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Legume Evolution: From Wild Ancestors to Modern Crops

Jingyi Zhang ✉
Tropical Legume Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China
✉ Corresponding email: jingyi.zhang@hitar.org

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Abstract Legumes hold a pivotal role in agriculture and human nutrition due to their ability to fix atmospheric nitrogen, enhancing soil fertility and providing protein-rich food. Understanding the evolutionary history of legumes is crucial for improving crop resilience and productivity. This study aims to trace the origins and early evolution of the legume family (Fabaceae), examining phylogenetic classifications, fossil records, and geographic diversification. The domestication process is analyzed, highlighting key traits selected for cultivation and identifying major centers of legume domestication globally. Advances in legume genomics are discussed, emphasizing their contributions to evolutionary studies and the role of genetic mutations in domestication. The evolution of agronomic traits, including yield, pest resistance, and nitrogen-fixing symbiosis, is explored through case studies of significant legume crops. Modern breeding techniques and biotechnology's impact on legume improvement are evaluated, alongside the integration of traditional knowledge. The importance of conserving wild relatives for genetic diversity and their utilization in breeding programs is underscored. Future directions in legume research, addressing challenges in cultivation and sustainability, and potential breakthroughs in legume science are outlined. This study concludes with a summary of key insights, implications for stakeholders, and a call to action for continued research and conservation efforts.

Keywords Legume evolution; Domestication; Genomics; Agronomic traits; Conservation

1 Introduction

Legumes have been integral to human and animal diets for millennia, serving as a cornerstone of traditional agriculture. They are highly valued for their nutritional content, providing essential proteins, complex carbohydrates, dietary fiber, and a range of vitamins and minerals. Despite their historical significance, the popularity of legumes has waned in recent decades, particularly in Europe, due to various socio-economic factors and the rise in meat consumption. However, legumes remain a sustainable and inexpensive alternative to meat, offering numerous health benefits, including antioxidant properties that help prevent chronic diseases (Maphosa and Jideani, 2017; Ferreira et al., 2021).

Understanding the evolutionary history of legumes is crucial for several reasons. Firstly, it provides insights into their adaptation mechanisms, which can inform breeding programs aimed at improving legume varieties for better yield, disease resistance, and nutritional quality. Secondly, knowledge of their evolutionary history can help in the development of sustainable agricultural practices, such as crop rotation and intercropping, which leverage the natural benefits of legumes for soil health and productivity. Lastly, this understanding can aid in overcoming cultural and societal barriers to legume consumption by highlighting their historical significance and nutritional superiority (Maphosa and Jideani, 2017; Ferreira et al., 2021).

The objective of this study is to underscore the pivotal role of legumes in transitioning towards more sustainable agri-food systems and diets, particularly in Europe. By compiling and analyzing various initiatives and strategies aimed at revitalizing legume production and consumption, this study seeks to highlight the multifaceted benefits of legumes and the obstacles that need to be addressed to achieve sustainable development goals. The significance of this study lies in its potential to influence policy-making, encourage public and private investments in legume research and technology, and ultimately, promote a shift towards healthier and more sustainable dietary patterns.

2 Origins and Early Evolution of Legumes

2.1 Phylogeny and classification of the legume family (Fabaceae)

The legume family, Fabaceae, is the third largest family of flowering plants, comprising approximately 800 genera and 20 000 species. Traditionally, Fabaceae has been divided into three subfamilies: Caesalpinioideae, Mimosoideae, and Papilionoideae, with the latter containing most of the major cultivated food and feed crops (Smýkal et al., 2015). Recent phylogenomic studies have provided a more robust framework for understanding the deep-branching relationships among these subfamilies, revealing that all six subfamilies of Fabaceae originated nearly simultaneously, challenging the traditional view of some subfamilies as 'basal' or 'early-diverging' (Figure 1) (Koenen et al., 2020). This simultaneous origin has significant implications for understanding the evolution of legume diversity and traits.

