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Evolutionary Genomics of Peas Insights into Domestication and Diversity

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Abstract Peas (*Pisum sativum L.*) have played a significant role in agriculture and scientific research due to their nutritional value and genetic model status. This study comprehensively examines the evolutionary history, genomic structure, domestication, and genetic diversity of peas. We discuss advances in genomic tools and resources, highlighting recent progress in sequencing technologies, genome-wide association studies (GWAS), and bioinformatics resources. Functional genomics and trait mapping efforts, including the identification of key genes, QTL mapping, and marker-assisted selection, are explored. The role of pea-microbe interactions, particularly in symbiotic nitrogen fixation and pathogen resistance, is also reviewed. Furthermore, modern breeding techniques, including genomic selection and CRISPR/Cas9, are presented alongside case studies of successful breeding programs. The study concludes with an analysis of current challenges in pea genomics and proposes future research directions to integrate genomics with phenomics for crop improvement. This study aims to provide a comprehensive understanding of pea genomics to enhance breeding strategies and ensure sustainable agricultural practices.

Keywords Pea genomics; Domestication; Genetic diversity; Functional genomics; Crop improvement

1 Introduction

Peas (*Pisum sativum* L.) have a rich history as one of the oldest domesticated crops, with their domestication dating back thousands of years. The evolutionary journey of peas has been marked by significant genetic changes driven by both natural selection and human intervention. Recent genomic studies have provided valuable insights into the complex evolutionary history of peas, revealing patterns of genetic variation and the impact of domestication on their genome. For instance, the first annotated chromosome-level reference genome assembly for pea has shed light on genomic rearrangements and the role of repetitive elements in pea genome evolution (Kreplak et al., 2019). Additionally, genotyping-by-sequencing data from diverse germplasm collections have helped trace the geographic expansion of pea cultivation and identify selective sweeps associated with domestication (Pavan et al., 2022). These studies underscore the intricate genetic dynamics that have shaped the evolution and domestication of peas.

Peas are a vital crop in global agriculture, serving as a significant source of protein for both human consumption and animal feed. They rank among the most widely cultivated pulses worldwide, with substantial contributions to food security and sustainable agriculture. The nutritional value of peas, including their high protein content and rich array of vitamins and minerals, makes them an essential component of diets in many regions (Tayeh et al., 2015). Moreover, peas have played a foundational role in the field of genetics, being the original model organism used by Gregor Mendel in his groundbreaking experiments on inheritance. Despite their historical significance, advancements in pea genomics have lagged behind other crops, but recent developments in genomic tools and resources are paving the way for enhanced breeding programs and crop improvement (Smýkal et al., 2012; Tayeh et al., 2015).

This study aims to provide a comprehensive overview of the evolutionary genomics of peas, with a focus on insights into their domestication and genetic diversity. The study will synthesize findings from recent genomic studies to elucidate the genetic mechanisms underlying pea domestication and the evolutionary processes that have contributed to their current diversity. By integrating data from various genomic analyses, including reference genome assemblies, genotyping-by-sequencing, and comparative genomics, this study will highlight key discoveries and their implications for pea breeding and crop improvement. The scope of the study encompasses the genetic architecture of domestication traits, the identification of selective sweeps, and the application of genomic tools in pea research and breeding. Through this synthesis, the study aims to advance our understanding of pea evolution and support ongoing efforts to enhance the genetic potential of this important crop.

2 Genomic Structure and Evolution

2.1 Basic genome structure of peas

The pea (*Pisum sativum* L.) genome is characterized by its large size and high content of repetitive DNA elements. The first annotated chromosome-level reference genome assembly for pea has provided significant insights into its genomic structure. This reference genome revealed that the pea genome is dominated by LTR-retrotransposons, particularly Ty3/gypsy elements, which are less diverse but more abundant than Ty1/copia elements. Notably, Ogre-like retrotransposons alone constitute over 20% of the genome. Additionally, the genome contains novel satellite repeats and variants of telomeric sequences, further contributing to its complexity (Macas et al., 2007; Kreplak et al., 2019).

2.2 Comparative genomics with related legumes

Comparative genomics has been instrumental in understanding the evolutionary relationships between peas and other legumes. Syntenic relationships between pea and other legume genomes, such as *Medicago truncatula* and soybean, have been established, revealing blocks of synteny that provide insights into the evolution of chromosome structure in legumes (Bordat et al., 2011; Smýkal et al., 2012; Tayeh et al., 2015). The development of the GenoPea 13.2 K SNP Array and high-density genetic maps has further facilitated the identification of syntenic networks and the localization of important agronomic traits (Tayeh et al., 2015). Additionally, a hierarchical alignment of legume genomes has illustrated genomic fractionation and gene loss patterns following polyploidization events, highlighting the evolutionary divergence among legume species (Wang et al., 2017).

