



Application of Quantitative Trait Loci Mapping and Marker-Assisted Selection in Genetic Diversity Assessment and Improvement of Leguminous Crops: A REVIEW

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ABSTRACT: Leguminous crops provide dietary protein and contribute to soil fertility through biological nitrogen fixation, but their productivity is constrained by drought, heat, soil stresses, pests, diseases and, in some crops, narrow genetic diversity. Conventional breeding has produced many improved cultivars, yet selection for complex traits is often limited by environmental effects, lengthy breeding cycles and difficult phenotyping. Molecular markers, QTL mapping and marker-assisted selection (MAS) complement conventional breeding by characterizing genetic variation and tracking favourable alleles. This review summarizes applications of these approaches in soybean, cowpea, groundnut, common bean, chickpea, pigeonpea, faba bean, pea and lentil, with emphasis on yield, drought adaptation, disease resistance, nutritional quality and other agronomic traits. SSR and SNP platforms have increased the resolution and throughput of diversity analysis and trait mapping. However, QTL $\times$ environment interactions, small-effect loci, inadequate phenotyping, limited marker validation and resource constraints restrict routine MAS, particularly for complex traits. Integrating QTL mapping and MAS with genome-wide association studies, genomic selection, pangenomics and high-throughput phenotyping offers a more effective route for using legume genetic resources and developing resilient cultivars.

KEYWORDS: genetic diversity, legumes, marker-assisted selection, molecular breeding, molecular markers, quantitative trait loci, SNPs.

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1. INTRODUCTION

Leguminous plants include economically important grain and oilseed crops such as soybean (*Glycine max*), cowpea (*Vigna unguiculata*), common bean (*Phaseolus vulgaris*), chickpea (*Cicer arietinum*), pigeonpea (*Cajanus cajan*), groundnut (*Arachis hypogaea*), lentil (*Lens culinaris*), pea (*Pisum sativum*) and faba bean (*Vicia faba*). They contribute protein, carbohydrates, minerals, vitamins and other compounds to human diets and are especially important where animal protein is less accessible (Bouchenak & Lamri-Senhadj, 2013; Kumar et al., 2011; Varshney et al., 2019).

Legumes form symbiotic associations with nitrogen-fixing bacteria, enabling atmospheric nitrogen to be converted into biologically available forms. When appropriately managed in rotations and intercropping systems, they can contribute to soil fertility and reduce dependence on synthetic nitrogen fertilizers (Kumar et al., 2011).

Productivity in many legume production systems remains below attainable levels. Drought, high temperature, salinity, declining soil fertility, insect pests, parasitic weeds and fungal, bacterial and viral diseases are important constraints. Climate variability may alter the distribution and intensity of these stresses. Breeding cultivars that combine high yield with stable resistance or tolerance is therefore a major objective (Varshney et al., 2019, 2021).

Conventional breeding depends largely on phenotypic selection and has produced numerous improved cultivars. However, selection can be inefficient when traits have low heritability, are expressed late, are costly or difficult to phenotype, or are strongly affected by the environment. Molecular breeding can complement conventional selection by characterizing genetic variation and identifying genomic regions associated with desirable phenotypes (Kumar et al., 2011; Varshney et al., 2013; Xu & Crouch, 2008).

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Molecular markers have transformed the characterization of legume germplasm. RFLPs, RAPDs and AFLPs were followed by SSRs and, increasingly, SNPs. SSRs and SNPs have been used in genetic diversity studies, linkage mapping, association mapping and breeding (Miklas et al., 2006; Varshney et al., 2021; Webb et al., 2016). Genome sequences for crops such as soybean, chickpea and pigeonpea have further accelerated marker discovery and genomic analysis (Schmutz et al., 2010; Varshney et al., 2012, 2013). QTL mapping connects phenotypic variation with molecular markers by locating genomic regions associated with quantitative traits. Once QTLs are validated, linked or functional markers may be used in MAS. MAS is most effective for major genes and large-effect, stable QTLs, whereas genome-wide approaches are generally better suited to highly polygenic traits (Kumar et al., 2011; Xu & Crouch, 2008).

This review examines molecular-marker diversity analysis, QTL mapping and MAS in leguminous crops, emphasizing crop-specific applications, major breeding objectives, practical limitations and integration with newer genomic approaches.

