polymorphism (SNP) markers, different SNP platforms, micro-array based markers, NGS-based markers, genotyping by sequencing (GBS), InDel markers etc. The marker resources available in chickpea and pigeonpea have been recently summarized (see Bohra et al. 2020a, Roorkiwal et al. 2020). Briefly, using different approaches, thousands of SSR (>3000 in chickpea, >3000 in pigeonpea) have become available over the years and DArT markers with >15360 features each for chickpea, pigeonpea and groundnut have been also developed by ICRISAT in collaboration with DArT Pvt Ltd, Australia. In addition to thousands of SSR and DArT markers, tens of thousands of SNP markers have also been developed by ICRISAT in collaboration with national/international partner’s using variety of approaches.

The availability of marker resources has led to the development of different types of genotyping platforms/assays (including Kompetitive Allele Specific PCR (KASP) assays, GoldenGate assays, Vera-code assays, 60K SNP chips using Affymetrix SNP platform and Axiom SNP array with thousands of SNPs) by public and private research organization/companies for their research/commercial use. Most of these genotyping platforms developed are based on SNP markers, since SNP markers considered as markers of choice and are amenable to high-throughput genotyping. The genotyping platforms available can be classified into low-density (1-10 SNPs), medium-density (2-10 K SNPs) and high-density (>20K SNPs) genotyping platform (Varshney et al. 2019). The low density genotyping platforms can be used in early generation testing, marker-assisted selection (MAS) and testing hybridity. The medium and high-density genotyping platforms have been extensively used in genetic diversity studies, genomic selection (GS), background selection, mapping genes/QTLs in different crop plants through genome-wide association studies (GWAS) and linkage mapping/QTL mapping. ICRISAT in collaboration with Intertek company is extending low-density (10 SNPs) genotyping for many crop species, including chickpea, pigeonpea and groundnut for foreground selection in early generations of breeding program (Varshney 2016, Varshney et al. 2019). Among the high-density genotyping platforms, the most recent SNP Arrays with genome-wide SNPs tiled on these have been developed in crops like chickpea (Roorkiwal et al. 2018a), pigeonpea (Saxena et al. 2018), field pea (Tayeh et al. 2015a). Moderate density genotyping platforms including genotyping by sequencing (GBS) and restriction-site-associated sequencing (RAD-Seq) have been also used successfully in chickpea for genetic studies (Roorkiwal



et al. 2020). In summary, different molecular marker systems have been used in the study of genetic diversity, population structure, development of genetic maps and QTL mapping/ GWAS for key traits in pulse crops including chickpea, and pigeonpea. The genes/QTLs once identified are deployed in molecular breeding programs aimed at enhancing targeted traits in different crop plants through marker-assisted selection (MAS), marker-assisted recurrent selection (MARS) and GS. It is expected that the improved versions of next-generation crop varieties could be developed with enhanced quality traits, better yield and disease resistance (Varshney et al. 2021).

## MOLECULAR GENETIC MAPS

The molecular genetic maps refer to linear arrangement of molecular markers (loci) on the chromosome that has been obtained on the basis of estimates of recombination fractions among the markers. These molecular genetic maps once developed can be used for different purposes including i) understanding genome organization, ii) study of evolution of species, iii) study of synteny between related species, iv) study of chromosomes/genome rearrangement across taxa, and more importantly v) discovery of genes/QTL through QTL interval mapping. During recent advances in genomics tools and technologies including advances in development of marker technologies, molecular genetic maps have been developed in almost all plants of significant academic and economic interest, and the list of plants is growing regularly. In many pulses also, linkage maps have been developed. For instance, in pigeonpea, the first genetic map was developed in year 2011 with 239 SSR loci (Bohra et al. 2012). Following this, several other maps were developed for pigeonpea (Bohra et al. 2012). However, these maps were not dense due to availability of less number of markers and due to less polymorphism available in the pigeonpea. However, with the availability of high-density genotyping platforms, the marker densities of the genetic maps in pigeonpea have now improved dramatically. The first high-density genetic linkage map of pigeonpea was developed using SNP markers and this map possess 910 marker loci with an average inter marker distance of 1.11 cM (Saxena et al. 2012). In addition to individual genetic maps, consensus genetic maps have also been developed in pigeonpea by merging more than one map (Arora et al. 2017). The genetic map with highest density in pigeonpea was constructed with 6818 SNP loci that span 974 cM of the genome (Yadav et al. 2019). A list of high-density genetic maps available in pigeonpea is available elsewhere (Bohra et al. 2020b).

