Plant Gene and Trait 2025, Vol.16, No.6, 274-283
http://genbreedpublisher.com/index.php/pgt

Review and Progress Open Access

Breeding Advances and Application Prospects of Flower Color Improvement in *Gerbera jamesonii*

Xingzhu Feng [1], Haimei Wang[1,2]
1 Hainan Institute of Biotechnology, Haikou, 570206, Hainan, China
2 Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China
Corresponding email: haimei.wang@hibio.org

Plant Gene and Trait, 2025, Vol.16, No.6 doi: 10.5376/pgt.2025.16.0029
Received: 29 Oct., 2025
Accepted: 05 Dec., 2025
Published: 18 Dec., 2025

Preferred citation for this article:
Feng X.Z., and Wang H.M., 2025, Breeding advances and application prospects of flower color improvement in *Gerbera jamesonii*, Plant Gene and Trait, 16(6): 274-283 (doi: 10.5376/pgt.2025.16.0029)

Abstract Gerbera daisies are cut flowers with extremely high ornamental value. Their rich and diverse flower colors are the core commercial characteristics. This article reviews the research progress of color improvement breeding of African chrysanthemums: starting from the types and metabolic mechanisms of pigments that form flower colors, it analyzes the genetic and cellular factors that affect flower colors; Then summarize the achievements and bottlenecks of traditional hybrid selection and molecular breeding in flower color improvement; Finally, in combination with market demand, the application prospects and breeding trends of new varieties are prospected. Studies show that the color of African chrysanthemums is mainly determined by anthocyanin and carotenoid pigments, and its synthesis is regulated by multiple genes and influenced by the environment. Traditional breeding has enriched the types of flower colors, but it is limited by complex genetic backgrounds and long breeding cycles. New technologies such as molecular markers, genetic engineering and gene editing are driving the transformation of breeding from empirical selection to precise design, making it possible to cultivate new varieties with more vivid and stable flower colors. In the future, through multi-omics integration and molecular design breeding, it is expected to accelerate the efficient improvement of African chrysanthemum color and meet the constantly changing market demands.

Keywords Gerbera Pattern improvement; Pigment metabolism; Conventional breeding; Molecular breeding; Application prospects

1 Introduction

Gerbera jamesonii, a perennial flower of the Compositae family, is also often called "Gerbera". It can always stand out in bouquets and flower baskets all year round. Ultimately, it's because its colors are eye-catching and there are many choices (Zhou et al., 2023). As one of the leading varieties among cut flower crops, its market position is often compared with that of roses, tulips, chrysanthemums and carnations (Gupta and Bashir, 2024). For consumers, many times the first thing they see is the pattern. Whether to buy or not, and whether it's worth it or not, the pattern often determines the first impression.

When making flower color improvements, breeders do not merely focus on "changing the color". Whether the hue should be rarer, whether the saturation can be richer and more vivid, and whether the lightness is brighter or softer all need to be taken into account (Zhou et al., 2022). But equally important are stability and neatness - some materials look good in certain environments but lose color when the season changes or the light and temperature change. Such materials are difficult to be used in production. Therefore, in breeding goals, "good-looking" and "enduring" are usually placed together: both expanding new color series and trying to keep their performance from being too exaggerated in different environments (Zhou et al., 2023).

This review does not follow the approach of "drawing conclusions first and then elevating", but rather breaks down the content: it begins by discussing how flower colors are formed and roughly how they are controlled genetically. Let's talk about how to evaluate the available germplasm resources and flower colors more accurately. Then, let's go through the progress of traditional hybrid selection and molecular methods in flower color improvement. Finally, let's return to the application level and discuss how the new variety can be industrialized and which paths breeding might take in the future.

