Legume Genomics and Genetics 2024, Vol.15, No.5, 221-231
http://cropscipublisher.com/index.php/lgg

Research Report **Open Access**

Genetic Improvement of Chickpeas: Traits, Targets, and Technology

Tianxia Guo ✉
Institute of Life Sciences, Jiyang College, Zhejiang A&F University, Zhuji, 311800, Zhejiang, China
✉ Corresponding email: tianxia.guo@cuixi.org

Legume Genomics and Genetics, 2024 Vol.15, No.5 doi: 10.5376/lgg.2024.15.0022
Received: 04 Sep., 2024
Accepted: 05 Oct., 2024
Published: 15 Oct., 2024

Preferred citation for this article:
Guo T.X., 2024, Genetic improvement of chickpeas: traits, targets, and technology, Legume Genomics and Genetics, 15(5): 221-231 (10.5376/lgg.2024.15.0022)

Abstract Chickpeas (*Cicer arietinum* L.) are a vital legume crop, contributing significantly to global food security and nutrition. However, chickpea cultivation faces numerous challenges, including yield instability, susceptibility to biotic and abiotic stresses, and the need for improved nutritional quality. This study explores key traits for chickpea improvement, focusing on enhancing yield, resistance to diseases and pests, tolerance to environmental stresses, and nutritional enhancement. It further reviews molecular and genomic approaches such as Marker-Assisted Selection (MAS), Genomic Selection (GS), Genetic Mapping, Quantitative Trait Loci (QTL) analysis, and CRISPR/Cas9 genome editing, highlighting their application in chickpea breeding programs. A case study on improving drought tolerance is presented, illustrating genetic, genomic, and breeding strategies to develop drought-resilient varieties. Emerging technologies like high-throughput phenotyping, multi-omics, and artificial intelligence are discussed for their potential to revolutionize chickpea breeding. The study also addresses challenges and opportunities, emphasizing the need for diverse germplasm utilization, effective policy support, and bridging the gap between research and farmer adoption. The study concludes by underscoring the pivotal role of integrative breeding technologies in shaping the future of chickpea improvement programs and ensuring sustainable agricultural practices.

Keywords Chickpea improvement; Biotic and abiotic stress tolerance; Molecular breeding; Genomic selection; Drought resilience

1 Introduction

Chickpea (*Cicer arietinum* L.) is the second most consumed legume crop globally, cultivated in over 50 countries. It is a vital source of essential nutrients, including vitamins A, C, E, K, B1-B3, B5, B6, B9, and minerals such as iron, zinc, magnesium, and calcium, which are beneficial for human health. Chickpeas are particularly important for diabetics due to their low glycemic index and high fiber content. Additionally, chickpeas contribute significantly to food security and the livelihoods of small-scale farmers in developing countries (Koul et al., 2022). The crop’s high protein content and essential fatty acids further enhance its nutritional value, making it a crucial component of the human diet (Madurapperumage et al., 2021).

Despite its nutritional benefits and agricultural importance, chickpea cultivation faces several challenges. The crop is often grown in marginal soils with low phosphorus availability, which severely hampers yields (Djouider et al., 2022). Biotic and abiotic stresses, including drought, heat, cold, and salinity, also significantly affect chickpea productivity (Arriagada et al., 2022). Although there have been advancements in developing stress-resistant varieties, there are still gaps that need to be addressed to improve yield and resilience (Koul et al., 2022). The genetic diversity within chickpea species offers potential for breeding programs, but the complexity of its genome and the need for precise phenotyping and novel breeding strategies pose additional challenges (Hiremath et al., 2011; Varshney et al., 2013).

This study aims to review the current state of chickpea genetic improvement, focusing on key traits, targets, and technologies. We will explore the nutritional and agricultural importance of chickpeas, the challenges faced in their cultivation, and the objectives of ongoing research efforts. The scope includes an examination of genomic technologies, such as genomics-assisted breeding, high-throughput phenotyping, and novel breeding strategies, which are essential for developing high-yielding, climate-resilient, and stress-tolerant chickpea varieties. By addressing these aspects, this paper seeks to provide a comprehensive overview of the advancements and future directions in chickpea genetic improvement.

2 Key Traits for Chickpea Improvement

2.1 Yield and yield-related traits

Yield potential in chickpeas is influenced by several key traits, including early maturity, photosynthetic efficiency, and resistance to both biotic and abiotic stresses. Early maturing varieties have been developed to escape terminal drought and heat stresses, which are critical in short-season environments (Gaur et al., 2012). Additionally, enhancing photosynthetic efficiency has been identified as a vital factor for increasing seed yield per plant. Genetic studies have pinpointed specific genes, such as those coding for chlorophyll A-B binding proteins, which are associated with improved photosynthetic efficiency and, consequently, higher seed yields (Basu et al., 2018).

Breeding for yield stability involves developing cultivars that can maintain high yields under varying environmental conditions. This includes incorporating resistance to major diseases and pests, as well as tolerance to abiotic stresses like drought and heat. Marker-assisted selection (MAS) is being utilized to combine resistance to multiple stresses, thereby improving the overall yield stability of chickpea cultivars (Millán et al., 2006). The integration of genomic technologies has also started to enhance the precision and efficiency of breeding programs aimed at yield stability (Gaur et al., 2012).

2.2 Resistance to biotic stresses

Chickpea production is significantly hampered by various biotic stresses, including fungal diseases like Fusarium wilt and Ascochyta blight, as well as pests such as the pod borer (*Helicoverpa* spp.) (Millán et al., 2006; Li et al., 2015; Choudhary et al., 2022). These diseases and pests can cause substantial yield losses, sometimes up to 100% under severe conditions.

Incorporating genetic resistance into chickpea cultivars is a primary objective in many breeding programs. Quantitative trait loci (QTL) for resistance genes have been identified and mapped, and molecular markers associated with these loci are being used for efficient pyramiding of resistance traits (Li et al., 2015; Choudhary et al., 2022). Advances in genomics, such as the development of high-resolution phenotyping tools and next-generation sequencing, are expected to further enhance the efficiency of breeding programs focused on biotic stress resistance (Gaur et al., 2012).

