Tree Genetics and Molecular Breeding 2025, Vol.15, No.6, 231-239
http://genbreedpublisher.com/index.php/tgmb

Case Study Open Access

Genetic Characterization and Breeding Practice of High-Anthocyanin Blueberry Germplasm

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Tree Genetics and Molecular Breeding, 2025, Vol.15, No.6 doi: 10.5376/tgmb.2025.15.0027
Received: 12 Oct., 2025
Accepted: 15 Nov., 2025
Published: 28 Nov., 2025

Preferred citation for this article:
Hong Z.M., Huang W.Z., and Fu J., 2025, Genetic characterization and breeding practice of high-anthocyanin blueberry germplasm, Tree Genetics and Molecular Breeding, 15(6): 231-239 (doi: 10.5376/tgmb.2025.15.0027)

Abstract Blueberries are rich in anthocyanins and have significant nutritional and health values. Increasing the anthocyanin content in blueberry fruits is of great significance for nutritional fortification and the development of functional foods. This article systematically analyzes the genetic characteristics and breeding strategies of blueberry germplasms with high anthocyanin content. Firstly, characterize the diversity of anthocyanin phenotypes in blueberry germplasm. Secondly, analyze the key gene nodes and their transcriptional regulatory networks in the anthocyanin biosynthesis pathway, and clarify the genetic mechanisms influencing anthocyanin accumulation. Then, through genetic mapping and genome-wide association analysis, the genetic loci that mainly control anthocyanin content are identified, and molecular markers are developed. Finally, explore the breeding practice paths of high-anthocyanin blueberries, including parental combination design, hybrid population improvement, multi-environment experimental evaluation, and standardized detection of anthocyanin quality, and look forward to future directions such as precise breeding and data platform construction. This research provides theoretical basis and technical support for the high-quality breeding and industrial development of blueberries.
Keywords Blueberry anthocyanin content; Genetic characteristics; Molecular breeding; Breeding of varieties

1 Introduction

When many people mention blueberries, their first reaction is that they are rich in anthocyanins. It is indeed because of this component that blueberries are often associated with antioxidant properties, eye protection, and anti-aging, and are even listed as representatives of healthy foods (Huang et al., 2016). In recent years, anthocyanins have not only been discussed in the field of nutrition, but also have been very popular in areas such as plant quality improvement and functional food development (Wang et al., 2022). Ultimately, on one hand, there is the research interest point, and on the other hand, there is the market and consumers' expectations for "healthier fruits". The two forces together have pushed blueberry anthocyanins to the forefront. The problem is that what people want is not just "anthocyanins", but "higher, more stable and more useful" anthocyanins. Therefore, it is quite natural to focus on germplasm resources with high anthocyanin content, as this directly affects whether new varieties with more prominent nutritional value can be cultivated and can also provide a raw material basis for subsequent product development.

However, breeding high-anthocyanin blueberries does not end with raising one indicator. High anthocyanins can indeed enhance the nutritional selling point and make it easier to create differentiation. They are also more popular when used as raw materials for functional foods. At the same time, such materials can also help us figure out "why anthocyanins are high", sort out the genetic reasons behind them, and make up for the shortcomings of traditional breeding in improving nutritional quality (Mengist et al., 2022). However, in reality, there are also some exceptional cases: the anthocyanin level of the same material may change when the environment is changed (Zhang et al., 2022). Sometimes, when anthocyanin levels increase, the yield, flavor or fruit size may not improve simultaneously; there may even be trade-offs (Mengist et al., 2020). So in breeding, it's more like doing a "balance problem", which requires both nutrition and the marketable traits to stand firm.

Based on these considerations, this study focuses on two things: first, to clarify the genetic causes of the high anthocyanin trait, and then to truly apply this information to the breeding of new strains. We assume that the differences in anthocyanin content are not random; they are influenced by some key genetic factors, and these factors can be identified and utilized. In terms of specific approaches, phenotypic identification should be conducted first to clarify the anthocyanin characteristics of different germplasms. Let's take a look at what differences might have occurred between the synthetic pathways and the regulatory levels. Subsequently, localization and association analysis are used to narrow down the range, identify key genes and develop available markers; Finally, the markers are put back into the breeding process for screening and improvement, promoting the formation of new high-anthocyanin strains.

