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Comparative Genomic Analysis of Wild and Cultivated Mung Bean (*Vigna radiata*)

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Abstract Mung bean (*Vigna radiata*) is an important edible and forage legume crop and has a wide history of cultivation and consumption in Asia and other regions. Wild mung beans, as a close relative of cultivated mung beans, retain rich genetic diversity and are of great value for studying the domestication process and genetic improvement of mung beans. This study, based on whole-genome resequencing and comparative analysis, systematically analyzed the genomic structure, gene family evolution, genetic diversity and population structure of wild and cultivated mung beans. The results show that the genome of cultivated mung beans has undergone significant structural variations compared to the wild type, including the expansion and contraction of some gene families. Population genetic analysis indicates that mung beans experienced significant genetic bottlenecks during domestication, leading to a decline in SNP and InDel diversity in cultivated varieties. Meanwhile, comparative analysis revealed that a number of key genes related to flowering period, seed size, nutritional quality and stress resistance presented differential selection signals between wild and cultivated mung beans. Further gene function annotation and pathway analysis suggest that these genes may have played a significant role in the adaptive evolution and cultivation improvement of mung beans. This study established a genomic comparison framework between wild and cultivated mung beans, providing new evidence for understanding the domestication mechanism of legume crops and offering a strong reference for molecular breeding and genetic improvement of mung beans.

Keywords Mung beans; Comparative genomics; Genetic diversity; Domestication; Molecular breeding

1 Introduction

Mung beans (*Vigna radiata*), which might have originally been just a wild plant somewhere in South Asia, have now become common legumes on dining tables in many regions, especially being widely consumed in Asia and Africa. It can not only be made into dry food and tender sprouts, but is also often used in traditional herbs. What is most valued about this plant is not only its fast growth and short cycle, but also its ability to fix nitrogen, which is very helpful for soil improvement and crop rotation. In addition, it can adapt to various climates and is quite drought-resistant. In terms of food security in developing countries, it plays a certain key role to some extent (Wu et al., 2020; Mwangi et al., 2021; Rohilla et al., 2022; Huppertz et al., 2023). When it comes to nutrition, mung beans themselves are no less impressive. The protein content in their dry seeds can reach 24%-27%, and they are also rich in various essential amino acids, iron, folic acid and other trace elements.

Cultivated mung beans and their ancestors, the wild subspecies *V. radiata* var. sublobata, have already developed a considerable genetic gap. This kind of differentiation does not occur entirely naturally; most of it is caused by human activities. To meet the demands of agriculture, people prefer traits that are early-maturing, high-yielding and less prone to podding. However, precisely because of these choices, the genetic basis of mung beans has narrowed (Liu et al., 2022; Huppertz et al., 2023; Jia et al., 2024). In other words, some traits that were considered "useful" were retained, but many other genetic resources were thus left aside. Comparative genomics technology comes in handy here. It can not only draw the genetic map of mung beans, but more importantly, it can help researchers identify genes related to key traits, such as loci related to flowering, disease resistance or nutrition. In recent years, whether it is the assembly of high-quality genomes, the alignment of pan-genomes, or genome-wide association studies such as GWAS, all have been used to screen out these candidate genes (Ha and Lee, 2019;

Chen et al., 2022; Chiteri et al., 2024). These tools do not make research more complicated; instead, they make breeding more directional and efficient.

This study systematically compared the genomes of wild and cultivated mung beans to clarify the genetic basis of domestication, trait selection and adaptation, including characterizing genomic diversity and population structure, identifying key gene and structural variations related to domestication and agronomic traits, and assessing the genetic improvement potential of wild germplasm. This study aims to provide fundamental knowledge for breeding mung bean varieties with strong stress resistance, high yield and rich nutrition by integrating comparative genomics, thereby promoting sustainable agriculture and food security.