2.3 Major evolutionary events in pea genomics

The evolutionary history of peas has been shaped by several major events, including genomic rearrangements, translocations, and transpositions. Phylogenetic analyses have shown that the pea genome has undergone significant gene dynamics, likely associated with genome size expansion during the divergence of the Fabeae tribe from its sister tribes (Figure 1) (Kreplak et al., 2019). The integration of genotyping-by-sequencing data from different germplasm collections has provided a comprehensive view of pea biodiversity and population structure, reflecting genetic variation based on geographic patterns and identifying putative selective sweeps associated with domestication and breeding (Pavan et al., 2022). Furthermore, the discordant evolution of organellar genomes in peas, driven by hybridization events and plastid-nuclear incompatibility, has contributed to the complex evolutionary landscape of the species (Bogdanova et al., 2018; Bogdanova et al., 2020).

In summary, the genomic structure and evolution of peas have been shaped by a combination of repetitive DNA accumulation, syntenic relationships with related legumes, and significant evolutionary events such as genomic rearrangements and hybridization. These insights not only enhance our understanding of pea genomics but also provide valuable information for crop improvement and conservation efforts.

3 Domestication of Peas

3.1 Historical perspectives on pea domestication

Pea (*Pisum sativum* L.) is one of the oldest domesticated crops, with a history that dates back to the Neolithic period. The domestication of peas is believed to have occurred in the Fertile Crescent, a region known for the early development of agriculture. Historical evidence suggests that peas were among the first crops to be cultivated by humans, alongside other staple crops such as wheat and barley (Pavan et al., 2022; Hellwig et al., 2022). The spread of pea cultivation from its center of origin to other parts of the world followed a pattern similar to other domesticated crops, facilitated by human migration and trade.

