

Feature Review

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Improving Cotton Yield and Fiber Quality Based on QTL Mapping and Genomic Selection

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Received: 09 Mar., 2025

Accepted: 21 Apr., 2025

Published: 12 May, 2025

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Preferred citation for this article:

Zhang X., Wang J.M., and Fu J., 2025, Improving cotton yield and fiber quality based on QTL mapping and genomic selection, Cotton Genomics and Genetics, 16(3): 117-125 (doi: [10.5376/cgg.2025.16.0012](https://doi.org/10.5376/cgg.2025.16.0012))

Abstract Cotton is a globally significant cash crop, but breeding efforts are often challenged by the complexity of achieving both high yield and superior fiber quality. This study explores the integration of quantitative trait loci (QTL) mapping and genomic selection (GS) as advanced tools to improve cotton breeding efficiency. We reviewed the principles and applications of QTL mapping for dissecting complex yield- and fiber-related traits, and assessed its limitations such as environmental interactions and low resolution. Genomic selection was examined in terms of predictive models, implementation in breeding pipelines, and advantages over traditional methods. A synergistic approach combining QTL mapping with GS was proposed to enhance selection accuracy and genetic gain, with emphasis on key traits such as boll number, fiber strength, and drought tolerance. We also discussed technological advancements including high-throughput phenotyping, SNP arrays, and machine learning for data analysis. A case study in Upland cotton demonstrated successful integration of QTL and GS, resulting in 15-20% gains in yield and fiber quality. Despite challenges such as genotype-by-environment interactions and model limitations, this study underscores the potential of integrative, genomics-driven strategies to sustainably advance cotton improvement programs.

Keywords Cotton breeding; QTL mapping; Genomic selection; Fiber quality; Genetic improvement

1 Introduction

Cotton is the most common natural fiber crop in the world and an important raw material for the textile industry. Its production feeds millions of people in the world. Because of its wide planting range and many uses in industry and agriculture, its economic value is very large. Therefore, how to improve cotton yield and fiber quality has always been a key issue for breeders and producers (Zhang et al., 2019b; Li et al., 2022).

However, it is not easy to improve both yield and fiber quality at the same time. This is because the genetic structure of cotton is relatively complex, and the two traits of yield and quality often affect each other. Sometimes, if one is improved, the other will decrease. In addition, the genetic diversity of cultivated cotton is not large, and the traits are affected by many genes and environmental factors, so it is difficult to make breakthroughs using traditional breeding methods. Now, people need new varieties that can produce high yields, provide good fiber, and adapt to changes more than ever before (Diouf et al., 2018; Yang et al., 2022).

In recent years, advances in molecular genetics have brought new tools to breeding, such as quantitative trait loci (QTL) mapping and genomic selection. These methods can help us better understand the genetic basis of cotton traits. By constructing high-density genetic maps and conducting genome-wide association studies (GWAS), researchers have found some stable QTLs and candidate genes related to yield and fiber quality. These results have promoted marker-assisted selection (MAS), making breeding more efficient. These methods allow breeders to focus on specific gene regions for improvement and integrate good genes from different germplasm resources (including interspecific hybrids) to improve cotton yield and quality (Li et al., 2016; Liu et al., 2018; Zhang et al., 2019a; Lu et al., 2022).

The purpose of this study is to summarize the recent progress in improving cotton yield and fiber quality through QTL mapping and genomic selection. We synthesize recent research results and focus on several key gene regions,

candidate genes, and specific breeding methods, especially those strategies that can improve both traits together. The application of genomic tools in actual breeding programs has very good prospects and is expected to break the traditional problem of "you can't have your cake and eat it too" and achieve a win-win situation and continuous improvement in yield and quality.

2 Quantitative Trait Loci (QTL) Mapping in Cotton

2.1 Fundamentals of QTL mapping and its role in dissecting complex traits

In cotton breeding, traits such as yield and fiber quality are simple to say, but they involve many genes and complex environmental factors. One gene alone cannot explain too many problems. Scientists usually build a genetic map first, which is made up of many molecular markers. Why do they do this? Because this way they can find out which gene regions are related to the target traits step by step. QTL positioning is a method that comes in handy in this process. It is actually a genetic analysis method used to locate gene regions that affect specific traits. Of course, it is not a panacea, but when faced with complex traits, this tool is indeed much better than traditional methods (Sun et al., 2012).