2 Characterization of Germplasm Resource Basis and Phenotypic Characteristics

2.1 Composition of germplasm sources and representative sampling principles

The germplasm sources used in this study are rather diverse: northern highbush, southern highbush, rabbit eye, and dwarf highbush blueberries are all present, and some wild relatives have also been added. The materials include not only common main cultivated varieties both at home and abroad, but also selected characteristic germplasms with particularly prominent anthocyanin content. When sampling, we did not focus on just one standard but considered both the genetic background and the target traits: on the one hand, we spread out based on kinship and geographical origin to ensure that different gene pools can be covered as much as possible (Boches et al., 2006); On the other hand, under the premise of coverage, it is more inclined to choose materials with a large difference in anthocyanin levels for comparison (Yousef et al., 2014). The overall sampling scale and structure have also been adjusted to ensure that these test materials can basically reflect the variation range of blueberry anthocyanin properties.

2.2 Key dimensions and typing framework of anthocyanin phenotypes

The anthocyanin phenotype of blueberries can be roughly divided into three aspects: total content, composition, and the distribution of its "landing points" in the fruit. Let's start with the total anthocyanin content. This is the most intuitive and commonly used method to determine exactly how much anthocyanin has accumulated (Spinardi et al., 2019). The composition is more like a "formula ratio", observing how much different anthocyanins each account for in the fruit. Blueberries usually contain several common types of anthocyanins, such as cyanidin glycosides, but they are not exactly the same. In a few genotypes, anthocyanins with acylation modification can also be found (Dare et al., 2024). As for distribution, the key lies in which is more or less, the peel or the flesh: most of the anthocyanins are mainly found in the peel, while the flesh is lighter in color (Wang et al., 2012). The flesh of a few wild species is also very purple, and the entire fruit is purplish red. When these items are combined, anthocyanin phenotypic typing can be performed on the germplasm, facilitating subsequent genetic analysis (Liu et al., 2025).

2.3 Phenotypic determination process norms and data quality control

The anthocyanin content of blueberry fruits was measured according to the same set of procedures. For each variety, it is not just about picking one or two fruits. Instead, mature fruits are taken from multiple representative plants and mixed together to make a sample. The fruits are frozen immediately after being picked, mainly to prevent the anthocyanins from being degraded if left for too long. Then, quantitatively weigh the fruit samples and extract the anthocyanins with acidified ethanol (Nicoué et al., 2007).

The total anthocyanin content was measured by the pH difference method (Lee et al., 2016). To determine the specific components, different anthocyanin monomers should be separated by HPLC and then tested. The entire determination is not "completed in one test". Parallel samples and repeated determinations will be conducted, and the instrument will be calibrated with standard substances to keep the extraction conditions consistent. When encountering obviously abnormal data, eliminate them first, then calculate the average value, and try to make the results solid and stable.

3 Anthocyanin Biosynthesis Pathways and Genetic Regulatory Mechanisms

3.1 Key nodes and metabolic branches at the structural gene level

Anthocyanins can be regarded as the products of the later stage in the flavonoid synthesis pathway, which are gradually "pushed" out through a series of enzymatic reactions. There are several crucial steps in the middle: DFR and ANS first treat substrates such as dihydroflavonols into anthocyanin aglycones, and then UFGT performs glycosylation to convert them into more stable anthocyanins (Nguyen et al., 2023). The final type of anthocyanin is not exactly the same. F3’h and F3’5'h affect the degree of hydroxylation of the B-ring, and thus different types of anthocyanins come into being (Zorenc et al., 2017). However, this path can also be "diverted". For instance, FLS will carry some intermediate products to the flavonol branch, and ANR can reduce anthocyanin aglycones to proanthocyanidins, which is equivalent to competing with anthocyanin synthesis for substrates (Lafferty et al., 2022). The final content and composition of anthocyanins often depend on the activity and expression levels of these key enzymes.