2 The Biological and Metabolic Basis of the Formation of African Chrysanthemum Color

2.1 Main pigment systems and interactions

The color of gerbera daisies' petals mainly depends on two sets of pigments being used: one is anthocyanin and other flavonoid pigments, which often pull the petals towards cooler tones such as red, pink and purple (Zhong et al., 2020). Another set is carotenoids, which make it easier to produce warmer colors such as yellow and orange (Kishimoto et al., 2007). They don't always operate independently; sometimes they stack together to rewrite the result. For instance, when there are only carotenoids in the petals, they are mostly yellowish in color. However, once anthocyanins accumulate simultaneously, the color may lean towards orange-red. There are also some flavonoid compounds that do not show much color themselves (such as chalketone, flavonols, etc.) that are "mixed in", acting as auxiliary pigments and interacting with anthocyanins to produce a coloration effect, resulting in a richer and more layered appearance in the end (Huang and Hong, 2025).

2.2 Key structural genes and metabolic pathways

The anthocyanins in African daisies are basically produced through the common phenylpropane-flavonoid pathway, where a series of structural genes take turns to function: CHS, CHI, F3H, F3’H/F3’5’H, DFR, ANS, etc. The final type and quantity of anthocyanins largely depend on whether these genes are highly expressed in the pathway and how strong the enzyme activity is (Laitinen et al., 2008). There are also some rather "bottleneck" situations: for instance, if F3'5'H is missing or doesn't work well, it will be very difficult to synthesize the blue-purple series (related to delphinium), and the color pattern naturally won't expand towards blue. At the same time, it is not solely dependent on structural genes to run on their own. There are also regulators controlling the field upstream. Transcription factors like R2R3-MYB and bHLH often form complexes, jointly pushing multiple structural genes together to determine whether anthocyanins can accumulate in large quantities (Zhong et al., 2020). As for carotenoids, the route is changed to the isoprene metabolic pathway. After the precursors are generated, they undergo steps such as cleavage, cyclization, and hydroxylation. Among them, the different activities of key enzymes like CCD will cause differences in the amount of pigment accumulation and the intensity of the color. By seizing these key points to adjust the expression, the color pattern presentation can often be significantly changed.

2.3 Cellular and physiological factors affecting phenotypes

The color of anthocyanins in the vacuole is basically the "switch" of pH: when the vacuole is acidic, it is more likely to be red; when it is close to neutral, it will move towards purple; and when the environment is alkaline, it will be more like blue. In addition to pH levels, metal ions also get involved. For instance, ions like aluminum and iron can complex with anthocyanins to form more stable blue-purple complexes. The color is not only more distinct but also less likely to drift (Akbari et al., 2012). Looking further at the cellular level, the shape of the petal's epidermis can also affect what your eyes see. If the epidermal cells are shaped like conical papillae, the light reflection will be suppressed and absorbed more, making the color appear darker and more saturated. If the surface is relatively flat and has more reflection, the pattern often appears paler. That is to say, the pigment itself is not the only answer. The combination of the cellular environment and structure ultimately determines the flower color of the gerbera.

3 Genetic Laws of Flower Color and Germplasm Resources: Sources and Plasticity of Improved Materials

3.1 Genetic patterns of flower color traits

The color inheritance of gerberas is not so much like it can be explained by "just one rule": in some cases, it seems to be determined by a single gene, while in many other cases, it is the result of multiple genes pulling together. For instance, when the major gene changes, the flower color may change instantly - if the gene controlling anthocyanin synthesis mutates, the petals may turn white directly due to the lack of pigment. Once the function is restored, the colored phenotype often returns as well (Tyrach and Horn, 1997). However, more subtle differences, such as whether the color is deep or not and which tone it leans towards, are usually not determined by a single gene. Instead, it is the cumulative effect of multiple genes, along with their interactions, that eventually "adjusts" the pattern to that form (Zhou et al., 2023).