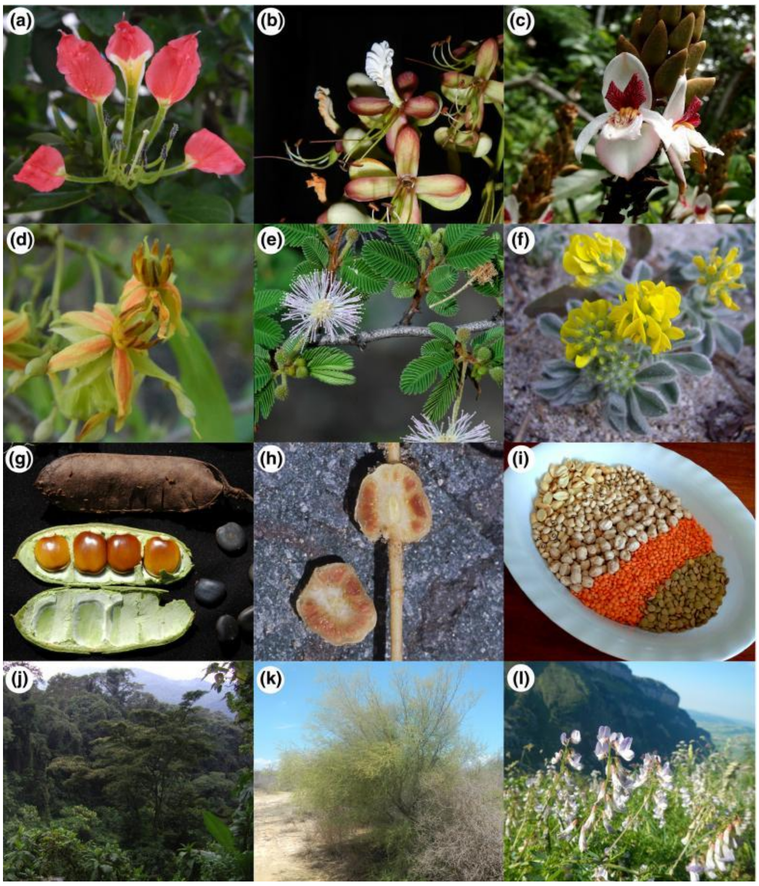

Figure 1 Diversity, ecology and economic importance of legumes (Adopted from Koenen et al., 2019)

Image caption: (a-f) The family is subdivided into six subfamilies: (a) Cercidoideae (*Bauhinia madagascariensis*); (b) Detarioideae (*Macrolobium angustifolium*); (c) Duparquetioideae (*Duparquetia orchidacea*); (d) Dialioideae (*Baudouinia sp.*); (e) Caesalpinioideae (*Mimosa pectinatipinna*); and (f) Papilionoideae (*Medicago marina*). (g) While the family has a very diverse floral morphology, the fruit (*Brodriguesia santosii*), which comes in many shapes and is most often referred to as a 'pod' or 'legume', is the defining feature of the family. (h) A large fraction of legume species is known to fix atmospheric nitrogen symbiotically with 'rhizobia', bacteria that are incorporated in root nodules, for example in *Lupinus nubigenus*. (i) Economically, the family is the second most important of flowering plants after the grasses, with a wide array of uses, including timber, ornamentals, fodder crops, and, notably, pulse crops such as peanuts (*Arachis hypogaea*), beans (*Phaseolus vulgaris*), chickpeas (*Cicer arietinum*) and lentils (*Lens culinaris*). (j-l) Ecologically, legumes are also extremely diverse and important, occurring and often dominating globally across disparate ecosystems, including: wet tropical forest, for example, *Albizia grandibracteata* in the East African Albertine Rift (j); savannas, seasonally dry tropical forests, and semi-arid thorn-scrub, for example. *Mimosa delicatula* in Madagascar (k); and temperate woodlands and grasslands, for example, *Vicia sylvatica* in the European Alps (l). Photographs: (a, b, d, i-l) Erik Koenen; (c) Jan Wieringa; (e-h) Colin Hughes (Adopted from Koenen et al., 2019)

2.2 Fossil records and molecular evidence of early legume evolution

Fossil records and molecular evidence have been pivotal in tracing the early evolution of legumes. The earliest evidence of the legume family dates back to the Late Campanian period, with fossil legume fruits discovered in northern Mexico, suggesting that Mexico could be a center of Fabaceae radiation (Centeno-González et al., 2021). Additionally, the Cretaceous-Paleogene (K-Pg) boundary mass extinction event played a crucial role in the evolution of plant diversity, including legumes. Multiple whole genome duplication (WGD) events around this period are hypothesized to have contributed to the survival and diversification of legume lineages (Koenen et al., 2020). These WGDs, along with subsequent polyploidization events, have been confirmed through phylogenomic analyses, further elucidating the complex evolutionary history of legumes (Cannon et al., 2015; Zhao et al., 2021).

