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Deciphering the Genetic Interactions That Control Soybean Agronomic Traits

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Abstract Soybeans are a crop of global significance, highly valued for their diverse applications in food, feed and industrial products. The productivity of soybeans is determined by complex agronomic traits, including yield, drought resistance, disease resistance and quality. Understanding the genetic interactions that regulate these traits is crucial for promoting soybean breeding programs. This study explored the genetic basis of these agronomic traits, with a focus on Mendelian genetics, quantitative trait loci (QTLs), and epigenetic interactions. Meanwhile, molecular mechanisms such as gene regulatory networks, transcription factors, and environmental interactions were studied, and these factors jointly affect trait expression. Through the advancements in genomics, high-throughput sequencing technology and bioinformatics platforms, an in-depth analysis of genetic interactions has been conducted. A case study on yield improvement demonstrated the identification and functional verification of cooperative gene interactions, highlighting their practical application in the cultivation of high-yield soybean varieties. Although there are still challenges in decoding polygenic traits and translating genetic insights into practice, this study highlights the potential of integrating multi-omics data and genome editing tools in enhancing the stress resistance and productivity of soybeans. This research provides a foundation for future soybean breeding innovation to meet global agricultural demands.

Keywords Soybean; Genetic interactions; Agronomic traits; Genomics; Breeding strategies

1 Introduction

When it comes to soybeans (*Glycine max* [L.] Merr.), although they may seem ordinary, you might not know how important they are. Whether it is making tofu or extracting oil, it is indispensable (Diers et al., 2018; Almeida-Silva et al., 2020). But then again, the demand for soybeans is increasing now (He et al., 2019) Not only humans eat it, but also animal feed is used, and it is widely used even in industry. Of course, the soybeans grown in different places vary quite a lot. So now everyone is trying to cultivate better varieties (Li et al., 2023; Rani et al., 2023b). In fact, perhaps no one paid attention to it in the early years, but the protein and fat content of soybeans is indeed astonishingly high, which is why it is so popular.

When it comes to soybean yield, it's not just about how many pods are produced. You see, things like plant height, whether the root system grows well, and even the weight of each bean are directly related to how many soybeans can be harvested in the end (Rani et al., 2023a). Of course, these manifestations are not solely determined by genes. The location and weather conditions are also particularly important. Let's take flowering time as an example. The difference between early and late flowering can be significant, as well as the time it takes from planting to harvesting, including what we often refer to as "hundred grain weight", all of which secretly affect yield (Rahama et al., 2022). Many people may not have noticed, but the root system underground is actually crucial, especially in times of drought or poor soil conditions. Good root growth is necessary to absorb sufficient nutrients (Kim et al., 2023b).

Those engaged in soybean breeding all know that merely looking at surface traits is not enough. The manifestations grown in the ground are actually the result of various genes "fighting" behind them-some genes cooperate with each other, while others undermine each other (Rani et al., 2023b). Nowadays, with advanced technology, detection methods like GWAS, combined with SNP chip technology, can help us identify those gene markers that control important traits (Kim et al., 2023a). However, to be honest, the performance of the same variety can vary greatly when grown in different places. This is the competition between genes and the environment. Through years of research, it has been found that understanding these genetic patterns clearly is particularly useful for breeding new varieties that are disease-resistant, drought-resistant and high-yielding (Diers et al., 2018; Hong and Huang, 2024). Of course, the genetic network is extremely complex. Sometimes a single gene can influence several traits, and this is the most troublesome part.

This study aims to clarify the genetic pathways behind the important agronomic traits in soybeans. Simply put, I want to understand why genes affect how tall soybeans grow and how many beans they produce. There have been many new discoveries now, such as specific gene markers and candidate genes, as well as complex interaction networks between them. However, it is interesting that the same gene may behave completely differently in different environments-a variety that grows well on this land may not work on another piece of land. So in addition to studying the genes themselves, we also need to consider the impact of the planting environment. Ultimately, conducting these studies is aimed at cultivating better soybean varieties with high yields, strong disease resistance, good adaptability, and the ability to cope with different planting conditions around the world. After all, the global demand for soybeans is increasing, and relying solely on old varieties is definitely not enough.