3.2 Cultivated varieties and wild relatives resources

Many of the commonly cultivated Gerbera daisies nowadays can actually be traced back to the contributions of a few original parents. For instance, materials like *Gerbera jamesonii* and G. viridiflora have undergone distant hybridization (Carrodeguas-González and Zúñiga Orozco, 2020). It is precisely because the sources are relatively concentrated that in order to make the flower color more "broad", special attention is paid to the collection of germplasm in breeding: not only existing cultivated varieties are considered, but also wild relatives are included. They themselves come with a richer variety of flower colors, which is equivalent to preparing a gene pool for new varieties. If the hybridization strategy is chosen appropriately, there is an opportunity to introduce unique pigment types or key regulatory genes from wild varieties into cultivated ones, creating new flower colors that are not present in the original varieties (Zhou et al., 2023). However, distant hybridization is not always smooth sailing. It often encounters problems such as incompatibility and infertility in the offspring. Therefore, it is often necessary to rely on methods like embryo rescue and setting up "bridge parents" to clear the way, so that wild resources can be truly utilized.

3.3 Linkage and trade-off of flower-related traits

The color of the flower is often not singled out for selection; it is frequently associated with other ornamental and agronomic traits. Genetically speaking, flower color genes may be precisely linked to genes related to flower shape, flowering period, resistance, and vase life. Therefore, once you focus on choosing a certain color, other traits may also change along with it. In breeding, such a situation has been witnessed: the color does indeed become more outstanding, but the disease resistance declines instead, or the lifespan of cut flowers shortens. This is mostly related to chain effects or even multiple issues within a single gene tube. To be stable, breeders must first identify these "not-so-friendly" correlations and try to break them down as much as possible. For instance, they can use continuous backcrossing to dilute the unfavorable background and then combine it with comprehensive selection for screening. The ultimate goal is very realistic: there can be an increase in color, but don't sacrifice other key traits (Figure 1) (Bhattarai et al., 2020; Zhou et al., 2023).

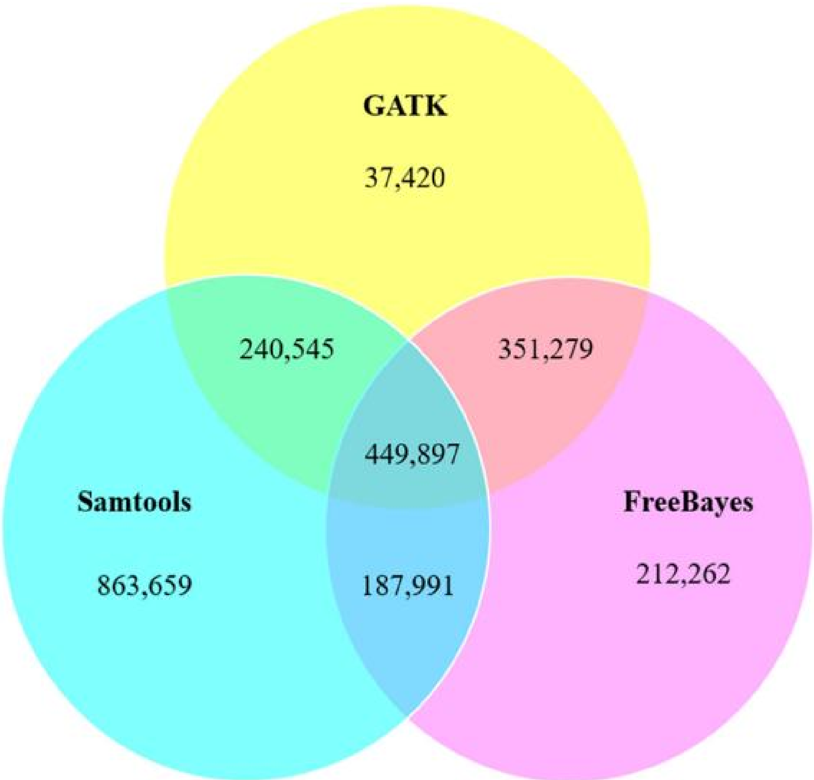

Figure 1 Venn diagram showing the distribution of SNPs in gerbera. SNPs were identified by GATK, Samtools and FreeBayes pipelines between powdery mildew resistant (UFGE 4033) and susceptible (06–245-03) gerbera breeding lines (Adopted from Bhattarai et al., 2020)