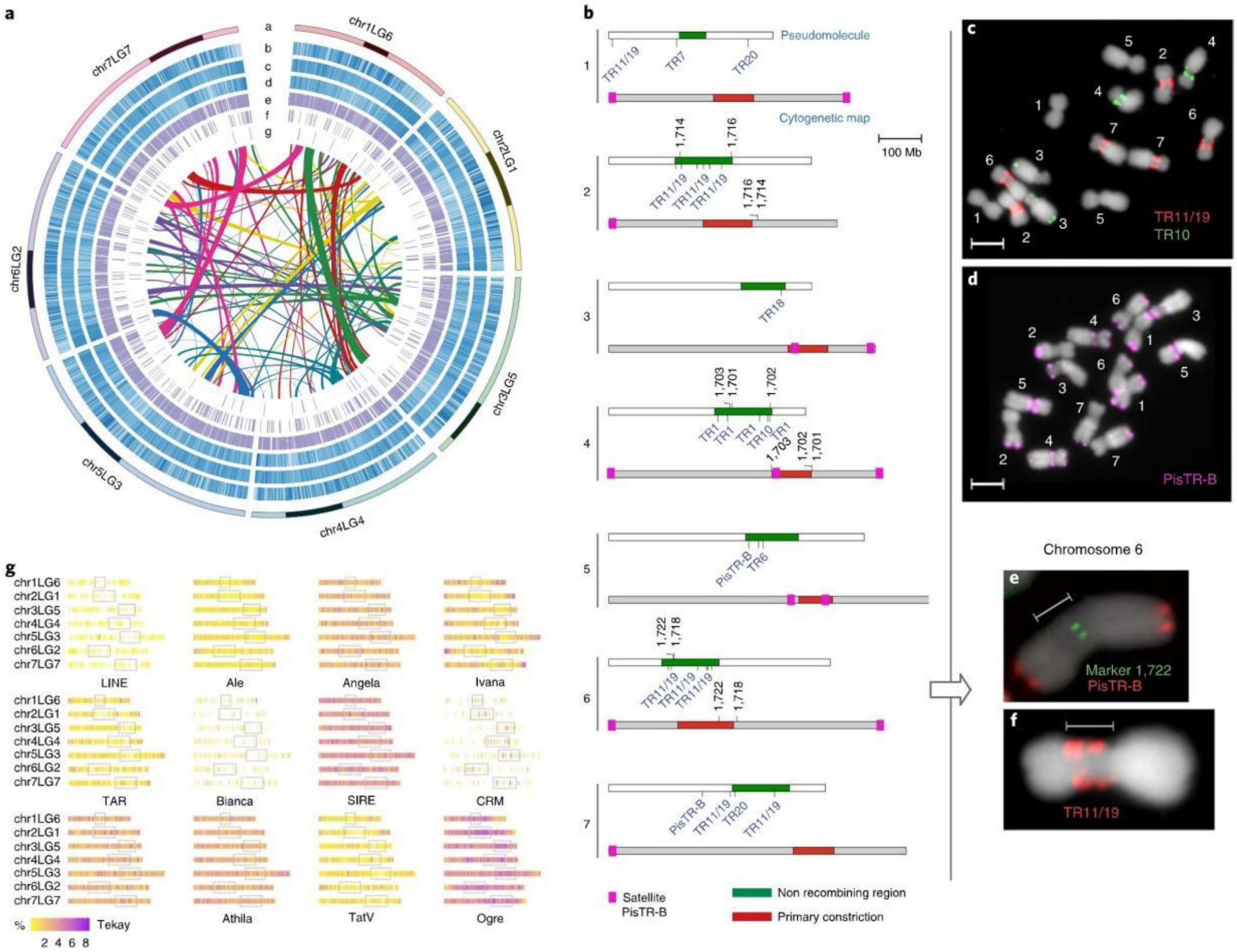

Figure 1 Pea genome features (Adopted from Kreplak et al., 2019)

Image caption: a, Circos view of the pea genome. Pseudomolecule color-code is shaded at estimated centromere positions. Lanes depict circular representation of pseudomolecules (a) and the density of retrotransposons, transposons, genes, ncRNA, tRNA and miRNA coding sequences (b-g). Lines in the inner circle represent links between synteny-selected paralogs. b, Estimated positions of centromeres in the assembly and their comparison to pea cytogenetic map is schematically represented, with pseudomolecules as white bars and cytogenetic maps of pea chromosomes as gray bars. Non-recombining regions representing the centromeres are marked in green. Positions of centromeric single-copy FISH markers are indicated above the pseudomolecules in black and positions of arrays of centromeric satellites present in the assembly are shown below them in blue. Positions of primary constrictions on the cytogenetic maps are labeled in red. PisTR-B satellite loci used to discriminate individual chromosomes are shown in purple boxes on the gray bars. c, FISH localization of the satellite repeats TR11/19 (red) and TR10 (green) on metaphase chromosomes (gray). d, Discrimination of chromosomes within the pea karyotype using FISH with PisTR-B probe (purple). e, Example of FISH detection of the single-copy marker (1 722, green) in the centromere of chromosome 6. f, Chromosome 6 with labeled centromeric repeat TR11/19. g, The density of different TE lineages inferred from the detection of their protein-coding domains along pseudomolecules (Adopted from Kreplak et al., 2019)

3.2 Genetic evidence of domestication

Genetic studies have provided significant insights into the domestication process of peas. The use of next-generation sequencing (NGS) and genotyping-by-sequencing (GBS) has allowed researchers to analyze the genetic diversity and population structure of pea germplasm collections. These studies have identified single nucleotide polymorphisms (SNPs) and other genetic markers that are associated with domestication traits (Pavan et al., 2022; Rispail et al., 2023). For instance, genome-wide scans have revealed selective sweeps in regions of the genome that are linked to key domestication traits such as shoot branching, cotyledon color, and resistance to lodging (Pavan et al., 2022).

Moreover, phylogenetic analyses have suggested that there may have been multiple independent domestication events in peas. This is supported by the detection of distinct genetic bases for domestication in different pea subpopulations, indicating that different groups of peas were domesticated separately (Hellwig et al., 2022). The genetic structure of wild and domesticated pea populations shows clear differentiation, with wild peas exhibiting greater genetic diversity compared to their domesticated counterparts (Hellwig et al., 2022; Rispail et al., 2023).

3.3 Key traits selected during domestication

Several key traits have been selected during the domestication of peas to enhance their suitability for cultivation and consumption. These traits include:

Seed Dispersal and Dormancy: One of the primary traits selected during domestication is the reduction of seed dispersal mechanisms and seed dormancy. Wild peas typically have dehiscent pods that shatter to disperse seeds, whereas domesticated peas have indehiscent pods that retain seeds, facilitating easier harvesting. Additionally, domesticated peas exhibit reduced seed dormancy, allowing for more uniform germination and cultivation (Hradilová et al., 2017).

Pod and Seed Characteristics: Domestication has also led to changes in pod and seed characteristics. Domesticated peas often have larger seeds and pods compared to their wild relatives. These changes are associated with increased seed yield and improved ease of harvesting (Rana et al., 2017). Genetic studies have identified specific genes and metabolic compounds that are involved in these traits, such as proanthocyanidins and flavonoids in seed coats (Hradilová et al., 2017).