3.2 Coupling relationship between transcriptional regulatory networks and signaling pathways

How do anthocyanins in blueberries pile up? Many times, it's not that a certain enzyme "suddenly becomes stronger", but rather that the upstream transcriptional regulation is in charge. The core is a common combination: R2R3-MYB, bHLH and WD40 form an activation complex, which "ignites" the structured gene promoter and pulls the transcription up (Zhang et al., 2021). However, it is not working in isolation. Environmental signals such as light exposure and endogenous hormone signals like ABA will all get involved and influence synthesis at the level of transcription factors. For instance, in the case of exogenous ABA treatment, a common outcome is a significant increase in the anthocyanin content of the fruit (Han et al., 2021). Structural genes and this set of MBW-related factors as a whole will be upregulated, especially key MYBs such as VcMYBA are more likely to be activated, and the accumulation will naturally increase. Conversely, there are also MYB inhibitors "stepping on the brakes", competing for binding sites to suppress expression. Overall, it is the multi-layered transcription factor network and the combination of light and hormone signals that enable anthocyanins to adjust in a timely manner in response to development and environmental changes.

3.3 Genetic variation types and potential functional consequences assessment

The differences in anthocyanin content are roughly genetic from two ends: one end in structural genes and the other in the regulatory layer. If there are problems with structural genes, such as the deletion of genes encoding enzymes or the alteration of key sites, the synthetic capacity will decline. In severe cases, the color of the fruit will become significantly lighter, or it may hardly color at all (Chu et al., 2024). Another more common situation is when the "switch" changes: missing promoters, transposon insertions, etc., will raise or lower the expression levels of key genes, and anthocyanins will naturally increase or decrease accordingly (Figure 1) (Castillejo et al., 2020). Blueberries are still polyploid. This matter is a bit more complicated. Allele loss and copy number changes may also rewrite metabolic fluxes (Wang et al., 2024). In conclusion, it is the accumulation of these different types of variations that has widened the gap in anthocyanin content within natural populations and left behind allele resources that can be directly utilized for breeding.

4 Analysis of Genetic Characteristics and the Association Rules with Traits

4.1 Methods for assessing Population structure and genetic diversity

This part mainly involves first "clarifying the inventory" of the blueberry germplasms to be tested, to see how close and far they are to each other. The approach is to genotype the material using molecular markers, with SSR or SNP being the most commonly used ones, and then calculate some genetic diversity indicators based on this (Bian et al., 2014). Then, without rushing to a conclusion, cluster analysis and PCA will be used to pull out the relationships and take a look: which materials are more similar and which are far apart, and those with similar genetic backgrounds will be grouped into the same group. At the same time, conduct a group structure analysis to estimate how many potential subgroups might exist and what materials each subgroup is approximately composed of and in what proportion. Combining these results can provide a relatively complete description of the genetic diversity level and structural characteristics of this batch of germplasm, and also facilitate avoiding detours when conducting association analysis, material selection, and breeding later on (Vega-Polo et al., 2020).