2.2 Key yield- and fiber-related QTLs identified in diverse cotton populations

Many researchers have found QTLs related to yield and fiber in different cotton varieties and planting environments. These QTLs are stable and have obvious effects on traits. For example, a study used a high-density genetic map to find more than 100 QTLs related to fiber quality, some of which were found multiple times in different generations and environments, indicating that they are reliable (Jia et al., 2024). Chromosome regions such as A7, D8 and C7 are "hotspots" for fiber length, strength and yield, and have been highlighted (Jamshed et al., 2016). Some QTL regions affect both yield and fiber quality, but their effects may be in opposite directions, indicating that there is a certain contradiction and balance between these traits (Figure 1) (Zhang et al., 2019b). QTLs that are stable in different environments are particularly suitable for marker-assisted selection and are of great value for breeding.

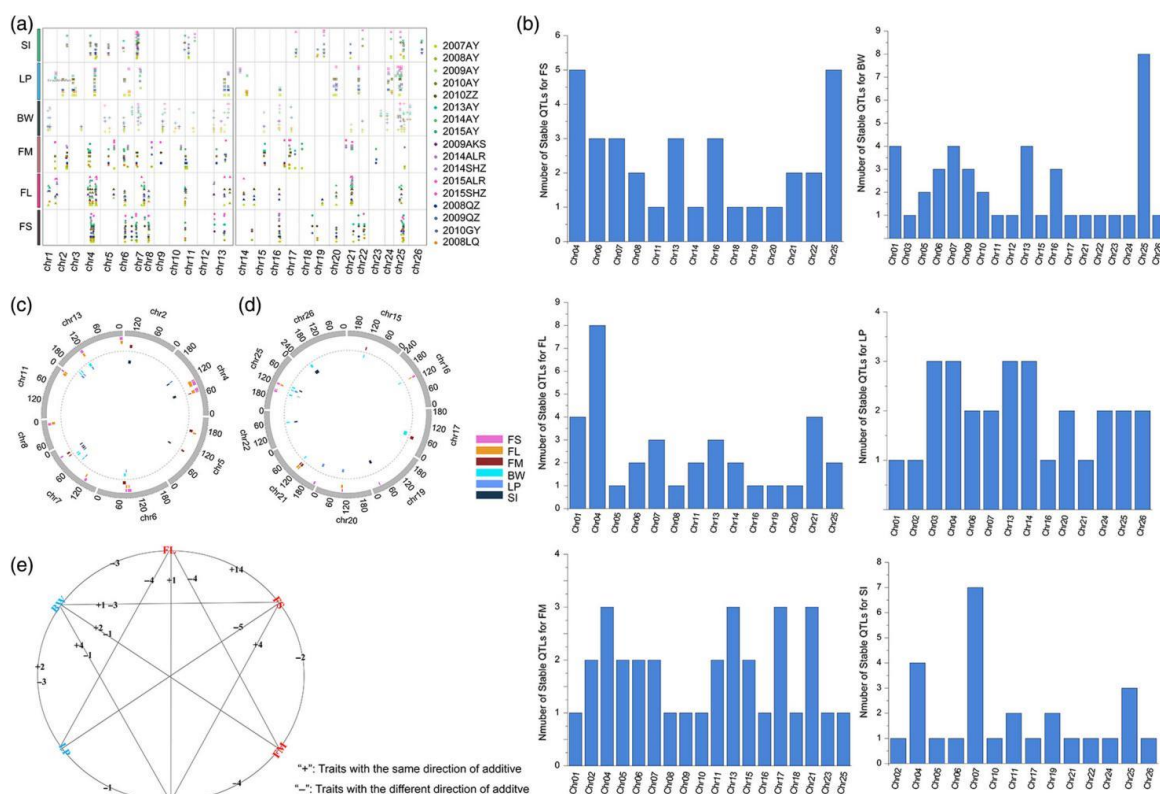


Figure 1 Detailed information about the QTLs and QTL clusters. (a) The position of the QTLs on the consensus genetic map. (b) The distribution of the stable QTLs for the six traits on the 26 chromosomes. (c) The position of QTL clusters on the consensus genetic map of At. (d) The position of QTL clusters on the consensus genetic map of Dt. (e) The number of two-pair-trait QTL clusters with the same and different direction for additive effect (Adopted from Zhang et al., 2019b)

2.3 Limitations of QTL mapping, including environmental interactions and resolution

Although QTL mapping has many advantages, it also has some disadvantages. For example, its resolution may not be high, which is related to the number of materials and population types you use. If there are not enough samples, the QTL region found may be relatively large, containing many genes, and it is difficult to say which one is working (Zhang et al., 2016). In addition, the environment has a great influence on QTL. Some QTLs are obvious in one place, but the effect is different in another place or year (Shen et al., 2007). Only a small number of QTLs can be stably expressed in various environments, so it is difficult to find stable QTLs that can be used in breeding. In addition, traits such as yield and fiber quality are often affected by multiple genes together, and their effects will interfere with each other, which makes the application of QTL in actual breeding more complicated (Wu et al., 2022).