4 Phenotypic Identification and Quality Evaluation System

4.1 Standardization of flower color phenotypes

To accurately assess the color of gerberas, it is not enough to merely rely on "whether they look similar to the naked eye". First, a unified standard for phenotypic identification must be established. A common practice in breeding is to first use standard color cards (such as RHS color cards) to compare and name the flower colors, making it convenient for different people and different batches to refer to the same color. However, this step is not absolutely objective, so digital imaging is often added, or a colorimeter/spectrophotometer is used to measure color parameters to obtain comparable quantitative data (Zhou et al., 2022). When actually recording, the CIELAB system is often used for expression. For instance, L* represents lightness, a* reflects the change from green to red, and b* reflects the change from blue to yellow. In this way, differences such as hue and saturation can be more easily "written clearly" (Figure 2) (Jahan et al., 2020). In addition, the environment has a significant impact on color patterns. Therefore, when evaluating, it is necessary to conduct repeated measurements at multiple locations and in multiple batches, trying to eliminate occasional fluctuations and retain more stable and representative color results.

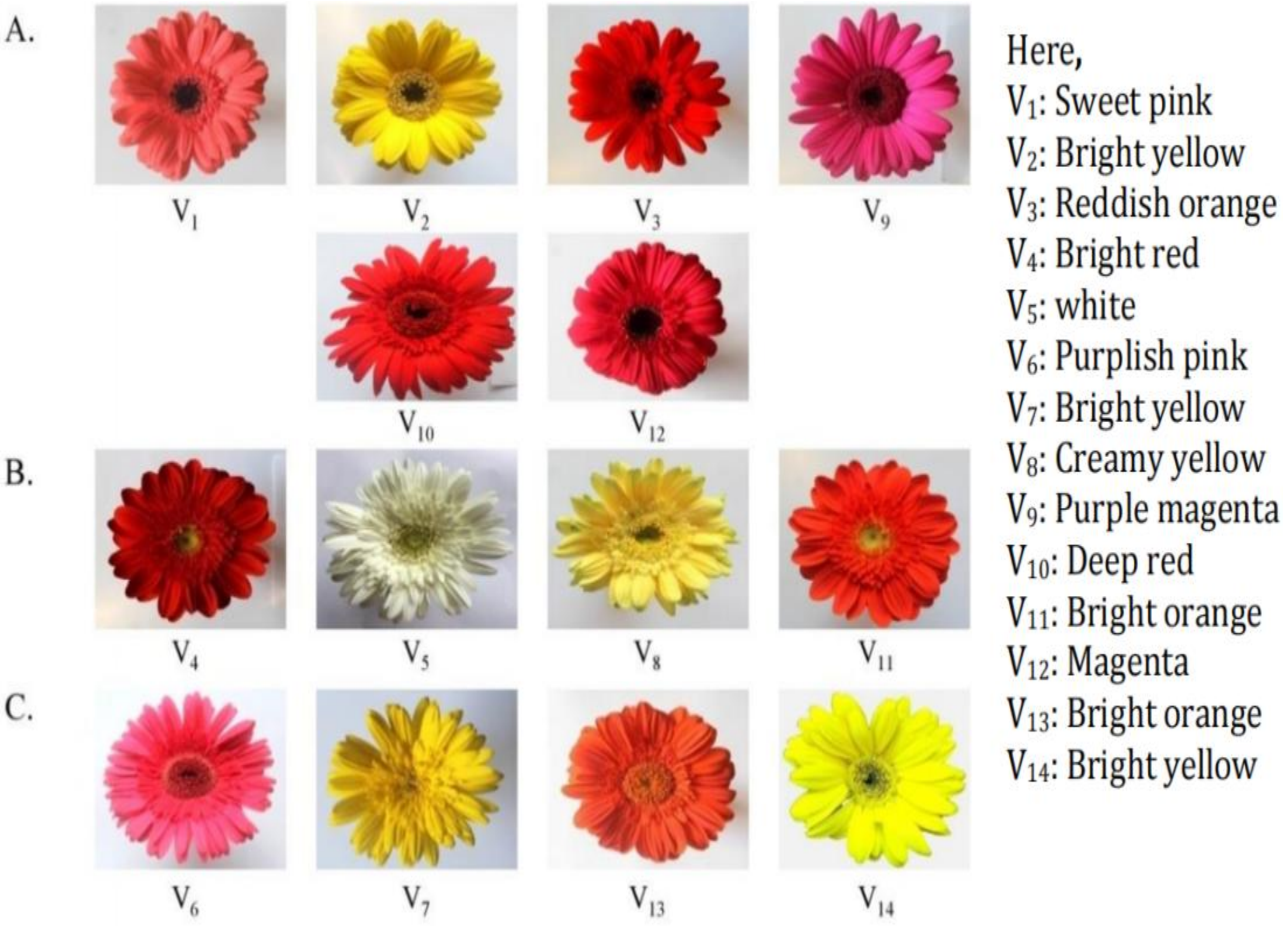

Figure 2 Classification of Gerbera according to the disc color (Adopted from Jahan et al., 2020)

4.2 Pigment Quantification and omics tools

To clarify the "material differences" behind the color of African chrysanthemums, HPLC or LC-MS can often be used directly: the amount of anthocyanins, carotenoids and other pigments in the petals and their respective components can all be quantitatively compared. If you don't just focus on the known components, you can also use non-targeted metabolomics to pull out the spectra of pigment-related metabolites of different varieties to see which metabolites are more closely related to the color differences (Zhou et al., 2022). If the transcriptome is also included, the candidate genes that may be involved in accumulation and regulation can be screened out incidentally. More importantly, the two sets of data should be examined together: by comparing the changes in the metabolome with the gene expression patterns, the differences in flower color phenotypes can be "matched", thereby identifying the key genes that affect the synthesis of anthocyanins or carotenoids (Zhong et al., 2020). This way, subsequent molecular breeding will have a more specific target.