Adaptation to Cultivation: Traits that enhance the adaptability of peas to different environmental conditions and cultivation practices have also been selected. These include traits related to plant architecture, such as shoot branching and resistance to lodging, which improve the overall productivity and resilience of the crop (Pavan et al., 2022; Rispail et al., 2023).

In summary, the domestication of peas has involved the selection of multiple traits that enhance their suitability for human use. Genetic studies have provided valuable insights into the evolutionary history and genetic basis of these traits, highlighting the complex interplay between natural and human-mediated selection in shaping the domesticated pea.

4 Genetic Diversity in Peas

4.1 Sources of genetic diversity

Genetic diversity in peas (*Pisum sativum* L.) arises from various sources, including wild relatives, landraces, and cultivated varieties. Wild peas, such as *P. fulvum*, contribute significantly to the genetic pool, offering traits that may have been lost during domestication (Rispail et al., 2023). The genetic diversity within the cultivated genepool is substantial, but wild material provides novel traits that can be incorporated into breeding programs (Smýkal et al., 2012). The integration of wild alleles into cultivated peas through intermediate subspecies like *P. sativum* subsp. *jomardii* and *P. sativum* subsp. *arvense* has been crucial during domestication (Rispail et al., 2023).

4.2 Assessment of genetic diversity using molecular markers

Molecular markers are essential tools for assessing genetic diversity in peas. Various types of markers, including Simple Sequence Repeat (SSR), Retrotransposon Based Insertion Polymorphism (RBIP), and Single Nucleotide Polymorphism (SNP) markers, have been employed to characterize pea germplasm (Smýkal et al., 2012; Burstin et al., 2015). SSR markers, known for their high polymorphism, have been widely used to study genetic structure and diversity (Rana et al., 2017). SNP markers, particularly those developed through genotyping-by-sequencing (GBS) and SNP arrays, provide high-resolution insights into genetic variation and have been instrumental in constructing genetic maps and understanding genome organization (Pavan et al., 2022). The GenoPea 13.2 K SNP Array, for instance, has facilitated the identification of ohnologue-rich regions and local duplicates within the pea genome (Tayeh et al., 2015).

4.3 Geographic distribution of genetic variation

The geographic distribution of genetic variation in peas reflects their evolutionary history and domestication patterns. Studies have shown that genetic variation in pea populations is structured based on geographic patterns, with distinct populations exhibiting different evolutionary histories. For example, the average decay of linkage disequilibrium (LD) varies significantly among genetically distinct populations, indicating diverse evolutionary trajectories (Pavan et al., 2022). The genetic diversity within pea collections often clusters into subpopulations corresponding to different geographic regions, with frequent genetic exchange between populations (Rana et al., 2017; Rispail et al., 2023). This geographic structuring is crucial for understanding the expansion of pea cultivation from its domestication center to other regions worldwide (Pavan et al., 2022).

In summary, the genetic diversity in peas is shaped by contributions from wild relatives, landraces, and cultivated varieties, assessed through various molecular markers, and structured by geographic distribution. These insights are vital for breeding programs aimed at improving pea varieties for future agricultural challenges.

5 Genomic Tools and Resources

5.1 Advances in sequencing technologies for peas

Recent advancements in sequencing technologies have significantly enhanced our understanding of the pea genome. The integration of next-generation sequencing (NGS) data from different genotyping-by-sequencing (GBS) libraries has allowed researchers to explore pea biodiversity on an unprecedented scale. For instance, a study combined GBS data from two *Pisum* germplasm collections, resulting in a dataset of 652 accessions and 22 127 markers. This comprehensive dataset facilitated the analysis of population structure and genetic variation, revealing geographic patterns and evolutionary histories of pea diversification (Pavan et al., 2022). Additionally, the use of 454 sequencing has enabled a detailed characterization of repetitive DNA in the pea genome, identifying major repeat families and providing insights into the genome’s architecture and function (Macas et al., 2007).

5.2 Genome-wide association studies (GWAS) in peas

Genome-wide association studies (GWAS) have become a pivotal tool in identifying genetic variants associated with important traits in peas. Traditional GWAS approaches require high-density genotyping of large numbers of individuals, which can be resource-intensive. However, innovative methods such as extreme-phenotype GWAS (XP-GWAS) have been developed to overcome these challenges. XP-GWAS involves genotyping pools of individuals with extreme phenotypes, allowing for the discovery of trait-associated variants without extensive genotyping resources (Yang et al., 2015). This method has proven effective in other crops and holds promise for application in peas. Furthermore, the integration of GWAS with population genomics has provided a comprehensive view of the genetic basis of fitness, local adaptation, and phenotypic traits in legumes (Cortinovis et al., 2020).