2.3 Tolerance to abiotic stresses

Drought and heat are major abiotic stresses that limit chickpea productivity. Mechanisms for drought tolerance include early maturity to escape terminal drought and the development of deep root systems to access water from deeper soil layers (Millán et al., 2006). Heat tolerance is often achieved through the selection of genotypes that can maintain reproductive success under high temperatures (Gaur et al., 2012). Improving water-use efficiency (WUE) is crucial for chickpea cultivation in arid and semi-arid regions. Breeding programs are focusing on traits such as reduced stomatal conductance and increased root depth to enhance WUE. Marker-assisted selection is being employed to identify and incorporate these traits into elite chickpea lines.

2.4 Nutritional quality and biofortification

Chickpeas are a vital source of protein and micronutrients, especially in developing countries. Breeding efforts are aimed at enhancing the protein content and bioavailability of essential micronutrients like iron and zinc. Genomic tools are being used to identify candidate genes associated with these nutritional traits, facilitating their incorporation into high-yielding cultivars (Figure 1) (Acharjee and Sarmah, 2013; Varshney et al., 2013; Halladakeri et al., 2023). Anti-nutritional factors such as phytic acid can reduce the bioavailability of essential nutrients in chickpeas. Breeding programs are targeting the reduction of these compounds to improve the nutritional quality of chickpeas. Advances in molecular breeding and the use of functional markers are aiding in the identification and selection of genotypes with lower levels of anti-nutritional factors.

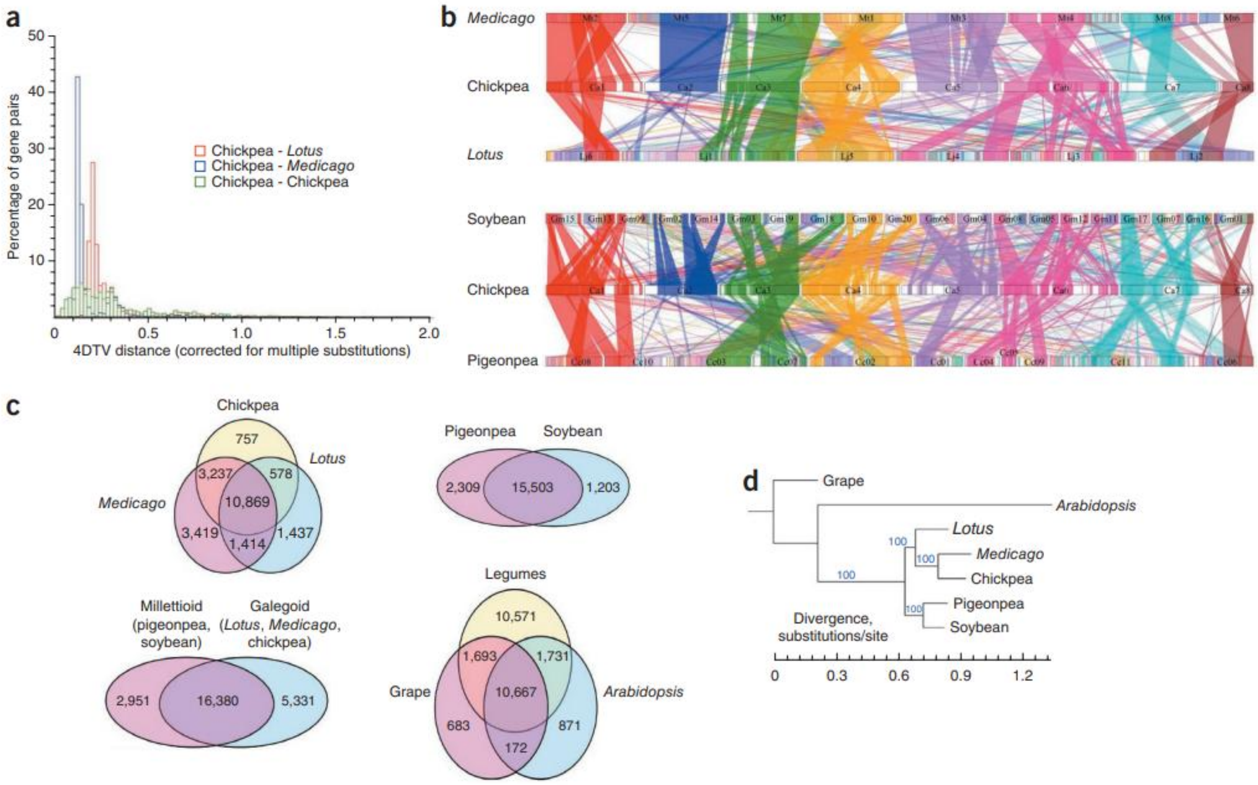

Figure 1 Comparison of chickpea, legume and other dicotyledonous genomes (Adopted from Varshney et al., 2013)

Image caption: (a) Age distribution of 4DTV for genes from three legume species (chickpea, *M. truncatula* and *L. japonicus*) genomes. (b) Synteny blocks shared between chickpea and other sequenced legume genomes, including *M. truncatula*, *L. japonicus*, soybean and pigeonpea. (c) Shared and unique gene families in legume species chickpea, *M. truncatula*, *L. japonicus*, soybean, pigeonpea; in millettioid and galegoids, and in legumes, *A. thaliana* and grape. (d) Phylogenetic tree of seven species (Adopted from Varshney et al., 2013)

3 Molecular and Genomic Approaches in Chickpea Breeding

3.1 Marker-assisted selection (MAS)

Marker-Assisted Selection (MAS) is a technique that uses molecular markers to assist in the selection of desirable traits in crop breeding. In chickpeas, MAS has been effectively used to improve traits such as drought tolerance, *Fusarium* wilt resistance, and *Ascochyta* blight resistance. The advent of next-generation sequencing (NGS) technologies has significantly enhanced the efficiency of MAS by enabling the identification and utilization of single nucleotide polymorphisms (SNPs) and other molecular markers (He et al., 2014; Sudheesh et al., 2021).