2. LITERATURE SEARCH STRATEGY

This article was developed as a narrative review rather than a systematic review or meta-analysis. Searches were conducted in Web of Science, Scopus, PubMed, Google Scholar and CAB Abstracts for publications available through December 2023. The search covered literature published from January 1990 through December 2023, with earlier studies considered when they established foundational marker systems, genetic maps or QTL and MAS applications.

Search concepts included combinations of terms such as legume genetic diversity, molecular markers in legumes, quantitative trait loci, QTL mapping, marker-assisted selection, marker-assisted backcrossing, SNP, SSR, genomics-assisted breeding, drought tolerance, disease resistance, yield QTL and individual crop names. Searches were supplemented by screening reference lists of relevant reviews and primary studies. Peer-reviewed articles and scholarly reviews addressing genetic diversity, genomic resources, QTL discovery, marker validation and marker-assisted breeding were prioritized.

Titles and abstracts were screened for relevance, followed by full-text assessment of potentially eligible publications. Studies were included when they focused on soybean, cowpea, groundnut, chickpea, common bean, pigeonpea, lentil, pea or faba bean and reported genetic-diversity analysis, molecular-marker development or application, QTL mapping, marker–trait association, marker validation or MAS relevant to crop improvement. Studies were excluded when they concerned non-leguminous crops, lacked a clear connection to genetic diversity or crop improvement, were duplicate records, or provided insufficient methodological or trait information. No formal risk-of-bias assessment or quantitative synthesis was performed.

Recent literature was emphasized for advances in high-density genotyping, genome-wide association studies and genomic breeding, while earlier publications were retained where they established important genomic resources or demonstrated applications of QTLs and MAS. Because this was a narrative review, study selection and interpretation involved author judgment and were not governed by a preregistered protocol or independently replicated screening. Consequently, publication bias, database coverage differences, inconsistent terminology, heterogeneous populations and environments, and selective emphasis on well-studied crops may have influenced the evidence summarized. The narrative approach is useful for integrating diverse methods and breeding contexts but does not provide the exhaustive, reproducible study identification or effect-size estimates of a systematic review or meta-analysis.

3. GENETIC DIVERSITY AND MOLECULAR TOOLS FOR LEGUME IMPROVEMENT

Genetic diversity refers to heritable variation within and among populations, accessions, landraces, cultivars and related species. It is fundamental to plant breeding because improvement requires variation from which favourable alleles can be selected. Genetic diversity also provides alleles for adaptation to changing environments, pests and pathogens (Varshney et al., 2019, 2021).

Domestication and repeated selection have reduced diversity in portions of the gene pools of several cultivated crops. This narrowing can restrict useful alleles and increase vulnerability to emerging stresses. Wild relatives, landraces, breeding lines and germplasm-bank accessions are therefore important resources for broadening breeding populations (Bertioli et al., 2016; Varshney et al., 2019). Phenotypic descriptors were historically used to characterize diversity, but their expression can be strongly influenced by the environment. DNA markers provide a more direct assessment of inherited variation, allowing researchers to identify genetically distinct accessions, quantify population structure, reveal relationships among genotypes and assist parent selection (Assefa et al., 2019; Varshney et al., 2019). Diversity analysis also supports QTL discovery because mapping populations require contrasting parents and sufficient marker polymorphism, while association mapping depends on historical variation and recombination (Varshney et al., 2021).

Molecular-marker technology has progressed from RFLPs, RAPDs and AFLPs to SSRs and SNPs. RFLPs provided reliable codominant markers but were laborious, RAPDs were simpler but could have reproducibility problems, and AFLPs generated many polymorphic loci without requiring prior sequence information. SSRs became widely used because they are generally polymorphic, reproducible and codominant (Kumar et al., 2011; Miklas et al., 2006). They supported germplasm characterization, population-structure analysis and linkage-map construction, particularly before genome-wide SNP resources became available (Miklas et al., 2006; Webb et al., 2016).

