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Global Germplasm Flow of Pineapple (*Ananas comosus*) and Its Impact on Modern Cultivars

Chuchu Liu [1,2], Zhonggang Li [1]
1 Cuixi Academy of Biotechnology, Zhuji, 311800, Zhejiang, China
2 Hainan Institute of Tropical Agricultural Resources, Sanya, 572000, Hainan, China
Corresponding email: chuchu.liu@cuixi.org
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Abstract Pineapple (*Ananas comosus*), as the third largest tropical fruit in the world, relies on global exchange and sharing of germplasm resources for its industrial development. However, due to the main use of asexual reproduction, current cultivated varieties generally have problems such as narrow genetic basis, weak disease and stress resistance. This study systematically reviewed the origin, transmission pathways, and genetic diversity patterns of pineapple germplasm resources, with a focus on analyzing the potential value of wild relatives and local varieties in modern breeding. By combining molecular markers and genomic technology, the genetic structure and classification characteristics of the main cultivated populations were further revealed, and the practical application of SNP markers in germplasm identification and variety breeding was demonstrated through typical cases. Research suggests that promoting the rational utilization of global germplasm resources, integrating cutting-edge methods such as genome selection, gene editing, and low-temperature preservation, is the key to breaking through current breeding bottlenecks and enhancing variety adaptability. This study aims to establish a more stable international cooperation mechanism to achieve sustainable protection and efficient utilization of germplasm resources, laying the foundation for the long-term stable development of the pineapple industry.
Keywords Pineapple (*Ananas comosus*); Germplasm resources; Genetic diversity; Disease resistance; Global dissemination; Germplasm conservation

1 Introduction

Pineapple (*Ananas comosus*) stands out as one of the world's most beloved tropical fruits- trailing just behind bananas and mangoes in terms of global production and trade. Grown across a wide stretch of tropical and subtropical regions, pineapples are cultivated on everything from small family farms to massive plantations. In countries such as Costa Rica, the Philippines, Thailand, and Brazil, pineapple farming isn't just big business- it's a vital source of income for countless communities. In Costa Rica, pineapple cultivation covers an area of 44,500 hectares, contributing about 1.7% of the country's GDP and creating a large number of jobs (Chen et al., 2020).

There are still some problems with pineapple cultivation, most pineapples are propagated by cuttings, not seeds. Therefore, their genetic differences are very small. Because of the low genetic diversity, it is more difficult to breed new and stronger varieties. This also means that pineapples are more vulnerable to pests, diseases and climate change (Zhou et al., 2015). Some varieties, like Smooth Cayenne, are almost universally used. But because there are very few differences between these varieties, they are more susceptible to disease or damage. Common problems include wilting, rot and insect pests. Environmental factors such as drought, saline soil and heat waves are also exacerbating these problems. Therefore, it is more important than ever to improve the stress resistance of pineapples.

Germplasm resources refer to all the genetic materials in pineapple plants, such as wild types, ancient local varieties, traditional strains, and modern hybrids. These different sources provide rich and useful traits. Some have different flesh textures or flavors, while others are better at resisting pests or coping with bad weather (Chen et al., 2019a). Natural selection and farmer cultivation have shaped this diversity over a long period of time. Today, the variety groups we are familiar with include Smooth Cayenne, Queen, Red Spanish, and Pernambuco, each of which has unique characteristics that adapt to specific climates or market needs. Some wild types, such as *Ananas macrodontes* and *Ananas bracteatus*, are particularly valuable. They are highly adaptable, resistant to diseases and drought-tolerant, and are therefore important resources for breeding better quality pineapple varieties.

Thanks to new technologies in molecular biology, scientists can now study the genetic characteristics of pineapples in greater depth. Molecular marker methods such as SSR (simple sequence repeats) and SNP (single nucleotide polymorphisms) can identify tiny genetic differences with high precision (Scherer et al., 2015; Ismail et al., 2020). With these tools, breeders can screen target traits more scientifically and greatly speed up the process when breeding new varieties.

