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Genetic Control of Tuber Size and Yield in Potatoes

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Abstract Potato (*Solanum tuberosum* L.) tuber size and yield are influenced by multiple genetic and environmental factors. This study reviews key genes and regulatory networks affecting tuber traits, including quantitative trait loci (QTL) analysis and transcription factor networks involved in tuber development. The application prospects of gene-editing technologies for improving tuber yield and quality are also explored. Existing research highlights the significant gene-environment interactions on tuber traits, while high-throughput genome-wide association studies (GWAS) and marker-assisted selection (MAS) have become effective tools for optimizing breeding strategies. The study further analyzes the impact of different genetic mechanisms on polygenic traits and the integration potential of traditional and modern molecular breeding techniques to address challenges in yield improvement and stress-resistant breeding. By reviewing recent research progress, this work aims to provide theoretical support for cultivating high-yield and high-quality potato varieties and proposes future research directions.
Keywords Potato; Tuber traits; Genetic control; Molecular breeding; Gene editing

1 Introduction

Potatoes (*Solanum tuberosum* L.) are staple foods in many places, especially in developing countries. Many of the carbohydrates, vitamins and even minerals people eat come from them. This is not only because they are delicious and have high nutritional value, but also because they have strong adaptability to the environment and a short growth cycle. Moreover, the yield is not low. For this reason, potatoes have become the world's third largest food crop after rice and wheat. However, if you want to make it produce more and have better quality, you still have to rely on genetic improvement.

The yield of tubers, the amount of starch, and the size of tubers are actually quite complicated. They are not determined by a single gene, but are related to the interaction of a large number of genetic factors and environmental factors. Some studies have been done in more detail. For example, QTL analysis has found several key locations-such as on chromosomes 3, 4, 5 and 10, which control important traits such as tuber size and yield.

Of course, how these genetic loci were found is inseparable from the credit of genetic maps and association studies. Through these methods, researchers have identified many gene regions that affect trait expression. This opens a window for understanding the genetic control mechanism of potatoes and provides an entry point for precision breeding.

This study mainly revolves around these traits, focusing on finding the key genetic loci that affect tuber size and yield. The research team used advanced technologies such as GWAS, hoping to find truly useful genes and alleles. The goal is actually very practical: to help breed potato varieties with high yield, more uniform size, and better resistance to stress.

2 Factors Affecting Potato Tuber Size and Yield

2.1 Environmental factors (light, soil, climate, etc.)

Whether potatoes grow well or not, the environment is the key. This is actually not difficult to understand. The amount of sunlight, the quality of the soil, and whether the climate is suitable will affect whether the tubers can develop smoothly. For example, light. Once the sunshine time becomes shorter, tubers are easier to form. This may be related to some regulatory signals, such as microRNA and epigenetic regulators (Kondhare et al., 2021). Of course, light is only one factor. Soil is also very important. The high potato yield in Acireale, Sicily, is likely directly related to the fertile soil there (Scavo et al., 2022). The impact of climate may be more intuitive-it is common for tuber yields to decrease in drought years, which also makes people more aware of the practical significance of irrigation and water management in planting (Aliche et al., 2019).

2.2 The dominant role of genetic factors in tuber size and yield

Of course, in addition to the environment, the "foundation" of the variety itself also plays a significant role. Some genes are directly linked to tuber size and yield. Genes such as ABF4 and CDF1, which have been studied more, have shown the ability to improve yield and quality under normal and adverse conditions (García et al., 2018; Carrillo et al., 2023). In addition, researchers have found a number of genetic markers related to yield, which can be used to determine whether certain traits will appear or whether a variety has a greater advantage in the market. This information is very useful for breeding. Potatoes of different genotypes perform differently in different environments. Some varieties are more "tough" and can produce stable yields even if they are planted in other places (Tatarowska et al., 2024).

2.3 The comprehensive effect of genetic and environmental interactions on yield

Having said that, environment and genetics are important, but whether they are "compatible" is also critical. Often, differences in potato yields are the result of a combination of genotype and environment. Scientists call this phenomenon genotype × environment interaction (GEI).