MAS has led to the development of chickpea varieties with improved resistance to various biotic and abiotic stresses. For instance, marker-assisted backcrossing (MABC) has been used to introgress QTL regions for drought tolerance and disease resistance into elite chickpea lines (Varshney et al., 2013). However, the application of MAS is limited by the complexity of quantitative traits, which are controlled by multiple genes with small effects. This complexity often requires the integration of other breeding approaches, such as genomic selection (GS), to fully exploit the potential of MAS (Varshney et al., 2017; Budhlakoti et al., 2022).

3.2 Genomic selection (GS)

Genomic Selection (GS) is a breeding method that uses genome-wide marker data to predict the breeding values of individuals. Unlike MAS, which focuses on specific markers linked to traits of interest, GS incorporates all available marker information into prediction models. This approach allows for the selection of individuals with superior genetic potential even before phenotypic evaluation, thereby accelerating the breeding cycle (Varshney et al., 2017; Sandhu et al., 2022). GS has shown promise in improving yield and stress tolerance in chickpeas. Studies have demonstrated high prediction accuracies for traits such as seed yield and days to maturity using GS models. The integration of GS with high-throughput phenotyping and genotyping technologies can further enhance the efficiency of chickpea breeding programs, making it a valuable tool for developing climate-resilient chickpea varieties (Roorkiwal et al., 2016; Budhlakoti et al., 2022; Biswas et al., 2023).

3.3 Genetic mapping and QTL analysis

Quantitative Trait Loci (QTL) mapping involves identifying regions of the genome that are associated with specific traits. In chickpeas, QTL mapping has been used to identify loci linked to important agronomic traits such as drought tolerance, disease resistance, and yield components. The development of dense genetic maps has facilitated the identification of these QTLs, providing valuable targets for MAS and GS. QTLs play a crucial role in the genetic improvement of chickpeas by enabling the targeted introgression of beneficial alleles into breeding lines. For example, QTLs associated with *Ascochyta* blight resistance have been successfully introgressed into chickpea cultivars, enhancing their resistance to this devastating disease. The identification and utilization of QTLs are essential for the development of chickpea varieties with improved performance under various environmental conditions (Varshney et al., 2017; Sandhu et al., 2022; Zhong, 2024).

3.4 CRISPR/Cas9 and genome editing

CRISPR/Cas9 is a powerful genome-editing tool that allows for precise modifications of specific genes. In chickpeas, CRISPR/Cas9 has the potential to target and edit genes associated with key traits such as disease resistance, drought tolerance, and yield. This technology offers a rapid and efficient means of introducing desirable genetic variations, thereby accelerating the breeding process (Varshney et al., 2017; Budhlakoti et al., 2022). Recent advances in CRISPR/Cas9 technology have demonstrated its potential in crop improvement. For instance, gene editing has been used to enhance disease resistance and stress tolerance in various crops, including chickpeas. The successful application of CRISPR/Cas9 in chickpeas could lead to the development of superior cultivars with enhanced agronomic traits, contributing to increased productivity and sustainability in chickpea farming.

4 Case Study: Enhancing Drought Tolerance in Chickpeas

4.1 Importance of drought tolerance in chickpea cultivation

Drought is a significant constraint in chickpea cultivation, leading to substantial yield losses. Chickpea, primarily grown in arid and semi-arid regions, is highly susceptible to terminal drought stress, which can result in up to 50% reduction in production (Varshney et al., 2013; Sachdeva et al., 2020). The increasing frequency and intensity of droughts due to climate change further exacerbate this issue, affecting various growth stages of the crop, including flowering and podding (Karalija et al., 2022). The economic and social implications of drought tolerance in chickpeas are profound. Chickpeas are a crucial source of protein for many resource-poor farmers in developing countries. Enhancing drought tolerance can stabilize yields, ensuring food security and economic stability for these communities. Moreover, drought-tolerant varieties can reduce the need for irrigation, conserving water resources and reducing production costs (Asati et al., 2022; Tiwari et al., 2023).

4.2 Genetic basis of drought tolerance

Research has identified several key genes and pathways involved in drought tolerance in chickpeas. For instance, transcription factors such as WRKY, DREB2A, and CarNAC3 have been shown to play significant roles in regulating drought responses (Borhani et al., 2019). Additionally, the ASR gene has been characterized for its involvement in drought stress regulation, with increased expression under drought conditions (Sachdeva et al., 2020). Genomic studies have also identified QTL clusters, particularly on CaLG04, which are associated with multiple drought tolerance traits (Varshney et al., 2013). Advancements in genomic resources and tools have facilitated the breeding of drought-tolerant chickpea varieties. Whole genome resequencing and the development of high-density genetic maps have enabled the identification of SNPs and QTLs associated with drought tolerance (Thudi et al., 2023). Marker-assisted selection (MAS) and genome-wide association studies (GWAS) are powerful tools that have been employed to enhance the precision and efficiency of breeding programs (Asati et al., 2022).

4.3 Breeding strategies for drought tolerance

Conventional breeding approaches for drought tolerance in chickpeas include the selection of genotypes with desirable traits such as deep root systems and high root biomass, which are beneficial for managing terminal drought stress (Asati et al., 2022). Field trials in various environments have been used to evaluate the performance of different genotypes under drought conditions, identifying those with superior drought tolerance (Arif et al., 2021). Integrating genomic and phenotypic data has become a cornerstone of modern breeding strategies. The use of multi-parent advanced generation intercross (MAGIC) populations and high-resolution mapping has allowed for the precise identification of drought tolerance traits (Thudi et al., 2023). Combining phenotypic data with genomic information enables the selection of genotypes with the best combination of traits for drought tolerance (Tiwari et al., 2023).