4.3 Stability and commercialization indicators

Before a new variety is truly launched to the market, the color pattern should not merely be considered as "good-looking at present". Stability and durability must first pass the test. The first thing to do is consistency: for the same variety, when it is propagated in different generations or planted in different batches, the color should be basically the same, and there should be no color deviation between batches. Then it needs to be placed in different environments to test it out and see if the color is sensitive to changes such as temperature and light. Even more ideally, the original color can still be maintained under different cultivation conditions. Another often overlooked but crucial point is the postharvest performance, especially the resistance to fading during transportation and bottling. Some dark flowers do tend to fade easily under strong light or high temperatures, so simulated transportation and bottling preservation tests are usually conducted to observe how much color can be retained within a few days after harvest. Only those that can simultaneously meet the requirements of stable flower color, good environmental adaptability and not easy to fade after harvest can be truly qualified for large-scale production and sales (Mohammadi et al., 2021; Xia et al., 2024).

5 Progress in Traditional Breeding: Selection Routes and Key Bottlenecks

5.1 Hybrid breeding and systematic selection

The most commonly used and traditional approach to improving the flower color of gerberas is still hybrid breeding. Breeders usually first select parents with complementary flower color advantages for sexual hybridization, but it's not just a matter of randomly pairing. They also look at the compatibility of the parents and screen out the more promising combinations first. The real trouble lies in the offspring: in isolated populations, due to genetic recombination, there will be a large number of changes in flower color. Therefore, it is often necessary to deal with a large number of plants, systematically screen each one, and pick out the individual whose color is closest to the target. The selection of superior individual plants is not over yet. The next step is to make the traits "stand firm". Commonly used methods include self-pollination, pedigree selection, or simply asexual reproduction to fix and purify them. Only through such strict selection and repeated identification from generation to generation can new materials with more stable genetic backgrounds and stable color patterns be obtained, and then new varieties can be advanced (Zhou et al., 2023).