2.3 Geographic origins and diversification of wild legumes

The geographic origins and diversification of wild legumes are deeply rooted in their evolutionary history. The tribe Fabeae, which includes ancient and important crops like lentil, pea, and broad bean, is believed to have originated in the East Mediterranean region during the Miocene epoch (23~16 million years ago) (Schaefer et al., 2012). From there, legumes spread across Eurasia, into tropical Africa, and the Americas through multiple long-distance dispersal events. This widespread distribution is supported by the high representation of legumes in ex situ germplasm collections, with over 1 000 000 accessions worldwide (Smýkal et al., 2015). The diversification of legumes is also marked by rapid evolutionary changes in their chloroplast genomes, which have undergone significant genomic diversification, contributing to the adaptability and success of legume species in various environments (Guo et al., 2007).

In summary, the origins and early evolution of legumes are characterized by a complex interplay of phylogenetic relationships, fossil records, and molecular evidence. The simultaneous origin of subfamilies, the impact of the K-Pg mass extinction event, and the geographic diversification from the East Mediterranean region have all played crucial roles in shaping the evolutionary trajectory of the Fabaceae family.

3 Domestication of Legumes

3.1 Transition from wild ancestors to domesticated crops

The domestication of legumes, like many other crops, involved a series of evolutionary and selective processes that transformed wild species into the cultivated varieties we rely on today. This transition was marked by significant genetic and phenotypic changes driven by human selection. For instance, the common bean (*Phaseolus vulgaris*) underwent a transformation that included the selection of traits such as reduced pod dehiscence, which was crucial for cultivation in arid regions (Parker et al., 2019). Similarly, the domestication of grain legumes like soybean (*Glycine max*) involved the selection of traits that facilitated adaptation to different latitudinal zones, such as changes in flowering time (Lu et al., 2020). The process of legume domestication has been extensively studied through genomic and archaeobotanical analyses, revealing the complex interplay between human selection and natural genetic variation (Fuller, 2007; Rendón-Anaya et al., 2017).

3.2 Key traits selected during domestication

Several key traits were selected during the domestication of legumes to enhance their suitability for agriculture:

Seed Size: Increased seed size was a common trait selected in many domesticated legumes. This trait was particularly important for improving yield and ease of harvest. For example, archaeobotanical evidence suggests that seed size in legumes like mung beans (*Vigna radiata*) and urd beans (*Vigna mungo*) increased significantly during the early stages of domestication (Fuller, 2007).

Pod Dehiscence: The reduction of pod dehiscence, or the tendency of pods to shatter and disperse seeds, was a critical trait selected in many legumes. This trait was essential for reducing seed loss during harvest. Studies on common bean and pea (*Pisum sativum*) have shown that multiple genetic loci control pod dehiscence, and selection for reduced dehiscence was a key step in their domestication (Hradilová et al., 2017; Parker et al., 2019; Parker et al., 2021).

Flowering Time: Adaptation to different growing seasons and latitudes required changes in flowering time. In soybean, for example, the selection of genes controlling flowering time allowed the crop to expand into new regions with varying day lengths and growing conditions (Weller and Ortega, 2015; Lu et al., 2020).

3.3 Major centers of legume domestication around the world

The domestication of legumes occurred independently in several regions around the world, each contributing to the diversity of legume crops we have today. In the Near East, the Fertile Crescent was a major center for the domestication of legumes such as lentils (*Lens culinaris*), peas (*Pisum sativum*), chickpeas (*Cicer arietinum*), and faba beans (*Vicia faba*) (Smýkal et al., 2015). In East Asia, China domesticated soybean (*Glycine max*), which has become one of the most important legume crops globally (Smýkal et al., 2015). South Asia, particularly India, was a center for the domestication of mung beans (*Vigna radiata*) and urd beans (*Vigna mungo*) (Fuller, 2007). In Africa, specifically West Africa, crops like cowpeas (*Vigna unguiculata*) and pearl millet (*Pennisetum glaucum*) were domesticated, with cowpeas being particularly significant for their adaptability to arid conditions (Fuller, 2007; Smýkal et al., 2015). Central and South America saw the domestication of common bean (*Phaseolus vulgaris*) and lima bean (*Phaseolus lunatus*), contributing significantly to the global legume crop pool (Figure 2) (Smýkal et al., 2015; Rendón-Anaya et al., 2017). These centers of domestication highlight the global importance of legumes and the diverse genetic resources that have been harnessed through human agricultural practices.

