

Legumes: Embracing the genome era

Legumes (Fabaceae, formerly Leguminosae) are a diverse, widely distributed, and economically important family of annual or perennial herbaceous plants, xerophytes, and forest trees. As a steady source of proteins, vitamins, minerals, and either lipids or starch, as well as their ability to fix nitrogen, legume grains play a major role in advancing health and nutrition, food security, and environmental sustainability, also providing forage for livestock and serving as cover crops to control weeds and erosion. The production potential of legume crops is constrained by several abiotic and biotic stress factors. Deployment of molecular breeding approaches for legume improvement has generally lagged behind the more successful cereal and oilseed crops. However, with the recent advances in next generation sequencing and genotyping technologies, legume genomics is advancing quite rapidly. Over the past decade, reference genome sequences have become available for more than 45 legume species (NCBI Genome Database; <https://www.ncbi.nlm.nih.gov/genome/browse/#!/overview/Fabaceae>). The application of DNA and RNA sequencing is providing considerable insights into the hidden genetic, epigenetic and structural variation underlying various complex traits for legume improvement. This special Issue on legume genomics, comprising nine reviews, four original research articles and a resource article, addresses some of the most important advances and applications in the field.

Food legumes are divided into two groups, oilseeds and pulses. Soybean (*Glycine max* [L.] Merr.), the most widely grown and used oilseed, was the first legume species for which a reference genome sequence became available almost a decade ago (Schmutz et al., 2010). Multiple soybean genome assemblies have become available since then, which has facilitated linkage mapping, QTL analysis and gene discovery, thereby accelerating the creation of improved varieties. The review article by Bhat and Yu (2021) summarizes recent progress made in soybean whole genome re-sequencing and highlights the significance and challenges in applying high-throughput genotyping and phenotyping methods in marker assisted breeding and genomics selection for soybean improvement.

Pulses are the dry edible seeds of food legumes. They have been an essential part of the human diet for centuries, especially in the Asian and African continents. Reference genome sequences have been generated for the major pulse crops, including common bean (*Phaseolus vulgaris* L.) (Schmutz et al., 2014), chickpea (*Cicer arietinum* L.) (Varshney et al., 2013), dry pea (*Pisum sativum* L.) (Kreplak et al., 2019), cowpea (*Vigna unguiculata* [L.] Walp.) (Lonardi

et al., 2019), and pigeon pea (*Cajanus cajan* [L.] Millsp.) (Varshney et al., 2012). Improving yield and nutritional quality are the primary targets for legume improvement. Yield is a complex trait that is both positively and negatively controlled by multiple genetic loci. Reinprecht et al. (2021) report structural and functional characterization of an anti-yield gene in common bean Phvul.009G190100 and its homolog Phvul.009G202100. The expression of these BZIP transcription factors is negatively correlated with yield in common bean. Viscarra-Torrico et al. (2021) provide an example of common bean with increased cysteine and methionine concentration. Burstin et al. (2021) provide a summary of the progress and objectives of the consortium PeaMUST, which is focused on improving the tolerance of pea to major biotic and abiotic stresses, making use of the recently published pea genome sequence (Kreplak et al., 2019) and associated bioinformatics and germplasm resources.

Lentil (*Lens culinaris* Medikus) and faba bean (*Vicia faba* L.) are emerging pulse crops for which genome sequences are lacking but significant advances have been made in recent years. Kumar et al. (2021) and Khazaei et al. (2021) review the available genetic and genomic resources for lentils and faba bean, respectively, and discuss the current status of the deployment of genomic tools in marker assisted breeding. Lupins and lablab are other underutilized pulse crops for which there is an increasing interest for human consumption. The genomes of two lupin species, *Lupinus angustifolius* L. and *Lupinus albus* L., have been recently sequenced. Kamphuis et al. (2021) provide an overview of the lupin genome and transcriptome resources and their use in germplasm improvement and breeding. Lablab, *Lablab purpureus* (L.) Sweet, a leguminous crop grown for food and feed in African countries, has also recently been sequenced (Chang et al., 2018). This crop has great genetic diversity that enables it to withstand high temperature and low rainfall conditions. Missanga et al. (2021) review the genomic and agronomic potential of this crop and discuss ways to enhance genetic resources for production sustainability, particularly under drought stress conditions.