5.3 Pea genomic databases and bioinformatics resources

The development of genomic databases and bioinformatics tools has been instrumental in advancing pea research. One notable resource is the translational genomics toolkit, which leverages syntenic relationships between pea and other model legumes such as *Medicago truncatula*. This toolkit allows researchers to map pea genes onto a consensus genetic map and identify candidate genes for various traits (Bordat et al., 2011). Additionally, the GWAS Atlas is a curated resource that integrates genome-wide variant-trait associations across multiple species, including plants and animals. This database provides a valuable platform for accessing high-quality GWAS data, facilitating genetic research and breeding applications in peas (Tian et al., 2019).

In summary, the integration of advanced sequencing technologies, innovative GWAS methods, and comprehensive genomic databases has significantly enhanced our understanding of pea genomics. These tools and resources are crucial for unraveling the genetic basis of domestication and diversity in peas, paving the way for future research and breeding efforts.

6 Functional Genomics and Trait Mapping

6.1 Identification of genes associated with key traits

The identification of genes associated with key traits in peas has been significantly advanced through the use of translational genomics and functional mapping. Translational genomics leverages the genetic information from well-characterized model plants to identify candidate genes in less-studied crops like peas. For instance, a study mapped 5 460 pea Unigenes onto a consensus map using syntenic relationships with *Medicago truncatula*, identifying candidate genes for traits such as nodulation regulation (Bordat et al., 2011). Similarly, functional mapping has been employed to develop gene-anchored markers, facilitating the identification of genes involved in primary metabolism and other essential functions (Aubert et al., 2006). These approaches have enabled the discovery of genes underlying important agronomic traits, including virus resistance and plant architecture (Smýkal et al., 2012; Smýkal and Konecna, 2014).

6.2 QTL mapping and marker-assisted selection

Quantitative Trait Loci (QTL) mapping has been a cornerstone in understanding the genetic control of complex traits in peas. A meta-analysis of QTLs identified 27 metaQTLs for traits such as seed weight, seed number, and seed protein content, with some QTLs having confidence intervals of less than 2 cM, making them highly precise for marker-assisted selection (MAS) (Klein et al., 2020). Another study focused on salinity tolerance in field peas identified QTLs on linkage groups Ps III and VII, with flanking SNP markers suitable for MAS (Leonforte et al., 2013). The integration of QTL mapping with genomic prediction techniques has further enhanced the accuracy of breeding programs, as demonstrated by high prediction accuracies for traits like thousand seed weight and flowering date (Tayeh et al., 2015).

6.3 Functional characterization of candidate genes

The functional characterization of candidate genes involves validating their roles in trait expression through various genomic and post-genomic approaches. For example, the use of BAC libraries, transcriptome, and proteome datasets has facilitated the identification and functional analysis of genes in peas (Smýkal et al., 2012; Smýkal and Konecna, 2014). Comparative genomic analyses with related legume species have also been instrumental in pinpointing candidate genes for traits such as salinity tolerance and domestication-related characteristics (Leonforte et al., 2013; Amkul et al., 2020). These efforts are complemented by advanced techniques like QTL-seq, which allows rapid mapping of QTLs through whole-genome resequencing, thereby accelerating the identification of genes associated with key agronomic traits (Takagi et al., 2013).

In summary, the integration of translational genomics, QTL mapping, and functional characterization has provided profound insights into the genetic basis of key traits in peas, paving the way for more efficient and targeted breeding strategies.

7 Pea-Microbe Interactions

7.1 Role of symbiotic relationships in pea evolution

Symbiotic relationships have played a crucial role in the evolution of peas (*Pisum sativum* L.), particularly through interactions with nitrogen-fixing bacteria and mycorrhizal fungi. These mutualistic associations have significantly influenced the genetic diversity and adaptability of pea plants. For instance, the presence of symbiotic genes such as LykX, which encodes a receptor for bacterial Nod factors, has been linked to various growth and yield parameters in pea cultivars (Zhukov et al., 2021). Additionally, the evolution of symbiotic traits in legumes, including peas, has been shaped by the horizontal transfer of key symbiotic genes among rhizobia, facilitating the spread of nitrogen-fixing capabilities (Remigi et al., 2016). The genetic diversity within pea populations is further enriched by the presence of heritable symbionts, such as those found in pea aphids, which contribute to the overall genetic variation and adaptability of the host plants (Russell et al., 2013).