2 Genome Structure and Conserved Features Analysis

2.1 Comparison of genome size and chromosome-level structure

The recently completed intergranular telomere to telomere (T2T) genome assembly of mung bean cultivated varieties now presents a comprehensive set of data: a genome size of approximately 500 Mb, distributed across 11 chromosomes, with a total of 28 740 protein-coding genes annotated. Nearly half (49.17%) of the regions were repetitive sequences, especially the long-terminal repetitive retrotransposon (LTR-RT) accounted for a large proportion. However, if mung beans are compared with their close relatives, such as adzuki beans, their collinearity in chromosomal structure is still very high, basically in a one-to-one correspondence. This stable structure also indicates from the side that the chromosomal arrangement within the genus Vigna has not been much "disturbed" and is relatively conserved (Liu et al., 2022).

2.2 Identification of conserved gene families and homologous gene clusters

In fact, it is not only the structural aspect that shows a conservative trend, but also the gene family has a similar tendency. In the comparative analysis of mung beans and other dicotyledonous plants, 32 253 orthogonal groups were identified, among which 87.4% of the mung bean coding genes were classified into a certain gene family. Among these families, 1 532 are unique to mung beans and mainly participate in biological processes such as starch and sucrose metabolism, amino acid synthesis, and ribosome assembly. Of course, not all families remained unchanged. Some expanded, while others shrank. Tandem repeats contribute significantly to expansion, especially in plant-pathogen interactions and secondary metabolism. Transcription factor families like NAC and BBX are typical examples that are highly conserved among various species. They are not only conserved but also often undergo purification selection. Most of the retained ones have practical effects on development or stress responses (Yin et al., 2021; Tariq et al., 2022; Yin et al., 2024).

2.3 Differences in structural variations (deletions, inversions, duplications)

The difference in structural variation (SV) between wild mung beans and cultivated mung beans can actually be seen through comparison, especially after conducting an integrated analysis of multiple germplasms. It's not to say that all variations are related to domestication, but the absence, inversion and repetition of some key regions are very likely to have accumulated gradually during the process of artificial selection. And don't forget that transposition factors like LTR-RT, these "moving" genetic elements, have been secretly causing trouble all along. Their amplification may not only affect the expression activity near the genes, but even lead the entire genome to evolve in another direction. Take those genes that regulate flowering time or color for example. PAV events occur particularly frequently. This is likely not a coincidence but the result of long-term selection. As for the expansion of gene families, fragment duplication is one of the driving forces, which has been mentioned in many studies. But then again, although there are many repeated genes, most of them are not messed up - their functions are rather stable because they are basically still under the pressure control of purified selection (Jia et al., 2024).

3 Gene Family Evolution and Functional Divergence

3.1 Comparative analysis of gene family expansion and contraction

Gene families do not exist statically, especially in mung beans, where their expansion and contraction are particularly obvious. Comparative genomic data show that among 32 253 orthogonal groups, 2 218 families experienced expansion and another 1 093 shrank (Liu et al., 2022; Tariq et al., 2022; Yin et al., 2024). The most obvious expansion is mostly related to plant-pathogen interactions, isoflavone synthesis, terpene metabolism, unsaturated fatty acid pathways, etc., all of which are related to plants' responses to the environment and the diversity of their nutritional composition. Behind such expansions are often serial repetitions or fragment repetitions at work. However, even if duplication occurs, the vast majority of gene pairs still retain their original functions because they are all under the pressure of purification selection. In contrast, although the number of shrinking families is also considerable, they are not as prominent in terms of functional enrichment.

3.2 Differences in stress-responsive gene families

When it comes to responding to adversity, some genetic families of mung beans are actually quite "versatile". The OSCA family is an example. There are a total of 13 members, and many of them will be activated under drought or salt stress (Yin et al., 2021). However, although these members are repetitive, their expressive behaviors are different from each other. Clearly, they are no longer cast from the same mold - functional differences have already been established. Looking at the BBX family, the number is slightly smaller, with 23 members. The expansion mainly relies on fragment repetition. This type of gene is highly sensitive when treated with ABA, PEG or NaCl, especially *VrBBX5*, *VrBBX10* and *VrBBX12*. They can often be seen in the expression profile and seem to be particularly active under stress conditions (Yin et al., 2024). In addition, the NAC family is even larger, with as many as 81 members. Its role can be found in almost all kinds of coercive scenarios. According to the hint of the co-expression network, they may not be the scraps but the "backbone" in the stress resistance strategy of mung beans.