4.4 Field trials and validation studies

Several case studies have demonstrated the success of breeding programs in developing drought-tolerant chickpea varieties. For example, the genotype ICC 4958 has shown high chlorophyll content and enzyme activities under drought stress, making it a promising candidate for drought tolerance (Tiwari et al., 2023). Additionally, genotypes such as CH55/09 have been identified as highly productive under stress conditions through field trials (Arif et al., 2021). Future research aims to further enhance drought tolerance in chickpeas by exploring new genetic resources and employing advanced biotechnological approaches. The ongoing development of transgenic and genome-edited chickpea varieties holds promise for achieving higher levels of drought tolerance. Continued efforts in field trials and validation studies will be crucial for the successful deployment of these advanced breeding strategies (Figure 2) (Karalija et al., 2022; Sachdeva et al., 2022).

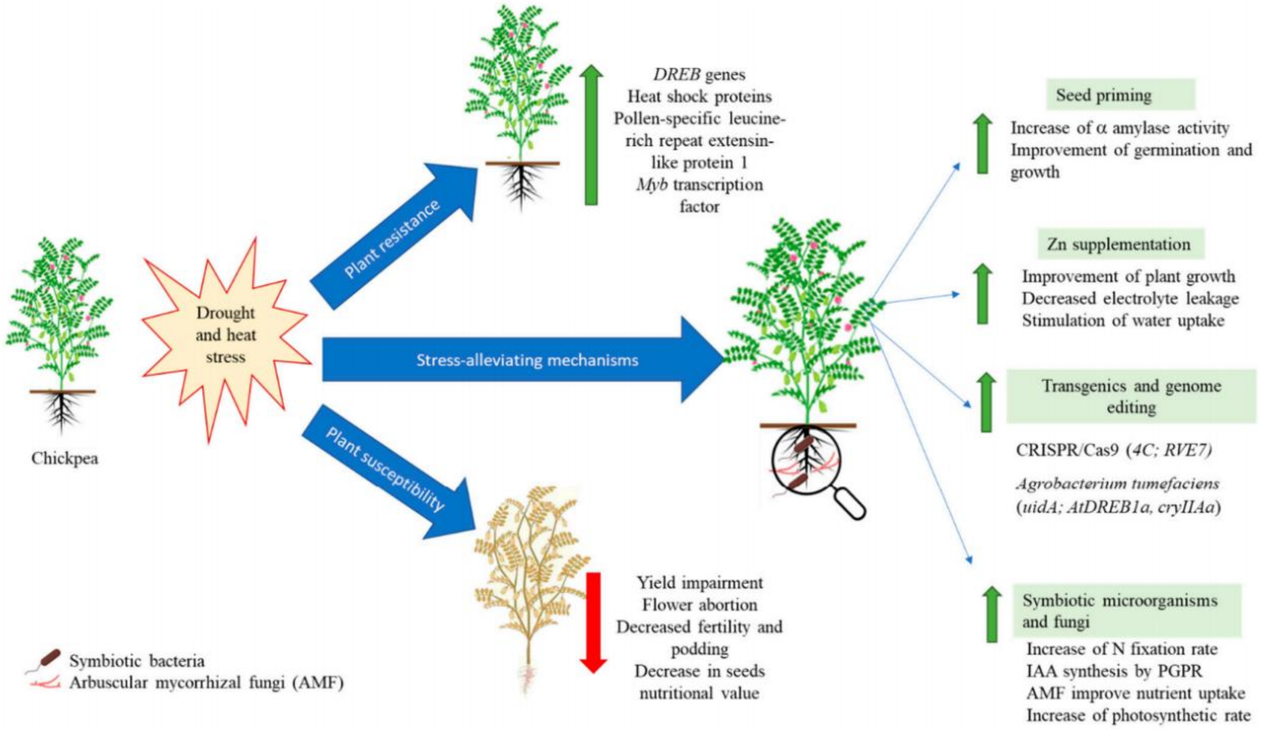

Figure 2 Chickpea tolerance of drought and heat and alleviation strategies (Adopted from Karalija et al., 2022)

5 Emerging Technologies and Future Directions

5.1 High-throughput phenotyping and genotyping

High-throughput phenotyping (HTP) has revolutionized the way we assess plant traits, enabling precise and rapid screening of large populations. This technology employs sophisticated non-invasive imaging, spectroscopy, and robotics to collect high-quality phenotypic data, which is crucial for understanding plant responses to various stresses and improving crop resilience (Mir et al., 2019). For instance, HTP systems have been used to evaluate vegetative drought tolerance in chickpea, providing insights into growth, physiological traits, and recovery under different water regimes (Lauterberg et al., 2023). These advancements in phenomics are pivotal for precision agriculture, allowing for the identification of superior genotypes with enhanced stress tolerance and productivity.

The integration of high-throughput genotyping and phenotyping technologies into breeding programs has significantly accelerated genetic gains in chickpea. Modern breeding approaches, such as marker-assisted selection and genomic selection, rely heavily on these technologies to identify and select desirable traits (Varshney et al., 2012; Hou et al., 2024). For example, the development of high-density SNP arrays and genotyping platforms has facilitated the creation of detailed genetic maps and the identification of quantitative trait loci (QTLs) associated with important agronomic traits (Roorkiwal et al., 2017). By combining high-resolution phenotypic and genotypic data, breeders can enhance selection efficiency and develop superior chickpea varieties more rapidly (Varshney et al., 2018; Roorkiwal et al., 2020).

5.2 Systems biology and multi-omics approaches

Systems biology approaches that integrate transcriptomics, proteomics, and metabolomics are transforming chickpea breeding by providing a comprehensive understanding of the molecular mechanisms underlying important traits. These multi-omics strategies enable the identification of key genes, proteins, and metabolites involved in stress responses and other agronomic traits (Roorkiwal et al., 2020; Singh et al., 2022). For instance, advances in next-generation sequencing and high-throughput genotyping have led to the development of extensive genomic resources, including transcriptome assemblies and SNP markers, which are essential for multi-omics studies (Varshney et al., 2012). The integration of these omics data sets facilitates a holistic view of the plant's biology, aiding in the discovery of novel targets for genetic improvement.

