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# Recent Advances in Hybrid Breeding of Kiwifruit: Strategies and Outcomes

Xingzhu Feng, Dandan Huang
Hainan Institute of Biotechnology, Haikou, 570206, Hainan, China
Corresponding email: dandan.huang@hibio.org
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**Abstract** Hybrid breeding is an important method to improve the quality, yield and stress resistance of kiwifruit fruits. This study summarizes some new progress in intraspecific and interspecific hybridization of kiwifruit at present. Techniques such as embryo rescue, polyploid breeding, and molecular marker-assisted selection have all played a significant role in breeding. This study also elaborates on how genomic technology and phenomics tools make breeding more accurate and faster, and analyzes the common problems encountered in practice through typical breeding cases. This study aims to provide some ideas and references for the future improvement and innovation of kiwifruit hybrid breeding.
**Keywords** Kiwifruit (*Actinidia spp.*); Hybrid breeding; CRISPR/Cas9; Polyploidy; Interspecific hybridization; Marker-assisted selection; Genetic improvement

## 1 Introduction

Kiwifruit (*Actinidia* spp.) is rich in nutrition and has high economic value. It originated in China, has a special taste, a high content of vitamin C, and contains a variety of health-beneficial components. It is very popular all over the world. The cultivation area of kiwifruit has expanded significantly. The major producing countries, New Zealand, Italy and China, have also benefited a lot from their agriculture. People have learned more about the nutritional value of kiwifruit, and it is often used in various dishes and beverages. The growth in global market demand for kiwifruit has made its economic status more prominent (Wang et al., 2020).

Hybrid breeding has become an important way to improve the quality of kiwifruit. The hybridization between *Actinidia arguta* and *Actinidia purpurea* can breed new varieties that are more cold-resistant, have larger fruits and more attractive appearances. Latocha and Jankowski (2011) demonstrated that this type of variety has improved agronomic traits and is more in line with consumers' requirements for taste and appearance. These are precisely the keys to whether the variety can succeed in the market. Shu et al. (2023) hold that current breeding relies on advanced technologies, which are beneficial for identifying important metabolic pathways and regulatory mechanisms related to fruit quality and nutrition, and can improve target traits such as fruit flavor and nutritional content.

This study expounds the latest progress in hybrid breeding of kiwifruit, mentions the methods and techniques used in the breeding process, analyzes the influence of hybrid breeding on fruit quality and other aspects, as well as the future development direction and possible problems of kiwifruit breeding. This study aims to summarize the achievements in kiwifruit breeding, identify areas that can be further improved, and make the newly bred varieties more suitable for the market and more acceptable to consumers.

## 2 Historical Perspective

### 2.1 Early breeding efforts and traditional methods

The earliest varieties of kiwifruit (*Actinidia* spp.) were mostly selected from wild species or naturally pollinated varieties. Hanley (2018) found that the early breeding work encountered many difficulties such as the long time from seed to flowering and fruiting of kiwifruit and dioecious plants. Its genetic composition is complex, with high heterogeneity. It is a climbing plant, and polyploid problems, etc., all make the breeding process troublesome.

The traditional breeding method is to select individuals with good growth and good traits from the natural population for reproduction. “Hayward” kiwifruit is a variety selected through natural selection.

### 2.2 Milestones in kiwifruit breeding history

In the 1970s, New Zealand established a formal breeding program, which promoted the birth of many new varieties and introduced yellow-fleshed and red-fleshed kiwifruits that had significantly improved in appearance and flavor compared to the original green-fleshed types (Hanley, 2018). The development of in vitro culture technology has made the breeding of kiwifruit more efficient. Wu’s research in 2018 found that the combination with polyploid breeding methods enriched the variety types and improved the overall quality of the fruits. The linkage maps established by RAD technology have helped breeders identify genetic markers related to the target traits and made mark-assisted selection (MAS) more accurate and reliable (Scaglione et al., 2015).