3 Genomic Selection: Principles and Implementation

3.1 Theoretical basis and advantages over traditional selection methods

In the matter of breeding, everyone hopes to select good varieties faster, but the traditional method is slow and relies on trait performance, which is observed from generation to generation. Later, genetic marker-assisted selection was introduced, but it only focuses on a few "key genes". But the problem is that not all traits are determined by a few genes. For complex traits such as yield and stress resistance, there are many genes behind them that play a role at the same time, and even each gene does not contribute much. At this time, genomic selection (GS) becomes more appropriate. It does not "pick the key points" like the traditional method, but takes into account the markers of the entire genome, which is more comprehensive. Moreover, it can predict which individuals have potential without measuring phenotypes (Goddard and Hayes, 2007). Using GS for selection is more efficient and accurate - especially when facing traits that do not have a single "dominant gene", traditional methods are often unable to cope with it (Meuwissen et al., 2016).

3.2 Models and statistical approaches in genomic prediction

To use GS, you have to build a model. But you can't just build it casually, you have to be able to handle massive amounts of genomic data. Several common models now, such as GBLUP, Bayesian models, and machine learning methods, actually have the same purpose - to predict the breeding value of an individual based on the marker information of the whole genome (Wang et al., 2018). However, the actual operation may be more complicated than you think. A common problem is that there are too many markers, but not enough phenotypic data. This imbalance will affect the accuracy of modeling. To compensate, some models will also consider non-additive effects, interactions between genes and the environment, or multiple traits together (Larkin et al., 2019). Of course, whether the effect is good or not depends on whether the model you choose is appropriate, the population structure, the density of markers, and the strength of the trait heritability itself (Robertson et al., 2019). It doesn't mean that everything will be fine if GS is used, but the details must be coordinated.

3.3 Integration into breeding pipelines for rapid genetic gain

Integrating GS methods into the breeding process allows us to select good lines earlier and more accurately, so that the time and cost of breeding excellent varieties will be much less. GS can be used at every stage of breeding, whether it is early selection or later verification, and is especially suitable for those traits that are expensive or difficult to measure (Crossa et al., 2017). If a dynamically updated training population is used, the prediction model is optimized regularly, and other new technologies, such as high-throughput phenotyping technology, are combined, the entire breeding efficiency will become higher and the genetic gain will be greater (Bassi et al., 2016). Therefore, GS is changing the way modern breeding is done and providing new means for the changing needs of agriculture (Voss-Fels et al., 2018).

4 Combining QTL Mapping and Genomic Selection

4.1 Marker-assisted selection guided by major QTLs

Marker-assisted selection (MAS) is a method of guiding breeding based on the located major effect QTL. It can help select genes that are beneficial to yield and fiber quality into target varieties (Cao et al., 2024). Breeders can find plants with ideal traits by selecting molecular markers that are closely linked to these important QTLs. This

not only speeds up the breeding process, but also reduces the work of a large number of phenotyping tests (Li and Sillanpää, 2012). However, the effectiveness of MAS mainly depends on the accuracy of QTL positioning and whether these QTLs can be stably expressed under different environments.

4.2 Enhancing genomic prediction accuracy using known QTLs

When doing genomic selection, adding known QTLs to the model as fixed effects or priority markers can make the prediction results more accurate, especially for those traits where the main effect QTL can explain a large part of the phenotypic differences (Kemper et al., 2015). Studies have found that if these QTL markers related to the target traits are used instead of randomly selected markers from the whole genome, the prediction effect will be better (Chen et al., 2022). Because these specific markers are more representative of the real genetic differences. In addition, using some multivariate statistical methods or Bayesian models, QTLs with multiple effects can also be used at the same time to improve the prediction accuracy of multiple related traits.