2 Genetic Basis of Agronomic Traits in Soybean

2.1 Defining agronomic traits

When it comes to whether soybeans grow well or not, it actually depends on many aspects. First and foremost, the most intuitive aspect is the yield-which is directly related to the number of pods per plant, the height of the plant, and the weight of a single bean (Hu et al., 2021; Fu et al., 2022; Rani et al., 2023a). However, nowadays the weather is becoming increasingly abnormal, and soybean varieties that can withstand drought conditions are particularly precious (Ouyang et al., 2022; Sun et al., 2022). Pests and diseases are also a headache, often reducing the harvest. Interestingly, the value of soybeans is not only determined by the yield. The protein and oil content in the soybeans is the key to determining the selling price (Zhu et al., 2021). Sometimes, varieties with high yields may not have as good nutritional value. This is quite contradictory.

2.2 Overview of mendelian genetics and quantitative trait loci (QTLs) in soybean

When it comes to the genetic characteristics of soybeans, at first, everyone followed Mendel's approach, thinking that a trait was controlled by a single gene. But in actual farming, it is found that those important characteristics of soybeans-such as when they flower, how tall they can grow, and how many beans they produce-are often the result of the combined action of many genes (Hu et al., 2021; Zhu et al., 2021). These complex genetic characteristics are now all referred to as quantitative trait loci (QTLS). Through QTL mapping technology, researchers gradually identified the locations of these characteristics on the genome (Fu et al., 2022). Interestingly, with the emergence of new technologies such as GWAS and SLAF-seq, the localization accuracy has been getting higher and higher, and a number of new key genes have been discovered as a result (Ouyang et al., 2022). However, on the other hand, although many QTLS have been found, when it comes to applying them to breeding, the complex interactions among these genes still need to be considered (Rani et al., 2023a).

2.3 Role of epistasis in complex trait determination

When it comes to soybean breeding, the relationships among genes are much more complicated than one might imagine. Different genes can influence each other, and this phenomenon, known as superposition, makes breeding particularly challenging. Look at such seemingly simple features as seed size and shape. In fact, they are the result of multiple genes "fighting" (Figure 1) (Li et al., 2020). What's more troublesome is that some key QTLS can affect several traits simultaneously, which explains why when one trait is improved, other traits will also change (Fu et al., 2022). However, then again, only by understanding these genetic interactions can the genetic potential of soybeans be truly exploited (Diers et al., 2018).

Studying the traits of soybeans nowadays is no longer as simple as it was in Mendel's time. From yield to drought resistance, behind each important feature lies a bunch of genes competing. Fortunately, new technologies keep emerging, allowing us to see these complex genetic relationships more clearly. Although the road ahead is still long, these discoveries have indeed opened up new ideas for cultivating better soybean varieties.