### 2.3 Transition from conventional to modern breeding techniques

The genome of kiwifruit has been sequenced, and the cost of genotyping is now much lower than before. Hanley (2018) found that techniques such as MAS and genomic selection (GS) have begun to be used in actual breeding, which is beneficial for breeders to find plants with ideal traits more quickly and also accelerates the selection and breeding of new varieties. Varkonyi-Gasic et al. (2018) edited the gene *CENTRORADIALIS-like* through CRISPR/Cas9, enabling kiwifruit to flower earlier and become a compact plant type, which made breeding faster and cultivation more convenient. Zhao et al. (2022) demonstrated that molecular cellular genetic techniques such as FISH and GISH have now also been optimized. These techniques are useful for a clearer understanding of the genetic structure and evolutionary relationships of kiwifruit, as well as for improving the accuracy and efficiency of breeding.

## 3 Genetic Diversity and Parent Selection

### 3.1 Overview of genetic diversity in kiwifruit

Kiwifruit belongs to the Actinidiaceae family. The *A. chinensis* complex has rich genetic diversity, and these genetic differences are crucial for resource conservation and the long-term development of kiwifruit. When Hu et al. conducted an analysis using SSR in 2022, they discovered a large number of genetic variations, identified 888 alleles, and the expected heterozygosity was as high as 0.846. However, the actual measured heterozygosity was only 0.622, indicating that there was inbreeding among the materials. Liao et al. (2019)’s study on wild kiwifruit (*A. eriantha*) also found that it has significant variations in fruit traits. The obvious linkage disequilibrium found at some SSR loci indicates that these traits are related to specific gene regions.

### 3.2 Criteria for selecting parent plants

The parents should have a relatively high genetic diversity for the offspring to be more likely to develop the desired good traits. Liao et al. (2019) and Hu et al. (2022) used molecular markers such as SSR to determine which plants had more abundant genes. The internal traits of fruits such as sugar content, carotenoids and chlorophyll can affect the sweetness, color and nutrition of the fruits. Liao et al. (2019) found that materials with good fruit quality in wild species were often selected as parents. Whether the pollen germination rate is high or not and whether it is compatible with the female parents are very important when selecting male parents. Iliescu et al. (2022) identified male materials with a pollen germination rate exceeding 90%, which performed better during pollination and were highly suitable for use as the male parent. Hanley (2018) indicated that in order to make the newly bred varieties more stable and disease-resistant, the breeding program would select disease-resistant materials from parents of different sources for use.

### 3.3 Role of wild relatives and existing cultivars

Wild kiwifruits such as *A. eriantha* bring rich genetic resources and have many special traits that can be used in breeding. Liao et al. (2019) argued that wild materials have good fruit quality and significant genetic differences, and are of great value for developing new varieties. The kiwifruit varieties that have been promoted in the market have stable traits, good fruit shape, taste or yield, and are also relatively recognized by consumers. In breeding practice, these two types of materials are usually combined. Wild species provide new traits, while cultivated species offer stability. Through hybridization, they complement each other's strengths. Hu et al. (2022) indicated that the core resource bank of the *Actinidia chinensis* complex is to lay a solid foundation for future genetic improvement and resource conservation.

## 4 Hybridization Techniques

### 4.1 Controlled pollination methods

Controlled pollination involves artificially transferring the pollen of selected male plants onto the stigma of the target female plants to ensure that the offspring have the required genetic combination. It is a fundamental step in cultivating new varieties with specific traits. Iliescu et al. (2022) specifically tested the pollen germination rates of different male hybrids and their compatibility with female plants in a kiwifruit breeding project in Romania, which could ensure successful pollination and the smooth development of seeds. Marcellán et al. (2022) found that male parents can affect the success of pollination, as well as the quantity and germination of seeds, indicating that the choice of pollination control is crucial to the overall hybridization outcome.