This study explored the spread and evolution of pineapple germplasm resources around the world and revealed how these flows led to the formation of today's cultivated varieties. The study also analyzed the current level of genetic diversity in pineapple crops and evaluated the application of new molecular tools in breeding work. We believe that all this information will be of great reference value for building a stronger and more sustainable pineapple industry.

2 Historical and Geographical Spread of Pineapple Germplasm

2.1 Origin and early domestication of pineapple

Pineapple (*Ananas comosus*) originated in the lowland tropical regions of South America, mainly distributed in southern Brazil, Paraguay, and northern Argentina. Archaeological evidence and local indigenous records indicate that the domestication history of pineapples can be traced back thousands of years. The indigenous tribes of pre Columbian times, such as the Tupi Guarani and Arawak people, were the first to breed wild pineapples for larger fruit, higher sweetness, and less seed content. The domestication process in this region has the characteristic of "one-step operation", which is to continue through asexual reproduction (such as bud sucking and creeping), so that excellent traits remain stable between generations (Chen et al., 2019a).

Thanks to its natural hardiness, pineapple thrived in a range of environments, which helped it spread well beyond its birthplace. Long before European explorers ever arrived, pineapples had already made their way across much of South America and the Caribbean (Maia et al., 2023). People were growing them in diverse ecosystems—from the lush Amazon basin to the foothills of the Andes and across countless islands.

The Carib people likely helped bring pineapple to many Caribbean islands. There, it wasn't just food. People also used it as medicine and to make fermented drinks. This early farming and plant selection added a lot to the plant's genetic variety. Because people kept choosing and growing plants with useful traits in many different places, many unique local types developed. This early diversity later became very helpful. It gave breeders a base to create modern varieties for farming today.

2.2 Global dissemination and introduction pathways

The story of pineapple's global rise began during the Age of Exploration. In 1493, Christopher Columbus encountered the pineapple for the first time on the island of Guadeloupe. Struck by its vibrant flavor and unusual appearance, he brought samples back to Europe three years later (Carvalho, 2020). Though Europeans admired the fruit, the temperate climate wasn't suitable for growing it successfully- at least, not without artificial heat.

In the early 1500s, Portuguese explorers and traders started taking pineapples to places outside their original home. They brought the fruit to warm areas like West Africa, India, and Southeast Asia. These places had the right kind of weather for growing pineapples, so the plants did well there. As time passed, pineapples began to grow in more and more places. Because the soil, weather, and farming styles were different in each area, the pineapples started to change and new local types appeared. By around the 1550s, people were already growing pineapples in faraway places like India and St. Helena, a small island in the Atlantic (Carvalho, 2020; Li et al., 2022). As the Portuguese continued exploring Asia, they eventually brought the pineapple to China during the late Ming Dynasty. By the 1700s, the pineapple had become a common fruit in many tropical places. People were growing it all over Southeast Asia, in the Caribbean, and on islands in the South Pacific.

In the 1800s, new technology changed everything. Steamships and refrigeration made it possible to store pineapples longer and ship them farther. This helped turn pineapple into a valuable global crop. Around this time, Hawaii became a major center for pineapple farming. The variety 'Smooth Cayenne' was grown on a large scale, and Hawaii also built big canning factories. These factories helped pineapple enter markets all over the world.

In the 20th century, the pineapple industry grew rapidly. Countries such as Costa Rica, the Philippines, and Thailand began to grow pineapples on large-scale farms and soon became major exporters worldwide. However, this rapid expansion also brought some negative effects. The entire industry gradually became dependent on a few popular pineapple varieties. These varieties were selected because of their beautiful appearance, sweet taste, and good transportation tolerance. While these characteristics improved planting efficiency and commercialization convenience, they led to a sharp decline in pineapple genetic diversity. The highly homogenous variety structure makes pineapples more vulnerable to pests, diseases and climate change, increasing the instability and risk of agricultural production.