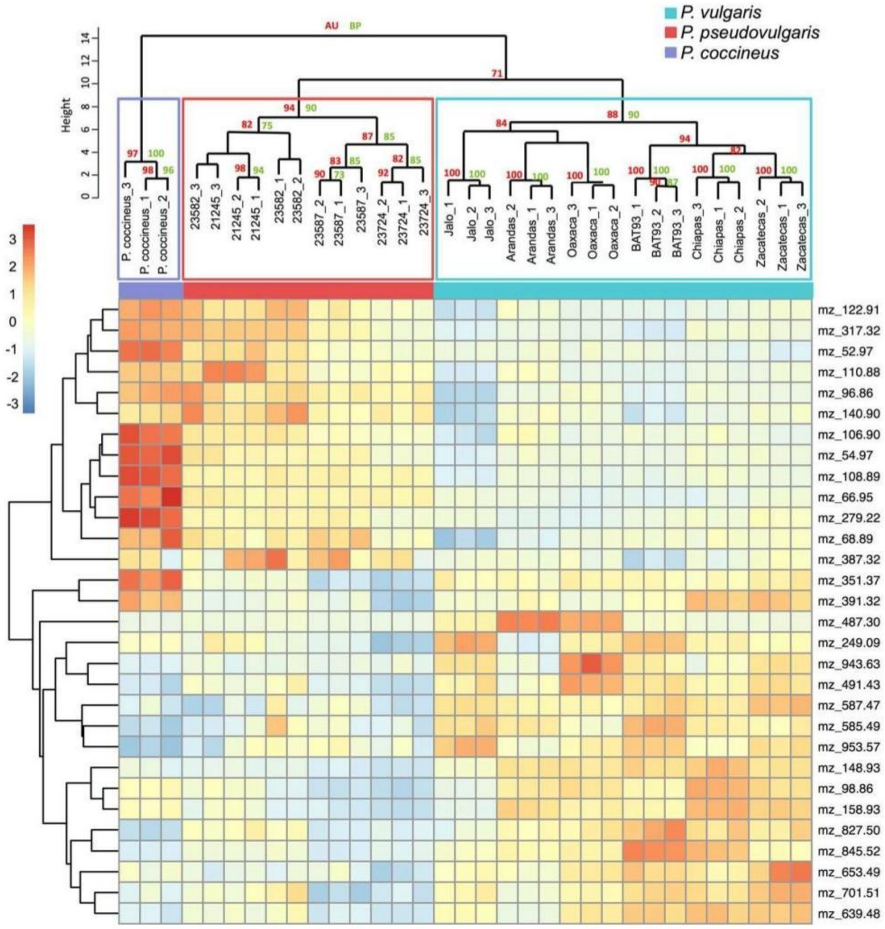

Figure 2 Metabolomic profiles of Phaseolus species (Adopted from Rendón-Anaya et al., 2017)

Image caption: The heatmap shows the 30 most informative mass signals from extracts of young trifoliate leaves that explain inter-species differences between *P. vulgaris*, *P. pseudovulgaris*, and *P. coccineus*. The associated horizontal dendrogram reproduces the phylogeny of the accessions, while the vertical dendrogram clusters mass signals according to their abundance. Approximately unbiased probabilities (AU) and bootstrap support (BP)⩾70 are displayed in the horizontal dendrogram (Adopted from Rendón-Anaya et al., 2017)

4 Genetic and Genomic Insights

4.1 Advances in legume genomics and their contributions to understanding evolution

Recent advancements in legume genomics have significantly enhanced our understanding of legume evolution. The sequencing of genomes from various legume species, such as soybean (*Glycine max*), wild peanut (*Arachis duranensis* and *Arachis ipaensis*), and barrel medic (*Medicago truncatula*), has laid a solid foundation for further genomic exploration (Wang et al., 2017). The development of a reference genome for pea (*Pisum sativum*) has provided insights into genomic rearrangements and the role of repetitive elements in legume genome evolution (Kreplak et al., 2019). Additionally, the completion of genome sequences for key legumes has revealed the importance of whole-genome duplication events in shaping legume genomes and the evolution of legume-specific traits (Young and Bharti, 2012). These genomic resources have facilitated the identification of genetic variations and adaptive genes, which are crucial for crop improvement programs (Mousavi-Derazmahalleh et al., 2018).

4.2 Comparative genomics between wild ancestors and modern crops

Comparative genomics between wild ancestors and modern crops has shed light on the genetic changes associated with domestication. For instance, the genomic history of the common bean (*Phaseolus vulgaris*) has unveiled its closest sister species and identified domestication-associated haplotypes (Rendón-Anaya et al., 2017). Similarly, the study of grain legume domestication has highlighted the genetic diversity bottlenecks created during domestication and the significance of wild relatives as reservoirs of novel genetic variation for crop breeding programs (Bohra et al., 2022). Comparative analyses have also revealed the divergent evolutionary levels among legumes and the impact of polyploidization on gene retention and copy number variation of important gene families (Wang et al., 2017). These findings underscore the importance of understanding the genetic basis of domestication to inform future breeding strategies.