5.2 Backcrossing and gradual infiltration breeding

Backcrossing and gradual infiltration is a common method to "transplant" a particular flower color from wild species or other varieties into an excellent cultivation background. The approach is not complicated: First, cross the donor parent carrying the target flower color gene with a stable cultivated strain (recipient parent) to obtain F_1. After that, they kept crossing back towards the receptor parent. For each generation, they selected two types of single plants that were both "passable" - on the one hand, they had to carry the target flower color, and on the other hand, their agronomic traits should be as similar as possible to those of the receptor. With more backcrossing rounds, the target flower color genes can gradually establish themselves in a favorable background, and at the same time, the advantages of the original variety can be retained to the greatest extent (Jugulam et al., 2015; Zhou et al., 2023). During the process, it is also necessary to keep a close eye on some "incidental problems", such as the unfavorable traits brought about by exogenous genes. By continuous selection, these flaws can be gradually diluted from generation to generation within the group, or the links between them and the target genes can be gradually broken down. Eventually, the desired color pattern can be obtained while the overall performance is brought back to a normal level.

5.3 Comprehensive improvement strategy for multiple traits

Nowadays, when it comes to gerbera breeding, the thinking is no longer as simple as "making the color beautiful". The flower color needs to be improved, and the yield, disease resistance and quality of cut flowers must also keep up. Otherwise, it will be very difficult to put it into practical use. In practical operation, a common approach is to use a comprehensive selection index or simply screen in stages: for the early generations, the color pattern is prioritized first for a preliminary selection. Once the materials are shortlisted, we will then look at the hard indicators such as output, stress resistance and bottle insertion life, and directly eliminate those with poor overall performance. After repeating this process several times, what remains will be materials that are eye-catching in color and reliable overall (Zhou et al., 2023). Recent years' practice has also shown that when the color and other traits are modified in a coordinated manner, it is often easier to produce varieties that are favored by the market - not only are the colors richer and more vivid, but also the vase life, plant form and other aspects have been improved compared with past materials (Chung and Lee, 2019).

6 Advances in Molecular Breeding and Biotechnology: From "Empirical Selection" to "Precise Design"

6.1 Molecular markers and QTL/GWAS analysis

Molecular markers have been quite "useful" in the research on the color of African chrysanthemums in recent years. At least, they have made genetic analysis and breeding no longer entirely dependent on later flower observation. A common approach is to first conduct a hybrid population and then use QTL analysis to identify loci: Some major loci have already been located, which are closely related to the quantitative indicators of flower color, such as the differences in values like L*, a*, and b*, as well as the changes in anthocyanin and carotenoid content (Zhou et al., 2022). From another perspective, conducting GWAS in natural germplasm populations can also uncover a batch of molecular markers and candidate loci with obvious correlations. In this way, in breeding, "color selection" can be accomplished earlier and faster: after developing available DNA markers, using MAS to test the genotype at the seedling stage can roughly predict the color trend of mature plants, significantly improving the screening efficiency and shortening the breeding cycle considerably (Zhou et al., 2023).

6.2 Gene function verification and regulatory network

When using genetic engineering on gerberas, it is often not just about "changing the color", but more importantly, to understand the genetic relationships behind the flower color and draw the regulatory network at the same time. The approach is also quite straightforward: for the suspected related genes, either overexpress them or use RNA interference to silence them. By observing how the color of the petals changes, one can infer exactly what role they play. For instance, when a certain R2R3-MYB transcription factor (like GMYB10) is overexpressed externally, anthocyanins tend to accumulate more, and the color of the petals becomes significantly darker. Conversely, if the key enzyme genes in the anthocyanin synthesis pathway (such as CHS) are suppressed by RNAi or VIGS, the color may become lighter, and in severe cases, it may even approach white. Such experiments, one positive and one negative (function gain and function loss), can basically explain the role of structural genes and regulatory factors more solidly. The more challenging part lies in the "connection" : Researchers are still sifting through interacting transcription factors, possible signaling molecules, etc., piecing these dots together to form a more complete network diagram, aiming to explain as clearly as possible how the pattern expression is tuned.