2.3 Major regions of pineapple genetic diversity

South America remains the core area of pineapple genetic diversity - this is not surprising, as pineapples originated here. In places like Brazil, Paraguay and their surrounding areas, a large number of wild and traditional local varieties are still preserved. These native pineapples vary greatly in shape and size, have diverse growth habits, and have good adaptability to adversity, which is extremely valuable for breeding work. Among them, some wild varieties, such as *Ananas bracteatus* and *Ananas macrodontes*, are very popular (Zhou et al., 2015; Carvalho, 2020). They have natural resistance to insects and diseases and can survive well in harsh climatic conditions.

Southeast Asia has also gradually developed into an important pineapple diversity region. Countries such as Thailand and the Philippines are not only major pineapple growers, but also have a rich variety of pineapple varieties. Over the years, local farmers have continuously selected and improved varieties based on consumer taste preferences and market demand, and gradually formed a number of types with local characteristics. Among them, well-known varieties such as Queen and Red Spanish are widely popular because of their unique flavor, long shelf life, and suitability for both fresh consumption and export (Nashima et al., 2022). In Brazil, Pérola pineapple is a representative variety of the Pernambuco group. Although it is not very common in the international market, it is still very popular in the local area, mainly because of its sweet aroma and soft sour taste, which meets the taste needs of local consumers.

Hawaii also played an important part in the history of modern pineapple farming, especially during the 1900s. The Pineapple Research Institute (PRI), based in Hawaii, became a center for new ideas and breeding work (Paull et al., 2022). PRI created better pineapple varieties that worked well for large farms and factories. Its biggest success was the 'Smooth Cayenne' type, which led the canned pineapple market for many years. Although Hawaii doesn't grow as many pineapples now, its research still matters. Now, research centers and seed banks around the world have taken over. They continue the job of saving and sharing pineapple genetic resources.

3 Genetic Structure and Classification of Pineapple Germplasm

3.1 Genetic diversity and classification criteria

When people classify pineapple varieties, they mostly look at what they can see- like how big the fruit is, whether the leaves have spines, the sugar and acid balance, the flesh color, and how much fiber is in it. Because pineapple has been grown in so many places, and for such a long time, local varieties have taken on their own shapes and traits. Different growing conditions and histories have led to some clear differences between regions, both in how the plants look and in their genetics. Right now, the most common pineapple types in commercial farming fall into four main groups: Smooth Cayenne, Queen, Red Spanish, and Perola (Figure 1). Among them, Smooth Cayenne stands out- it's grown widely and known for its big fruit, sweet taste, and soft texture with little fiber (Kinley et al., 2022).

Figure 1 Fruit and plant characteristics of three accessions of pineapple evaluated at Agriculture Research and Development Centre, Samtenling, Bhutan in 2018: (a) fruits of PV1 at maturity (left) and at green stage (right), (b) fruits of PV2 at green stage (left) and at maturity stage (right), (c) fruits of PV3 at green stage (left) and at maturity stage (right), (d) spine distribution and its density on leaf of PV1, PV2 and PV3 from top to bottom respectively, (e) plants of PV1, (f) plants of PV2, and (g) plants of PV3 (Adopted from Kinley et al., 2022)

Image caption: It illustrates the differences in fruit morphology, leaf spine density, and plant structure among three local pineapple cultivars from Bhutan (PV1, PV2, PV3). PV1 has large, brightly colored fruits with nearly spineless leaves, resembling the Smooth Cayenne type; PV2 bears medium-sized, fibrous fruits with purplish spines along the leaf margins, aligning with the Red Spanish type; PV3 produces small, aromatic, golden-yellow fruits with compact, spiny leaves, characteristic of the Queen type. The image visually highlights the taxonomic classification and potential utilization directions of the three cultivars (Adapted from Kinley et al., 2022)

One of the factors that keeps pineapple traits stable for a long time is its reproduction method. Unlike seed reproduction, farmers usually use asexual reproduction to grow pineapples. Asexual reproduction is the use of the mother plant's nutritional organs such as suckers and runners for planting. In this way, the traits of the plant can be kept consistent between generations. However, even under the premise of asexual reproduction, certain variations will occur over time. Factors such as natural mutations, cross-pollination, and artificial breeding will gradually introduce new traits. Ismail et al. (2020) used SSR molecular marker technology to analyze 65 pineapple types, revealing two major genetic groups, proving that even cultivated pineapples can maintain a high level of genetic diversity during the planting process, providing a scientific basis for future variety improvement and genetic resource management.