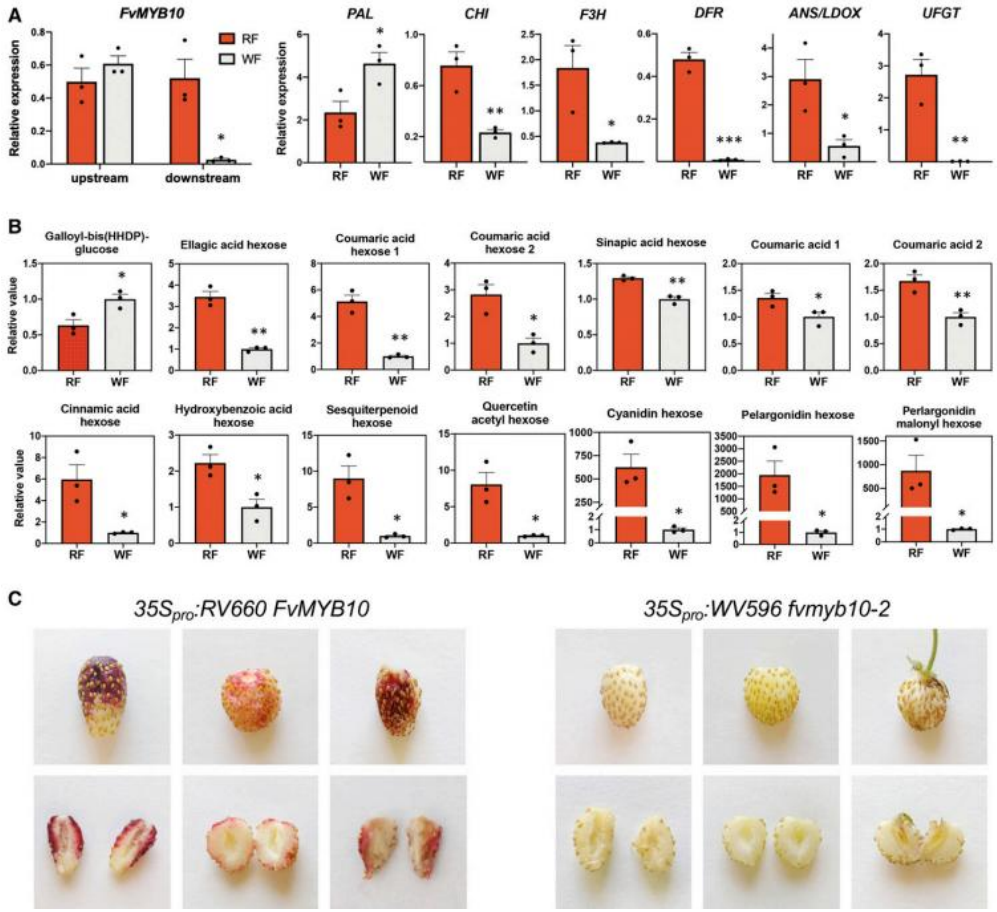

Figure 1 Effect of FvMYB10 Mutation on Structural Genes and Metabolites in *F. vesca* (Adopted from Castillejo et al., 2020)

4.2 Statistical framework for genetic effects decomposition and environmental interaction

The fluctuation of anthocyanin content is not entirely determined by "strong genes necessarily higher", as the environment can also play a role. Therefore, statistical methods such as analysis of variance are generally used to break down the total variation into genetic effects, environmental effects, and genotype × environment interaction (G×E), and then estimate the heritability based on this. The actual result is often that the heritability is mostly at a medium level, but the environmental influence is obvious, and G×E is also frequently significant (Connor et al., 2002a). To avoid being misled by a single location or a single year, stability analysis will be conducted using data from multiple environmental tests to see which materials remain stable under different conditions. When modeling, directly incorporating environmental factors into the model can also make the estimation of the main effects and interaction effects of genes more reliable (Mengist et al., 2020). In this way, it is possible to more clearly see which factors affect this trait, and it is also convenient to more steadily screen out genotypes with high anthocyanins and less likely to "drop easily when changing environments" during breeding.

4.3 Correlation and trade-off analysis between target traits and commercial traits

An increase in anthocyanins does not necessarily mean "all good things". It often has a domino effect on the properties of other products. For instance, in terms of nutritional quality, anthocyanins often rise along with indicators such as total phenols and soluble solids. Therefore, high-anthocyanin varieties often have a stronger flavor and higher antioxidant activity (Zeng et al., 2020). However, when it comes to the size of the fruit, the opposite relationship may occur: many small-sized blueberries have higher anthocyanins per unit weight. A very direct reason for this is that the proportion of the peel on small fruits is larger. One more point to note is that materials with high anthocyanins sometimes have thicker peels and a harder texture, which may affect the fresh taste and storability (Hirzel et al., 2023). When conducting breeding, one cannot merely focus on the anthocyanin indicator. While increasing the content, one should also take into account the fruit size, flavor, and yield, striving to maintain a balance.