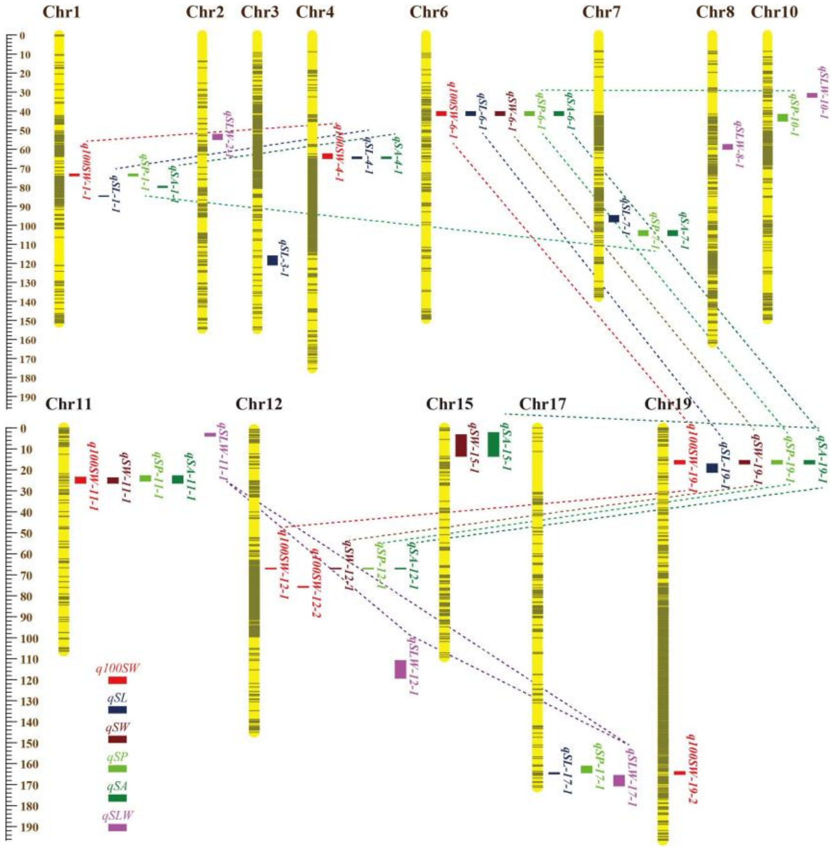

Figure 1 Locations and interactions of QTLs detected for seed traits in NJRISX (Adopted from Li et al., 2020)

Image caption: Different colorful dot lines represent the interaction between respective QTLs. The ruler on the left is shown in units of cM (Adopted from Li et al., 2020)

3 Molecular Mechanisms Underpinning Genetic Interactions

3.1 Gene regulatory networks controlling soybean development

The growth process of soybeans is like a carefully arranged 'gene symphony'. Recent research has found that genes like *GmCOL1* act as strict conductors, specifically responsible for suppressing flowering time (Wu et al., 2019). Interestingly, in addition to these visible genes, there are also some "behind the scenes players"-such as small molecules such as miRNAs and lncRNAs. Although they do not directly code proteins, they can secretly regulate important characteristics such as seed color and yield (Figure 2) (Ku et al., 2022). These regulatory factors are like stage supervisors, influencing the growth and development of soybeans by controlling the stability and translation efficiency of mRNA. For example, under drought conditions, certain miRNAs may suddenly become active, adjusting the expression levels of stress related genes. These findings make us understand that improving soybean varieties cannot only focus on coding genes, the entire regulatory network must be taken into account.

3.2 Role of transcription factors and signaling pathways

The growth regulation of soybeans is like a precise 'molecular symphony', and transcription factors (TFs) are the conductors of this performance. For example, the transcription factors of the AP2/ERF family not only regulate how soybeans grow, but also respond to various environmental pressures (Yang et al., 2021). Interestingly, these transcription factors rarely go it alone-they often work in teams to regulate downstream genes through complex signaling networks. Just like the recently discovered GmPLATZ, this transcription factor is particularly interesting as it acts as a "seed size regulator" that affects the size of beans by activating cell division related genes and gibberellin synthesis genes (Hu et al., 2023). In fact, these regulatory mechanisms are more complex than we imagine. The same transcription factor may play completely different roles at different stages of development, and sometimes it may also "string" with other signaling pathways. For example, a transcription factor responsible for drought resistance may also affect flowering time. This characteristic of "specialization and versatility" not only brings challenges to breeding work, but also provides new opportunities. After all, if a key regulatory node can be found, it may be possible to improve multiple agronomic traits simultaneously.

3.3 Impact of environmental interactions on genetic pathways

The growth performance of soybeans is like an "environmental detector", and the same genes may be completely different in different places-this land is a high-yield variety, and changing land may cause wilting (Rani et al., 2023b). Interestingly, some varieties are particularly selective and can only reach their maximum potential in specific environments. Through GWAS analysis, it was found that certain genomic regions act as "environmental sensors" that adjust trait performance based on different planting conditions (Ravelombola et al., 2021; Fu et al., 2022). For example, drought resistant genes are particularly active in arid areas, but may become lazy in humid areas. These findings make breeding work more like 'precise matching'. Not only do we need to consider the genes themselves, but we also need to consider their "temperaments" in different environments. Now we know that soybeans are regulated by a triple network of genes, transcription factors, and environmental signals from flowering time to disease resistance. Sometimes a gene needs to "listen" to both internal developmental signals and external environmental signals before deciding how to express it. Although this complexity is a headache, it also provides new ideas for cultivating varieties with stronger adaptability, such as finding key regulatory nodes that can stably function in multiple environments.