7.2 Genomic insights into nitrogen fixation

The ability of peas to form symbiotic nodules with *Rhizobium leguminosarum* sv. *viciae* (Rlv) is a key trait that enhances nitrogen fixation. Studies have shown that the efficiency of nitrogen fixation and the competitiveness for nodulation are distinct traits influenced by both plant and bacterial genetic determinants (Bourion et al., 2018). The genomic analysis of pea nodules has revealed a variable gene family encoding nodule-specific cysteine-rich (NCR) peptides, which play a critical role in bacteroid differentiation and nitrogen fixation (Zorin et al., 2022). Furthermore, the identification of nearly 200 genes required for symbiotic nitrogen fixation in legumes, including peas, has advanced our understanding of the molecular mechanisms underlying this complex trait (Roy et al., 2019). These genes are involved in various processes such as microbial infection, nodule development, and the regulation of nitrogen fixation, highlighting the intricate genetic network that supports this symbiotic relationship (Kouchi et al., 2010).

7.3 Pathogen resistance and plant immunity

The interaction between peas and their symbiotic partners also influences their resistance to pathogens and overall plant immunity. The genetic and molecular mechanisms that regulate symbiotic specificity in legume-rhizobium interactions are diverse and involve a wide range of host and bacterial genes and signals (Wang et al., 2018). These mechanisms not only ensure successful symbiosis but also contribute to the plant's ability to fend off pathogenic attacks. Comparative genomic analyses have provided insights into the genetic determinants of infection susceptibility and the evolutionary pressures exerted by host-pathogen interactions (Sironi et al., 2015). Additionally, the presence of symbiotic genes and their allelic variations can impact the effectiveness of symbiotic interactions and the plant's overall health and productivity (Zhukov et al., 2021). Understanding these interactions is crucial for improving the resilience and yield of pea crops in agricultural settings.

In summary, the evolutionary genomics of peas reveals the significant impact of symbiotic relationships on their domestication and diversity. The intricate genetic networks governing nitrogen fixation, pathogen resistance, and plant immunity underscore the importance of these interactions in shaping the evolutionary trajectory of peas.

8 Applications in Breeding and Crop Improvement

8.1 Modern breeding techniques for peas

Modern breeding techniques for peas have evolved significantly with the advent of genomic selection (GS) and high-density genotyping. GS has emerged as a promising technique to enhance the accuracy and efficiency of marker-based selection. By utilizing genome-wide molecular marker data, GS predicts the breeding values of candidate lines, thereby accelerating the breeding cycle and improving selection gains. For instance, a study involving a collection of 339 genetic resource accessions demonstrated high genomic prediction accuracies for traits such as thousand seed weight (TSW), number of seeds per plant (NSeed), and date of flowering (Tayeh et al., 2015). The study highlighted the importance of the size and composition of the training population in maximizing prediction accuracies, which is crucial for developing effective GS strategies in pea breeding (Tayeh et al., 2015).

8.2 Genomic selection and CRISPR/Cas9 in pea improvement

The integration of genomic selection and CRISPR/Cas9 technology offers a powerful approach for pea improvement. Genomic selection leverages high-density marker scores to predict the breeding values of lines, incorporating all marker information to avoid biased estimates and capture more variation due to small-effect quantitative trait loci (QTL). This method has shown promise in accelerating the breeding cycle and enhancing gains per unit time (Varshney et al., 2017).

CRISPR/Cas9, a versatile genome editing tool, has revolutionized crop improvement by enabling precise and efficient gene editing. This technology allows for the rapid introduction of beneficial traits, such as disease resistance, abiotic stress tolerance, and improved nutritional quality, into pea varieties (Figure 2) (Arora and

Narula, 2017; Rodríguez-Leal et al., 2017; Wan et al., 2021). The simplicity and high mutation efficiency of CRISPR/Cas9 make it an attractive option for developing new germplasm resources and enhancing agronomic traits (Arora and Narula, 2017). Additionally, advancements in CRISPR/Cas9, such as base editors and prime editors, have further improved the specificity and efficiency of gene editing, offering new opportunities for pea breeding (Biswas et al., 2021).