### 4.2 In vitro fertilization and embryo rescue

In vitro fertilization and embryo rescue are suitable for addressing problems such as long seed dormancy time and low germination rate. They are carried out in a controlled laboratory environment, where embryos are taken out for individual cultivation to ensure their smooth development into healthy seedlings. Marcellán et al. (2022) demonstrated that in vitro embryo culture methods have been successfully employed in kiwifruit breeding to cultivate interspecific hybrids, which are suitable for selecting rootstocks with ideal traits.

### 4.3 Genetic markers and molecular tools in hybridization

Genetic markers, molecular tools and other technologies enable breeders to more accurately identify the parental origin of hybrid plants and screen out individuals with ideal traits more quickly. Zhao et al. (2022) found that fluorescence in situ hybridization (FISH) and genomic in situ hybridization (GISH) have been optimized for application in kiwifruit, which can clearly distinguish chromosomes and determine which genes come from which parent. Chłosta et al. (2021) demonstrated that sex-linked molecular markers can identify female sources in callus or regenerated plants and determine at an early stage which plants are worth preserving, thereby enhancing breeding efficiency.

### 4.4 CRISPR/Cas9 and gene editing

CRISPR/Cas9 can modify the genes of kiwifruit in a targeted manner, which is beneficial for breeders to obtain the desired traits more quickly. In 2018, Varkonyi-Gasic et al. modified the *CENTRORADIALIS-like* gene through CRISPR/Cas9 technology, successfully transforming kiwifruit into a compact plant and enabling it to flower earlier, accelerating the breeding process. It can also create new traits that traditional breeding cannot achieve. CRISPR/Cas9 is expected to help cultivate new kiwifruit varieties that are more disease-resistant, have better fruit quality and can adapt to different environments (Varkonyi-Gasic et al., 2018; 2021)

## 5 Strategies for Hybrid Breeding

### 5.1 Objectives: disease resistance, yield improvement, fruit quality

Improving disease resistance can reduce the losses caused by diseases and make planting more stable. When the output increases, the income of fruit farmers will also be higher and the economic benefits will be better. The improvement of fruit quality such as good taste, delicate texture and rich nutrition can meet consumers' preferences and make it easier to stand out in the market. They are the most core directions in kiwifruit breeding.

### 5.2 Breeding for abiotic stress tolerance

Zhang et al. (2019) found that the transcription factor AcMYB3R of type R1R2R3-MYB could enhance the drought and salt tolerance of *Arabidopsis thaliana*, indicating that it might have a similar effect in kiwifruit and could be used to cultivate more drought-resistant and salt-tolerant varieties (Figure 1). Jin et al. (2021) demonstrated that the bZIP type transcription factor AchnABF1 is crucial for plants to cope with osmotic stress and low temperatures, providing theoretical support for the development of cold-resistant kiwifruit varieties.

Recent research by Liu et al. (2023) indicates that the gene *AcePosF21* can activate the synthesis of ascorbic acid under cold conditions, which is useful for reducing oxidative damage to plants and enhancing the resistance of kiwifruit to low-temperature environments.