4 Advances in Genomics and Bioinformatics Tools

4.1 High-throughput sequencing technologies in soybean genomics

Nowadays, conducting soybean research is not as difficult as it used to be. New technologies have made genomic analysis both fast and accurate. Take the SoySNP50K chip for example. It screened out 51 important markers from various soybean materials at once, and these markers were all linked to visible and tangible traits such as plant height and grain weight (Rani et al., 2023a). What's more interesting is that through whole genome sequencing of 250 soybean samples from different sources, new genes such as *GSTT1* and *CKX3* were unexpectedly discovered. Surprisingly, they are related to the complex trait of yield (Yang et al., 2021). However, on the other hand, although finding so many SNP loci and candidate genes is a good thing, it still depends on their performance in different varieties when they are actually applied to breeding (Ravelombola et al., 2021). Just as it was recently discovered, some genes that perform well in the south are completely different when planted in the north.

4.2 Functional genomics approaches to unravel genetic interactions

Nowadays, the methods for studying the functions of soybean genes are getting more and more advanced. Take this TILLING-by-Sequencing+ technology for example. It can precisely identify the mutations we need from tens of thousands of mutants like a sieve (Lakhssassi et al., 2021). What is particularly interesting is that for some mutants found by this method, the fatty acid composition in the seeds has completely changed, which provides a new idea for improving the quality of soybean oil. Even more amazing is the CRISPR/Cas9 "gene scissors", combined with the transformation technology of Agrobacterium roots, which makes the study of soybean root systems particularly convenient. In the past, studying root system genes was very troublesome. Now, we can precisely edit the target genes directly and modify them however we want. For instance, recently someone used this method to knock out the genes that control root growth. As a result, it was found that not only did the root system change, but the drought resistance of the entire plant was also affected. The greatest advantage of this technology is its speed. It can verify the function of a gene within just a few months, which is much more time-saving than traditional methods. However, it should be noted that although technology has advanced, the complex interactions among soybean genes still often leave people confused. Sometimes, modifying one gene can affect several unexpected traits.

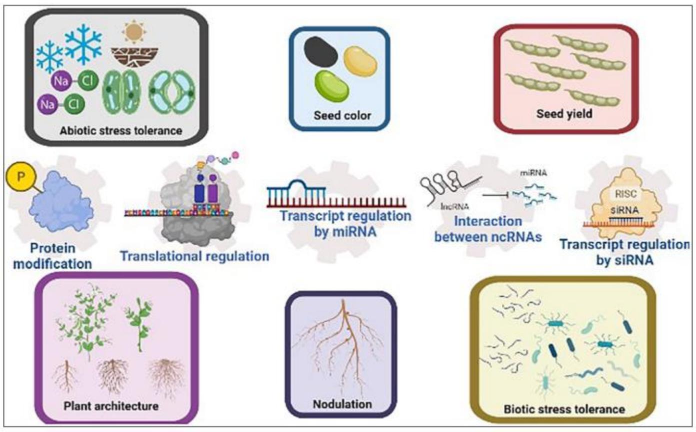

Figure 2 Common agronomic traits selected in soybean breeding include seed color and yield, plant architecture, nodulation efficiency, and the tolerance to abiotic and biotic stresses (Adopted from Ku et al., 2022)

Image caption: These traits have been reported to be regulated by post-transcriptional regulatory mechanisms such as transcript regulation by ncRNAs, proteins modification, and translational regulation. The interaction between ncRNAs further increases the versatility of post-transcriptional regulations. This figure is created with BioRender.com (Adopted from Ku et al., 2022)

4.3 Integrative bioinformatics platforms for soybean trait analysis

Processing soybean genetic data now relies heavily on powerful analytical tools. Take SoyMAGIC as an example, this platform is quite interesting as it uses a special hybrid population design (MAGIC) that can precisely locate the gene regions that affect agronomic traits (Hashemi et al., 2022). However, on the other hand, having genetic data alone is not enough. The most powerful feature of these platforms is their ability to integrate the actual performance data of plants, so as to find the truly important genetic markers. It is interesting that the same genotype may perform significantly differently in different environments, and current analytical tools can help us identify which varieties perform better under specific conditions (Rani et al., 2023b). Speaking of technological progress, from gene sequencing to data analysis, this whole set of methods has indeed made breeding work different. Although it is not yet possible to fully predict all traits, at least now we can screen out potential new varieties faster.