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SNPs now support high-throughput diversity analysis, linkage mapping, GWAS and genomic prediction because they occur abundantly throughout plant genomes and are suitable for automated genotyping. Next-generation sequencing, genotyping-by-sequencing and SNP arrays have enabled large numbers of variants to be surveyed. In faba bean, gene-based SNPs and high-density maps have strengthened resources for diversity analysis, association mapping, comparative genomics and molecular breeding (O'Sullivan & Angra, 2016; Webb et al., 2016).

Reference genomes have further increased the value of marker-based approaches. The soybean genome sequence provided a framework for investigating its duplicated genome (Schmutz et al., 2010), while genome resources for pigeonpea and chickpea supported marker discovery and analysis of genomic regions relevant to breeding (Varshney et al., 2012, 2013).

4. QTL MAPPING AND MARKER-ASSISTED SELECTION

Many economically important plant characteristics are quantitative rather than discrete. They show continuous variation because they are influenced by multiple genes and environmental conditions. A QTL is a genomic region containing one or more genetic factors that contribute to variation in a quantitative phenotype (Kumar et al., 2011; Xu & Crouch, 2008).

QTL mapping combines phenotypic measurements with molecular-marker data. A typical study develops or selects a mapping population, phenotypes it for the target trait, genotypes individuals with molecular markers, constructs or uses a linkage map and tests associations between genomic regions and phenotypic variation (Xu & Crouch, 2008). Mapping populations may include F₂ populations, backcrosses, recombinant inbred lines, doubled haploids and multiparent populations. Recombinant inbred lines are particularly useful because they can be evaluated repeatedly across environments, allowing investigation of QTL stability and genotype × environment interactions.

High-density SNP genotyping and reference genomes can improve localization of genomic regions, but QTL detection alone does not establish breeding value. Effect size, consistency across environments, marker–QTL distance, genetic background and phenotyping accuracy determine whether a QTL can be used effectively. Many QTLs for complex traits explain only small proportions of phenotypic variance and are therefore difficult to exploit individually through MAS (Varshney et al., 2021; Xu & Crouch, 2008).

MAS uses molecular markers associated with genes or QTLs to select individuals carrying favourable alleles, often before full phenotypic expression of the target trait (Kumar et al., 2011; Xu & Crouch, 2008). It is most advantageous when phenotyping is expensive, destructive or difficult; when traits are expressed late; when environmental variation complicates selection; or when several resistance genes must be combined. It can also facilitate selection for recessive alleles in heterozygous individuals (Miklas et al., 2006; Xu & Crouch, 2008).

Foreground selection identifies individuals carrying the target gene or QTL. Background selection uses markers distributed throughout the genome to identify individuals with a high proportion of the recurrent-parent genome during backcrossing. Recombinant selection can reduce unwanted donor DNA surrounding the target locus. In gene or QTL pyramiding, markers assist in combining several favourable loci within one genotype (Xu & Crouch, 2008). Marker-assisted backcrossing can therefore introduce desirable loci from donor parents into established cultivars while retaining much of the recurrent-parent background (Varshney et al., 2013; Xu & Crouch, 2008).

5. CROP-SPECIFIC APPLICATIONS

5.1 Soybean

Soybean is a major oilseed and protein crop whose extensive genomic resources have made it a model for molecular improvement among grain legumes. The soybean genome sequence provided a foundation for high-density marker development and analysis of its duplicated genome (Schmutz et al., 2010).

QTLs and molecular markers have been investigated for seed protein and oil composition, flowering and maturity, plant architecture, yield components, disease resistance and abiotic-stress responses. SNP resources and extensive germplasm collections have also supported GWAS and genomic prediction (Varshney et al., 2021). Although genome duplication can complicate interpretation of gene function, sequence resources, high-throughput genotyping and functional-genomic tools support identification of candidate genes and diagnostic markers (Schmutz et al., 2010; Varshney et al., 2021).

5.2 Chickpea

Chickpea is an important pulse crop in dryland systems and is frequently exposed to terminal drought and diseases. Genomic-resource development has made it a prominent example of genomics-assisted breeding among food legumes (Varshney et al., 2013, 2019).

A widely cited example concerns the “QTL-hotspot,” a genomic region associated with root and drought-related traits. Marker-assisted backcrossing was used to introgress this region from ICC 4958 into the elite cultivar JG 11 (Varshney et al., 2013), illustrating how QTL information can be incorporated into a breeding strategy. Markers and QTLs have also been investigated for

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Fusarium wilt and Ascochyta blight resistance, seed characteristics and other agronomic traits. The chickpea reference genome and resequencing resources have facilitated sequence-based breeding (Varshney et al., 2013, 2019).