4.3 Role of genetic mutations and adaptations in legume domestication

Genetic mutations and adaptations have played a pivotal role in the domestication of legumes. The identification of stress-responsive proteins through proteomic approaches has provided insights into the molecular mechanisms of stress tolerance and adaptation in legumes (Jan et al., 2022). Additionally, the genetic control of flowering time, which is crucial for adaptation to various eco-geographic locations and agricultural practices, has been extensively studied in legumes such as pea and soybean (Weller and Ortega, 2015). The discovery of legume-specific gene families and the role of gene duplication, including whole-genome duplication events, have been instrumental in the evolution of legume-specific traits (Young and Bharti, 2012). These genetic insights are essential for developing modern cultivars with improved yield, quality, and stress tolerance. By integrating genomic and genetic data, researchers can better understand the evolutionary processes that have shaped legume genomes and leverage this knowledge to enhance crop improvement efforts.

5 Evolution of Agronomic Traits

5.1 Development of traits related to yield, pest resistance, and environmental tolerance

The evolution of agronomic traits in legumes has been driven by the need to enhance yield, pest resistance, and environmental tolerance. Genetic improvement efforts have focused on integrating modern genomics, phenotyping, and systems modeling to develop high-yielding and resilient legume varieties. For instance, the integration of genomics and high-throughput phenomics has accelerated genetic gains in legumes, leading to improved varieties that perform well under diverse environmental conditions (Varshney et al., 2018). Additionally, the use of crop rotation and intercropping practices has been shown to enhance soil fertility and pest resistance, thereby improving overall crop yield and sustainability (Rodriguez et al., 2020; Kebede, 2021).

5.2 Evolution of nitrogen-fixing symbiosis in legumes

The symbiotic relationship between legumes and nitrogen-fixing bacteria, primarily rhizobia, is a key evolutionary trait that has significantly contributed to the success of legumes in various agroecosystems. This symbiosis allows legumes to fix atmospheric nitrogen, enriching the soil and reducing the need for synthetic fertilizers. The evolution of this complex trait has been shaped by genetic and environmental factors, with nearly

200 genes identified as essential for symbiotic nitrogen fixation (SNF) in legumes (Roy et al., 2020). Comparative genomics studies have revealed that nodulation, a critical component of SNF, may have originated from a common ancestor and was subsequently lost in many descendant lineages (Velzen et al., 2018). This finding challenges the traditional view of multiple independent origins of nodulation and suggests a single evolutionary event followed by parallel losses.

5.3 Case studies of specific legume crops

Soybean is one of the most extensively studied legume crops, particularly in the context of SNF. Research has identified numerous genes involved in the nodulation process and the regulation of symbiosis in soybean (Roy et al., 2020). Advances in genetic and genomic tools have facilitated the development of soybean varieties with enhanced nitrogen-fixing capabilities and improved resistance to environmental stresses.

Chickpea is another important legume crop that has benefited from genetic improvement efforts. The integration of genomics and phenotyping has led to the development of chickpea varieties with improved drought tolerance and pest resistance, which are crucial for maintaining productivity in rainfed regions (Varshney et al., 2018). Additionally, the use of intercropping and crop rotation practices has further enhanced the sustainability and yield of chickpea cultivation (Rodriguez et al., 2020; Kebede, 2021).

Lentil cultivation has also seen significant advancements through the application of modern breeding techniques. The development of lentil varieties with enhanced nitrogen-fixing abilities and resilience to environmental stresses has been a key focus of research. Comparative genomics studies have provided insights into the genetic basis of nodulation and SNF in lentils, contributing to the development of improved varieties (Marx et al., 2016; Velzen et al., 2018).

In summary, the evolution of agronomic traits in legumes has been driven by the need to enhance yield, pest resistance, and environmental tolerance. The symbiotic relationship with nitrogen-fixing bacteria has played a crucial role in the success of legumes, and ongoing research continues to uncover the genetic and environmental factors that shape this complex trait. Case studies of specific legume crops, such as soybean, chickpea, and lentil, highlight the significant progress made in developing high-yielding and resilient varieties through the integration of modern genomics, phenotyping, and sustainable agricultural practices.