5 Case Study: Gene-Gene Interaction in Soybean Yield Improvement

5.1 Identifying key yield-related genes and their interactions

To increase soybean yield, the key is to identify the genes that play a decisive role. The recent research is quite interesting, such as the discovery of some important SNP markers using GWAS method, which are not only related to yield, but also affect characteristics such as maturity time and plant height (Ravelombola et al., 2021). Speaking of which, some wild soybean varieties contain good genes, and introducing these excellent genes into cultivated varieties can indeed increase yield (Diers et al., 2018). However, the most surprising thing is that genes like *Glyma.01g199200* and *Glyma.10g065700*, although not previously studied, are closely related to yield traits in their location (Rani et al., 2023a). Of course, these findings are just the beginning, as soybean yield is influenced by too many factors and the interactions between genes are much more complex than imagined.

5.2 Experimental validation of synergistic gene functions

It is not enough to rely solely on calculations to understand how these genes affect soybean yield. Experimental verification is needed. For example, in the study of the NAM population containing 5 600 inbred lines, many genetic markers related to yield were indeed found (Figure 3) (Diers et al., 2018). Interestingly, even machine learning is now being used to predict yield by analyzing combinations of various traits, and the results are surprisingly good (Yoosefzadeh Najafabadi et al., 2021). However, what is most surprising is that some QTLs act like "transportation hubs" and can simultaneously affect several important agronomic traits (Fu et al., 2022). Of course, to truly apply these findings to breeding, they still need to be tested through field experiments, as there is always a gap between laboratory data and actual yields.

5.3 Outcomes and implications for breeding high-yield soybean varieties

Now, those engaged in soybean breeding can be said to have a new weapon. The key genes discovered and their interactions have made breeding efforts more targeted. Take SNP markers for example. Combined with genomic selection technology, the breeding of high-yield varieties is now much more accurate than before (Yoosefzadeh-Najafabadi et al., 2021). Interestingly, some newly discovered gene loci recently, such as those controlling adaptability genes, have provided new ideas for breeding (Copley et al., 2018; Lodhi et al., 2023). However, to be honest, although the laboratory data is impressive, to truly cultivate new varieties that are both high-yielding and stress-resistant, repeated field verifications are still necessary. After all, the global demand for soybeans has been on the rise, and relying solely on old methods will definitely not keep up. Now that these genetic discoveries have been made, at least breeders have seen new hope and know which direction to focus their efforts on.

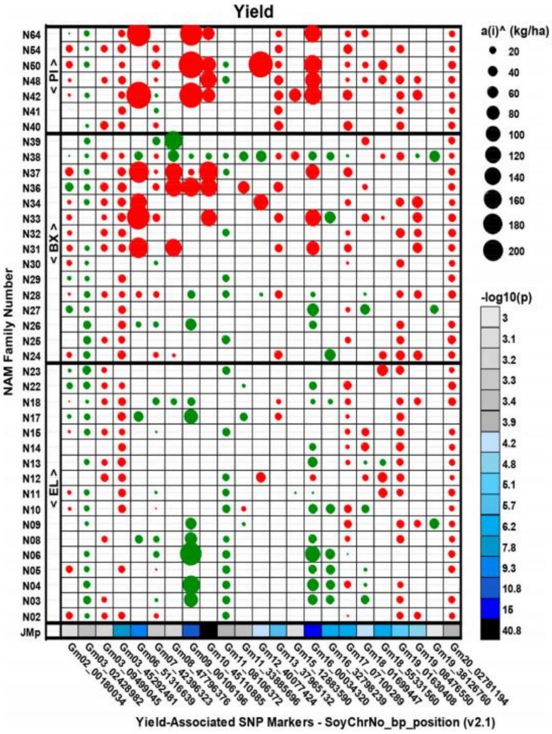

Figure 3 Marker trait associations for yield (Adopted from Diers et al., 2018)