5 Positioning Verification and Construction of Molecular Breeding Tools

5.1 Research design for qtl mapping and genome-wide association analysis

To identify the gene loci that control anthocyanin content, it is generally not advisable to use only one method. A common approach is to conduct QTL mapping and GWAS together for mutual comparison, which is more stable. QTL mapping is more "within the family". It measures the anthocyanin content of each individual in a specific hybrid isolation population and conducts whole-genome marker typing. First, the genetic map is built up, and then it detects which segments correspond to the trait changes (Montanari et al., 2022). GWAS takes a different approach, using natural germplasm populations in combination with high-density marker whole-genome scans for association analysis, and employs a mixed linear model to suppress the interference caused by population structure (Mengist et al., 2022). If the results on both sides can match, it indicates that the positioning is more reliable and it is easier to narrow down the range. When designing experiments, multiple environmental repetitions must also be taken into account; otherwise, it is very likely that only sites that are "significant under specific conditions" will be identified. Identifying QTLs that are stable across environments is more like a key site that can truly be applied in breeding (Figure 2) (Babiker et al., 2025).

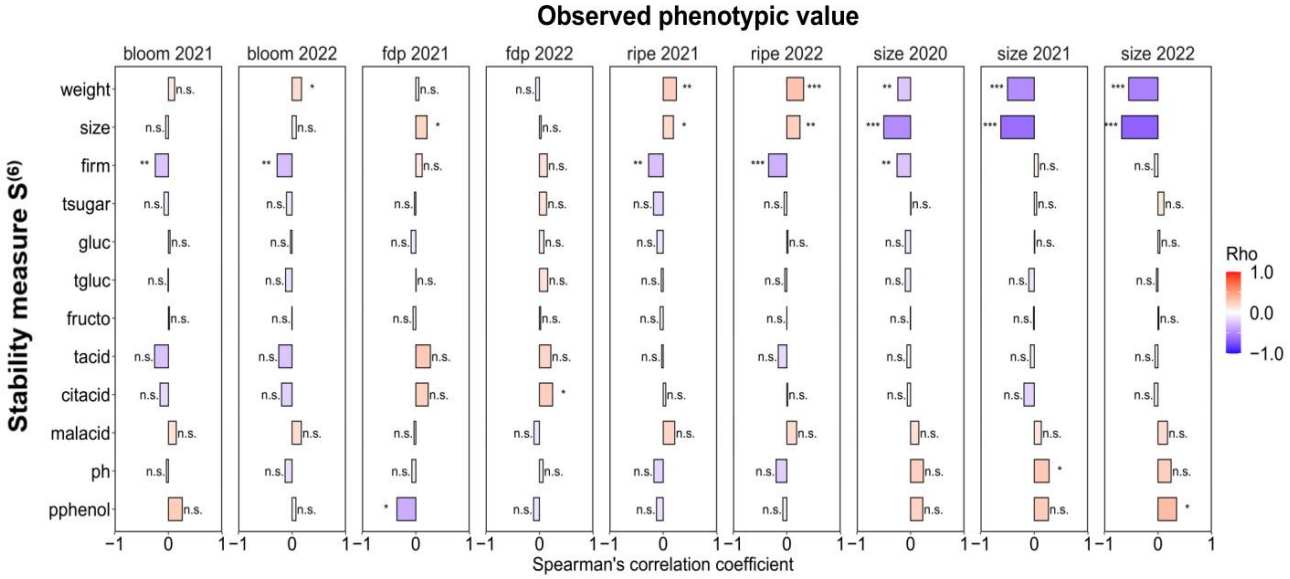

Figure 2 Relationship between phenotypic stability across years and phenology traits/fruit size (Adopted from Babiker et al., 2025)

Image caption: Single, double, and triple asterisks indicate significance at 5%, 1%, and 0.1% level. weight, berry weight; size, berry size; firm, berry firmness; tsugar, total sugar content; gluc, D-glucose content; tgluc, total glucose content; fructo, D-fructose content; tacid, total acid content; citacid, citric acid content; malacid, malic acid content; ph, juice pH; pphenol, total polyphenol content (Adopted from Babiker et al., 2025)