6.3 Conception of gene editing and synthetic biology

In the past, the color of African chrysanthemums was mostly achieved through gradual hybridization. Now, gene editing has made "targeted color modification" more realistic. For instance, if a site-directed mutation is made to the regulatory genes in the anthocyanin pathway, the level of pigment accumulation may change. For instance, if the genes related to carotenoid degradation (such as CCD) are knocked out, there is a chance for more yellow pigment to accumulate and the color to be brighter. There are also precedents in ornamental plants: morning glories were once used with CRISPR/Cas9 to knock out anthocyanin-related genes, changing their blue-purple color to light yellow (Khusnutdinov et al., 2021). It is even possible to follow the synthetic biology approach and introduce key enzymes like F3'5'H to attempt to "make up" for the previously absent blue-purple color (Giovannini et al., 2021). However, when it comes to gerberas, there are still obstacles such as the efficiency of the transformation system, the simultaneous modification of multiple genes, and the approval and supervision. Only when the technology and policies become more favorable will it be more like true precision breeding.

7 Application Prospects: Industrialization Path, Market Demand and Iteration of Breeding Strategies

7.1 Market and consumption trends

Nowadays, when choosing the color of gerberas in the market, people are increasingly dissatisfied with "just looking good", and they prefer something new and distinctive. Therefore, those new products with unique patterns are more likely to be remembered. In terms of breeding, they will focus on market gaps, such as petal colors that are closer to blue or even darker (which are still rare or even non-existent at present). Once developed, they often have strong commercial appeal (Noda, 2018). Meanwhile, many breeders do not merely promote individual varieties but create "sets" - a gradient of the same color series from light to dark. This makes it more convenient for flower shops to use for color matching and also makes flower art more convenient. The preferences in different scenarios are actually quite intuitive: wedding celebrations prefer soft tones like pure white and pink. On occasions like Valentine's Day when expressing love, people prefer red tones. For celebration and opening ceremonies, flower baskets often use brighter and more festive colors such as red, orange and yellow. Seizing these segmented demands to create new varieties of theme color series and festival-specific color series usually can enhance the added value and competitiveness of the products more effectively (Zhou et al., 2022).

7.2 Production end implementation and variety promotion

The selection of new varieties is just the first step. Whether they can be turned into industrial achievements depends more on the subsequent system. First of all, the propagation of seedlings must be smooth: Use methods such as tissue culture for rapid expansion, and try to provide virus-free and genetically consistent seedlings, so that the new variety can be in a stable state and the batches can be easily controlled when it enters commercial cultivation (Laishram et al., 2013). Promotion and protection should also be advanced simultaneously. Breeding units should apply for new plant variety rights as early as possible to safeguard intellectual property rights first. At the same time, by conducting demonstration planting with flower enterprises and participating in flower exhibitions, the exposure and recognition of the new flower colors can be increased. The production end still cannot be relaxed. Quality standards such as seedling quarantine, cultivation norms, and post-harvest treatment must be clearly defined. Otherwise, the color and quality will be inconsistent with each batch after they are put on the market, and the reputation will quickly decline. Finally, there is logistics and the terminal. Only when cold chain transportation and the flower shop's preservation system are in place can the flower color effect be maintained from the field all the way to the consumers (Leonard et al., 2011). Only by connecting these links can new varieties of colors and patterns more easily move from "laboratory achievements" to commercialization.

7.3 Risks and challenges

The improvement of African chrysanthemum color has really reached the stage of promotion and industrialization, and there are quite a few troubles. Let's start with the environmental aspect: Some "special colors" are actually very picky about conditions. Even a slight change in temperature or light can cause the color to fall out of the ideal range. If they are promoted in a different climate region, the color pattern will deviate, which will directly affect the appearance and price (Naing et al., 2018). Further down the line is the issue of genetics. Gerberas themselves have a high degree of heterozygosis and hybridization, and their flower color is entangled with a bunch of gene interactions and other traits. Therefore, unexpected side effects may occasionally occur during the breeding process. In addition, many varieties reproduce asexually. Over time, they are prone to accumulate mutations or be affected by viruses, and both flower color and plant performance may deteriorate (Maske et al., 2018). Beyond technology, there are also practical obstacles: in some countries, the approval of flower color improvements made through genetic modification or gene editing is more cautious, and the market acceptance of "genetically modified flowers" is also unstable, making it even more difficult to bet on their promotion. In the end, the accounts still need to be calculated - high-end technology requires a large investment and has a long cycle. It is not always certain whether the new designs can recoup the research and development costs. In terms of response, we can only adopt multiple approaches: conduct multi-point trials to screen out adaptability, stabilize the foundation by removing viruses and ensuring the quality of seedlings, and then combine with popular science communication to reduce public concerns. Only in this way can the improvement of flower color be more sustainable.