Image caption: The estimated magnitude of each allelic effect (in kg/ha) is depicted by circle symbol diameter, with negative and positive effects rel- ative to the common parent (IA3023) respectively depicted by red and green. The observed-log10(p) values for the each of the 23 marker-trait associa- tions across the 39 founder families are column color-coded by magnitude in the row labeled JMp (acronym for Joint Mapping p value) (Adopted from Diers et al., 2018)

6 Challenges in Deciphering Genetic Interactions

6.1 Limitations of current experimental approaches

Although the current methods for studying soybean genes are advanced, they are not omnipotent. Take the commonly used GWAS and GS techniques for example. Although many important genes can be identified, it is quite difficult to operate in practice-thousands of samples are often required, and a large number of genotypes have to be done (Ravelombola et al., 2021). For instance, there was a previous study that conducted tens of thousands of SNP analyses on 250 soybean materials and indeed found significant clues. However, if the year or batch of materials were changed, the results might be quite different. What is more troublesome is that for complex traits like yield controlled by multiple genes, it is particularly difficult to accurately locate the relevant QTL (Fu et al., 2022). Sometimes, even if a promising gene is found in the laboratory, when it is tested in the field, the result is just passable. These restrictions have forced researchers to consider whether they should develop some more precise and stable new methods.

6.2 Complexity of polygenic traits in soybean

Those important characteristics of soybeans-such as yield, maturity time and plant height-are not determined by just one or two genes. This is like a group of people having a meeting to make a decision, each expressing some opinions, and finally combining them to form the result (Diers et al., 2018). When conducting previous research using the NAM population, although many related gene markers were found, it is still not fully understood how these genes "meet" with each other. What is more complicated is that some gene loci are particularly "meddlesome" and can affect several traits simultaneously (Fu et al., 2022). For instance, for the same QTL, both plant height and flowering time might be managed, which makes breeding work seem like solving a series of problems-moving one might lead to a whole series. Although technology has advanced nowadays, it is still not an easy task to fully understand the "interpersonal relationships" among these genes.

6.3 Translating genetic insights into practical breeding programs

Applying the discoveries from genetic research to breeding is no easy task. Although GWAS and GS technologies have identified many important markers, they always encounter various troubles when applied in practice. For instance, a new gene locus discovered in early-maturing varieties, which theoretically can improve the maturity period and yield, is found to be unstable when applied to the field-if it works well in one plot, it may fail in another. What is even more troublesome is that the genetic differences between cultivated soybeans and wild germplasm are too large, making it particularly difficult to select alleles (Diers et al., 2018). Now even those factors that regulate small Rnas and epigenetics have to be taken into account (Ku et al., 2022), but these mechanisms themselves are like a black box, and it is not clear exactly how they operate.

Ultimately, the current challenges mainly come from three aspects: the limitations of the experimental methods themselves, the complexity of trait inheritance, and the bottleneck of transformation from the laboratory to the field. To break through these, it is probably necessary to put more effort into genotyping technology, draw the genetic map more precisely, and at the same time, find ways to truly integrate and utilize various omics data. After all, breeding is not about conducting experiments; ultimately, it is necessary to grow truly good varieties.

7 Future Directions and Applications

7.1 Integrating multi-omics data for deeper genetic insights

The study of soybeans has become increasingly sophisticated nowadays. Analyzing genomic, transcriptomic and proteomic data together is like piecing together the pieces of a jigsaw puzzle-the recent HypWAS method is quite interesting. It can predict grain yield by analyzing spectral data (Yoosefzadeh-Najafabadi et al., 2021). In fact, the experimental data accumulated over the years has piled up like a mountain. The key is how to string them together. For instance, some genes have very high expression levels, but the corresponding protein activities are very low. This contradictory phenomenon precisely indicates that multi-omics joint analysis is needed. However, to be fair, although the technology is getting more and more sophisticated, the ultimate goal is very simple: to help breeders avoid detours and cultivate good varieties more quickly. After all, compared with the previous "blind men touching the elephant" style of breeding, at least more clues can be seen now.