5.2 Organization of the evidence chain for candidate gene selection and functional validation

Once the target region is circled, the next step is not to "review all the genes", but to first narrow down the candidate genes to a more reasonable range. Usually, genomic annotations are reviewed first, and then screening is carried out in combination with common knowledge about the anthocyanin pathway: if there are transcription factors like MYB or structural enzyme genes such as DFR, ANS, and UFGT in the QTL region, they are generally given priority as candidates (Zhang et al., 2025). Then, from another perspective for verification: compare the expression levels of candidate genes with high and low anthocyanin materials to see if the expression changes are consistent with the traits; At the same time, pair the sequences of the candidate genes to see if there are any key differences between the high and low materials as further support (Plunkett et al., 2018). The last step is the "hard verification", which involves conducting functional tests through experiments such as genetic modification or gene silencing: whether overexpression can increase anthocyanins and whether silencing will significantly reduce them. Only by integrating annotations, expressions, sequence differences and functional results can the target genes be truly identified.

5.3 Process implementation of molecular marker systems and selection strategies

Once the target gene is determined, the "high anthocyanin" can then be developed into a set of operational marker-assisted breeding processes. The first step is to create the markers: Select the molecular markers that are most closely linked to high anthocyanin alleles, such as specific SNPs, or more convenient PCR markers, so that the target genotype can be screened out in the seedling stage (Wang et al., 2019). In actual breeding, marker detection should be directly integrated into the process - when facing a large number of offspring seedlings, DNA should be extracted first for marker detection, and those without the target allele should be eliminated in advance. Keep the plants carrying the target gene and then enter the field for assessment. Even in the field stage, anthocyanins should not be the sole focus. Conventional phenotypic selection should be carried out simultaneously, taking into account commercial traits such as fruit size, flavor, and texture. The significance of MAS lies precisely here: faster, more accurate, fewer detours, and the breeding cycle can also be shortened. Finally, by integrating laboratory testing with field selection to form a standardized process, efficiency will naturally be higher (Montanari et al., 2022).

6 Breeding Practice Paths and Strain Evaluation Systems

6.1 Breeding target system and parent combination Construction logic

To carry out high-anthocyanin breeding, the goal must be clearly set first, and there is not just one indicator. The anthocyanin content should of course be significantly increased, but the prerequisite is not to bring down the fruit size, flavor and yield at the same time. How to pair the parents has thus become more realistic: A common practice is to select one material with "abundant anthocyanins but average overall traits", and the other is a main cultivated variety with mature fruit quality, stable performance but only medium anthocyanins. The two sides are crossed to complement each other's strengths (Hera et al., 2025). High anthocyanin content does not necessarily mean it is effective. When matching parents, genetic compatibility and heterosis should also be taken into account at the same time; otherwise, the survival rate of hybridization and the performance of the offspring will be affected (Stevenson and Scalzo, 2012). Only when the parent combination is done scientifically can we truly have a solid foundation if we want to cultivate new varieties with high anthocyanin content, good taste and stable yield in the future.

6.2 Integration of hybrid separation population improvement and selection methods

When improving the hybrid offspring, it is generally not the case that only the "fruit observation and plant selection" in the field are relied upon. Molecular markers and conventional phenotypes are used together. MAS is applied first during the seedling stage: Marker testing is conducted to directly eliminate plants without the target allele, reducing the population size first and saving a lot of energy later on (Ferrão et al., 2021). After the plants bear fruit, conduct actual measurements on the remaining individual plants: the anthocyanin content should be measured, and the fruit size, flavor, and texture should also be evaluated together. Finally, select the strain with more stable and better overall performance. As for how to choose, it also depends on the characteristics of the traits: if the anthocyanin content is relatively stable in genetics, it is more advisable to choose individual plants. But if the environmental impact is obvious, don't be too hasty. Switch to family selection or conduct more experiments to enhance reliability. Sometimes, a step of "remelting" is taken, where the selected superior individuals are reincarnated for hybridization to continue aggregating favorable alleles (Lobos and Hancock, 2015). By connecting molecular techniques with traditional breeding in this way, the isolated population can be gradually improved, and the selection will be faster and more accurate.