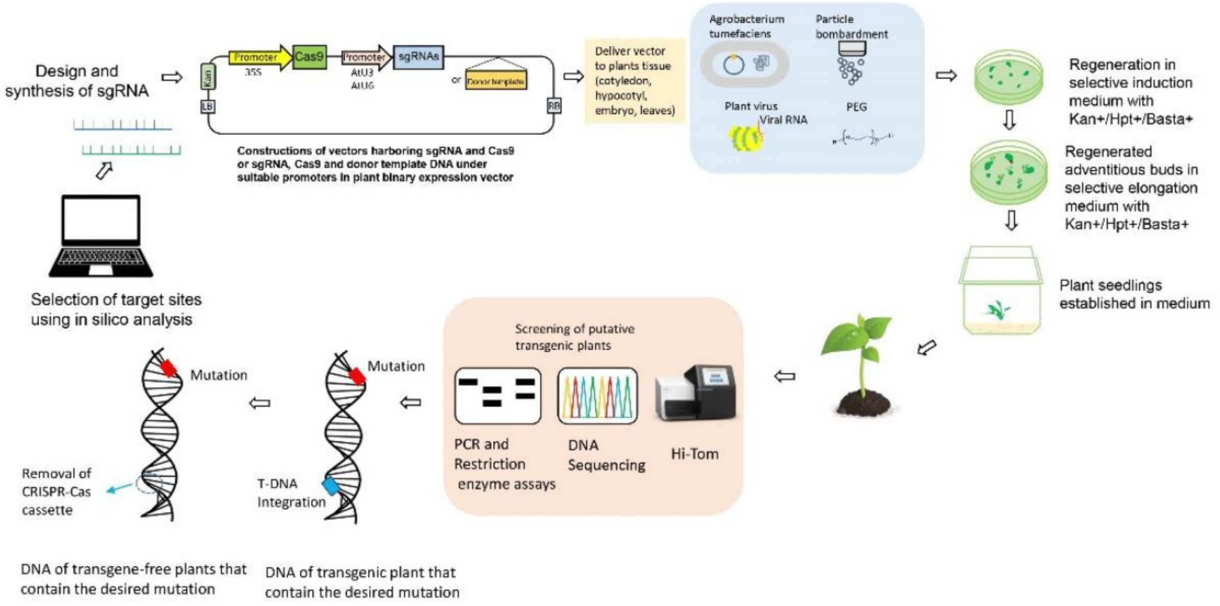

Figure 2 CRISPR-Cas9 mediated genome editing (Adopted from Wan et al., 2021)

Image caption: (I) Selection of the desired genomic DNA target, and recognition of protospacer adjacent motif (PAM) sequences before 20 bp sequences. Design of the sgRNA using online bioinformatics tools. (II) Cloning of designed sgRNAs, and binary vector construction using promoters. (III) The delivery of CRISPR-Cas editing reagents into plant cells. The vector can be transferred into the plant via *Agrobacterium tumefaciens*, nanoparticles, biolistic bombardment, or polyethylene glycol (PEG). Alternatively, plant RNA viruses have been used to induce heritable genome editing. When the cassette harbouring the sgRNA, RNA mobile element, and tobacco rattle virus (TRV) is transformed into the Cas9 expressing plants, the systemic spread of sgRNA will introduce heritable genome editing. (IV) Plant transformation and development of transgenic plants. (V) Genotyping of transgenic plants. (VI) Transgene-free plants with the desired mutation are obtained (Adopted from Wan et al., 2021)

8.3 Case studies of successful breeding programs

Several successful breeding programs have demonstrated the potential of modern breeding techniques in improving pea varieties. For example, a study on the genetic diversity and trait genomic prediction in a pea diversity panel utilized newly developed SNP markers to characterize diverse pea accessions and predict phenotypes such as TSW, NSeed, and BegFlo. The study showed that high-throughput SNP arrays could significantly enhance the efficiency of marker-assisted selection in peas (Burstin et al., 2015).

Another case study highlighted the application of CRISPR/Cas9 in crop quality improvement, where the technology was used to modulate traits such as appearance, palatability, and nutritional components in various crops (Liu et al., 2021). This approach has accelerated crop breeding progress by enabling precise gene editing and the development of non-genetically modified (Non-GMO) crops with desired traits (Jaganathan et al., 2018).

Overall, the integration of genomic selection and CRISPR/Cas9 technology in pea breeding programs has shown great promise in enhancing yield potential, improving stress resistance, and developing high-quality pea varieties. These advancements underscore the importance of modern breeding techniques in addressing the challenges posed by global climate change and meeting the demands of sustainable agriculture.

9 Challenges and Future Directions

9.1 Gaps in current genomic knowledge

Despite significant advancements in pea genomics, several gaps remain. The first annotated chromosome-level reference genome for pea has provided a foundation for understanding legume genome evolution and the molecular basis of agronomically important traits (Kreplak et al., 2019). However, the complexity of the pea genome, characterized by intense gene dynamics and large genome size, poses challenges for comprehensive genomic studies. Additionally, while translational genomics has identified numerous candidate genes and syntenic relationships, the functional characterization of these genes remains incomplete (Bordat et al., 2011). The integration of different genotyping-by-sequencing datasets has expanded our understanding of pea biodiversity, yet the loss of information during this process indicates that more comprehensive datasets are needed (Pavan et al., 2022). Furthermore, the identification of genomic regions under selection in domesticated pea groups suggests that there are still undiscovered genetic bases of domestication (Hellwig et al., 2022).