This type of interaction has been observed in many places, for example, the same variety in the Mediterranean and Poland can produce very different results (Ma, 2024; Tatarowska et al., 2024). To figure out which varieties perform best in which environments, researchers use analytical methods such as AMMI and GGE biplots. These tools can help identify varieties that can both produce stable high yields and adapt to different conditions. For breeders, this kind of analysis is very valuable, especially when faced with uncertainties such as climate change.

3 Genetic Basis of Potato Tuber Size and Yield

3.1 Some key regulatory factors of tuber size (such as StCDF1)

When it comes to potato tuber size, the gene *StCDF1* cannot be avoided. This gene was first noticed because of its role in photoperiod regulation of tuberization-it can inhibit *StCO1/2* and then increase the expression of *StSP6A*, thereby promoting tuber formation (Kondhare et al., 2019). But things are not that simple. *StCDF1* has a significant positive correlation with another gene called *StBEL5*, which is also a key regulatory factor in the tuber development process.

The two seem to form a synergistic regulatory mechanism. Another interesting discovery is that when *AtCDF1* of *Arabidopsis* is ectopically expressed in potatoes, the tubers actually show stronger "sink" characteristics in the field-in short, more photosynthetic products are transported to the tubers, and eventually the tubers become larger and the yield increases (Carrillo et al., 2023).

3.2 Research progress on QTL positioning

In fact, it is not just a single gene. Quantitative trait loci (QTL) positioning is also helping us understand which genetic regions are related to tuber yield and shape. For example, there is a major QTL on chromosome 10 that is strongly correlated with tuber shape, and some signals can also be seen on chromosomes 4 and 6 (Park et al., 2024). In addition to shape, traits such as weight and specific gravity have also been located on chromosomes 5 and 3.

Interestingly, GWAS studies often use Manhattan plots to find SNP sites that are particularly highly correlated with target traits. Taking tuber yield and quality as an example, the hotspot area on chromosome 5 often appears with starch content and late blight resistance; chromosomes 4 and 10 are more inclined to tuber appearance (Yuan et al., 2024). These genetic "hotspots" may be breakthroughs in functional gene research in the future (Figure 1).