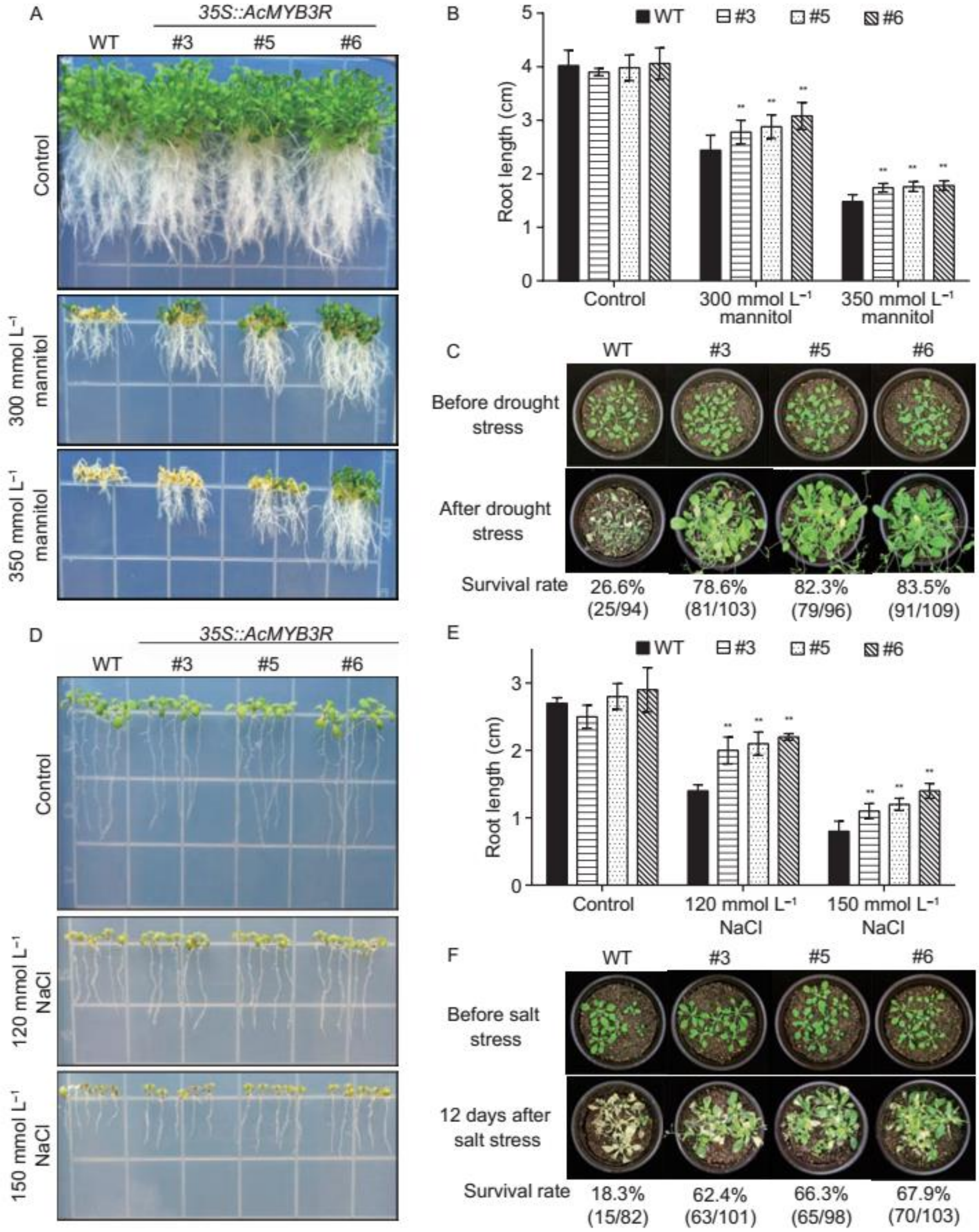



Figure 1 Overexpression of AcMYB3R results in enhanced drought or salt tolerance (Adopted from Zhang et al., 2019)

Image caption: A and B, phenotypes and the root length of wild type (WT) and AcMYB3R-overexpressing lines (#3, #5 and #6) under mimic drought stress on 0.5× MS medium. C, phenotype of WT and AcMYB3R-overexpressing lines (#3, #5 and #6) before and after drought stress treatments in pots. D and E, phenotypesm and the root length of WT and AcMYB3R-overexpressing lines (#3, #5 and #6) under salt stress on 0.5× MS medium. F, phenotype of WT and AcMYB3R-overexpressing lines (#3, #5 and #6) before and after NaCl treatment in pots. Data in Fig. 4-B and E are mean±SD from three independent experiment. **, signifcant differences at P<0.01 by Student's t-test (Adopted from Zhang et al., 2019)

### 5.3 Breeding for biotic stress tolerance

Breeders are striving to identify and utilize genes related to disease resistance and introduce them into new varieties to enhance the resistance of plants. Molecular markers and genomic tools have helped researchers identify many key genes. Zhang et al. (2019) discovered the role of AcMYB3R in abiotic stress and pointed out that it may have potential in enhancing the resistance of plants to phytopathogens. This genetic information can enable breeding work to be carried out more specifically, and kiwifruit varieties that are more resistant to diseases and pests can be selected and bred.