In chickpea, narrow genetic base and low level of intra-specific genetic polymorphism, development of good high-density genetic mapping remained a challenge (Verma et al. 2015). However, advent of NGS technologies led to the development of thousands of markers and availability of high-density marker linkage maps in chickpea. For instance, one of the most comprehensive genetic map having 1,291 markers on eight linkage groups spanning a total of 845.56 cM distance was developed at ICRISAT (Thudi et al. 2011). Varshney et al. (2014a) after screening thousands of markers, could find only few hundred polymorphic markers and ultimately were able to map 241 and 168 markers on ICCRIL03 and ICCRIL04 mapping populations respectively. However, with the availability of NGS tools and technologies like genotyping-by-sequencing genotyping platform, several high-density genetic maps could be developed. For instance, using GBS, a high-density genetic map having 1007 mapped markers spanned around 727.29 cM was developed (Jaganathan et al. 2015). Similarly, using GBS technology, one of the most saturated/densest intra-specific linkage maps reported with 3,363 loci at an average marker density 0.33 cM (Verma et al. 2015). Several other linkage maps and consensus maps using multiple genetic mapping have been developed in chickpea (Mallikarjuna et al. 2017). In addition, integrated physical, genetic and genome sequence map of chickpea has also been developed (Varshney et al. 2014b).

More recently, using NGS-based genome sequencing and resequencing technologies, millions of SNP markers have been discovered in chickpea and used in preparation of high-density SNP array. Using high-density SNP array platform “Axiom CicerSNP Array”, genetic maps for ICCRIL03 and ICCRIL04 populations were constructed. For ICCRIL03 mapping population, a total of 13679 SNPs were successfully placed on eight linkage groups covering 1033.67 cM (Roorkiwal et al. 2018a).

Like chickpea and pigeonpea, genetic linkage maps including medium-density and high-density linkage maps have been developed successfully in other legumes crops including groundnut and lentil. The development of these genetic linkage maps involved the use of a variety of molecular markers /genotyping platforms including SNP arrays.

### Mapping of genes: from QTL mapping to sequence-based trait mapping

Identification of genes/QTLs through QTL interval mapping is now a routine. However, several inherent disadvantages are associated with QTL mapping including i) Time and labor intensive, ii) less recombination events and hence less

diversity sampled, iii) use of controlled crosses whose development takes several years, iv) problem of polymorphism while developing linkage maps, etc. Some of these disadvantages have been overcome through the use of recently emerged association mapping (genome-wide association studies; GWAS) as an alternative to QTL mapping. The use of association mapping/GWAS has become very popular in the last two decades and now GWAS has been used in almost all crop plants for discovery of gene/QTLs of all important traits. In grain legume crops both mapping approaches including QTL mapping and GWAS have been used for gene discovery and several important genes/QTLs have been discovered for important targeted traits. For instance, using QTL interval mapping, genes/QTLs have been identified for drought/drought related traits and yield under drought (Mir et al. 2012, Varshney et al. 2014b). It is important to mention that a “QTL-hotspot” was identified on linkage group-4 that harbors 12 major QTLs for drought tolerance related traits explaining up to 58.20% phenotypic variation. This important hot-spot region was later fine mapped using important genotyping platform “genotyping-by-sequencing (GBS)”, sliding window based bin mapping and GWAS based gene enrichment analysis of skim sequenced data of RIL population (Jaganathan et al. 2015, Kale et al. 2015). QTLs/genes for drought and heat responsive traits have also been identified using GWAS and candidate gene sequencing approaches (Thudi et al. 2014). Genes/QTLs have also been identified for important diseases in chickpea like Fusarium wilt (FW), Ascochyta blight (AB), botrytis gray mold (Anuradha et al. 2011, Sabbavarapu et al. 2013, Varshney 2016). In addition gene/QTLs have also been identified for phenology related traits, seed traits etc. (Verma et al. 2015, Ortega et al. 2019, Sivasakthi et al. 2019, Roorkiwal et al. 2020).