3.3 Evolutionary features of genes related to yield and quality

The evolution of gene families is not only related to resistance, but also to yield and quality. During the domestication process of mung beans, some genes related to flowering time or color have undergone PAV variations, and these variations are actually conducive to early flowering and wider adaptation in different environments (Liu et al., 2022). Looking at the genes involved in starch synthesis, sucrose metabolism, amino acids and secondary metabolism, many are concentrated in the specific or expanded families of mung beans. That is to say, these functions may be related to its characteristics of high protein and high nutritional density (Liu et al., 2022). In terms of some more "practical" traits, such as pod cracking, the PDH1 gene has been explicitly named as one of the key domestication sites regulating this trait (Li et al., 2024), because it is directly related to whether the pods can be harvested smoothly.

4 Genetic Diversity and Population Structure

4.1 Distribution patterns of SNPs and InDels in wild and cultivated mung bean

In mung beans, the distribution of genetic variations is not even and is not as simple as imagined. Resequencing data revealed that there were over one million proprietary SNPS in the cultivated population, while the number of structural variations (SVS) in the wild population was significantly higher (Jia et al., 2024). It is worth noting, however, that most of the variations are low-frequency variations (sub-allele frequencies <0.05), among which deletion type SV is the most common. Across the entire genome, the distribution of SNPS and SVS is highly consistent, but there are also some regions that are "abnormally active", with a particularly large accumulation of variations. These hotspots may reflect traces of past domestication or strong selection. Although technological means are becoming increasingly advanced, such as high-quality genome assembly which enables us to observe millions of SNPS and tens of thousands of Indels, it is still not easy to explain the biological significance behind these variations.

4.2 Population structure and phylogenetic analysis

Wild mung beans and cultivated mung beans are actually quite clearly distinguished in terms of genetics. When analyzed with markers such as SNP, SV, and SSR, the two are basically classified into different groups, and the gene exchange between them is also very limited (Chen et al., 2015; Liu et al., 2022). Analysis tools such as PCA graphs and phylogenetic trees further verified this differentiation pattern. The population clustering of cultivated varieties is usually more concentrated, while the genetic background of wild species is more complex and the differences are also greater. The geographical origin can also be seen in the population structure - for example, Chinese strains and non-Chinese strains often belong to different groups, and even there are many detailed differences among local varieties native to China (Jia et al., 2024).

4.3 Evidence of domestication bottlenecks and loss of genetic diversity

When it comes to the loss of genetic diversity, the situation of mung beans is actually quite typical. Throughout the entire domestication process, mung beans have experienced a distinct genetic bottleneck. The nucleotide diversity of cultivated species is much lower than that of wild species, and the number of private SV has also decreased significantly (Jia et al., 2024). Not only that, indicators such as PIC values and allelic variations are also generally low in the cultivation materials (Chen et al., 2015; Chiteri et al., 2022), indicating that the loss of diversity is not only a "reduction in quantity", but also becomes more homogeneous at the genotype level (Figure 1). The reason for this might be related to the strong selection of some domesticated traits and the restricted introduction of wild gene banks. This situation also reminds us that in the future, the improvement of mung beans may have to rely more on wild germplasm to make up for the lack of diversity.