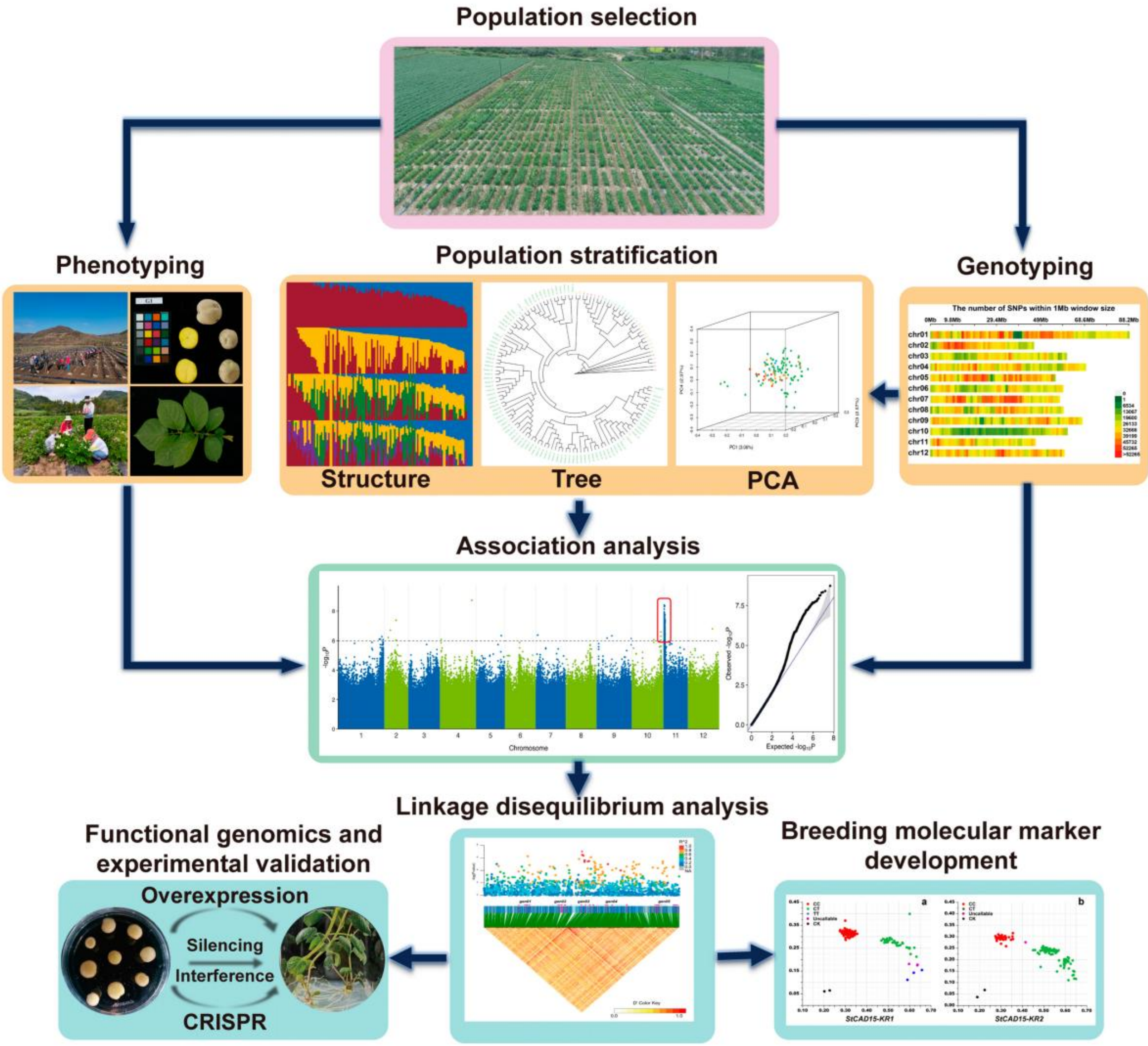

Figure 1 Overview of the steps for potato GWAS (Adopted from Yuan et al., 2024)

3.3 Polygenic control mechanism of tuber size and yield

One or two genes alone cannot explain tuber development. Studies have shown that this is a regulatory pattern involving multiple genes and distributed throughout the genome. It is said that there may be hundreds of genes involved, and most of these genes are distributed on all 12 chromosomes, like a cluster (Schönhals et al., 2017). To make it more complicated, some genes can be "interfered" or "modified" by other genes-the so-called epistasis. In some diploid potato populations, it was found that nearly 80% of yield-related QTLs had epistatic effects (Marand et al., 2019), which shows that this type of genetic interaction is very common. In addition, tuber yield and starch content are not completely consistent: some genes may be beneficial to one trait but not to another. However, some SNP sites that "take both ends into account" have been found to positively affect both traits at the same time.

4 Case study: Exploration of High-Yield and High-Quality Cultivation of potato Varieties

4.1 Background at a glance: difficulties in potato cultivation in Heilongjiang

Although Heilongjiang is one of the important potato producing areas in China, the planting conditions here are not ideal. Due to cold weather, short growing season, pests and diseases, and drought, farmers often face the risk of reduced production. These problems are not just occasional, but may occur every year. Traditional breeding methods are not efficient and often unable to cope with these complex factors (Nahirñak et al., 2022). At present, people are increasingly in need of potato varieties that can withstand adversity and have high yields, not only to have enough food, but also to ensure agricultural income and food security in this region (Slater et al., 2017; Haas et al., 2020).

4.2 Breeding process: grasping the key points of yield with "MAS"

To solve the problem, we must start from the source. As a new breeding tool, marker-assisted selection (MAS) has been gradually used in recent years to improve the tuber size and yield of potatoes. Its advantage is that it does not rely entirely on long-term field trials, but uses genetic markers to screen out plants that may perform well in advance. Through QTL analysis, researchers found some key genetic regions related to tuber appearance and specific gravity, which facilitates the focus of subsequent breeding. MAS is also used to locate disease resistance genes, such as resistance genes to late blight, which has played a major role in reducing disease losses (Beketova et al., 2021). However, this technology itself is not omnipotent. It usually has to be combined with traditional methods to truly achieve the goal of high yield and high quality.