Similarly, in pigeonpea, genes/QTLs have been identified for variety of traits using different trait mapping approaches. For instance genes/QTLs have been identified for important diseases like Fusarium wilt (FW) and sterility mosaic disease (SMD) (see Raju et al. 2010, Dubey et al. 2011, Varshney 2016, Pazhamala et al. 2017, Mir et al. 2017, Bohra et al. 2020a, Saxena et al. 2021). Genes/QTLs have been also identified for plant height, growth habit, flowering, earliness and determinacy through candidate gene sequencing and whole genome scanning approaches (Bohra et al. 2011, Kumawat et al. 2012, Mir et al. 2013b, Mir et al. 2014, Mir et al. 2017). In addition, genes/QTLs have also been identified for drought, salinity, cold, agronomic traits such as fertility restoration (Priyanka et al. 2010, Bohra et al. 2011, Kumawat et al. 2012, Deeplanaik et al. 2013, Mir et al. 2017, Saxena et al. 2020). The use of wild relatives like *C. cajanifolius* and *C. acutifolius* through advance back-cross QTL mapping has also been attempted in pigeonpea to map genes for agronomically important traits including yield and yield contributing traits (Saxena et al. 2020).

In view of genomics revolution in legume crops, the NGS-based high-throughput genotyping approaches are being used for genetic/trait mapping. This sequence-based trait mapping has been used in chickpea, pigeonpea by either sequencing of the whole population or pooled samples belonging to two extreme bulks for the trait of interest (see Pandey et al. 2016, Varshney et al. 2019, Roorkiwal et al. 2020, Bohra et al. 2020b). The NGS-based trait mapping overcomes several disadvantages like time consuming and costly nature of traditional approaches of trait mapping and therefore preferred in recent times for trait mapping. Sequenced-based trait mapping approaches have also been used in chickpea, pigeonpea and groundnut for identification of candidate genes/genomic regions for rust and late leaf spot resistance (see Pandey et al. 2016, Varshney 2016, Roorkiwal et al. 2020, Bohra et al. 2020c).

## GENOME SEQUENCING INITIATIVES IN PULSES

### Whole genome sequencing

#### Chickpea

Chickpea is one of the most important legume crops with its small (desi) and large sized (kabuli) seeds constituting the main market types. Varshney et al. (2013d) reported 532-Mb genome assembly in CDC Frontier (Kabuli chickpea) by whole genome shotgun sequencing approach, and assembly contained a total of 28,269 genes. The assembly had 7,163 scaffolds greater than 1Kb and 3,659 scaffolds greater than 2 Kb. Nearly 73% of the assembly comprised of larger scaffold size, being N50 of 39.99 Mb. Of the total genes reported, 89.73% were annotated with 4.93 as the mean number of exon per gene and 236 bp as the average exon size. The assembly harboured 187 disease-resistance genes and large-scale DNA markers were discovered including 48,298 SSRs and 76,084 SNPs. Similarly, Jain et al. (2013) reported draft genome sequence of ICC 4958 (desi) having size of 520 Mb, capturing 70% of total genome size. Their genome assembly had 27,571 predicted genes and the repeat elements comprised of 210 Mb. During comparative analysis with other dicot genome



numbers of gene predicted were lower but the average transcript length was reported to be higher and nearly equal to soybean. Another genome assembly by Parween et al. (2015) captured 511 Mb of ICC 4958 (desi) and 327 Mb-genome was assembled for PI 489777, a wild chickpea (Gupta et al. 2017). Among all the assemblies, Varshney et al. (2013d) have sequenced most of the genome approximately 74% of the total. Further, Misra et al. (2014) developed a Chickpea Genomic Web Resource (CGWR) to visualize the desi genotype (ICC 4958) genome and have comparatively analyzed the wild and cultivated genotypes of chickpea and other legume crops. Following the availability of the whole genome assemblies, researchers have developed several databases to catalogue genome-wide DNA markers for applications in research and breeding such as chickpea microsatellite database (CicArMiSatDB) (Doddamani et al. 2014) and Microsatellite Database (CMsDB) (Parida et al. 2015). Other databases on chickpea genomic resources include CicArVarDB encompassing SNP and InDel (Doddamani et al. 2015), and ISM-ILP database (Srivastava et al. 2016) that provides information on 119,169 and 110,491 ISMs from protein-coding genes desi (23,129) and kabuli (20,386) chickpeas.