5.3 Common Bean

Common bean has received considerable attention because of its nutritional importance and susceptibility to numerous diseases. Marker-assisted approaches have been particularly developed for disease resistance (Assefa et al., 2019; Miklas et al., 2006).

Resistance loci and QTLs have been characterized for anthracnose, angular leaf spot, common bacterial blight, rust and viral diseases. Earlier RAPD and SCAR markers provided tools for disease-resistance selection, while SSR and SNP systems increased precision and throughput (Assefa et al., 2019; Miklas et al., 2006). Modern breeding increasingly integrates QTL information with GWAS, genomic prediction and functional genomics. Because resistance can vary among gene pools and pathogen populations, resistance loci require validation in the genetic backgrounds and environments where they will be deployed (Assefa et al., 2019).

5.4 Groundnut

Groundnut improvement is complicated by relatively narrow variation within cultivated germplasm and its allotetraploid genome. Molecular markers and mapping populations have nevertheless supported analysis of resistance traits (Bertioli et al., 2016; Khedikar et al., 2010).

Late leaf spot and rust are important foliar diseases. In a recombinant inbred population derived from TAG 24 × GPBD 4, QTL analysis identified genomic regions associated with resistance. A major rust-resistance QTL was reported, and the SSR marker IPAHM 103 was associated with the region and evaluated in additional breeding material, supporting its potential use in marker-assisted introgression (Khedikar et al., 2010).

Subsequent work has examined drought adaptation, disease resistance, seed quality and yield-related traits. The usefulness of individual markers across breeding populations depends on validation in the relevant genetic backgrounds and environments.

5.5 Cowpea

Cowpea is important in sub-Saharan Africa as a food, feed and income crop and can perform under relatively dry conditions. Its productivity is constrained by drought, insects, diseases and parasitic weeds such as *Striga gesnerioides* (Fatokun et al., 2018; Kumar et al., 2011).

Molecular-marker studies have characterized cowpea germplasm and identified diversity useful for parent selection. Markers associated with *Striga* resistance and other traits illustrate the potential of marker-assisted breeding. SNP markers, high-density maps and genome resources are supporting investigation of yield, maturity, resistance and adaptation traits (Fatokun et al., 2018; Varshney et al., 2021).

5.6 Pigeonpea

Pigeonpea is an important food and forage legume in tropical and semi-arid regions. Its draft genome sequence provided a framework for marker discovery and trait analysis (Varshney et al., 2012).

Molecular breeding has targeted Fusarium wilt, sterility mosaic disease, fertility restoration, yield components and drought adaptation. Marker-assisted methods have also been applied to hybrid breeding and purity assessment. Genomic resources have therefore supported the transition toward genomics-assisted pigeonpea improvement (Bohra et al., 2020; Varshney et al., 2012).

5.7 Faba Bean, Pea and Lentil

Faba bean, pea and lentil are important cool-season legumes. Molecular improvement was initially constrained by limited genomic resources and, particularly in faba bean, genome complexity. SSR, SNP and gene-based marker development has improved resources for these crops (O'Sullivan & Angra, 2016; Webb et al., 2016).

High-density consensus mapping in faba bean has provided resources for QTL discovery, association mapping and comparative genomics (Webb et al., 2016). QTLs have been reported for disease resistance, flowering, maturity, seed traits and abiotic-stress responses. In pea and lentil, genome assemblies, SNP genotyping and association mapping are expanding opportunities for breeding disease-resistant, stress-tolerant and nutritionally improved cultivars (Varshney et al., 2021).

6. TRAIT-SPECIFIC APPLICATIONS AND BREEDING PRIORITIES

6.1 Disease and Pest Resistance

Disease resistance is one of the most effective targets for MAS. When resistance is controlled by a major gene or large-effect locus, DNA markers can enable screening without exposing every breeding generation to the pathogen (Assefa et al., 2019; Khedikar et al., 2010; Miklas et al., 2006).