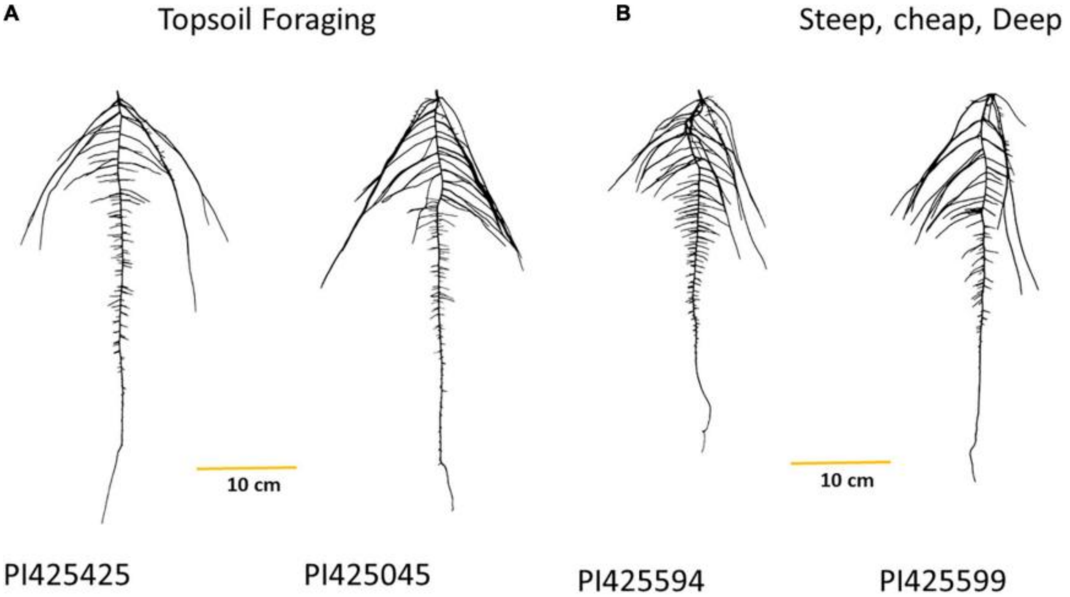

Figure 1 Mung bean iRoot ideotypes, (A) top two genotypes in the topsoil foraging and (B) top two genotypes in the steep, cheap, and deep after ranking the genotypes in the IA mung bean panel (Adopted from Chiteri et al., 2022)

5 Case Study: Key Domestication Traits Revealed by Comparative Genomics

5.1 Variations in genes related to flowering time and growth duration

Not all mung bean materials can flower normally in different environments, and this actually involves variations in photoperiodic regulatory genes. Comparative genomic studies have shown that nine genes closely related to flowering time carry significant presence/absence variations (PAVs), which have been subject to selective pressure during domestication, especially those associated with early flowering traits. Early flowering is a very practical feature among mung beans that adapt to seasonal changes or differences in planting areas. The results of GWAS further indicated that the direct homologues of genes such as FERONIA receptor-like kinase and photosensitive pigment A (PhyA) are the key to the differences in flowering time, and the SNPS related to them statistically explain a large number of phenotypic differences (Liu et al., 2022; Chiteri et al., 2024). These findings provide clear genetic targets for adjusting the growth period of mung beans.

5.2 Selection signatures in genes controlling seed size and nutritional quality

In fact, domestication has also left many genetic imprints on seed quality. Structural variations and the accumulation of SNPS in pathways such as fatty acid, lignin, and phenylpropanoid metabolism reflect the direction of domestication selection, and these variations affect seed composition and nutritional values (Jia et al., 2024). GWAS also verified this: homologous genes such as *SWEET10* related to crude starch content and loci related to mineral concentration were frequently selected in cultivated species (Wu et al., 2020; Liu et al., 2022). It is worth mentioning that the PDH1 gene plays a core role in the pod cracking trait, and cracking is directly related to the preservation and harvest rate of seeds (Figure 2). It is also regarded as a classic case of parallel domestication (Li et al., 2024).