6 Modern Breeding and Biotechnology

6.1 Impact of modern breeding techniques on legume improvement

Modern breeding techniques have significantly impacted legume improvement by broadening the genetic base and enhancing desirable traits. Introgression breeding, which involves the incorporation of genetic material from wild relatives into cultivated varieties, has been particularly successful. This method has led to the development of improved cultivars in various legumes such as chickpea, pigeonpea, peanut, lentil, mungbean, urdbean, and common bean. For instance, in mungbean, distant hybridization has resulted in seven improved commercial cultivars, while in urdbean, three such cultivars have been reported (Pratap et al., 2021). Additionally, the use of cytoplasmic male sterility genes from crop wild relatives (CWRs) has significantly benefited pigeonpea breeding (Pratap et al., 2021). The integration of genomics, phenomics, and speed breeding techniques has further accelerated genetic gains in legumes, making them more resilient to environmental stresses and improving their yield potential (Varshney et al., 2018; Singh et al., 2022).

6.2 Role of biotechnology and genetic engineering in legume crop development

Biotechnology and genetic engineering have played crucial roles in the development of legume crops by enabling precise modifications at the genetic level. Techniques such as transgenic technology, somatic hybridization, and intragenesis have shown promise in introducing beneficial traits into legume crops. For example, horizontal gene transfer through these biotechnological methods has facilitated the introgression of useful genes, enhancing traits such as disease resistance and stress tolerance (Pratap et al., 2021). The integration of modern genomics approaches, including genome editing tools like CRISPR/Cas9, has further revolutionized legume breeding by allowing targeted modifications to improve specific traits (Varshney et al., 2018; Singh et al., 2022). These advancements have not only increased the efficiency of breeding programs but also expanded the genetic diversity available for crop improvement (Muñoz et al., 2017).

6.3 Integration of traditional knowledge with modern science for legume breeding

The integration of traditional knowledge with modern scientific approaches has proven to be a valuable strategy in legume breeding. Traditional knowledge, which encompasses the understanding of local crop varieties and their adaptation to specific environments, provides a rich source of information that can complement modern breeding techniques. For instance, pre-breeding activities that utilize promising landraces and wild relatives have been initiated to develop new gene pools with a high frequency of useful genes and broader adaptability (Sharma et al., 2013). Combining this traditional knowledge with advanced molecular markers and genomics tools has enhanced the efficiency of introgression and reduced linkage drags, thereby improving the overall genetic enhancement of grain legumes (Sharma et al., 2013; Smýkal et al., 2015). This holistic approach ensures that the benefits of both traditional and modern practices are harnessed to develop resilient and high-yielding legume varieties.

7 Conservation of Wild Relatives

7.1 Importance of preserving wild legume species for genetic diversity

Preserving wild legume species is crucial for maintaining genetic diversity, which is essential for the resilience and adaptability of cultivated crops. Wild relatives of legumes harbor a wealth of genetic variation that has been lost in domesticated varieties due to genetic bottlenecks and selective breeding (Smýkal et al., 2015; Bohra et al., 2022; Rajpal et al., 2023). This genetic diversity includes alleles that confer resistance to diseases, tolerance to abiotic stresses, and other beneficial traits that can be utilized to improve crop performance and sustainability (Muñoz et al., 2017; Zhang et al., 2019). For instance, wild soybean (*Glycine soja*) retains higher genomic diversity compared to its domesticated counterpart, making it a valuable resource for soybean improvement (Nawaz et al., 2020).

7.2 Strategies for conserving wild legume germplasm

Several strategies are employed to conserve wild legume germplasm, including ex situ and in situ conservation methods. Ex situ conservation involves the collection and storage of seeds or other plant materials in gene banks, which allows for the preservation of genetic resources outside their natural habitats (Smýkal et al., 2015; Nawaz et al., 2020). For example, the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) has initiated pre-breeding programs to develop new gene pools in chickpea, pigeonpea, and groundnut using wild relatives (Sharma et al., 2013). In situ conservation, on the other hand, focuses on protecting wild species in their natural habitats, ensuring the maintenance of their ecological interactions and evolutionary processes (Muehlbauer et al., 2004; Muñoz et al., 2017). Both approaches are complementary and essential for the long-term conservation of genetic diversity in legumes.