3.2 Molecular markers and phylogenetic relationships

Modern molecular marker technologies, like SSR, SNP and AFLP, provide powerful tools for distinguishing different types of pineapples. In the past, scientists mainly relied on external morphological characteristics, such as the shape, size or color of the fruit, to determine the differences between varieties, but now they can be analyzed directly at the DNA level. For example, SNP (single nucleotide polymorphism) markers can identify repeated fragments in DNA, thereby revealing the genetic relationship between different pineapple types. Some studies have even pointed out that today’s cultivated pineapples may be derived from multiple wild pineapple species rather than a single ancestor (Zhou et al., 2015).

AFLP (amplified fragment length polymorphism) markers are also often used to cluster pineapple types, and the resulting groups often coincide with familiar cultivar groups, such as Cayenne and Queen (Rattanathawornkiti et al., 2016). AFLP technology has the ability to construct genetic “fingerprints”, so it is widely used in variety identification, germplasm resource protection and breeding material identification.

3.3 Key germplasm groups and their characteristics

Pineapple germplasm resources mainly include commercially cultivated types, traditional local varieties (landraces) and wild species. At present, most of the pineapples grown in the global market are concentrated in a few varieties, mainly Smooth Cayenne and MD-2. These varieties are favored because they have high yields, moderate fruit size, strong transport adaptability, and are suitable for international export. However, as mentioned earlier, over-reliance on a few varieties also brings obvious disadvantages: reduced genetic diversity makes crops more vulnerable to pests and diseases (Zhao and Qin, 2018).

In contrast, traditional local varieties and wild species have richer genetic variation. These old varieties have stronger ability to adapt to adversity and have unique flavor characteristics. Varieties like Queen perform well in arid areas of Africa and are suitable for dry and hot climates; while Red Spanish, which originates from Central America, is known for its strong insect resistance. Wild species also have extremely high breeding potential. For example, *Ananas bracteatus* performs well in disease resistance (Chen et al., 2019b), and *A. macrodontes* is drought-resistant, salt-tolerant, and has strong adaptability. It provides an important genetic basis for improving the stress resistance and quality of existing commercial varieties, and is a key support for future breeding and improvement work.

In the modern breeding process, multiple molecular markers are used to conduct in-depth research on the genetic structure of these populations, and it is found that there are abundant genetic variations within these varieties. The Cayenne population has specific morphological characteristics and is classified as an independent cluster in phylogenetic analysis (Rattanathawornkiti et al., 2016). Hybrid breeding, gene introduction, and gene editing of these germplasm resources can improve the stress resistance of varieties, improve fruit quality, and enhance their adaptability to climate change.

4 Modern Pineapple Cultivars and Their Genetic Basis

4.1 Commercially important pineapple cultivars

The global pineapple industry mainly relies on several highly commercialized varieties, which are superior in fruit quality, storage resistance and processing adaptability. Among them, Smooth Cayenne was once the most widely planted variety. Its juicy flesh, sweet and sour balance, and low fiber content make it the main choice for canning and export trade. However, this variety is sensitive to a variety of diseases (such as pineapple wilt), which limits its further promotion.