The application of multi-omics approaches in chickpea breeding has led to significant advancements in trait discovery and improvement. By leveraging transcriptomics, proteomics, and metabolomics data, researchers can identify candidate genes and pathways associated with traits such as drought tolerance, disease resistance, and nutritional quality (Roorkiwal et al., 2020; Singh et al., 2022). For example, genomics-assisted breeding has successfully introgressed QTLs for drought tolerance into elite chickpea varieties, resulting in lines with higher yield under stress conditions (Thudi et al., 2014). These multi-omics approaches are crucial for developing climate-resilient and high-yielding chickpea cultivars.

5.3 Machine learning and artificial intelligence in breeding

Machine Learning (ML) and Artificial Intelligence (AI) are increasingly being used in chickpea breeding to develop predictive models and decision support tools. These technologies can analyze large and complex data sets, including genomic, phenotypic, and environmental data, to predict the performance of breeding lines and guide selection decisions (Roorkiwal et al., 2020; Varshney et al., 2018). For instance, ML algorithms can be used to predict the genetic potential of lines for specific traits, thereby enhancing the efficiency of breeding programs. The integration of AI in breeding pipelines helps in optimizing resource allocation and accelerating the development of improved chickpea varieties.

AI plays a crucial role in accelerating genetic gains in chickpea breeding by enabling more precise and efficient selection processes. By utilizing AI-driven tools, breeders can identify the best-performing genotypes with greater accuracy and speed, thus reducing the breeding cycle time (Varshney et al., 2018). AI technologies, such as deep learning and neural networks, can also uncover complex patterns and interactions within the data that are not easily detectable through traditional methods (Roorkiwal et al., 2020). This capability is particularly valuable for addressing the challenges posed by climate change and ensuring the development of robust and high-yielding chickpea varieties.

6 Challenges and Opportunities in Chickpea Improvement

6.1 Genetic diversity and germplasm utilization

Genetic diversity is crucial for the success of breeding programs as it provides the raw material for selection and adaptation to changing environmental conditions. Diverse germplasm lines offer a wide range of alleles that can be harnessed to improve agronomic traits such as yield, disease resistance, and stress tolerance. For instance, the evaluation of a chickpea core collection identified diverse agronomically superior germplasm, which can be used to develop high-yielding cultivars with a broad genetic base (Upadhyaya et al., 2007). Additionally, the use of specialized germplasm subsets like mini core collections and reference sets has facilitated the identification of trait-specific germplasm, aiding in trait mapping and allele mining for resistance to biotic and abiotic stresses (Upadhyaya et al., 2011).

Effective germplasm management involves the development and utilization of core collections, which represent a subset of the entire germplasm collection while maintaining genetic diversity. For example, a core subset of chickpea was developed using geographic distribution and quantitative traits, preserving the genetic variation available in the entire collection (Upadhyaya et al., 2001). Moreover, the integration of genomic tools such as single nucleotide polymorphisms (SNPs) and diversity arrays technology (DArT) has enabled the creation of integrated genetic maps, facilitating the identification of genes associated with important traits (Upadhyaya et al., 2011). The use of multi-parent advanced generation intercross (MAGIC) populations has also been shown to enhance genetic diversity and bring novel alleles for developing superior chickpea varieties (Samineni et al., 2021).

6.2 Bridging the gap between research and adoption

Extension services play a vital role in bridging the gap between research and adoption by disseminating new technologies and practices to farmers. Farmer participatory breeding involves the active participation of farmers in the breeding process, ensuring that the developed varieties meet their needs and preferences. This approach has been shown to enhance the adoption of new chickpea varieties, as farmers are more likely to adopt varieties that they have helped to develop and that are suited to their local conditions (Roorkiwal et al., 2020).

Policy support and adequate funding are essential for the sustained improvement of chickpea. Governments and funding agencies need to prioritize chickpea research to address the challenges of low productivity and climate change. Investments in modern breeding technologies, such as genomic selection and breeding by design, can accelerate the development of climate-resilient chickpea varieties (Roorkiwal et al., 2020). Additionally, policies that support the conservation and utilization of genetic resources can enhance the effectiveness of breeding programs (Upadhyaya et al., 2011).

6.3 Ethical and biosafety considerations

The use of genetic modification (GM) in chickpea improvement raises several ethical and biosafety concerns. These include the potential impact on biodiversity, the unintended effects on non-target organisms, and the socio-economic implications for smallholder farmers. It is essential to conduct thorough risk assessments and engage with stakeholders to address these concerns. The development of GM chickpea varieties should be guided by principles of transparency, safety, and sustainability (Roorkiwal et al., 2020). Regulatory frameworks play a critical role in ensuring the safe development and deployment of GM chickpea varieties. These frameworks should be based on scientific evidence and include provisions for monitoring and managing potential risks. Public perception of GM crops is also a significant factor influencing their adoption. Efforts to improve public understanding of the benefits and risks associated with GM chickpea, through education and transparent communication, can help build trust and acceptance. By addressing these challenges and leveraging the opportunities, chickpea improvement programs can develop high-yielding, resilient, and nutritious varieties that contribute to food security and sustainable agriculture.

7 Concluding Remarks

The genetic improvement of chickpeas has seen significant advancements through the integration of modern genomic technologies with traditional breeding methods. Key achievements include the development of high-resolution phenotypic and genetic data, which have facilitated the identification of genes and biological pathways associated with important breeding traits. The use of molecular markers and quantitative trait loci (QTL) mapping has enhanced the efficiency of gene transfer and trait pyramiding, particularly for resistance to biotic and abiotic stresses. The draft genome sequence of chickpea has provided a valuable resource for trait improvement, highlighting candidate genes for disease resistance and agronomic traits. Additionally, the development of specialized germplasm subsets and the application of next-generation sequencing technologies have opened new avenues for trait mapping and allele mining. Recent breeding programs have also enhanced genetic diversity in both desi and kabuli varieties, reflecting the impact of modern breeding efforts.