## Pigeonpea

Pigeonpea was the first pulse and second legume crop whose genome was sequenced. Using a *de novo* assembly approach and based on Illumina sequencing platform, Varshney et al. (2012) assembled 605.78 Mb of the popular pigeonpea variety ICPL 87119 (Asha), representing 72.7% the total genome size of pigeonpea (833.07 Mb). This assembly contained a total of 137,543 scaffolds with N50 of 516.06 Kb. Of the total scaffolds, 6,534 were longer than 2kb. In this draft genome assembly, 51.67% of the total genome was represented by the transposable elements (TE) whereas the total GC content was 32.8%. The genome assembly had 48,680 genes with coding sequence size of 959.39 bp and 3.59 exons per gene. Besides protein-coding genes, further annotation identified 862 microRNAs, 763 tRNA, 329rRNA and 363 small nuclear RNA (snRNA) in the pigeonpea genome. On comparative analysis with soybean genome (Schmutz et al. 2010), the number of exons per gene was 3.59 which was less than that of soybean (5), whereas lengths of exon (267.39 bp) and intron (536.89 bp) were found to be higher. Another draft genome assembly of pigeonpea by Singh et al. (2012) based on 454 GS-FLX technology. They identified 1,213 defence-responsive genes and 152 genes having possible association tolerance against abiotic stress. The availability of the reference genome sequence has opened enormous opportunity for the development of large-scale DNA markers, such as 309,052 SSRs and 28,104 SNPs across 12 genotypes. Varshney et al. (2017) have resequenced the genomes (with the coverage depth of 5X to 12X) of 292 pigeonpea accessions including wild species, cultivated breeding lines and landraces. Following the whole genome sequencing approach, Kumar et al. (2016) have reported the first hap map using 20 accessions representing parents of MAGIC, NAM, RIL, 18 wild and 2 cultivated lines. Similarly, first pangenome of pigeonpea contained 86.6% core genes and 13.4% variable genes.

## Field pea

Field pea is used as a genetic model for genetic studies since 1980s, however its large genome size (4.45 Gb) has hampered the progress of pea genomics as compared to the other pulse crops. Earlier researches have reported that this difficulty occurs because pea genome is mostly dominated by mobile and repetitive elements mainly Ty3/gypsy family of transposons (Macas et al. 2007). More recently, Kreplak et al. (2019) have built a high-quality chromosomal-level genome assembly of the reference genotype 'Caméor' that spanned 3.92 Gb of the genome. The genome assembly was made using a combination of short read sequences (Illumina sequences) with 281X genome coverage and long read sequences (PacBio RSII) with 13X genome coverage. The key features of this assembly included N50 of scaffolds being with 415,920 bp, total length of pseudomolecules was 3.23 Gb, and the lengths of transposon regions were 2.45 Gb and 171 Mb of class II and class I, respectively. The genome pea assembly consisted of 44,756 genes, 30,687 of which were annotated. The reference pea genome provides a strong foundation to elucidate the phylogeny and evolutionary relationship of pea with other crops, and a variety of important genes for future improvement.

## Common bean

Common bean is a short-day plant grown mainly in African and American countries. Nearly 8,000 years ago, wild pools independently isolated themselves in two geographical locations i.e., Mexican and South American. Schmutz et al. (2014) presented a genome analysis of an Andean ecotype common bean (G19833) to cover accessions ranging from Mexico to Argentina. Using whole genome shotgun approach, the authors assembled common bean genome on

11 pseudomolecules, with a mean coverage of 21X. The assembly size was reported to be 472.5 Mb, of which 468.2 Mb was assigned to pseudomolecules. By resequencing 60 wild accessions and 100 landraces the study confirmed the evolutionary relationship of the Mesoamerican and Andean gene pools.

## Mungbean

Mungbean is a warm season fast growing legume in Asia belonging to subgenus *Ceratotropis* of genus *Vigna*. Kang et al. (2014) assembled 431-Mb of the diploid *V. radiata* var. *radiata* (VC 1973) using Illumina and GS FLX platforms, with the corresponding libraries providing 320-fold and five-fold coverage of the total genome. Furthermore, a wild relative (*V. radiata* var. *sublobata*, accession *TC1966*) of the domesticated mungbean was sequenced covering 82% (423-Mb) of the total 501 Mb genome. Similarly, a 792-Mb genome of the tetraploid *V. reflexo-pilosa* var. *glabra* (accession V1160) was assembled into 29,166 scaffolds. A total of 22,427 genes were predicted based on homology-based search and RNA-Seq data of different tissues.