4.3 Strategies to incorporate both tools into cotton improvement programs

To combine QTL mapping and genomic selection, some supporting strategies need to be adopted. First, QTL mapping can be used to identify key genetic loci, and then these loci can be given priority when making genomic predictions, which can improve the accuracy and efficiency of predictions (Lan et al., 2020). Second, linkage mapping and association mapping can be combined. This method can better narrow the scope of QTL and help find important candidate genes, thereby improving their application value in actual breeding (Daware et al., 2020). In addition, multivariate analysis and Bayesian methods are also very useful. These models can predict multiple traits at the same time and can also take advantage of the pleiotropy of genes and their commonalities (Kemper et al., 2018). Finally, the breeding process needs to be constantly updated. New QTL data and the latest phenotypic information can be added regularly to adjust the training population and model so that the prediction effect can continue to keep up with environmental and genetic changes and maintain good genetic gain.

5 Traits Targeted for Improvement

5.1 Yield components: boll weight, number of bolls, and lint percentage

Whether a cotton variety produces a lot or not depends on how many bolls it has on a plant, how many bolls there are, how heavy each boll is, and what the lint percentage is. These are not new problems, and the older generation of breeders have been thinking about them for a long time. Traditional breeding methods are still in use, of course, but there are more tools now than before. For example, now we can use genotyping technology, combined with gene editing methods, to directly target key sites related to these traits (Singh et al., 2020). We don't have to look at the performance of each plant, we can also judge which plant has potential. To put it bluntly, this method helps breeders save time and improve efficiency, and the goal is also very direct-select varieties with higher yields.

5.2 Fiber quality traits: length, strength, micronaire, and uniformity

Whether cotton can be sold in the market depends not only on the amount of production, but also on the fiber quality. Textile mills are very concerned about indicators such as length, strength, and micronaire. If the uniformity is not good, there may be a problem with the machine. These traits are actually more difficult to change than yields - because there are many details and high requirements. However, in recent years, genomics has made rapid progress, and breeders can locate the genes that control these traits more quickly. Take CRISPR/Cas for example, it can specifically modify a specific gene without touching other parts (Sedeek et al., 2019). If operated properly, the two goals of yield and quality can actually be achieved at the same time.

5.3 Agronomic resilience: drought tolerance, pest resistance, and maturity timing

Whether cotton is easy to grow is not just about whether it can produce high yields. Some places are dry, some places are prone to pests and diseases, and some places take too long to mature and cannot be harvested in time. These problems are complex and simple at the same time - the key is whether there is a way to take into account multiple traits at the same time. The climate has changed, and the environment is not as stable as before, and cotton must keep up. At this time, genomics and new technologies come in handy. Scientists will use whole genome screening to pick out genes that can help plants "take on things" (Li et al., 2024). The final variety must be the type that can survive, grow, and produce fruits in all kinds of land.

6 Technological Advances Supporting QTL and Genomic Approaches

6.1 High-throughput phenotyping platforms for precise trait evaluation

In recent years, technological developments have driven the emergence of high-throughput phenotyping platforms. This platform can quickly and accurately measure many agronomic traits on a large scale. It usually combines advanced imaging technology and various sensors to more clearly evaluate complex traits such as yield and fiber quality. By providing stable and reliable phenotypic data, these platforms also make genetic analysis more efficient, helping breeders better perform QTL positioning and genomic selection (Singh et al., 2022).

6.2 Next-generation sequencing and high-density SNP arrays

Not all genes are easy to find. The genetic markers behind some traits are very deep, especially in the QTL region or even in the details of a gene - it was difficult to figure out in the past. Until the emergence of next-generation sequencing technology (NGS), the situation changed. This technology can do a lot of things, such as constructing a very detailed genetic map, or directly locating very close molecular markers (Jaganathan et al., 2020). Of course, NGS alone is not enough. High-density SNP chips and whole-genome sequencing methods have also been added to improve the resolution of QTL positioning and speed up gene discovery (Kumar et al., 2017). With these tools, researchers can perform genotyping in large populations, which is very helpful for QTL analysis and genomic selection of cotton and even other crops (Nguyen et al., 2019).

6.3 Bioinformatics tools and machine learning in data integration

Nowadays, we have more and more genomic and phenotypic data. In order to integrate and analyze these data clearly, advanced bioinformatics tools and machine learning methods must be used. The improvement of computer technology has also brought better statistical models and algorithms, which can process large amounts of data, make gene positioning more accurate, and also improve the effect of genomic prediction (Altaf et al., 2024). Machine learning is widely used to integrate multiple omics data, narrow the scope of QTL, and predict the performance of complex traits, which is very helpful for QTL positioning and genomic selection in crop improvement.