## 6 Recent Advances and Technologies

### 6.1 Application of CRISPR and gene editing

The CRISPR/Cas9 technology can create directed mutations in the genes of kiwifruit, which is beneficial for breeders to obtain ideal new traits. Varkonyi-Gasic et al. (2018) modified the *CENTRORADIALIS-like* gene in kiwifruit using CRISPR/Cas9, transforming the perennial plant that originally grew in a vine-like pattern into a compact plant, enabling it to flower rapidly at the top and shortening the juvenility period. Wang et al. (2018) optimized the pairing method of sgRNA and Cas9, making CRISPR/Cas9 more efficient when editing multiple genes at one time and achieving a higher accuracy rate of mutations. Zhou et al. (2020) demonstrated that CRISPR/Cas9 can accelerate the breeding speed and improve the agronomic traits of kiwifruit, and it is a very promising new tool.

### 6.2 Use of genomics and bioinformatics in hybrid breeding

Popowski et al. (2021) established a high-density genetic map using genotyping-by-sequencing (GBS) and identified QTL loci related to fruit quantity, weight, and storage hardness in hexaploid kiwifruit. Hanley (2018) demonstrated that advancements such as the completion of kiwifruit genome sequencing and the decreasing cost of genotyping have made breeding faster and more cost-effective. Cheng et al. (2019) and Jeon et al. (2023) both hold that GS predicts the breeding value of each plant by analyzing a large number of markers across the entire genome, and can also take into account both major and minor effector genes. Merrick et al. (2022) found that this method has begun to be applied in kiwifruit, which is expected to improve the efficiency and accuracy of hybrid breeding.

### 6.3 Marker-assisted selection (MAS) and genomic selection (GS)

MAS is suitable for selecting traits controlled by one or a few genes and determining whether kiwifruit seedlings are male or female (Cheng et al., 2019). Merrick et al. (2022) hold that traits such as the size, taste, and disease resistance of fruits, which are determined by many genes together, need to be marked with GS, which takes all gene markers into account and is more comprehensive. Hasan et al. (2021) found that techniques such as molecular markers have improved the accuracy of screening and made the breeding process faster. The combination of MAS and GS can pick out plants with different advantages at different stages, making the breeding effect better. Hanley (2018) indicated that the kiwifruit varieties eventually bred would better meet the demands of growers and the market.