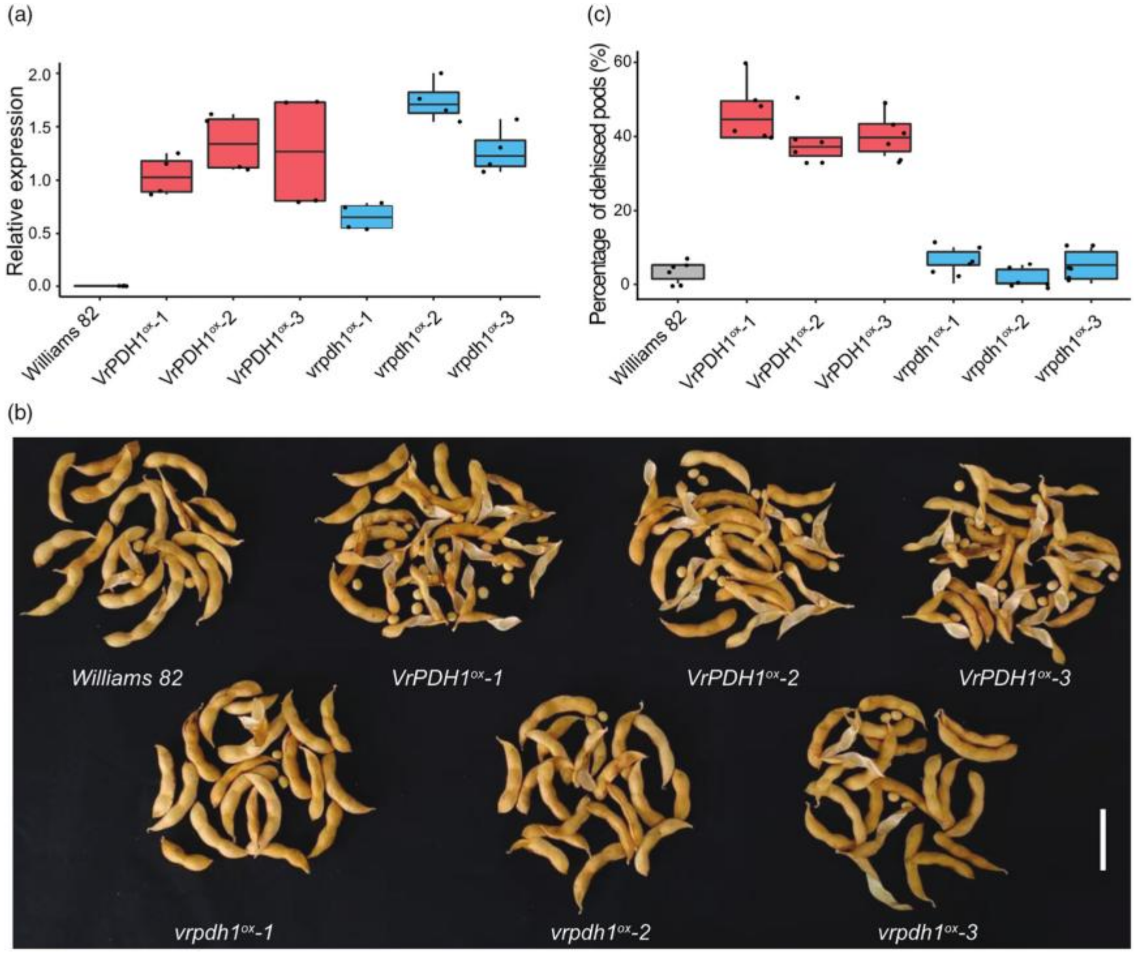

Figure 2 Function evaluation of *VrPDH1* in controlling pod dehiscence in mung bean. (a) The expression levels of *VrPDH1*/*vrpdh1* in transformed plants. (b) The pod dehiscence phenotype in transgenic soybean lines. (c) The percentage of dehisced pods in transgenic soybean lines (Adopted from Li et al., 2024)

5.3 Functional differences in genes associated with disease resistance and stress tolerance

If we really talk about the differences between cultivated mung beans and wild mung beans, it's not as simple as just looking at who grows better or who produces more. The differences are also quite obvious in the genes related to adversity. Gene families like NAC and B-box (BBX) have always played important roles in responding to environmental challenges such as drought and diseases. In wild mung beans, the structures and expression patterns of these genes are significantly more diverse (Tariq et al., 2022; Yin et al., 2024). For instance, *VrNAC1.4*, *VrBBX5*, *VrBBX10* and *VrBBX12* have relatively high expression activity in wild materials and are associated with stress resistance and disease resistance. But once it comes to cultivating mung beans, the situation is a bit different. The diversity of such genes has been weakened, which is a typical "genetic bottleneck". Although this might have lost some potential for resistance, from another perspective, it also serves as a reminder for subsequent precision breeding (Jia et al., 2024).