In recent years, MD-2 has become the most mainstream pineapple variety in the global market. This variety was bred and promoted by Del Monte, and its current planting area has exceeded that of all other varieties. Yow et al. (2021) pointed out that compared with the traditional Smooth Cayenne, MD-2 fruits are sweeter, have a longer shelf life after harvest, and perform better in dealing with common problems such as browning of the core. Genetic studies further show that MD-2 has unexpected genetic diversity and complex genetic structure, which is an important reason for its high adaptability and wide market acceptance. The success of MD-2 not only reflects the application effect of modern molecular breeding technology in actual production, but also reflects the results of comprehensive consideration of fruit quality, storage and transportation performance and planting stability in commercial breeding.

There are also several regionally dominant varieties in Southeast Asia, Africa, and Latin America, such as Queen, which has smaller fruits but rich flavor and is mainly used for fresh consumption. Red Spanish has strong disease resistance and good transportability, and is favored by growers in the Caribbean. Pernambuco has soft, sweet flesh with low acidity and is very popular in the Brazilian market (Ali et al., 2020).

4.2 Germplasm contributions to modern varieties

Modern pineapple breeding relies heavily on germplasm resources from different regions. Traditional local varieties and wild relatives provide a crucial genetic basis for the improvement of existing commercial varieties. Zhou et al. (2015) found that wild types such as *Ananas comosus* variant *A. bracteatus* and *A. ananassoides* have passed on some valuable traits to modern cultivated varieties. These wild relatives enrich the genetic diversity of cultivated varieties, especially in terms of resistance to fungal, bacterial and viral diseases, providing key traits that were originally scarce in commercial varieties.

With the help of genetic tools such as SNP molecular markers, researchers can also trace the source of specific traits. These markers reveal the genetic composition of different pineapple strains and greatly improve the accuracy and targeting of breeding work.

For example, the whole genome map of the MD-2 variety released by Yow et al. (2021) has become one of the core reference resources for current pineapple research. The map clearly marks the gene regions associated with important traits, providing guidance for breeders, so that future pineapple breeding can be promoted more systematically and efficiently.

4.3 Genetic bottlenecks and breeding limitations

One big problem in the pineapple industry today is that people rely too much on just a few kinds of pineapples. This has caused what scientists call a “genetic bottleneck”, meaning there isn’t much genetic difference between the plants (Zhou et al., 2015). Varieties like Smooth Cayenne and MD-2 are grown almost everywhere, so the genetic makeup of pineapple crops is very limited (Zhang and Ming, 2018; Valentino et al., 2023).

Because of this, pineapples have a harder time dealing with new diseases or changes in the environment. They don’t have enough natural variety to stay strong in the face of problems (Chen et al., 2017). Breeding pineapples is also hard. They don’t pollinate themselves and are mostly grown from parts of the plant like suckers or runners. This means it takes a long time to create new types. Each new variety needs to go through many rounds of testing and selection, which is a long and tiring process.

Scientists are actively exploring how to increase genetic diversity through sexual reproduction and using molecular tools to study key gene families. For example, the ATP-binding cassette transporter (ABC) gene family has been shown in recent years to be closely related to plant stress response and disease resistance mechanisms (Chen et al., 2017).

5 The Role of Germplasm Exchange in Pineapple Breeding

5.1 Hybrid breeding and hybridization strategy

Pineapple breeding mainly relies on hybridization and genetic recombination to combine the excellent characteristics of different varieties to cultivate new varieties with high yield, high quality and strong stress resistance. For example, the EU-funded pineapple germplasm project studied the genetic structure of Ananas and Pseudananas and applied resistance screening technology to enhance the disease resistance of pineapples (Carlier et al., 2012). Molecular characterization techniques (such as restriction fragment length polymorphism (RFLP) and PCR-RFLP) facilitate the identification of genetic markers, thereby more accurately selecting target traits during hybridization.

With better tools now available, like marker-assisted selection (MAS) and genomic selection (GS), it's easier to find and select the traits breeders want. These methods save time and improve accuracy. In fact, similar approaches have worked well in other crops. For example, Bertioli et al. (2021) used wild species in peanut breeding to develop varieties that could resist disease- an effort that's helped boost food security.