7 Case Study: Enhancing Yield and Fiber Quality in Upland Cotton

7.1 Overview of a breeding program combining QTL mapping and genomic selection

Recently, some upland cotton breeding programs have combined QTL mapping and genomic selection (GS) to successfully improve lint yield and fiber quality. These programs usually first construct genetic maps using high-density SNPs and perform genome-wide association studies (GWAS) to identify QTLs associated with major traits. Then, molecular markers and GS models are used to screen for superior genotypes (Figure 2). For example, multi-parent hybrid populations and recombinant inbred lines are often genotyped with markers linked to QTLs associated with fiber length, fiber strength, boll weight, and lint percentage. This can bring favorable alleles together and reduce the negative impact between yield and quality (Zhang et al., 2019a).

7.2 Key results

In the years of cotton improvement, QTLs that can stably control yield and fiber traits are rare. But some of the ones that have been verified do play a key role. For example, one study combined several outstanding loci - FL5, FL3, FL2 (these affect fiber quality) and BW1, LP1 (related to yield). The performance after the merger is very impressive: fiber length increased by more than 10%, strength increased by 17%, and lint percentage also improved (Zhao et al., 2024). However, not every study has such neat data. Some work has also discovered a larger number of QTLs. For example, a study identified 106 QTLs related to yield and quality, of which 46 can explain more than 10% of trait differences alone. After picking out those stable ones as the priority targets in the model, the screening efficiency of GS has been significantly improved. Moreover, more than once, researchers have noticed that some QTLs have "pleiotropy" - that is, they affect multiple traits at the same time. If we can find this gene and combine it with high-quality germplasm materials, improving both yield and quality will no longer be an "impossible triangle".

7.3 Impact

It used to be said that yield and fiber quality are in a tug-of-war, and it is difficult to balance them. But this is not unsolvable, it just depends on whether there are means. Through the combination of QTL positioning and genomic

selection, some people have indeed done it. A batch of upland cotton varieties were selected under this strategy. By aggregating key gene loci, they finally showed that the yield and fiber quality were 15%-20% higher than the old varieties (Wang et al., 2021). This was difficult to achieve in the past, after all, the two traits always have a sense of "constraining each other". Now, technical means have broken through this hurdle, not only providing breeders with a clear operation path, but also allowing the cotton industry to take a big step towards "high efficiency and stable production".