## Adzuki Bean

Adzuki bean (*V. angularis* var. *angularis*) is grown in 30 countries worldwide. To accelerate the genomic research, Kang et al (2015) built a genomic assembly of Chinese cultivar “Jingnong 6”. With 168X coverage of the total genome, 443 Mb representing 75% of the total genome (591 Mb) was assembled into 3,883 scaffolds having N50 of 703 Kb. The repetitive content of the genome comprised of 207 Mb (44.51%), which was lower than other pulse crops such as chickpea, pigeonpea but almost similar to that of common bean. A total of 26,857 genes were predicted with high confidence and of these, 15,976 genes were assigned to pseudo chromosomes. Salient features of the genomic assemblies among selected legume crops are given in Table 2.

Another draft genome assembly of adzuki bean by Yang et al. (2015) based on HiSeq 2000 sequencing platform assembled 450 Mb contig sequences with N50 of 38 kb (168X coverage of total genome) representing 83% of the total genome size of adzuki bean (542 Mb). This assembly contained a total of 466.7 Mb scaffolds with N50 of 1.29 Mb, representing 86.11% of the total genome size. Of the total scaffolds, 6,534 were longer than 2kb. In this draft genome assembly, 34.57% of the total genome was represented by the retrotransposons whereas the total GC content was 34.8%. Besides 34,183 protein-coding genes, further annotation identified 312 microRNAs, 307 tRNAs, 3730 rRNAs and 314 small nuclear RNAs (snRNA) in the adzuki bean genome.

**Table 2.** Salient features of the genome assemblies of some pulse crops

Assembly features	Chickpea	Pigeonpea	Field Pea	Common Bean	Mungbean	Adzuki Bean
Genome Size	738 Mb	858 Mb	4.45 Gb	587 Mb	579 Mb	538 Mb
Genome sequenced	544.3 Mb	605.78 Mb	3.92 Gb	473 Mb	473 Mb	450 Mb
Number of Scaffold	7,163	137,542	24,623	708	2,800	37,533
N50 of (Scaffolds)	39.99 Mb	516 Kb	415,940 bp	50.4 Mb	1507 Kb	1.29 Mb
Number of exon per gene	4.93	3.59	4.33	5.5	-	-
Number of predicted genes	28,269	48,680	44,756	27,197	22,427	34,183
Transposable elements	49.41%	51.67%	84%	45.42%	43%	44.51%
GC% content	30.78%	32.80%	37.60%	-	33%	34.80%
References	Varshney et al. (2013d)	Varshney et al. (2012)	Kreplak et al. (2019)	Schmutz et al. (2014)	Kang et al. (2014)	Kang et al. (2015)

## TRANSCRIPTOMIC RESOURCES IN PULSES

To leverage legume functional genomics and to provide genes controlling important traits, transcriptomic resources have been developed in recent past. The global expression analysis in combination with gene expression atlas (Table 3), have elucidated the molecular mechanism underlying important plant responses that contribute towards sustainable agriculture production. Earlier, transcriptome assemblies were developed in pulse crops using a combination of Sanger and next generation sequencing platforms. For example, Dubey et al. (2011) developed a transcriptome assembly (CcTA)

**Table 3.** Gene expression atlas built in some pulse crops

Crop	Resource	Number of genes catalogued	References
Chickpea	<i>Cicer arietinum</i> gene expression atlas ( <i>CaGEA</i> )	32,873	Kudapa et al. (2018)
Pigeonpea	<i>Cajanus cajan</i> gene expression Atlas ( <i>CcGEA</i> )	28,793	Pazhmala et al. (2017)
Common bean	<i>Phaseolus vulgaris</i> gene Expression Atlas ( <i>Pv GEA</i> )	11,010	O' Rourke et al. (2014)

comprising of 127,754 tentative unique sequences (TUSs) and the transcriptome assembly offered sets of DNA markers including 8137 SSRs, 12,141 SNPs and 5845 ISR. Similarly, Dutta et al. (2011) developed a set of 3,771 genic SSR markers. Sinha et al. (2015a, b) in pigeonpea identified, sequenced and validated the set of 10 housekeeping genes in pigeonpea under salt and heat stress conditions. The study by Raju et al. (2010) reported 9,468 high quality ESTs and identified genes responsive to Fusarium wilt (19) and sterility mosaic disease (20), the two most prominent diseases of pigeonpea. More recently, transcriptome assemblies have been developed in pigeonpea based on RNA-Seq of transcriptomes from unopened flower buds of male sterile lines and cognate fertile lines (Bohra et al. 2021a, Bohra et al. 2021b).