4.3 Actual effect: selection and promotion of new varieties

In practice, MAS has indeed helped a lot. Researchers have selected a number of stable and high-yield varieties through MAS in multiple breeding projects. Interestingly, one of the cases used the *ABF4* gene of Arabidopsis thaliana, and the tuber yield under stress conditions did not decrease but increased, and the storage and processing quality also improved simultaneously (García et al., 2018). From the field point of view, screening depends not only on genes, but also on trait performance (Figure 2). Figure A shows the distribution of fresh weight of tubers in different populations. Such diversity is actually very beneficial for breeding, and the most promising individuals can be selected from them. Part B lists some key steps from field selection to molecular verification, such as environmental multi-point experiments, candidate gene expression analysis, and the assistance of metabolomics data. Figure C uses a Venn diagram to compare the intersection and differences between different screening strategies. The three methods of PPt, MPt and MPs have their own focuses. Combining them can take into account sensitivity and specificity, and it is not easy to miss key genes, and it can also filter out a lot of environmental interference. Figure D further shows the difference in tuber yield under different stress conditions. The results are obvious. The varieties bred by MAS are much better than traditional methods in terms of yield and stability, especially in plots with frequent drought and diseases. Further gene map analysis also helped to identify some genetic markers that may be related to drought tolerance (Haas et al., 2020). In the end, some new varieties with strong adaptability and good yield were promoted and performed well in actual production. They were not only disease-resistant and stress-resistant, but also took into account market demand (Tessema et al., 2022).

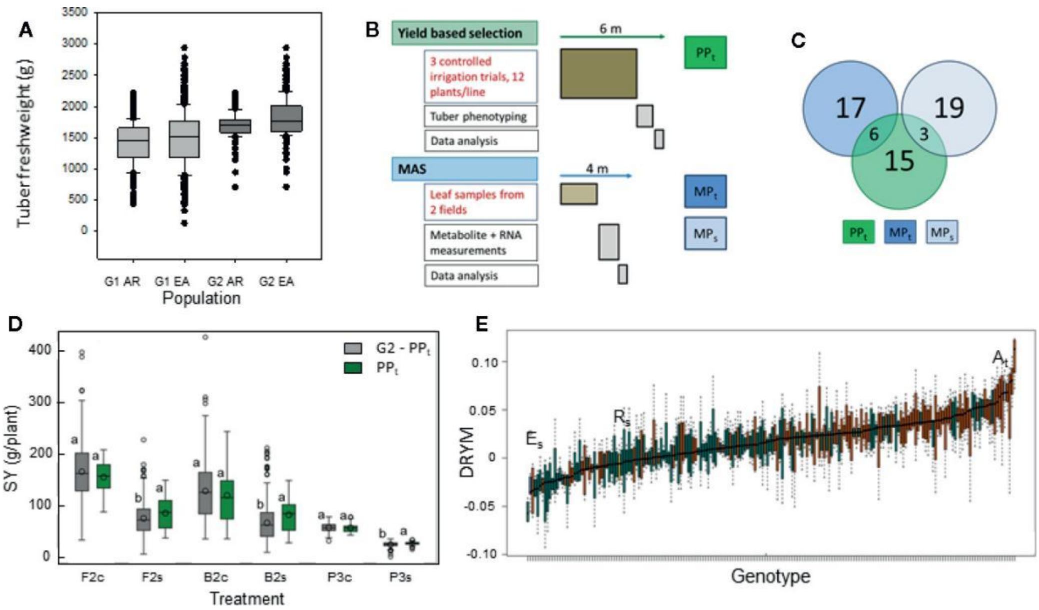

Figure 2 Selection experiment comparing phenotypic selection and MAS from a potato population segregating for drought tolerance (Adopted from Haas et al., 2020)

5 Molecular Mechanisms Regulating Tuber Size and Yield

5.1 Hormone regulation mechanism: the role of gibberellins and cytokinins in tuber growth

Tuber development is affected by the combined effects of multiple hormones, not just one hormone. For example, gibberellins (especially GA_3) have a prominent effect on tuber dormancy and germination. Studies have shown that the transcription factor StTCP15 can regulate the ratio between ABA and GA_3 . When this ratio is lower, tubers will germinate earlier; conversely, if the expression of StTCP15 decreases, germination will be delayed (Wang et al., 2022). However, the role of cytokinins and auxins cannot be ignored. Auxin is often considered to be the "starting signal" for the formation of initial tubers, but it also needs to cooperate with other hormones, such as the interaction with gibberellins and strigolactones in runners, which will directly affect the final yield. In addition, some experiments have artificially increased the expression level of GA oxidase (such as what Kolachevskaya et al., 2019 did), and found that it does bring significant changes to tuber formation and productivity.