Future chickpea breeding programs stand to benefit greatly from the continued integration of genomic tools and technologies. The use of marker-assisted selection (MAS) and genomic selection (GS) will be crucial in accelerating the development of superior chickpea varieties with enhanced resistance to biotic and abiotic stresses. The identification and utilization of novel haplotypes from diverse germplasm resources will further enhance the genetic base of chickpea breeding programs. Additionally, the adoption of advanced breeding techniques such as speed breeding and CRISPR/Cas9-based genome editing holds promise for achieving rapid genetic gains and meeting the growing demand for chickpea. Collaborative efforts between public and private organizations will be essential in generating 'super chickpeas' with multiple transgenic traits to address various production constraints.

The role of technology in chickpea improvement cannot be overstated. The advent of next-generation sequencing and other genomic tools has revolutionized the way breeding programs are conducted, enabling more precise and efficient selection of desirable traits. The integration of functional omics, parental selection, forward breeding, and genome-wide selection is expected to bring a paradigm shift in the development of climate-resilient and high-yielding chickpea varieties. As we move forward, it is imperative to bridge the genome-to-phenome gap by integrating modern genomics technologies with molecular breeding efforts. The continuous improvement of breeding programs through sequence-based approaches and the adoption of innovative technologies will ensure sustained genetic gains and contribute to global food and nutritional security.

Acknowledgments

I am grateful to Julie for critically reading the manuscript and providing valuable feedback that improved the clarity of the text. I am also grateful to the anonymous reviewers for their constructive feedback that significantly improved the manuscript.

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.

References

Acharjee S., and Sarmah B., 2013, Biotechnologically generating ‘super chickpea’ for food and nutritional security, Plant Science, 207: 108-116.
https://doi.org/10.1016/j.plantsci.2013.02.003

Arif A., Parveen N., Waheed M., Atif R., Waqar I., and Shah T., 2021, A comparative study for assessing the drought-tolerance of chickpea under varying natural growth environments, Frontiers in Plant Science, 11: 607869.
https://doi.org/10.3389/fpls.2020.607869

Arriagada O., Cacciuttolo F., Cabeza R., Carrasco B., and Schwember A., 2022, A comprehensive review on chickpea (*Cicer arietinum* L.) breeding for abiotic stress tolerance and climate change resilience, International Journal of Molecular Sciences, 23(12): 6794.
https://doi.org/10.3390/ijms23126794

Asati R., Tripathi M., Tiwari S., Yadav R., and Tripathi N., 2022, Molecular breeding and drought tolerance in chickpea, Life, 12(11): 1846.
https://doi.org/10.3390/life12111846

Basu U., Bajaj D., Sharma A., Malik N., Daware A., Narnoliya L., Thakro V., Upadhyaya H., Kumar R., Tripathi S., Bharadwaj C., Tyagi A., and Parida S., 2018, Genetic dissection of photosynthetic efficiency traits for enhancing seed yield in chickpea, Plant, Cell and Environment, 42(1): 158-173.
https://doi.org/10.1111/pce.13319

Biswas P., Ahmed M., Afrin W., Rahman A., Shalahuddin A., Islam R., Akter F., Syed M., Sarker M., Ifterkharuddaula K., and Islam M., 2023, Enhancing genetic gain through the application of genomic selection in developing irrigated rice for the favorable ecosystem in Bangladesh, Frontiers in Genetics, 14: 1083221.
https://doi.org/10.3389/fgene.2023.1083221

Borhani S., Vessal S., Bagheri A., and Shokouhifar F., 2019, Differential gene expression pattern of drought responsive transcription factors in chickpea: an expressional analysis, Journal of Plant Growth Regulation, 39: 1211-1220.
https://doi.org/10.1007/s00344-019-10056-5

Budhlakoti N., Kushwaha A., Rai A., Chaturvedi K., Kumar A., Pradhan A., Kumar U., Kumar R., Juliana P., Mishra D., and Kumar S., 2022, Genomic selection: a tool for accelerating the efficiency of molecular breeding for development of climate-resilient crops, Frontiers in Genetics, 13: 832153. https://doi.org/10.3389/fgene.2022.832153

Choudhary A., Jain S., Dubey A., Kumar J., Sharma M., Gupta K., Sharma L., Prakash V., and Kumar S., 2022, Conventional and molecular breeding for disease resistance in chickpea: status and strategies, Biotechnology and Genetic Engineering Reviews, 39(2): 193-224. https://doi.org/10.1080/02648725.2022.2110641

Djouider S., Gentzbittel L., Jana R., Rickauer M., Ben C., and Lazali M., 2022, Contribution to improving the chickpea (*Cicer arietinum* L.) efficiency in low-phosphorus farming systems: assessment of the relationships between the P and N nutrition, nodulation capacity and productivity performance in P-deficient field conditions, Agronomy, 12(12): 3150. https://doi.org/10.3390/agronomy12123150

Gaur P., Jukanti A., and Varshney R., 2012, Impact of genomic technologies on chickpea breeding strategies, Agronomy, 2: 199-221. https://doi.org/10.3390/AGRONOMY2030199

Halladakeri P., Gudi S., Akhtar S., Singh G., Saini D., Hilli H., Sakure A., Macwana S., and Mir R., 2023, Meta-analysis of the quantitative trait loci associated with agronomic traits, fertility restoration, disease resistance, and seed quality traits in pigeonpea (*Cajanus cajan* L.), The Plant Genome, 16(3): e20342. https://doi.org/10.1002/tpg2.20342

He J., Zhao X., Laroche A., Lu Z., Liu H., and Li Z., 2014, Genotyping-by-sequencing (GBS), an ultimate marker-assisted selection (MAS) tool to accelerate plant breeding, Frontiers in Plant Science, 5: 484. https://doi.org/10.3389/fpls.2014.00484