## 7 Case Studies of Successful Hybrids

### 7.1 Detailed examination of notable kiwifruit hybrids

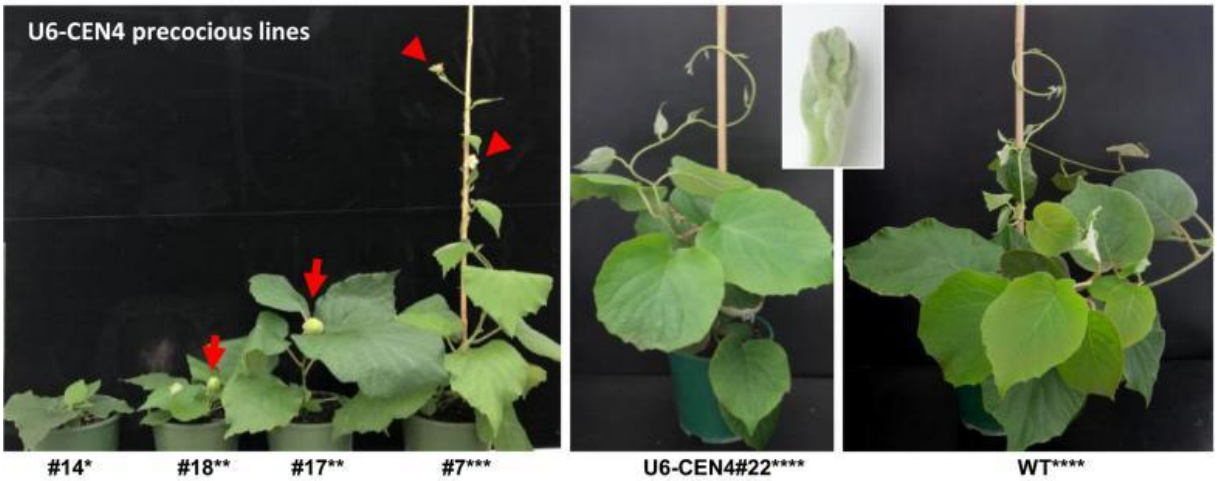
Marcellan et al. (2022) obtained varieties with changed rhizome structure by crossing *Actinidia arguta* with *A. chinensis* var. *deliciosa*, providing a new option for controlling plant size. In 2018, Varkonyi-Gasic et al. used CRISPR/Cas9 technology to conduct targeted mutations on the *AcCEN4* and *AcCEN* genes, transforming the traditional perennial climbing kiwifruit into a compact plant, achieving rapid apical flowering and shortening the breeding cycle (Figure 2). Iliescu et al. (2022) screened out male hybrid varieties with a relatively high pollen germination rate, which is crucial for enhancing field pollination efficiency and fruit yield.

### 7.2 Breeding strategies used and outcomes achieved

The hybridization of *A. arguta* and *A. chinensis* var. *deliciosa* was accomplished through conventional isploid hybridization, and new materials with ideal rhizome traits could be obtained without complex techniques such as embryo rescue (Marcellán et al., 2022). Another study was to mutate the *AcCEN4* and *AcCEN* genes using

CRISPR/Cas9 technology, making kiwifruit plants more compact and flowering earlier, and accelerating the breeding process (Varkonyi-Gasic et al., 2018). Iliescu et al. (2022) identified male varieties with high pollen germination rates and strong pollination capabilities through selective breeding, which are crucial for enhancing fruit setting rates and yields.

(a)




(b)

| | *AcCEN4* E1 | *AcCEN4* E4 | *AcCEN* E1 | *AcCEN* E4 | predicted genotype |
|---|---|---|---|---|---|
| U6-CEN4#14 * | E1-E4 del<br>indel | E1-E4 del<br>indel | wt | insertion (+156) | *cen4cen4/cencen* |
| U6-CEN4#18 ** | E1-E4 del<br>indel | E1-E4 del<br>indel | wt/indel | indel | *cen4cen4/cencen* |
| U6-CEN4#17 ** | E1-E4 del<br>indel | E1-E4 del<br>indel | wt/indel | wt | *cen4cen4/CENcen* |
| U6-CEN4#7 *** | indel | wt | wt | wt/indel | *cen4cen4/CENcen* |
| U6-CEN4#22 **** | wt/indel | wt | wt | wt | *CEN4cen/CENCEN* |
| U6-CEN4#19 **** | wt/indel | wt/indel | wt/indel | wt/indel | *CEN4_/CEN_* |

(c)