6.3 Multi-point and multi-year testing and quality evaluation index system

Selecting excellent strains is only the first step. Later, regional trials are still needed to "test their quality in different environments". The common practice is to change several regions and plant for several consecutive years: while measuring the anthocyanin content, all fruit quality indicators are comprehensively tested, and the yield is compared at the same time. When evaluating, do not just focus on a single aspect. Usually, a comprehensive index system is established, including nutritional aspects such as anthocyanins, sensory aspects flavor, fruit color, texture), and processing adaptability hardness, storability, etc.. Weights are assigned based on their importance, and finally a comprehensive score is calculated. After the statistical analysis run is completed, if a certain variety

can maintain a stable performance in all pilot projects and also ranks high in the overall score, it will be more qualified to enter the list of candidate new varieties (Mengist et al., 2022). Incidentally, it can also be seen that there are differences in its adaptation to different ecological conditions, and thus there will be a basis for where it is more suitable to be promoted in the future (Spinardi et al., 2019).

7 Industrial Applications, Standardization and Future Directions

To ensure the quality of high-anthocyanin blueberries is stable, it is not enough to merely rely on "measuring to be quite high". The key is to have standards and a system where everyone tests in the same way. First, establish industry standards: What level of anthocyanin content is considered "high anthocyanin"? Make the threshold clear, and then there will be a hard yardstick for the identification of new varieties and product certification later. The testing aspect also needs to be unified; otherwise, different laboratories will conduct their own tests, making it difficult to match up. A more practical approach is to fix the operation process, keep the methods as consistent as possible, and at the same time provide standard reference samples and quality control procedures. Conduct inter-laboratory comparisons again to verify whether the accuracy and repeatability are up to standard. The sample stage should not be overlooked either. It is best to include collection, processing and preservation in the norms to reduce human differences. With the consistency framework of standards and testing in place, the quality of high-anthocyanin blueberry products will be more reliable, and breeders and processing enterprises will also be better able to evaluate and implement them in accordance with the same set of rules.

Whether high-anthocyanin blueberries are good for processing or not also needs to be examined separately. One cannot just look at the fresh fruit indicators. It is usually put into different processing scenarios for a run: simulating the processes of juicing, drying, heat treatment, etc., to compare how much anthocyanin is retained before and after processing, and at the same time record whether the color has become lighter or darker. Ideally, after processing, the anthocyanin content is still quite high and the color remains bright. In this way, the product not only has a natural color but also nutritional selling points. In addition, the texture and flavor will also be "disturbed". For instance, whether the meat structure will break apart after freezing and thawing, the juice yield will be high or not, and whether the taste of the finished product is satisfactory all need to be evaluated together. If some high-anthocyanin varieties are less likely to fade and have better stability during heating and storage, they are more suitable for development in the direction of functional foods or natural pigments. Only after completing these processing adaptations can materials that can be both eaten fresh and processed be screened out, and the space for industrialization will also be greater.

To ensure that new high-anthocyanin blueberries keep emerging in the future, relying solely on conventional breeding may not be sufficient. Technology, data and intellectual property rights need to be developed simultaneously. In terms of breeding technology, it can be more "precise" : methods such as genomic selection, molecular design breeding, and gene editing can be used to increase the anthocyanin content more quickly. Especially in gene editing, if the key genes and target sites are relatively clear, there is an opportunity to make targeted improvements and directly obtain new materials with higher anthocyanins. Of course, no matter how advanced the technology is, it still needs data to support it. Therefore, it is necessary to build a breeding data platform to integrate germplasm information, phenotypic data and genomic data, which will facilitate decision-making and also facilitate resource sharing, and the efficiency will be significantly better. Another aspect that is often overlooked is intellectual property rights: new varieties should have their own layout, and variety rights should be applied for when necessary. Key genes, detection methods and other technical points should also be patented in a timely manner. Don't wait until the results are released to make up for it. By integrating precision breeding, data platforms and intellectual property strategies into one, innovation will be more stable and promotion and implementation will be smoother.

Acknowledgments

We would like to express my heartfelt thanks to all the teachers who have provided guidance for this study.

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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