Hiremath P., Farmer A., Cannon S., Woodward J., Kudapa H., Tuteja R., Kumar A., Bhanuprakash A., Mulaosmanovic B., Gujaria N., Krishnamurthy L., Gaur P., Kavikishor P., Shah T., Srinivasan R., Lohse M., Xiao Y., Town C., Cook D., May G., and Varshney R., 2011, Large-scale transcriptome analysis in chickpea (*Cicer arietinum* L.), an orphan legume crop of the semi-arid tropics of Asia and Africa, Plant Biotechnology Journal, 9: 922-931. https://doi.org/10.1111/j.1467-7652.2011.00625.x

Hou J., Zhang J., Bao F., Zhang P., Han H., Tan H., Chen B., and Zhao F., 2024, The contribution of exotic varieties to maize genetic improvement, Molecular Plant Breeding, 15(4): 198-208. https://doi.org/10.5376/mpb.2024.15.0020

Karalija E., Vergata C., Basso M., Negussu M., Zaccai M., Grossi-de-Sá M., and Martinelli F., 2022, Chickpeas' tolerance of drought and heat: current knowledge and next steps, Agronomy, 12(10): 2248. https://doi.org/10.3390/agronomy12102248

Koul B., Sharma K., Sehgal V., Yadav D., Mishra M., and Bharadwaj C., 2022, Chickpea (*Cicer arietinum* L.) biology and biotechnology: from domestication to biofortification and biopharming, Plants, 11(21): 2926. https://doi.org/10.3390/plants11212926

Lauterberg M., Tschiersch H., Papa R., Bitocchi E., and Neumann K., 2023, Engaging precision phenotyping to scrutinize vegetative drought tolerance and recovery in chickpea plant genetic resources, Plants, 12(15): 2866. https://doi.org/10.3390/plants12152866

Li H., Rodda M., Gnanasambandam A., Aftab M., Redden R., Hobson K., Rosewarne G., Materne M., Kaur S., and Slater A., 2015, Breeding for biotic stress resistance in chickpea: progress and prospects, Euphytica, 204: 257-288. https://doi.org/10.1007/s10681-015-1462-8

Madurapperumage A., Tang L., Thavarajah P., Bridges W., Shipe E., Vandemark G., and Thavarajah D., 2021, Chickpea (*Cicer arietinum* L.) as a source of essential fatty acids-a biofortification approach, Frontiers in Plant Science, 12: 734980. https://doi.org/10.3389/fpls.2021.734980

Millán T., Clarke H., Siddique K., Buhariwalla H., Gaur P., Kumar J., Gil J., Kahl G., and Winter P., 2006, Chickpea molecular breeding: new tools and concepts, Euphytica, 147: 81-103. https://doi.org/10.1007/s10681-006-4261-4

Mir R., Reynolds M., Pinto F., Khan M., and Bhat M., 2019, High-throughput phenotyping for crop improvement in the genomics era, Plant Science, 282: 60-72. https://doi.org/10.1016/J.PLANTSCI.2019.01.007

Roorkiwal M., Bharadwaj C., Barmukh R., Dixit G., Thudi M., Gaur P., Chaturvedi S., Fikre A., Hamwieh A., Kumar S., Sachdeva S., Ojiewo C., Tar'an B., Wordofa N., Singh N., Siddique K., and Varshney R., 2020, Integrating genomics for chickpea improvement: achievements and opportunities, Theoretical and Applied Genetics, 133: 1703-1720. https://doi.org/10.1007/s00122-020-03584-2

Roorkiwal M., Jain A., Kale S., Doddamani D., Chitikineni A., Thudi M., and Varshney R., 2017, Development and evaluation of high-density Axiom® CicerSNP Array for high-resolution genetic mapping and breeding applications in chickpea, Plant Biotechnology Journal, 16: 890-901. https://doi.org/10.1111/pbi.12836

Roorkiwal M., Rathore A., Das R., Singh M., Jain A., Srinivasan S., Gaur P., Chellapilla B., Tripathi S., Li Y., Hickey J., Lorenz A., Sutton T., Crossa J., Jannink J., and Varshney R., 2016, Genome-enabled prediction models for yield related traits in chickpea, Frontiers in Plant Science, 7: 1666. https://doi.org/10.3389/fpls.2016.01666

Sachdeva S., Bharadwaj C., Patil B., Pal M., Roorkiwal M., and Varshney R., 2022, Agronomic performance of chickpea affected by drought stress at different growth stages, Agronomy, 12(5): 995.
https://doi.org/10.3390/agronomy12050995

Sachdeva S., Bharadwaj C., Singh R., Jain P., Patil B., Roorkiwal M., and Varshney R., 2020, Characterization of ASR gene and its role in drought tolerance in chickpea (*Cicer arietinum* L.), PLoS One, 15(7): e0234550.
https://doi.org/10.1371/journal.pone.0234550

Samineni S., Sajja S., Mondal B., Chand U., Thudi M., Varshney R., and Gaur P., 2021, MAGIC lines in chickpea: development and exploitation of genetic diversity, Euphytica, 217(7): 137.
https://doi.org/10.1007/s10681-021-02874-0

Sandhu K., Shiv A., Kaur G., Meena M., Raja A., Vengavasi K., Mall A., Kumar S., Singh P., Singh J., Hemaprabha G., Pathak A., Krishnappa G., and Kumar S., 2022, Integrated approach in genomic selection to accelerate genetic gain in sugarcane, Plants, 11(16): 2139.
https://doi.org/10.3390/plants11162139

Singh R., Singh C.A., Chandana B., Mahto R., Patial R., Gupta A., Gahlaut V.G., Hamwieh A., Upadhyaya H., and Kumar R., 2022, Exploring chickpea germplasm diversity for broadening the genetic base utilizing genomic resourses, Frontiers in Genetics, 13: 905771.
https://doi.org/10.3389/fgene.2022.905771