5.2 Regulatory function of transcription factor network in tuber development

If hormones are the source of signals, then transcription factors may be more like "conductors". They do not directly produce hormones, but determine the specific effects of hormone signals. For example, R2R3-MYB members in the MYB family often appear in studies related to tuber development, especially those processes related to hormone response or environmental stress (Sun et al., 2019). StTCP15 is also an example. As mentioned earlier, it affects the pathways of ABA and GA_3 , thereby affecting tuber dormancy. In addition, growth regulators such as GRF also have their own "division of labor": StGRF1, 2, and 5 are more likely to participate in tuber germination, while StGRF4 and 9 are more active during dormancy (Cui et al., 2024). The regulation of these factors is not linear or isolated. They often cross and cooperate with each other, allowing tubers to "self-regulate" size and yield in a complex environment.

5.3 Application of key gene editing technologies (such as CRISPR-Cas9)

In the past, the regulation of tuber development mainly relied on natural variation and traditional breeding, but now the situation is different. Tools such as CRISPR-Cas9 allow researchers to precisely "move" a gene, such as *StGA3ox3*, which controls GA biosynthesis. If this gene is regulated, the rhythm of tuber formation will also change (Malankar et al., 2023). Other studies have found that phasiRNA siRD29(-) can affect the expression of *StGA3ox3* in the early stage of tuber formation, which actually provides the possibility of RNA-level regulation. In addition to gibberellin synthesis genes, researchers have also tried to increase the expression of some auxin synthesis genes driven by tuber-specific promoters, and found that it can increase tuber yield (Zhang, 2024). In general, gene editing makes regulation more "specific", rather than relying on guesswork and screening as before.

6 Breeding Strategies for Potato Tuber Size and Yield

6.1 Traditional breeding: long-lasting, but also with many limitations

In the past, potato breeding was basically based on experience and eyes-whoever has a large tuber, high yield, and disease resistance is selected. Seed selection, hybridization, and then screening generation after generation, the process is not complicated, but slow. Moreover, the most reliable thing about this method is the intuitively visible "phenotype", such as the size of the tuber or the growth of the plant. But there are also many problems. Potatoes themselves are polyploids, and the genome is complex. In addition, the traits are easily affected by the environment. Sometimes the same variety grows differently in different plots (Schönhals et al., 2017; Tessema et al., 2022). This makes phenotypic breeding time-consuming and unreliable. Especially for "invisible" traits such as drought tolerance and tuber shape, it is easy to be missed, but they are linked to processing and sales and cannot be ignored (Aliche et al., 2019).

6.2 Molecular breeding: accurate and efficient, but the threshold is not low

In contrast, molecular breeding today is like installing navigation. The marker-assisted selection (MAS) method can "calculate" whether the plant will produce good tubers in the future when it is still young. For example, the size, shape, and density of the tubers have clear QTL regions and DNA markers, and breeders can screen seedlings in advance based on these "fingerprints" (Park et al., 2024). Genomic selection (GS) goes a step further and predicts the "potential value" of the plant before it grows out, so that strains with strong stress resistance can be selected under stress environments (such as drought) (Pandey et al., 2022). Even now, we can directly manipulate genes, use CRISPR-Cas9 or RNA interference (RNAi) to precisely target and adjust key sites that control tuber yield and quality, instead of relying on "chance".

6.3 Multi-target breeding: if you want everything, you have to know how to make trade-offs

However, in reality, breeding often cannot focus on just one trait. Large tubers and high yields are good things, but if the quality is not up to standard, problems will still arise in the processing stage. Therefore, the "multi-target" strategy is now advocated-while increasing yields, we must also consider tuber appearance, quality, and even adaptability to stress environments such as drought. In order to clarify the relationship between various traits, some studies have introduced path coefficient analysis to help breeders determine which traits have the greatest impact and which ones can be traded off (Shubha and Singh, 2018). In addition, there are studies that try to bring in metabolite and transcript information, instead of relying solely on traditional yield data. In drought years, it is also clearer to see who performs more stably (Haas et al., 2020). In this way, the varieties finally selected can not only produce more, grow better, and be more adaptable to climate change, and their overall performance will naturally be more competitive (Hanász et al., 2024).