Similarly in chickpea, 21,491 ESTs were developed as a rich resource for the identification of drought-responsive genes (Hiremath et al. 2011). A variety of DNA markers were identified including SSRs (728), SNPs (495), COS (387), and ISR (2088). Other transcriptome based studies in chickpea include Varshney et al. (2009) (20,162 ESTs) and Garg et al. (2011) (34,760 transcripts reads). In chickpea, SAGE combined with NGS has also been used for genome-wide high quality transcriptome profiling, which led to the identification of 3,858 drought-responsive genes in chickpea. Another SAGE analysis study by Afonso-Grunz et al. (2015) elucidated strongly upregulated gene glutathione S-transferases or genes implicated in phenylpropanoid and flavonoid biosynthesis pathway. A microarray based transcriptome analysis in root and leaf tissues have revealed 4,815 differentially expressed genes, out of which 88 and 52 genes were found to be differentially expressed in root and leaf tissues respectively. Another microarray based transcript study has confirmed a set of 109,210 and 386 genes expressed differentially in drought, cold and salinity stress respectively (Mantri et al. 2007). Advances in sequencing technologies in combination with improved computations tool have facilitated the development of gene expression atlas in different pulse crops such as common bean (O'Rourke et al. 2014) pigeonpea (Pazhmala et al. 2017) and chickpea (Kudapa et al. 2018).

## GEMOMIC BREEDING METHODS IN PULSE CROP IMPROVEMENT

### Marker-assisted backcrossing

Among various GAB (Varshney et al. 2021) approaches, marker assisted backcrossing (MABC) has been used to introgress major-effect QTL controlling a variety of biotic and abiotic stresses such as disease resistance and drought tolerance. For instance, Geletu, a drought tolerant line derived from MABC scheme in chickpea was released for cultivation in Ethiopia. The QTL hotspot genomic region harbouring a variety of drought tolerance associated traits was introgressed into an Indian chickpea cultivar from the donor ICC 4958 (Varshney et al. 2013c). Similarly, QTL controlling resistance against Fusarium wilt and Ascochyta blight were introgressed to chickpea cultivar C 214 following MABC approach (Varshney et al. 2014c). More recently, fast-track development of drought tolerant 'Pusa chickpea 10216' was demonstrated by transferring "QTL-hotspot" genomic region from ICC 4958. Development of various molecular breeding products in chickpea has been discussed in detail elsewhere (Bohra et al. 2019, Roorkiwal et al. 2020).

In field pea, application of GAB approach was demonstrated for selection of lodging resistance in early segregating generations, and the GAB approach was found to be more efficient than conventional phenotypic selection (Zhang et al. 2006). Other traits that have been introgressed in field pea using GAB approach include *Aphanomyces* root rot resistance (Hamon et al. 2013), frost tolerance (Lejeune-Hénaut et al. 2008, Tayeh et al. 2015b). Advanced backcross-QTL (AB-QTL) proposed by Tanksley and Nelson (1996), facilitates variety development and QTL introgression in a simultaneous manner. In field pea, an AB population was made by back crossing (BC<sub>2</sub>F<sub>6</sub>) an accession ATC 113 to a susceptible cultivar Pennant (Aryamanesh et al. 2012). Similar examples were reported in common bean for agronomic traits (Blair et al. 2006). Some examples of fast-track trait introgression using MABC/MAS approaches in pulse crops are provided in Table 4.