6 Molecular Mechanisms of Domestication and Adaptation

6.1 Genomic evidence of domestication selection signals

The domestication trajectory of mung beans is not a straight line. High-resolution notch-free genome assembly and population resequencing results on some key metabolic pathways have revealed obvious traces of selection. In pathways such as fatty acid synthesis, lignin biosynthesis, and phenylpropanoid metabolism, many gene regions overlap with structural variations (SVS) and SNPS, and this is precisely where selective clearance occurs intensively. During the domestication process, these genes were strongly screened. In fact, it was not only for agronomic purposes. Some variations simultaneously affected seed composition, plant morphology and even stress response (Jia et al., 2024). Looking at the overall trend, the total number of SVS in cultivated populations is far lower than that in wild species, and there is also a significant loss of private variations. This difference itself indirectly confirms the genetic bottleneck brought about by domestication.

6.2 Differences in adaptive genes between wild and cultivated types

Not every type of mung bean can remain calm in the face of environmental changes. Cultivated mung beans often seem "picky", while wild mung beans are much more flexible. From the comparative genomic data, it can be seen that the genetic diversity of wild populations is higher, and they carry more adaptive genes. Moreover, these differences are often hidden in regulatory regions rather than directly acting on coding sequences. Proteins with EF-hand domains associated with calcium signaling pathways occur more frequently and sometimes more complex in wild mung beans, which may be one of the reasons why they can cope with complex environments (Jia et al., 2024). In contrast, for cultivated types, in some metabolic pathways, the number of gene families has even decreased. However, it is not a one-sided weakening. For instance, the genes in the pathways related to plant-pathogen interaction and isoflavone synthesis show signs of expansion, which to some extent indicates that they are gradually finding their own rhythm in the artificial cultivation system (Liu et al., 2022).

6.3 Reconstruction of gene regulatory networks during domestication

Behind many domesticated traits, it is not merely a simple change in genetic coding. The adjustment at the regulatory level is the decisive link. Minor changes in the promoter sequence and the accumulation of PAV events often affect the arrangement of the entire regulatory network. Some genes, such as *PDH1* which controls pod cracking, not only have changes occurred in the coding region, but its upstream regulatory region has also been simultaneously "rewritten", which has been repeatedly mentioned in multiple transcriptome and genomic studies (Liu et al., 2022; Li et al., 2024). For instance, gene families such as B-box (BBX) that are involved in stress responses have undergone repeated expansion during the domestication process. Although most of the repetitive genes were eventually screened out by purification selection and retained the core function, these expansion phenomena themselves are sufficient to show that the regulatory system is not imstatic and it is also quietly reconstructed during the domestication process (Yin et al., 2024).

7 Applications of Comparative Genomics in Mung Bean Breeding

7.1 Development and utilization of molecular markers from domestication-related genes

The breakthroughs made in molecular breeding of mung beans in recent years are inseparable from the promotion of comparative genomics. This field has identified many types of variations related to domestication and agronomic traits, such as SNPS, InDel and PAV, involving a wide range of traits, including flowering time, grain size, disease resistance, and even nutritional quality. It is worth noting that these markers are no longer just on paper; they are increasingly being used in molecular marker-assisted selection (MAS) and population genetic diversity assessment (Chen et al., 2022; Rohilla et al., 2022). However, markers are merely entry points. Tools such as high-density genetic maps and GWAS are the "Bridges" that establish clear connections between markers and traits, especially playing an accelerator role in enhancing yield and resistance. In addition, markers such as SSR, SNP and transposon-derived markers have also begun to be used for genetic assessment of interspecific hybrid offspring, with a straightforward aim - to broaden the genetic basis of breeding materials (Fatmawati et al., 2021; 2023).