7.3 Utilization of wild relatives in breeding programs to enhance crop resilience

The utilization of wild relatives in breeding programs is a promising strategy to enhance crop resilience and address the challenges posed by climate change, pests, and diseases. Wild legumes possess traits that can be introgressed into cultivated varieties to improve their performance under adverse conditions (Choi et al., 2004; Rendón-Anaya et al., 2017; Rajpal et al., 2023). Advances in genetic and genomic technologies, such as whole-genome sequencing, quantitative trait loci (QTL) mapping, and marker-assisted selection (MAS), have facilitated the identification and transfer of beneficial alleles from wild relatives to domesticated crops (Sharma et al., 2013; Muñoz et al., 2017; Rajpal et al., 2023). For instance, the integration of omics technologies has expanded the capacity to monitor genetic changes and identify stress-responsive genes in wild legumes, which can be harnessed to develop stress-tolerant and high-yielding cultivars (Figure 3) (Zhang et al., 2019; Bohra et al., 2022). Additionally, pre-breeding efforts have successfully introgressed desirable traits from wild germplasm into breeding lines, overcoming barriers such as cross-incompatibility and linkage drag (Muehlbauer et al., 2004; Sharma et al., 2013). By preserving and utilizing the genetic diversity of wild legume species, breeding programs can develop more resilient and sustainable crop varieties, ensuring food security and agricultural productivity in the face of global challenges.

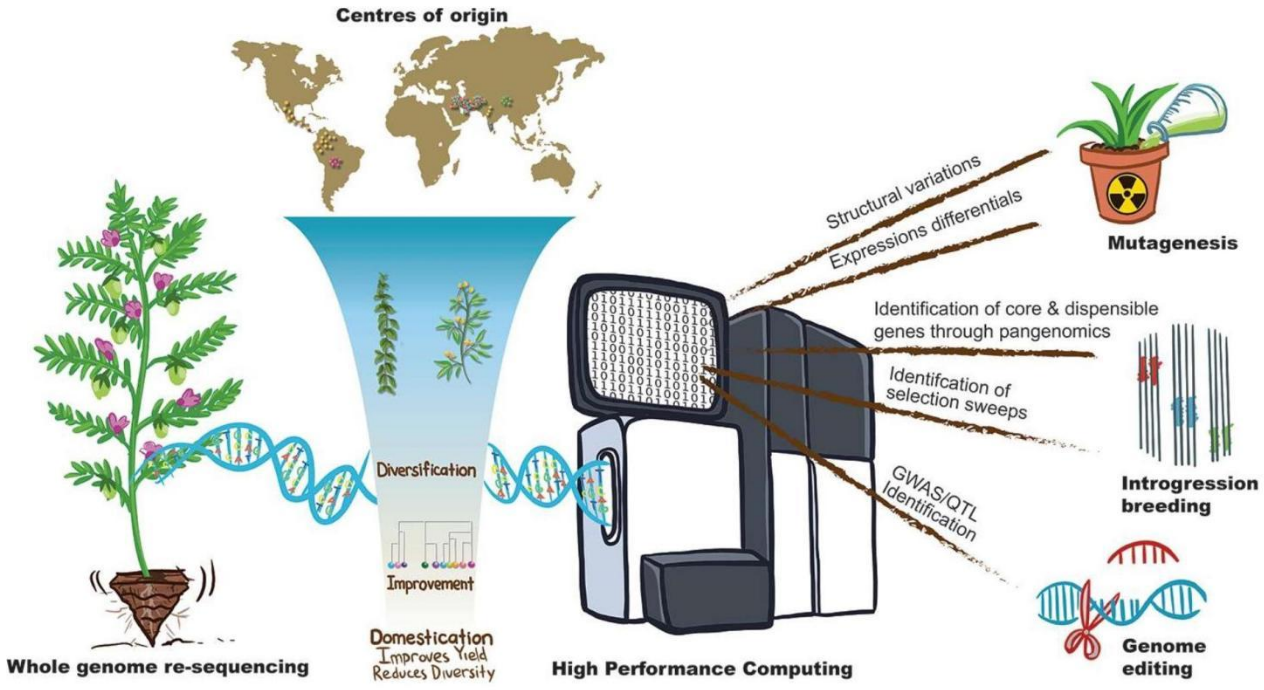

Figure 3 Understanding domestication of grain legumes for future improvement (Adopted from Bohra et al., 2022)

Image caption: Grain legumes have been domesticated in different centers of origins worldwide and then spread to diverse eco-geographies for crop production. Morpho-physiological traits during domestication and diversification/improvement show distinct phenotypes among wild and current breeding pools. In recent years, incorporation of omics-level data and pangenome has strengthened crop genetic research. Once the key domestication loci are precisely mapped, the CWRs can be readily converted into domesticated forms by transferring these loci into CWRs through gene editing, introgression and mutagenesis approaches. Rapid domestication of CWRs using advanced biotechnologies will be key to sustainable crop improvement (Adopted from Bohra et al., 2022)