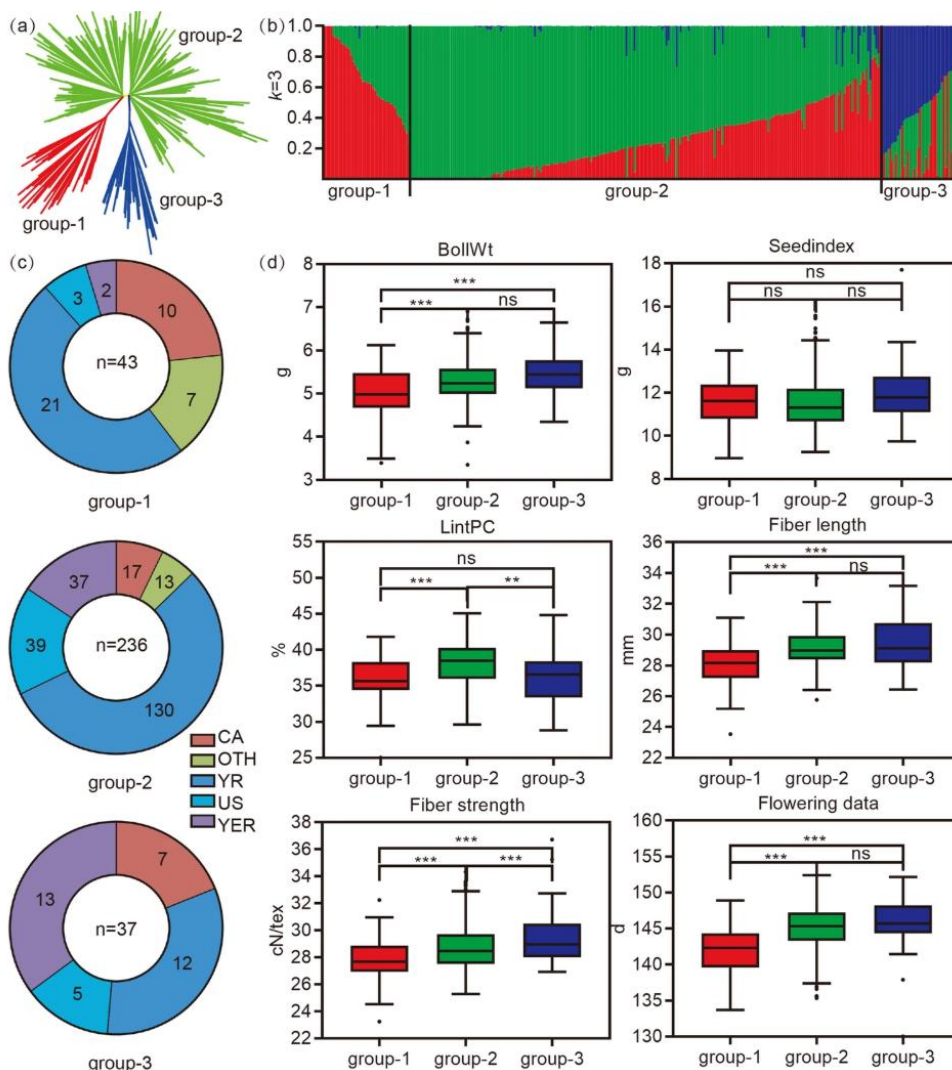


Figure 2 Phylogenetic relationships of 316 cotton accessions: (a) A neighbor-joining tree was constructed using whole-genome SNP data. The accessions were divided into three groups, group-1 (red), group-2 (cyan) and group-3 (blue); (b) Population structure of cotton accessions. The cotton samples were divided into three groups when $k = 3$; (c) Geographic origin of the three groups, Central Asia (CA), the United States (US), the Yellow River (YR), the Yangtze River (YZR) and other places (OTH); (d) Phenotype distributions of yield and fiber quality traits, the group divided by the structure of the 316 accessions, Boll weight (BW), Seed index (SI), Lint PC (LP), Fiber length (FL), Fiber strength (FS) and Flowering data (FD). Within boxplots, the bold line represents the median, box edges represent upper and lower quantiles, and whiskers are 1.5 times the quantile of the data. Outliers are shown as open dots (* $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$, two-sided t-test). The neighbor-joining tree (a) was constructed using the software PHYLIP (v3.696, <https://evolution.genetics.washington.edu/phylip.html>). Population structure of cotton accessions (b) was determined using the software Admixture (v1.30, <http://dalexander.github.io/admixture/index.html>). The others were created by the software GraphPad Prism 9 (ver. 9.0.0, <http://www.graphpad.com>) (Adopted from Wang et al., 2021)

8 Challenges and Future Prospects

8.1 Managing genotype-by-environment interactions in predictive breeding

It is not uncommon for the same cotton plant to grow differently in different fields. The problem is that it is difficult for breeders to predict its performance. Especially when genotype and environment are mixed together,

the variation of traits can be unexpectedly large. Whether it is QTL positioning or genomic selection, they are reliable in theory, but once the environment changes, the model may not work. Therefore, G×E interaction is an unavoidable hurdle. To solve it, the experimental design must be more detailed, and multi-environment testing is indispensable. Another point is that environmental data cannot be only put in the report, but must be included in the model. Otherwise, the selected materials may fail to perform well in a different planting area.

8.2 Need for multi-trait and multi-environment prediction models

Early prediction models were actually quite "simple" - one model for each trait, one model for each environment. But the reality is much more complicated than that. The breeding goal now is to "superimpose multiple traits", and environmental fluctuations are getting bigger and bigger. If we still follow the old method, the selected varieties may be good in one aspect, but poor in another. So what is needed now is a model that can look at multiple traits at the same time and take environmental changes into account. In this way, it is possible to take into account yield, quality, and stress resistance, and it is possible to select cotton varieties that perform stably in different regions and years. This is not to say that the model can solve everything, but it is indeed closer to actual needs than previous methods.

8.3 Prospects for integrating gene editing with marker-based breeding

In the future, cotton can be improved by combining gene editing technology (such as CRISPR/Cas) with molecular marker breeding methods. Gene editing can precisely modify key genes found through QTL mapping and genomic selection, so that varieties with ideal traits can be cultivated more quickly. Combining these two methods may break through the current bottleneck of trait improvement, combine useful genes more quickly, and better cope with the challenges brought by complex genetic structure and environmental changes.

Acknowledgments

We would like to thank the anonymous peer review for their critical comments and revising suggestion.

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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