5.2 Contributions of wild relatives to breeding

Wild relatives of cultivated crops are an important source of genetic diversity, providing excellent traits such as disease resistance, improved fruit quality and environmental adaptability. In pineapple breeding, *Ananas bracteatus* showed strong resistance to pineapple wilt (Fusariosis), while *Ananas macrodontes* had strong drought tolerance and salt tolerance (Qiao et al., 2021; Feng et al., 2022), and these traits can be used to improve the adaptability of modern pineapple cultivars.

Genomic tools have made this work much easier. With methods like marker discovery and trait mapping, breeders can find useful genes in wild plants and track them as they're added to commercial types. But for this to work well, the wild germplasm needs to be carefully studied and clearly recorded. As Migicovsky and Myles (2017) noted, having good genomic data on wild species is especially important for perennial crops like pineapple.

5.3 Challenges and opportunities in germplasm utilization

The sharing of germplasm resources has long been promoting the production and improvement of excellent pineapple varieties. However, there are still some practical obstacles, the most prominent of which is the legal level. Regulations on biodiversity and genetic resources are becoming increasingly stringent around the world. As more countries strengthen the management of the entry and exit of germplasm resources, the cross-border flow of seeds and plant materials has become increasingly difficult. This directly affects the ability of breeders to obtain the required genetic diversity and slows down the development of new pineapple varieties (Bertioli et al., 2021). In terms of resource protection, technologies such as in vitro preservation and cryopreservation are being widely used to preserve rare or precious germplasm resources to ensure that these genetic materials can still be used in future breeding work. Global cooperation is also becoming increasingly stronger. Institutions such as the International Plant Genetic Resources Institute (IPGRI) and the Food and Agriculture Organization of the United Nations (FAO) are promoting the establishment of global germplasm banks and encouraging the sharing of knowledge and germplasm materials (Shaw et al., 2023).

6 Impact of Germplasm Flow on Stress Tolerance

6.1 Genetic resources for abiotic stress tolerance

Some pineapple varieties from arid regions of South America and Africa have shown outstanding drought resistance (Lin and Ming, 2018). Among them, *Ananas macrodontes* is a typical example. It can grow deeper roots to obtain water from dry soil and survive well during long droughts (Zhao and Qin, 2018). At the same time, in Southeast Asia and some coastal areas of Africa, soil salinization is becoming an increasingly serious problem, which has become an important factor restricting pineapple cultivation. Studies have found that *A. bracteatus* has strong salt tolerance and its leaf epidermis is thicker, which helps to reduce water evaporation and can still maintain healthy growth in saline soils (Chen et al., 2019b). The Queen variety, which is widely grown in Southeast Asia, is resistant to high temperatures, while some traditional local varieties in South America also show moderate cold resistance.

At the molecular level, scientists are gradually revealing the genetic mechanisms of pineapple's response to drought and salt stress. Whole-genome studies have shown that the AcoCPK gene family plays an important role in regulating plant stress responses (Zhang et al., 2020). These genes have evolved over a long period of time to enhance the survival of pineapples under different climatic conditions. Interestingly, some studies have found that overexpression of the *AcWRKY31* gene may increase the sensitivity of plants to drought and salt stress, showing the complexity of plant stress response mechanisms (Huang et al., 2022; Macioszek et al., 2024).

Another key gene family is the DREB transcription factor family, which plays a core role in plant response to stress by regulating the activity of specific DNA elements. They are currently considered an important target for improving the stress tolerance of future pineapple varieties, providing a theoretical basis and technical direction for breeding new varieties that are more adaptable to drought, salinity, high temperature or low temperature environments (Chai et al., 2020).