7.2 Potential of genomic selection and molecular design breeding

If we talk about something further than MAS, it all depends on genomic selection. Now, with the addition of GWAS, high-throughput typing technology and the pan-genome, molecular design breeding of mung beans has also begun to truly "take root". The advantage of this type of method lies in the fact that it can predict the manifestation of complex traits in advance, and even select potential parents at the early stage of breeding, gradually integrating traits such as yield, nutrition, and stress resistance into a variety (Wu et al., 2020; Liu et al., 2022). Especially for those traits with complex genetic backgrounds, it is quite difficult to select them by traditional methods. Genomic selection models can greatly improve efficiency. Of course, behind this are abundant germplasm resources and reliable statistical modeling techniques-only when these two are well combined can strategies truly move from theory to practice (Ahmed et al., 2024).

7.3 Comparative genomics with other legume crops and complementary utilization

The genome of mung beans is actually not so "independent and unique" from that of other leguminous crops. Related species such as cowpea, adzuki bean and soybean often share a set of ancestral "genetic programs" in terms of seed size, flowering time and stress resistance. Many key functional regions and direct homologous genes have been revealed one by one in comparative genomes (Srivastava et al., 2018; Chiteri et al., 2024). Sometimes, the data of Mung Bean itself may not be so complete, but with the research results of these "neighbors", many molecular tools and experiences can be smoothly transferred over. Not only borrowing, but also mung beans themselves can find improvement clues from these collinear regions and shared QTLS. Even some hidden new alleles and molecular markers are discovered precisely through this cross-species comparison approach. The result is that an entire genetic toolbox has been continuously expanded, not only for mung beans but also for other legumes.

8 Conclusion

At first, in fact, no one expected that the genetic diversity within mung beans would be so complex. It was not until high-quality reference genomes and whole genome assembly were available that the truth was gradually pieced together - 83% of the genes belonged to the core sequence, while the remaining 17% had very obvious variations. This is just the beginning. Key traits such as early flowering, pod cracking, nutritional composition, and stress resistance mechanisms were later gradually traced back to specific genes and even variations at the PAV level. Interestingly, the selection signals are also very obvious in pathways such as fatty acid synthesis and phenylpropane metabolism. However, relying solely on gene structure is not enough; the expression level must also keep up. So GWAS and transcriptome analysis were also brought in, filling in the "dynamic information" link. Many candidate genes related to agronomic and nutritional traits were thus discovered (and indeed provided considerable assistance for subsequent molecular breeding).

Of course, clarifying these fundamental issues does not mean that all obstacles have been cleared. Many early studies were limited by the low density of markers, resulting in mediocre resolution of gene mapping. Even with more complete genome assembly nowadays, there are still not many candidate genes that have been truly verified for function, and the "identities" of many regulatory elements are still just speculations. In addition, the genetic resources of wild mung beans have not been fully exploited yet. The work of integrating genomic, transcriptomic and metabolomic data for multi-level trait analysis is still in its infancy. To be more realistic, even if potential genes are identified, it is still quite difficult to quickly transform them into breeding tools at present. Problems such as the inability to keep up with high-throughput phenotypic capabilities and the immaturity of statistical modeling tools have been constantly slowing down this transformation process.

However, one thing has become increasingly clear: genomic comparisons between wild and cultivated mung beans are constantly demonstrating the significance of wild germplasm resources. They have considerable potential in providing new alleles for stress resistance, disease resistance, and even nutritional improvement. The genetic bottlenecks and diversity losses that emerged during domestication once again remind us that we should not overlook the role of closely related wild materials in breeding. What needs to be done now is actually to link these genomic discoveries with more operational breeding strategies, such as MAS, genomic selection, and even gene editing. Only in this way can the development pace of high-yield and stress-resistant mung bean varieties be truly accelerated, and it is also possible to provide more stable confidence for food security and sustainable agriculture in addressing the challenges of climate change and pests and diseases.

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Conflict of Interest Disclosure

The authors affirm 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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