7 Challenges and Solutions

7.1 The impact of genetic background complexity on yield control

The yield of potato tubers is not determined by a single gene. Its genetic background is complex, and it is particularly sensitive to environmental conditions such as drought, which makes the situation even more difficult. Once drought occurs, not only the total amount of tubers decreases, but also the yield of the marketable part decreases. Studies have shown that the tuber size of plants with slower leaf maturation is more widely distributed, so that the proportion of large tubers is higher during drought, which is quite beneficial (Aliche et al., 2019). However, it is easier said than done to find the gene loci directly related to yield from these traits. Although the current genetic map has marked a lot of useful information, since most of these traits are caused by the joint action of many genes, the real difficulty is how to use this information to create drought-resistant and high-yielding varieties. This is why modern molecular technology is becoming more and more important (Naeem et al., 2021).

7.2 Balancing ecological adaptability and biodiversity conservation in breeding practices

For breeders, it is not only necessary to have high yields, but also to consider environmental adaptability. In addition, do not make the varieties too simple, otherwise it will be difficult to deal with new problems in the future. Technologies such as CRISPR-Cas9 and TALEN have indeed brought a lot of convenience to breeding-now it is possible to breed new varieties with high yields and strong adaptability without relying on genetic modification (Hameed et al., 2018; Ahmad et al., 2022). But the problem is also here: once these technologies are over-reliant, the genetic base may become narrower, and it will become passive when encountering new pests or climate change in the future. Therefore, how to maintain population diversity while using these technologies is a very realistic balancing problem in current breeding.

7.3 The potential of modern biotechnology

Now when it comes to increasing potato yields, it is impossible to bypass modern biotechnology. For example, epigenetics is quite interesting. Instead of changing the DNA sequence, it affects gene expression through "regulatory switches", which may improve stress resistance and yield stability (García et al., 2018). There are also multi-omics integration technologies-in fact, it is to put a lot of "omics" information together, such as genome, transcriptome, proteome and metabolome, etc. Through this integration method, researchers can have a clearer understanding of how the tuber grows and how it responds to various stresses (Pourazari et al., 2018). Although these methods sound advanced, in the final analysis, the purpose is to find out which regulatory points can be used to improve potato yield and quality.

8 Future Prospects and Suggestions

8.1 Deepen the research on the genetic basis of tuber size and yield

At present, many aspects of the genetic control of potato tuber yield have not been clarified. It is not to say that there is no clue at all-for example, some genetic markers related to tuber size distribution under drought conditions have been found on chromosome 3 (Aliche et al., 2019). But these are just the tip of the iceberg. To truly understand the genetic mechanism behind it, we must continue to study the genetic variation and heritability of these traits in depth (Gashaw et al., 2020; Tessema et al., 2022). This information is very critical for future breeding work, especially when selecting parents or formulating improvement strategies. CRISPR-Cas9 and RNAi tools have been used to improve the quantity and quality of tubers, and the effect is also good, but more verification and optimization are needed before they can be widely used.

8.2 Strengthen international cooperation and data sharing to promote potato breeding

Not every region can solve all problems on its own, especially for crops like potatoes that are sensitive to climate and diseases. This determines the importance of international cooperation. Some cross-border studies have played a demonstration role. For example, experiments in France and the Netherlands have made people more aware of the impact of different environments on tuber size, while in Ethiopia and the Himalayas, studies have highlighted the important value of genetic diversity (Shubha and Singh, 2018). Data sharing and germplasm exchange can help breeders find potential materials faster and help avoid duplication of research. In other words, cooperation is not just to save resources, but also to make breeding work go further and more steadily.

8.3 Combining genetic improvement with smart agricultural technology

Some things cannot be solved by breeding alone, but must rely on planting management technology. Precision agricultural tools such as remote sensing and automatic irrigation can actually monitor crop growth and environmental conditions in real time, which is also very helpful for breeding experiments. For example, after the *ABF4* gene in *Arabidopsis* was introduced into potatoes, it was found that both yield and stress resistance were improved, which shows that genetic modification and modern agricultural equipment can complement each other (Saifullah et al., 2024). Of course, some cultivation techniques, such as adjusting the planting density or tuber distribution pattern, can also further improve yield performance. In short, combining genetic improvement with intelligent technology is a breakthrough in the development of breeding.

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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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