**Table 4.** Some examples of fast-track trait introgression using MABC/ MAS in some pulse crops

Crop	Donor Parent	Recipient	Trait	DNA Marker	References
Chickpea	Vijay	Pusa 256	Resistance against Fusarium wilt ( <i>foc2</i> )	SSR	Pratap et al. (2017)
Chickpea	WR 315	C 214	Resistance against Fusarium wilt ( <i>foc1</i> )	SSR	Varshney et al. (2014c)
Chickpea	ILC 3279	C 214	Ascochyta blight ( <i>ABQTL-I and ABQTL-II</i> )	SSR	Varshney et al. (2014c)
Common bean	AND 277	Rudá	Resistance against angular leaf spot	STR	Gonçalves-Vidigal et al. (2011)
Common bean	AND 277	IAC-Milênio	Resistance against angular leaf spot	SNP	De Almeida et al. (2021)
Common Bean	BAT93	Jalo EEP558	Resistance against anthracnose and rust	SSR, RGA, AFLP	Hanai et al. (2010)
Common Bean	Bunsi	Midland	Resistance against white mold	AFLP, RAPD	Ender et al. (2008)
Common Bean	R31-83	Orion	Resistance against white mold	SNP	Vasconcellos et al. (2017)
Common Bean	G21212	BAT 881	Drought tolerance	RFLP,SSR,SNP	Díaz et al. (2018)
Lentil	<i>L. odemensis</i>	<i>L. culinaris</i> cv. alpo	Ascochyta blight resistance	SNP	Polanco et al. (2019)
Lentil	ILL2024	Cassab	Boron toxicity tolerance	SNP	Kaur et al. (2014)
Lentil	L 4149	PL 8	Rust resistance	SRAP , SSR	Dikshit et al. (2016)
Lentil	PDL-1 and PSL-9	L-4147 and L-4076	Salt Tolerance	SSR	Singh et al. (2020)
Pea	00-2067	Reward	Resistance against Aphanomyces root rot (ARR)	SSR, SNP	Wu et al. (2021)
Pea	Eritreo	Messire	Resistance against powdery mildew	SCAR, RAPD	Cobos et al. (2018)
Pea	955180	Majoret	Resistance against powdery mildew	SSR	Ek et al. (2005)
Pea	J12480	Lincoln	Resistance against powdery mildew	RAPD, SSR	Katoch et al. (2010)
Pea	955180	Majoret	Resistance against powdery mildew	SSR	Ek et al. (2005)
Pea	Parafield	Kaspa	Salt tolerance	SNP	Leonforte et al. (2013)

## Genomic selection

In the post-NGS era, the availability of reference genome sequence has provided the breeders with a variety of genome-wide DNA markers that are indispensable to effective plant selections and GAB. Several high-density genotyping systems are now available to assay a large number of genotypes in a cost and time-efficient manner (Rasheed et al. 2017). The development of cost-effective and customized genotyping platforms are all the more relevant in view of the concurrent refinements in plant breeding methods. For instance, genomic selection (GS) has recently emerged as a new breeding tool to improve genetic gain of plant breeding programs (Crossa et al. 2017). The genetic gain per unit time can be predicted based on the breeder's equation (Moose and Mumm 2008). The genetic gain of a breeding program can be enhanced by improving selection intensity (*i*) and selection accuracy (*r*) while shortening the length (*l*) of the breeding cycle (Santantonio et al. 2020, Sinha et al. 2021). The application of GS has shown encouraging results in legume crops. In chickpea, Roorkiwal et al. (2016) performed phenotyping of 320 elite breeding lines genotyped with 3,000 DArT Seq markers at two different locations, and the accuracies of GS models ranged from 0.13 (seed yield) to 0.91 (100-seed weight). A later GS study in chickpea by the same group incorporated G×E interactions into GS prediction models and also compared the impact of population structure and different genotyping platforms (GBS and DArT-Seq) on prediction accuracies (Roorkiwal et al. 2018b). In field pea, Tayeh et al. (2015c) reported prediction accuracies in the range of 0.65 (days to flowering) and 0.83 (1000-seed weight) based on the GS study involving 339 accessions genotyped using 13.2K SNP array. The study reported higher effect of size and composition of the training population on prediction accuracies than that of the GS prediction models and genotyping platforms. Another GS study performed on 215 field pea lines (assayed by the GBS) reported 0.56 as the highest prediction accuracy for ascochyta blight resistance. GBLUP and RKHS models performed better than the other models employed (RR-BLUP, Bayes A, Bayes B, Bayes C, BRR) (Carpenter et al. 2018). Recently, Annicchiarico et al. (2019) applied genomic prediction approach for improving grain yield, flowering initiation, lodging susceptibility, seed weight and winter plant survival for three environments, with GS models trained on 306 interconnected RILs. The study established the superiority of GS over the phenotypic selection. The utility of WGRS data in predicting hybrid performance and identification of high-yielding heterotic pattern has been demonstrated in pigeonpea (Saxena et al. 2021). The genome-wide predictions have been elucidated to be crucial for long term gain in hybrid breeding.