8 Future Directions and Challenges

8.1 Emerging trends in legume research and breeding

Recent advancements in legume research and breeding have focused on integrating modern genomic tools with traditional breeding methods to enhance genetic diversity and improve crop resilience. The use of wild relatives and gene pools has been emphasized to broaden the genetic base of legumes, which is crucial for overcoming the yield plateau and achieving higher genetic gains (Muñoz et al., 2017; Singh et al., 2022). Techniques such as pre-breeding, alien gene introgression, and speed breeding are being increasingly adopted to accelerate the development of improved legume varieties. Additionally, the application of genetic engineering and genome editing tools, such as CRISPR/Cas9, is expected to revolutionize legume breeding by enabling precise modifications of desirable traits (Singh et al., 2022).

8.2 Addressing challenges in legume cultivation and sustainability

Legume cultivation faces several challenges, including fluctuating climates, soil deterioration, and the need for sustainable agricultural practices. To address these issues, researchers are exploring the potential of crop wild relatives (CWRs) and exotic germplasm to introduce novel genetic variations that can enhance stress tolerance and adaptability to diverse environmental conditions (Muñoz et al., 2017; Pratap et al., 2021). Introgression breeding has shown promise in developing improved cultivars with enhanced agronomic traits, such as disease resistance and drought tolerance (Pratap et al., 2021). Moreover, integrating advanced genomic approaches with traditional breeding methods can help mitigate the genetic bottlenecks that have limited the genetic diversity of domesticated legumes (Muñoz et al., 2017).

8.3 Potential breakthroughs in legume science and agriculture

The future of legume science and agriculture holds several potential breakthroughs that could significantly impact global food security. One promising area is the development of specialized populations for transferring quantitative trait loci (QTLs) from CWRs into elite backgrounds, which can lead to the discovery of cryptic genetic variations and the development of superior cultivars. Additionally, the use of horizontal gene transfer techniques, such as transgenic technology and somatic hybridization, offers new avenues for introducing beneficial traits into legume crops. The integration of genomics, phenomics, and advanced breeding techniques is expected to drive a paradigm shift in legume breeding, ultimately leading to the development of more resilient and productive legume varieties (Pratap et al., 2021; Singh et al., 2022). By addressing these emerging trends, challenges, and potential breakthroughs, legume research and breeding can contribute to sustainable agriculture and global food security in the face of changing environmental conditions and growing population demands.

9 Concluding Remarks

The evolution of legumes from their wild ancestors to modern crops has been a complex journey marked by significant genetic, agronomic, and ecological advancements. Key insights from the reviewed literature highlight the importance of crop wild relatives (CWRs) and landraces in broadening the genetic base of legume crops. Introgression breeding has been particularly successful in incorporating novel genetic variations and improving agronomic traits in various legumes such as chickpea, pigeonpea, and mungbean. The integration of modern genomics, phenomics, and advanced breeding techniques has further accelerated genetic gains, making legumes more resilient to climatic stresses and enhancing their nutritional value. Evolutionary studies have provided a deeper understanding of the domestication processes and the genetic changes that have occurred, offering valuable insights for future breeding programs.

For researchers, the findings underscore the necessity of continuing to explore and utilize the genetic diversity present in wild relatives and landraces. Advanced genomic tools and techniques should be leveraged to identify and introgress beneficial traits into cultivated varieties. Breeders are encouraged to adopt pre-breeding and introgression strategies to overcome genetic bottlenecks and develop cultivars with enhanced resistance to biotic and abiotic stresses. Policymakers should support initiatives that promote the conservation of wild germplasm and facilitate the exchange of genetic resources across borders. Investments in research infrastructure and breeding programs are crucial to ensure food security and sustainable agricultural practices.

The journey of legume evolution is far from complete. Continued research is essential to unlock the hidden genetic potential of wild relatives and to develop innovative breeding strategies that can address the challenges posed by climate change and population growth. Conservation efforts must be intensified to protect the genetic diversity of wild legumes, which are invaluable resources for future crop improvement. Collaborative efforts among researchers, breeders, and policymakers are vital to create a sustainable and resilient legume production system. By fostering a multidisciplinary approach and investing in cutting-edge technologies, we can ensure the continued evolution and improvement of legume crops for the benefit of global food security and agricultural sustainability.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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