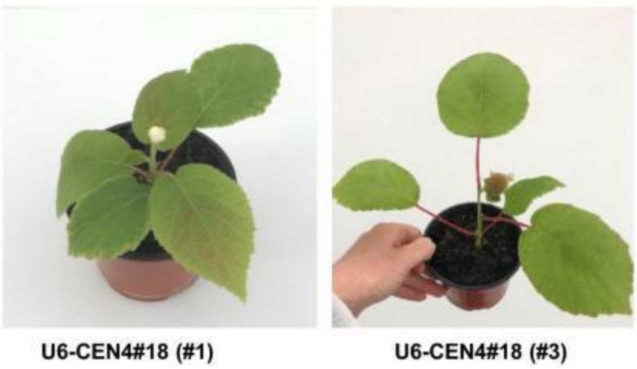



Figure 1 CRISPR/Cas9-mediated editing of *AcCEN4* and *AcCEN* genes (Adopted from Varkonyi-Gasic et al., 2018)
Image caption: (a) The height and architecture of U6-CEN4 plants. Arrows and arrowheads indicate fruit and flowers respectively. The insert shows a close-up image of the vegetative shoot tip in line 22. The asterisks denote the phenotypes: *, compact plant, early flowering, no fruit set; **, compact plant, early flowering; ***, vine habit, early flowering; ****, vine habit, no flowering. (b) Mutations identified in E1 and E4 sites in AcCEN4 and AcCEN alleles. (c) Rapid flowering and fruit development in U6-CEN4#18 lines after re-establishment and propagation in tissue culture (Adopted from Varkonyi-Gasic et al., 2018)

### 7.3 Challenges faced and how they were overcome

Maghdouri et al. (2021) found that after adjusting the cold wet lamination treatment method and improving the composition of the seedling substrate, problems such as low germination rate, uneven growth of seedlings, and incompatibility during grafting could be improved. Germination would be faster and the seedlings would be more uniform. The long juvenile period of kiwifruit and dioecious plants make the breeding cycle longer. The CRISPR/Cas9 technology can enable plants to flower earlier and even form bisexual flowers, accelerating the speed of breeding (Varkonyi-Gasic et al., 2018; 2021) Incompatibility problems are prone to occur when grafting between different species. Li et al. (2021) selected rootstocks and scions with closer genetic relationships and higher binding degrees for combination in order to increase the survival rate and improve the success rate of grafting.

## 8 Field Performance and Commercialization

### 8.1 Evaluation of hybrid varieties in field trials

Field trails will examine the agronomic traits of plants, such as their growth patterns, flowering times, and resistance to diseases. Varkonyi-Gasic et al. (2018) mutated the *CENRORADIALIS-like* gene in kiwifruit using CRISPR/Cas9 technology and found that this modification could make the plants more compact and enable earlier flowering, which was beneficial for both breeding and field performance. Iliescu et al. (2022) identified male hybrid varieties with high pollen germination rates, which are crucial during field pollination and can enhance fruit setting rates.

### 8.2 Fruit yield, quality, and market acceptance

Abbate et al. 's research in 2021 found that artificial pollination is more effective than natural wind or insect pollination, increasing fruit setting rate, fruit weight, fruit diameter and seed quantity, and improving the overall quality of the fruit. Maghdouri et al. (2021) found that improving the layering method of seeds during the seedling stage and combining it with appropriate seedling substrates can make seed germination more uniform, seedlings grow stronger, and lead to higher yields. Wu (2018) developed new kiwifruit varieties with various flesh colors such as green, yellow and red. Different colors make the fruits more attractive and more acceptable to consumers, resulting in better market performance.

### 8.3 Commercial success stories and economic impact

Hanley's breeding work in New Zealand in 2018 introduced yellow-fleshed and red-fleshed kiwifruits, which were more popular than the traditional green-fleshed varieties and also made the market larger. Wu (2018) indicated that establishing an efficient in vitro culture system enables faster breeding and brings new varieties to the market earlier to meet the demands of consumers. Xie et al. (2019) found that by identifying specific molecular markers, the identity of a variety can be confirmed. This is helpful in resolving legal disputes over varieties, ensuring the authenticity of kiwifruits sold on the market, protecting consumers' rights and interests, and making the market more trustworthy.