MAS can also support pyramiding of resistance genes. Markers distinguish plants carrying different combinations of loci even when their phenotypes are similar, allowing breeders to combine resistance loci that may broaden or stabilize protection. Pathogen monitoring remains necessary because resistance effectiveness can change as pathogen populations evolve (Assefa et al., 2019; Miklas et al., 2006).

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6.2 Drought Tolerance and Other Abiotic Stresses

Drought tolerance involves root architecture, water extraction, stomatal behaviour, osmotic adjustment, phenology and biomass partitioning. The chickpea QTL-hotspot represents an attempt to use a genomic region associated with multiple drought-related traits in breeding (Varshney et al., 2013).

The value of drought-related MAS depends on reliable phenotyping and validation across target environments. A QTL identified under one temperature, soil type or moisture regime may not perform consistently elsewhere. Multi-environment evaluation is therefore essential before deployment (Varshney et al., 2021). Similar considerations apply to salinity, heat and other abiotic stresses.

6.3 Yield and Yield Components

Yield is difficult to improve through individual QTLs because it is highly polygenic and strongly influenced by the environment. QTLs have nevertheless been reported for pod number, seed number, seed weight, biomass, harvest index and related traits (Kumar et al., 2011; Varshney et al., 2021).

MAS may be useful when major, stable QTLs contribute appreciably to a yield component. For overall yield, genomic selection may be more appropriate because it uses genome-wide marker information rather than relying on a small number of loci (Jannink et al., 2010; Varshney et al., 2021).

6.4 Nutritional and Quality Traits

Legume breeding increasingly considers nutritional quality alongside productivity. Seed protein, oil composition, micronutrient concentration, cooking quality and antinutritional factors can have genetic components suitable for genomic investigation (Bouchenak & Lamri-Senhadj, 2013; Kumar et al., 2011; Varshney et al., 2021).

Markers linked to stable major loci can facilitate early selection, whereas high-throughput phenotyping and genomic prediction may be more suitable for highly polygenic nutritional traits.

7. INTEGRATION WITH MODERN GENOMIC APPROACHES

7.1 Genome-Wide Association Studies

Traditional QTL mapping generally uses crosses between a limited number of parents and therefore captures only alleles segregating between those parents. GWAS uses diverse germplasm and historical recombination and can provide higher-resolution marker–trait associations (Varshney et al., 2019, 2021).

Combining QTL mapping and GWAS can strengthen confidence in regions detected by independent approaches. A QTL identified in a biparental population and supported by an association signal in diverse germplasm may be a stronger candidate for fine mapping and validation.

7.2 Genomic Selection

Genomic selection differs from conventional MAS. MAS focuses on selected markers associated with major genes or QTLs, whereas genomic selection uses genome-wide marker effects to predict genomic breeding values. It is therefore attractive for complex traits controlled by many small-effect loci (Jannink et al., 2010; Varshney et al., 2021).

MAS and genomic selection are complementary: MAS remains efficient for major genes and large-effect QTLs, whereas genomic prediction can capture more dispersed genetic variation underlying polygenic traits (Jannink et al., 2010; Varshney et al., 2021; Xu & Crouch, 2008).

7.3 High-Throughput Phenotyping

Accurate phenotyping remains a major limitation in QTL discovery. Genotyping has become increasingly rapid, but precise phenotyping across thousands of plants and multiple environments remains difficult (Cobb et al., 2013).

Remote sensing, imaging, automated environmental monitoring and related technologies can measure canopy temperature, biomass, growth, water status and stress responses. Integrating these measurements with genomic data may improve QTL detection and genomic prediction (Cobb et al., 2013; Varshney et al., 2021).

7.4 Pangenomics and Haplotype-Based Breeding

A single reference genome cannot represent all structural and sequence variation within a species. Pangenomic approaches can reveal presence–absence variation, structural variants and rare alleles that may be overlooked by a single reference (Varshney et al., 2021).

Haplotype-based breeding may identify favourable combinations of variants within genomic regions. These approaches could improve use of landraces and wild relatives and broaden the genetic base available to breeders (Bertioli et al., 2016; Varshney et al., 2021).

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7.5 Gene Editing

When QTL fine mapping and functional genomics identify causal genes or alleles, gene editing may provide another route to crop improvement. Genome editing does not replace diversity analysis, QTL mapping or MAS; these approaches can provide information needed to identify editing targets (Varshney et al., 2021).