6.2 Contributions to improved pest and pathogen resistance

Pineapple growers have long faced serious pests and diseases, with mealybugs, nematodes and root rot being the main threats to yield. Fortunately, some wild pineapple species - *Ananas bracteatu* and *Ananas ananassoides* - are naturally resistant to mealybugs. These resistance traits have been introduced into commercial breeding, and breeders hope to cultivate stronger varieties through genetic improvement, while reducing the use of pesticides and maintaining or even increasing yield levels. In the Caribbean, the Red Spanish variety is well known for its natural defense mechanism. Its thick skin and fibrous leaves are structural features that help to keep out nematodes (Charles et al., 2025). Similarly, traditional local varieties from Brazil and Colombia show strong resistance to root rot, and their genetic resources are now being used to improve the resistance of major cultivated varieties.

With the rapid development of genomics technology, breeders have more efficient tools to accelerate the process of disease-resistant breeding. Macioszek et al. (2024) pointed out that enhancing the expression of the *AcWRKY31* gene can effectively improve pineapple’s resistance to mealybugs. The plant calcium-dependent protein kinase (*CDPK*) gene has also been identified as a key regulatory factor in responding to pathogen infection and is an important target with potential in future disease-resistant breeding (Zhang et al., 2020).

7 Case Study

7.1 Identification and diversity of pineapple germplasm based on SNP markers

Globally, with the widespread planting of pineapples as economic fruit trees, countries have continuously introduced and improved cultivars, forming a complex germplasm flow network. How to accurately identify the genetic background of many pineapple varieties and clarify the relationship between different varieties is one of the basic tasks of modern breeding and resource protection.

Zhou et al. (2015) developed 58 stable SNP molecular markers for 94 pineapple materials from different sources for rapid identification of germplasm resources. The study specifically analyzed the differences between two materials HANA 96 and HANA 97 in the ‘Cayenne 7898’ group. Although the two are very similar in appearance, their flesh color is obviously different: one is white and the other is dark yellow (Figure 2). This somatic mutation was successfully identified by SNP markers, indicating that molecular methods can accurately track small variations in asexually propagated crops. This method provides a practical tool for variety management, germplasm protection and pineapple breeding.

7.2 Global germplasm flow promotes pineapple variety diversification and modern cultivation system optimization

The global exchange of pineapple germplasm resources has provided an important impetus for the cultivation of new varieties and the optimization of cultivation systems. A typical case is the study of the Japanese variety “Yugafu”. Nashima et al. (2022) used haplotype-resolved genome sequencing methods to deeply analyze the genetic background of the variety and identify key genes related to leaf morphology and flesh color. This information was used in molecular marker-assisted selection (MAS) to guide more precise breeding strategies. The study also confirmed that “Yugafu” was bred from the hybrid of the two parents “Cream pineapple” and “HI101”.