## 9 Challenges and Limitations

### 9.1 Genetic bottlenecks and breeding constraints

Kiwifruit takes a long time to grow from young seedlings to flowering and fruiting, and is dioecious (Hanley, 2018). The complexity of genes, the high degree of heterozygosity and the situation of polyploidy make the breeding of new varieties more troublesome. Maghdouri et al. (2021) found that its seeds contain dormant embryos, which sometimes germinate slowly and irregularly, and the seedlings grow unevenly, affecting the efficiency of seedling raising. Hu et al. (2022) indicated that with significant environmental changes nowadays, the growth areas of some wild kiwifruits have been destroyed, and the genetic diversity within the *Actinidia chinensis* complex is also at risk. These resources must be well protected to ensure the sustainable development of the kiwifruit industry.

### 9.2 Environmental and regulatory challenges

Extreme weather, bacterial canker disease and other problems have brought great pressure to the cultivation of kiwifruit (Hanley, 2018). These situations are difficult to deal with. If there are regulations on the use of advanced genetic technology in addition, the problem will be even more complicated. These techniques can select good varieties more quickly in breeding and improve the performance of plants (Varkonyi-Gasic et al., 2018; 2021) However, due to the strict regulations in agriculture and the environment, new technologies are sometimes difficult to be applied immediately, which will slow down the promotion speed of new varieties.

### 9.3 Consumer acceptance and market barriers

Nowadays, kiwifruit with better flavor, more colors and richer nutrition can be cultivated. However, when promoting it in the market, problems such as consumers' taste habits and insufficient cognition of new things are still encountered (Hanley, 2018). When it comes to genetically modified technology, many people are concerned about safety or environmental impact, making it more difficult for genetically modified kiwifruit to enter the market (Varkonyi-Gasic et al., 2018; 2021) There must be clear and simple publicity methods to solve these problems, so that everyone understands the benefits of new varieties and that they are safe, so that more people are willing to try and the breeding achievements can truly play a role.

## 10 Future Prospects

### 10.1 Emerging technologies and their potential impact

CRISPR/Cas9 gene editing has been used to make kiwifruit flower earlier and grow more compactically, potentially making kiwifruit cultivation in indoor environments a reality (Varkonyi-Gasic et al., 2018; 2021) Molecular cellular genetic techniques such as FISH and GISH enable scientists to have a clearer understanding of the genetic structure of kiwifruit, which is beneficial for making more accurate breeding decisions (Zhao et al., 2022). Establishing an efficient in vitro culture system can rapidly obtain a large amount of new materials through chromosome doubling or micropropagation, facilitating the development of new varieties (Wu, 2018).

### 10.2 Prospects for international collaboration in breeding programs

The sharing of genetic resources among countries, the exchange of experiences and the application of advanced technologies have enhanced the efficiency of breeding. Italy and Romania have jointly integrated resources and expertise and successfully bred high-quality kiwifruit varieties (Iliescu et al., 2022). Hanley (2018) believes that this kind of cooperation can solve global problems such as bacterial canker disease of kiwifruit and improve the disease resistance of varieties. Through international cooperation among different countries, they can leverage their respective genetic resource advantages and technological means to jointly develop robust varieties that are both high-yielding and disease-resistant.

### 10.3 Vision for the future of kiwifruit hybrid breeding

The future of kiwifruit hybrid breeding is likely to combine new technologies and international cooperation to jointly cultivate new high-quality varieties that are more suitable for the global market. Tools such as GS and MAS are useful for breeders to find kiwifruit with good traits such as better taste, brighter color and higher nutrition more quickly (Hanley, 2018). Hybridization among different species can be used in the future to cultivate rootstock materials that control growth or enhance disease resistance (Marcellan et al., 2022). Maghdouri et al. (2021) demonstrated that improvements in seed germination methods and the growth patterns of seedlings would make the propagation of new varieties smoother. With the breeding work becoming increasingly complex, people are paying more and more attention to sustainable development and using cryopreservation methods to preserve precious germplasm resources for a long time (Pathirana et al., 2020).

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### 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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