9.2 Integrating genomics with phenomics

The integration of genomic data with phenomic data is crucial for advancing our understanding of pea domestication and diversity. Recent studies have highlighted the importance of combining genomic and phenomic resources to elucidate the genetic architecture of complex traits (Turner-Hissong et al., 2019). Advanced molecular technologies, such as genome-wide association studies and population genetic screens, have revealed diverse mutations affecting domestication traits (Olsen and Wendel, 2013). However, the challenge lies in effectively integrating these genomic insights with phenotypic data to inform breeding strategies. The development of high-density SNP arrays and consensus genetic maps has provided valuable tools for genotyping and mapping, but their application in phenomic studies is still in its early stages (Tayeh et al., 2015). Moreover, the identification of genomic hotspots of differentiation in pea aphid host races underscores the potential for similar approaches in pea to uncover adaptive divergence and ecological isolation (Nouhaud et al., 2018).

9.3 Prospects for future research and crop improvement

Future research in pea genomics should focus on addressing the existing gaps and enhancing the integration of genomics with phenomics. One promising direction is the use of genomic selection (GS) to improve breeding accuracy and efficiency. Studies have shown that GS can significantly enhance the prediction accuracy of important traits, such as seed weight and flowering time, by leveraging genome-wide molecular marker data (Tayeh et al., 2015). Additionally, the development of community resources and collaborative efforts will be essential for advancing pea genomics. The creation of comprehensive genomic databases and bioinformatics tools, such as the translational toolkit for pea, will facilitate the identification and functional characterization of candidate genes (Bordat et al., 2011). Furthermore, the application of precision gene editing technologies holds great potential for targeted crop improvement by leveraging the genetic insights gained from evolutionary genomics studies (Turner-Hissong et al., 2019). Overall, the integration of advanced genomic and phenomic approaches, coupled with collaborative research efforts, will pave the way for significant advancements in pea domestication and crop improvement.

10 Concluding Remarks

The evolutionary genomics of peas (*Pisum sativum* L.) has provided significant insights into their domestication and genetic diversity. The integration of genotyping-by-sequencing (GBS) data from different germplasm collections has allowed for a comprehensive analysis of pea biodiversity, revealing geographic patterns of genetic variation and identifying selective sweeps associated with domestication and breeding. The development of the GenoPea 13.2 K SNP Array and high-density genetic maps has further elucidated the structure and organization of the pea genome, facilitating the identification of important agronomic traits. Despite the challenges posed by the large and repetitive nature of the pea genome, significant progress has been made in understanding its evolution and the genetic basis of key traits. Studies on genetic diversity and population structure have highlighted the substantial variation within the cultivated genepool and the potential of wild material to introduce novel traits.

Additionally, genomic prediction techniques have shown promise in improving the accuracy and efficiency of marker-based selection in pea breeding.

The findings from these studies have several important implications for pea breeding and conservation. The identification of genetic markers associated with desirable traits, such as resistance to biotic and abiotic stresses, can enhance marker-assisted selection (MAS) programs, increasing precision and shortening breeding cycles. The high genetic diversity observed in pea collections suggests that there is significant potential for the incorporation of novel traits from wild relatives, which can improve the resilience and adaptability of cultivated varieties. The development of genomic tools, such as the GenoPea 13.2 K SNP Array, provides valuable resources for plant scientists to strengthen pea as a model for genetics and physiology and to enhance breeding efforts. Furthermore, the insights gained from the study of domestication and genetic diversity can inform conservation strategies, ensuring the preservation of genetic resources and the evolutionary potential of wild pea populations.

In conclusion, the advancements in pea genomics have significantly contributed to our understanding of the evolutionary history, domestication, and genetic diversity of this important legume. The integration of genomic data from diverse sources has provided a comprehensive view of the pea genome, paving the way for the identification of key agronomic traits and the development of improved breeding strategies. Future research should focus on the continued exploration of genetic diversity within wild and cultivated pea populations, the refinement of genomic prediction models, and the application of advanced breeding techniques, such as gene editing, to further enhance pea breeding programs. Additionally, efforts should be made to ensure the conservation of genetic resources and the sustainable use of pea germplasm in the face of changing environmental conditions and agricultural demands.

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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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