8. CHALLENGES AND LIMITATIONS

The main limitations of QTL-based MAS are linked to trait complexity, environmental dependence, marker reliability and breeding capacity. Many important traits are highly polygenic, so individual QTLs may explain only a small proportion of phenotypic variation. QTL effects can also depend on temperature, soil type, moisture regime, pathogen population and genetic background. Consequently, associations identified in one population or environment may not transfer reliably to another.

Marker–trait associations may fail to transfer among genetic backgrounds, and recombination between a marker and the causal allele can reduce selection accuracy when the marker is not tightly linked. Phenotyping errors further reduce QTL-mapping power, making precise, replicated and multi-environment evaluation essential (Cobb et al., 2013; Xu & Crouch, 2008).

QTL discovery also does not ensure routine breeding use. Validation, fine mapping and conversion of research markers into inexpensive, breeder-friendly assays are necessary before deployment. Infrastructure, technical expertise, genotyping costs, bioinformatics capacity and reliable phenotyping facilities remain unevenly distributed, particularly in breeding programs serving regions where cowpea, groundnut and pigeonpea are major crops (Kumar et al., 2011; Varshney et al., 2021).

These limitations explain why MAS is most reliable for major genes and stable, large-effect QTLs, while genomic selection and other genome-wide approaches are generally more appropriate for complex traits.

9. PROSPECTS FOR LEGUME IMPROVEMENT

Future genetic improvement of legumes will increasingly depend on integration rather than a single technology. Germplasm characterization can identify diversity; high-density markers can reveal population structure; QTL mapping and GWAS can associate genomic variation with phenotypes; functional genomics can identify candidate genes; MAS can transfer major favourable alleles; and genomic selection can accelerate improvement of polygenic traits (Varshney et al., 2021).

Greater attention should be given to validation of QTLs across genetic backgrounds and target production environments. For African legume breeding, genomic studies using locally adapted germplasm and farmer-relevant environments are important because markers and QTLs discovered elsewhere may not transfer directly to local breeding material (Kumar et al., 2011; Varshney et al., 2019).

Wild relatives and landraces may contain alleles for heat, drought, pest and disease resistance that were reduced during domestication. Genomics-assisted pre-breeding can facilitate transfer of such diversity into elite populations while reducing undesirable linkage drag (Bertioli et al., 2016; Varshney et al., 2019).

Declining sequencing costs, breeder-friendly SNP assays, high-throughput phenotyping and improved computational methods may make molecular breeding more accessible. International collaboration and open genomic databases can reduce duplication of effort and support under-resourced breeding programs (Cobb et al., 2013; Varshney et al., 2021).

10. CONCLUSION

Genetic diversity is the foundation of sustainable legume improvement, while molecular markers provide tools for characterizing and using that diversity. QTL mapping identifies genomic regions associated with phenotypic variation, and MAS enables favourable alleles at validated loci to be tracked during breeding (Kumar et al., 2011; Xu & Crouch, 2008).

Applications across soybean, chickpea, common bean, groundnut, cowpea, pigeonpea, faba bean, pea and lentil demonstrate the value of these approaches for disease resistance, drought adaptation, yield components, quality traits and genomic resource development. Particularly illustrative examples include marker-assisted analysis of disease resistance and introgression of a chickpea genomic region associated with drought-related traits (Assefa et al., 2019; Khedikar et al., 2010; Varshney et al., 2013).

The review's central conclusion is that QTL mapping and MAS are powerful but targeted tools rather than universal solutions. Their effectiveness depends on trait architecture, phenotyping accuracy, QTL stability, marker–trait linkage and validation across relevant populations and environments. MAS is most valuable for major genes and stable, large-effect loci, whereas genomic selection and other genome-wide approaches are better suited to complex traits controlled by many small-effect loci.

QTL mapping and MAS should therefore be integrated with well-characterized germplasm, reliable phenotyping, GWAS, genomic selection, pangenomics, high-throughput phenotyping and functional genomics. Strategic integration of these technologies can connect genetic diversity more efficiently with crop improvement and support development of productive, nutritious and climate-resilient legume cultivars (Varshney et al., 2021).

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