Cowpea is an important food legume, particularly in sub-Saharan Africa where it is known as the poor man's meat. Annotated genome sequences of seven different cowpea accessions have already been publicly released (Lonardi et al., 2019, <https://phytozome-next.jgi.doe.gov/cowpeapan/>). These assemblies combined with other resources, including transcriptomes and genetic maps, have facilitated marker discovery and design as well as genome-wide association mapping studies to dissect genetic factors underlying important traits. Wu

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et al. (2021) converted approximately 40 k SNPs from the Illumina Cowpea iSelect Consortium Array into useful Kompetitive allele specific (KASP) markers, and validate a set of these markers for genetic diversity analysis and cultivar identification in asparagus bean, a vegetable-type cowpea. Muñoz-Amatruán et al. (2021) provide a phylogenetic analysis of cultivated cowpeas, mapping major loci for flowering time and other agronomic traits, based on high-density genotyping of a minicore composed of 368 diverse accessions.

With the exception of soybean and few major pulse crops, legume crops generally have suffered from limited genomic resources, research and breeding. Such undervalued orphan legumes are widely distributed across sub-Saharan Africa. Paliwal et al. (2021) focus on three such orphan crops, including Bambara groundnut (*Vigna subterranea* (L.) Verdc.), which has also been recently sequenced (Chang et al., 2018), African yam bean (*Sphenostylis stenocarpa* [Hochst. Ex A.Rich.] Harms) and Kersting's groundnut (*Macrotyloma geocarpum* [Harms] Maréchal & Baudet). They discuss constraints and prospects of producing these crops, and review the rewards of conservation and characterization of genetic resources of these indigenous African legume crops.

The foundational genetic, genomic and phenomic resources available for more than a dozen legume crops are housed in the Legume Information System (LIS; <https://legumeinfo.org>), and are integrated into various comparative genomic tools found therein. Berendzen et al. (2021) provide an overview of the LIS platform and discuss major data analysis features supported by the platform, including genome browsers, sequence-search tools, phylogenetic tree viewer, an interactive microsynteny and pan-genome viewer, and a novel genetic variant data viewer.

As comprehensive genomic and transcriptomic resources become increasingly available, the expansion to molecular characterization of other features, such as methylation pattern and chromatin accessibility, becomes essential to reveal the impact of epigenetic modifications on gene regulation. In recent years, a number of studies have focused on the epigenetic changes associated with plant development and adaptability to both biotic and abiotic stresses. Windels et al. (2021) provide a snapshot of such studies in different legume crops and highlight the impact of epigenetic mechanisms on legume productivity and adaptability.

CRISPR/Cas9 technology has rapidly transformed genome editing across biological systems. The adoption of this technology for legume improvement has been very slow due to the lack of availability of efficient protocols for plant transformation and regeneration of whole plants. Bhowmik et al. (2021) focus on the recent advances in CRISPR/Cas9-based gene editing technology, and discuss the challenges and opportunities for harnessing gene editing for improvement of different legume crops.

In summary, tremendous advancements in genome knowledge are taking place for legumes, extending steadily from the most widely consumed legume, soybean, to other species that are also relevant to food and nutritional security. This expansion of genome knowledge in many ways parallels the history of cartography. As aptly described by Carr (2010), maps, like clocks, have become such common “tools of

the mind” that their pervasiveness influences the development of human cognizance, becoming hard-wired into our brains. Does anyone now live a day unaware of what time it is, or travel anywhere without, at least mentally if not visually, conceptualizing a map? Likewise, with ever-expanding genomic knowledge in legumes, can anyone pursue a new variety without considering genetic maps, allelic variants and omics datasets? And, in the context of risks from embracing new tools of the mind, can we avoid being side-tracked by tantalizing layers of detail within genome information? Fortunately, the goals for legume improvement usually are quite circumspect—yield of plant-based protein and vegetable oil, environmental tolerance, pest and disease resistance—making it likely that legume genomic knowledge will continue to facilitate humankind's efforts to find balance between the needs of our burgeoning population and responsible stewardship of the Earth's fragile biosphere.


CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

n/a

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