Sudheesh S., Kahrood H., Braich S., Dron N., Hobson K., Cogan N., and Kaur S., 2021, Application of genomics approaches for the improvement in ascochyta blight resistance in chickpea, Agronomy, 11(10): 1937.
https://doi.org/10.3390/agronomy11101937

Thudi M., Gaur P., Krishnamurthy L., Mir R., Kudapa H., Fikre A., Kimurto P., Tripathi S., Soren K., Mulwa R., Bharadwaj C., Datta S., Chaturvedi S., and Varshney R., 2014, Genomics-assisted breeding for drought tolerance in chickpea, Functional Plant Biology, 41(11): 1178-1190.
https://doi.org/10.1071/FP13318

Thudi M., Samineni S., Li W., Boer M., Roorkiwal M., Yang Z., Ladejobi F., Zheng C., Chitikineni A., Nayak S., He Z., Valluri V., Bajaj P., Khan A., Gaur P., Eeuwijk F., Mott R., Xin L., and Varshney R., 2023, Whole genome resequencing and phenotyping of MAGIC population for high resolution mapping of drought tolerance in chickpea, The Plant Genome, 17(1): e20333.
https://doi.org/10.1002/tpg2.20333

Tiwari P., Tiwari S., Sapre S., Tripathi N., Payasi D., Singh M., Thakur S., Sharma M., Tiwari S., and Tripathi M., 2023, Prioritization of physio-biochemical selection indices and yield-attributing traits toward the acquisition of drought tolerance in chickpea (*Cicer arietinum* L.), Plants, 12(18): 3175.
https://doi.org/10.3390/plants12183175

Upadhyaya H., Bramel P., and Singh S., 2001, Development of a chickpea core subset using geographic distribution and quantitative traits, Crop Science, 41: 206-210.
https://doi.org/10.2135/CROPSCI2001.411206X

Upadhyaya H., Dwivedi S., Gowda C., and Singh S., 2007, Identification of diverse germplasm lines for agronomic traits in a chickpea (*Cicer arietinum* L.) core collection for use in crop improvement, Field Crops Research, 100: 320-326.
https://doi.org/10.1016/J.FCR.2006.08.008

Upadhyaya H., Thudi M., Dronavalli N., Gujaria N., Singh S., Sharma S., and Varshney R., 2011, Genomic tools and germplasm diversity for chickpea improvement, Plant Genetic Resources, 9: 45-58.
https://doi.org/10.1017/S1479262110000468

Varshney R., Kudapa H., Roorkiwal M., Thudi M., Pandey M., Saxena R., Chamarthi S.S.M., Mallikarjuna N., Upadhyaya H., Gaur P., Krishnamurthy L., Saxena K., Nigam S., and Pande S., 2012, Advances in genetics and molecular breeding of three legume crops of semi-arid tropics using next-generation sequencing and high-throughput genotyping technologies, Journal of Biosciences, 37: 811-820.
https://doi.org/10.1007/s12038-012-9228-0

Varshney R., Mohan S., Gaur P., Gangarao N., Pandey M., Pandey M., Bohra A., Sawargaonkar S., Chitikineni A., Kimurto P., Janila P., Saxena K., Fikre A., Sharma M., Rathore A., Pratap A., Tripathi S., Datta S., Chaturvedi S., Mallikarjuna N., Anuradha G., Babbar A., Choudhary A., Mhase M., Bharadwaj C., Mannur D., Harer P., Guo B., Liang X., Nadarajan N., and Gowda C., 2013, Achievements and prospects of genomics-assisted breeding in three legume crops of the semi-arid tropics, Biotechnology Advances, 31(8): 1120-1134.
https://doi.org/10.1016/j.biotechadv.2013.01.001

Varshney R., Pandey M., Bohra A., Singh V., Thudi M., and Saxena R., 2018, Toward the sequence-based breeding in legumes in the post-genome sequencing era, TAG, Theoretical and Applied Genetics, 132: 797-816.
https://doi.org/10.1007/s00122-018-3252-x

Varshney R., Roorkiwal M., and Sorrells M., 2017, Genomic selection for crop improvement, Crop Science, 49: 1-12.
https://doi.org/10.1007/978-3-319-63170-7

Varshney R., Thudi M., Nayak S., Nayak S., Gaur P., Kashiwagi J., Krishnamurthy L., Jaganathan D., Koppolu J., Koppolu J., Bohra A., Bohra A., Tripathi S., Tripathi S., Rathore A., Jukanti A., Jukanti A., Jayalakshmi V., Vemula A., Singh S., Yasin M., Sheshshayee M., and Viswanatha K., 2013, Genetic dissection of drought tolerance in chickpea (*Cicer arietinum* L.), Theoretical and Applied Genetics, 127: 445-462.
https://doi.org/10.1007/s00122-013-2230-6

Varshney R., Varshney R., Song C., Saxena R., Azam S., Yu S., Sharpe A., Cannon S., Baek J., Rosen B., Tar'an B., Millán T., Zhang X., Ramsay L., Iwata A., Wang Y., Nelson W., Farmer A., Gaur P., Soderlund C., Penmetsa R., Xu C., Bharti A., He W., Winter P., Zhao S., Hane J., Carrasquilla-Garcia N., Condie J., Upadhyaya H., Luo M., Thudi M., Gowda C., Singh N., Lichtenzveig J., Gali K., Rubio J., Nadarajan N., Doležel J., Bansal K., Xu X., Edwards D., Zhang G., Kahl G., Gil J., Singh K., Singh K., Datta S., Jackson S., Wang J., Wang J., and Cook D., 2013, Draft genome sequence of chickpea (*Cicer arietinum*) provides a resource for trait improvement, Nature Biotechnology, 31: 240-246.
https://doi.org/10.1038/nbt.2491

Zhong B.J.L., 2024, The fruit revolution in the genomic era: unveiling the journey of strawberry genetic improvement, International Journal of Horticulture, 14(2): 72-83.
https://doi.org/10.5376/ijh.2024.14.0009