8 Conclusions and Future Directions

To improve the color of African chrysanthemums more quickly and steadily, many key points actually lie in basic science. First of all, the question of "why some varieties are very stable while others change color when exposed to the environment" has not been explained clearly enough at present. How does pigment synthesis receive signals such as temperature and light, and whether there is epigenetic regulation involved, all need to be delved deeper to grasp the key points that truly affect stability. Another challenge is how multiple pigment pathways work together in the same petal: anthocyanins and carotenoids do not operate independently. Sometimes, when you try to stack one type, it ends up pressing down on another, and the flower color is "stuck" instead. Therefore, it is necessary to understand the interaction relationships among pathways and the laws of metabolic balance. Omics and systems biology would be more appropriate. Finally, genetic analysis needs to be more precise: Flower color is a quantitative trait, and small-effect genes and gene interactions are crucial. Relying solely on rough positioning is insufficient. A more feasible approach in the future is to combine high-throughput sequencing with precise phenotypes of large populations to create a more detailed genetic map, discover more minor loci and new allelic variations, and thoroughly explain the genetic structure of flower patterns.

To achieve rapid and accurate breeding of African chrysanthemum color, relying on a single technique is not enough. Several lines need to be combined into a system: phenotypes can be obtained in batches, multi-omics can be explained clearly, and finally, it can be applied to targeted improvement at the molecular level. The first step is often to speed up the phenotypic end by introducing a high-throughput measurement platform, using machine vision combined with AI to automatically measure color patterns and run data. This way, a large amount of materials can also provide relatively objective results more quickly. Then, the genomic sequencing, transcriptome, and metabolome data are compared with the floral phenotype. Bioinformatics analysis is used to sort out the gene network and metabolic pathways, and the truly key control factors are screened out. With these "key points", molecular design breeding seems more targeted: for instance, using gene editing to eliminate unfavorable alleles, or combining and aggregating favorable alleles to directly piece together a new genotype at the molecular level that is closer to the target color. Overall, it is to connect traditional experience with modern molecular methods, significantly accelerating the breeding pace of new varieties.

Looking ahead, for the improvement of African chrysanthemum color to always stay ahead, resources, platforms and breeding systems all need to keep up in the long term. Let's start with resources. Cultivated varieties and wild relatives should be combined to form a more extensive germplasm bank, especially those with extreme flower colors and special pigment mutants. After collecting them in place, the differences should be "marked" through molecular means. Only in this way can there be sufficient materials to choose from during breeding. The breeding process itself also needs to be more digitalized: put the flower color phenotype, genotype and environmental data into the same platform, and use methods such as genomic selection to predict the flower color of the offspring in advance, reduce blind trial matching, and make decision-making more efficient. Regional differences should not be overlooked either. With different climates, strategies need to be more regionalized, and targeted breeding should be carried out to maintain stable flower colors even in the local area. Finally, there should be a rhythm of variety updates. Once new varieties are introduced to the market, they should not be stopped. It is necessary to continuously monitor production performance and market feedback, and modify and upgrade the old varieties. Replace or supplement them when necessary. Only in this way can the product line remain vigorous and its competitiveness be more stable. Overall, only by laying a solid foundation in basic research, making good use of tools and establishing a smooth system can the improvement of patterns be more likely to achieve high efficiency, high stability and sustainability.

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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