### Rapid generation turnover (RGT) technologies

As mentioned in the previous section, approaches that reduce the length of the breeding cycle can contribute to accelerate the rate of genetic gain. These breeding protocols are collectively termed as speed breeding (SB). From the breeder's equation, the response to selection shows an inverse relation with the length of the breeding cycle (Moose and Mumm 2008). Hickey et al. (2019) have discussed the benefits of SB using artificial lighting and other rapid generation advancement (RGA) technologies with other modern breeding tools (genome editing, high-throughput phenotyping and GS) to accelerate the yield gains. The study by Watson et al. (2019) has demonstrated a considerable reduction in the breeding cycle time (up to 6 generation in a year) of cool season legumes such as chickpea and field pea (Watson et al. 2019). A more recent study by Samineni et al. (2020) applied RGA protocol on six chickpea accessions, two each from early, medium and late categories and the authors reported production of seven generations in a single year. Earlier in pea, RGA protocol (20-hr photoperiod, 21/16 ligh/dark, hydroponic system etc.) accelerated the development of mapping population of pea by 30–45 days per generation faster over standard single seed descent method (Mobini and Warkentine 2016). Exogenous application of plant growth regulators such as benzylaminopurine (BAP; cytokinin) in combination with cold treatment (8/4 °C day/night for 2 days) considerably reduced the generation time in faba bean through improving pollen viability and enhanced pod and seed setting (Mobini et al. 2015).

In pigeonpea, four genotypes from early maturity groups namely, ICPL 4, ICPL 151, ICPL 85024 and ICPL 87093 were subjected to RGA protocol under controlled conditions, and four generations were obtained in 349, 367, 313 and 338 days, respectively (Saxena et al. 2017). The study demonstrated shortening of generation time by combining harvesting of immature seeds and single pod descent method. Another SB-based strategy by Saxena et al. (2019) employed early maturing photoperiod-insensitive genotypes, and showed its potential to deliver new early maturing cultivars with the successful reduction of up to 4-5 years. SB recipes combined with single seed descent and MAS or GS will provide greater genetic gains over conventional methods of plant breeding (Varshney et al. 2021).

### Haplotype-based breeding

While the concept of haplotype assembly was proposed by Bevan et al. (2017), based on haplo-pheno analysis, superior haplotypes were identified in rice (Abbai et al. 2019) and pigeonpea (Sinha et al. 2020). Based on these superior haplotypes, Varshney et al. (2020) outline the concept of haplotype-based breeding for faster development of designer cultivars. This approach has tremendous advantages over MABC, which takes years and generations to transfer superior genes, and the process creates bottleneck effects and reduction of genetic diversity. Developing improved cultivars for future climate will require assembling gene(s) scattered throughout the genome, and efficient accumulation of such gene(s) will rely on approaches that exploit haplotypes. Haplotype-based breeding aimed at transferring superior haplotypes underlying genetic variations that are in strong linkage disequilibrium (LD) with the candidate genomic regions associated with the traits of interest (Varshney et al. 2021).

To accelerate future crop breeding, breeders need to shift from traditional DNA marker systems to haplotypes and pyramid them into a variety, opening doors to transfer novel genetic diversity from wild species, landraces and diverse accessions. More recently, the haplotype-based approach has been implemented in pigeonpea. For instance, Sequencing data of 292 accessions were mined to find superior haplotypes for 10 drought-responsive candidate genes (Sinha et al. 2020). Total five genes showed positive linkage disequilibrium for the seven drought responsive traits. A haplo-pheno analysis targeting candidate genomic regions/genes of association analysis revealed the superior haplotypes viz., *C. cajan\_23080-H2*, *C. cajan\_30211-H6*, *C. cajan\_26230-H11* and *C. cajan\_26230-H5* for plant traits that control drought response of pigeonpea. Identification of haplotypes creates novel avenues to tailor future cultivars harnessing growing genome-wide sequence information and historical phenotypic records (Varshney et al. 2021).

### FINAL CONSIDERATIONS

Pulses are crucial to provide affordable protein to growing human population worldwide. The pace of genetic improvement of pulses has lagged behind in comparison to cereal crops. Nevertheless, remarkable success has been made in recent years in developing modern genomic tools and breeding approaches that underpin genetic improvement of pulses. Trait discovery has been revolutionized following sequencing of multiple genomes, and elucidation of crop evolution and breeding history has offered novel breeding targets to hasten crop breeding progress. Improved pulses



cultivars resulting from GAB are now ready for cultivation in farmers' field. Initial examples of application of GS and SB for enhancing generation turnover in pulses breeding programs are encouraging, and enhanced adoption of these modern approaches will be crucial to improve the rate of genetic gain in pulses breeding programs. Besides SB and GS, application of HBB will pave the way for next generation breeding in pulses for the rapid delivery of ideal cultivars that adequately cater to the future needs in a timely manner.

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