7.2 CRISPR/Cas9 and genome-editing tools for targeted genetic interaction studies

Gene editing technology has truly brought about earth-shaking changes to soybean research in recent years. Take the "gene scissors" CRISPR/Cas9 for example. After editing the *GmEOD1* gene with it, not only did the soybean grains become larger, but also the protein and oil contents increased (Yu et al., 2023). Even more astonishingly, by fiddling with the *GmAITR* gene, soybeans can actually grow better in saline-alkali land (Wang et al., 2021). Now even the delivery system has been upgraded, using Agrobacterium rhizopus for transformation, and the efficiency is much higher than before (Chen et al., 2019; Niazian et al., 2022). To be honest, although the technology is very advanced, various unexpected situations still occur in actual operation-sometimes editing a gene can also affect other unexpected traits. However, in any case, these new tools have indeed put breeding work on a fast track. Varieties that used to take over a decade to complete can now be accomplished in just a few years.

7.3 Enhancing soybean breeding strategies for climate resilience

It's getting harder and harder to grow soybeans nowadays. We often encounter extreme weather. However, some new technologies have been quite effective recently. Gene editing tools like CRISPR/Cas9 have been able to help improve the stress resistance and yield of soybeans (Guan et al., 2022). Interestingly, last year someone used this method to adjust several genes, and soybeans actually grew well in saline-alkali land and drought conditions (Yao et al., 2023). Sure enough, gene editing alone may not be sufficient. Nowadays, it is popular to analyze genomic and proteomic data together, which makes it easier to identify those genes that can truly resist climate change (Ku et al., 2022). Although it sounds simple, various unexpected situations still arise in actual operation. For instance, some genes perform well in the laboratory but fail to adapt to the local environment in the field. Overall, however, the combination of these new technologies does provide new ideas for cultivating climate-adaptive soybeans (Do et al., 2019). After all, in the face of increasingly abnormal weather, the old varieties are indeed struggling a bit.

8 Concluding Remarks

There have been many breakthroughs in studying the genetic laws of soybean agronomic traits in recent years. Interestingly, by analyzing the NAM population, not only were genetic markers found to affect yield, but it was also unexpectedly discovered that these markers were associated with maturity, plant height, and even seed quality. GWAS analysis identified a number of key SNP loci in cultivated soybean and wild germplasm, which control important features such as flowering time and pod number. However, what is most surprising is that certain core QTLs, like transportation hubs, can simultaneously regulate multiple traits. Although GS and MAS technologies seem promising, in practical applications, it has been found that different varieties have significant differences in their response to these markers. For example, some SNPs that perform strongly in wild soybeans have a reduced effect when transferred to cultivated varieties. This also indicates that the genetic interaction network of soybeans is much more complex than we imagined.

Soybeans are pointed at globally as providing protein and oil. But to be honest, it's not easy to grow soybeans that are both high-yielding and disease resistant. Recently, it has been discovered that there are many good genes hidden in wild soybeans, and these "wild path" genes may solve major problems. Look, features like maturity, plant height, and bean size may seem simple, but behind them are all competing genes. It is interesting that the same gene may behave completely differently in different environments-varieties that grow well on this land may wilt in a different location. Understanding these genetic patterns now is particularly helpful for cultivating new varieties with stronger adaptability. After all, climate change is becoming increasingly severe, so we need to prepare in advance for soybean varieties that can perform stably in various environments. Although the research process is quite brain wracking, these efforts must be put in for food security.

Next, when studying soybean genes, we need to verify each of the candidate genes and QTLs we have found one by one. CRISPR/Cas9, this kind of "gene scissors", is now quite useful. You can modify it wherever you want and directly observe the effect after the modification. However, merely looking at genes is not enough. It is necessary to analyze the transcriptome, proteome and other data together to understand the complete process of trait formation. Interestingly, the same gene may behave vastly differently in various environments, so it is necessary to conduct experiments in more places. Ultimately, our goal is very practical-it is to cultivate soybean varieties with high yields, strong disease resistance and good nutrition. Although the road ahead is still long, at least now we know which direction to strive for.

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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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