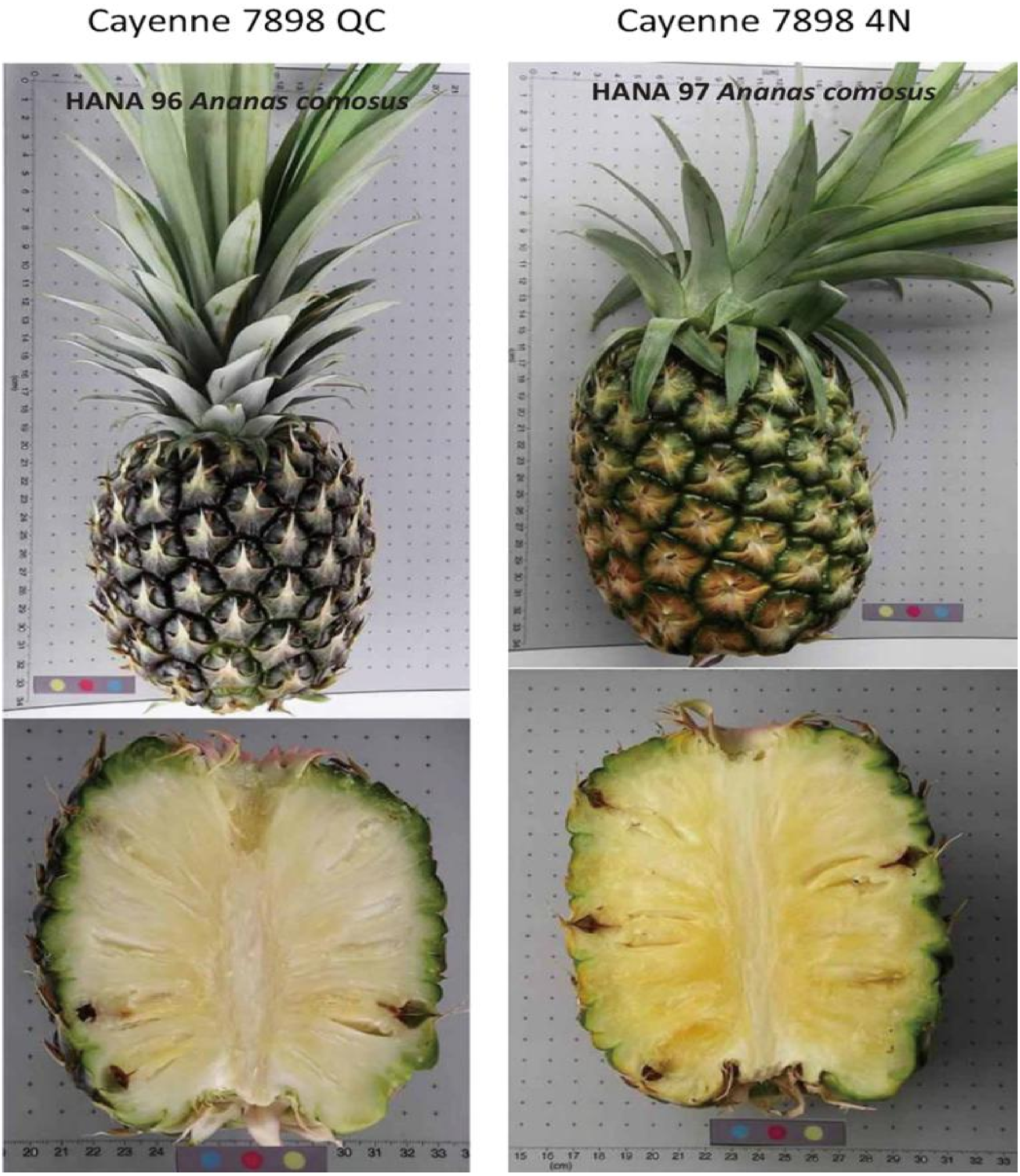

Figure 2 Phenotypic variation between somatic mutants HANA 96 and HANA 97 of the ‘Cayenne 7898’ pineapple clone. Both clones have similar fruit shape and skin color, but differ in flesh color (Adopted from Zhou et al., 2015)

Image caption: The visual difference in pineapple flesh color shown in the figure indicates that significant phenotypic variation can occur even in vegetatively propagated materials. This supports the necessity and effectiveness of using SNP markers to detect subtle genetic differences, contributing to accurate variety identification and the tracking of mutation events (Adapted from Zhou et al., 2015)

In terms of leaf margin morphology, the study found that the *AcWOX3* gene controls whether the leaves have thorns (i.e., “tubular” or “thornless” leaves). In thornless types such as Cream pineapple, due to the presence of inverted repeat sequences in the gene region, the RNA interference mechanism (RNAi) is activated, thereby inhibiting the expression of *AcWOX3*, resulting in smooth and thornless leaf margins. Under normal expression conditions, *AcWOX3* is active and the plant exhibits typical thorny leaves. In terms of flesh color, the study identified *AcCCD4* as a key gene that controls carotenoid degradation. In white-fleshed varieties, the gene is highly expressed, preventing carotenoids from accumulating, resulting in light-colored flesh. In yellow-fleshed varieties, *AcCCD4* is expressed at a low level, allowing carotenoids to accumulate, forming yellow flesh (Figure 3).

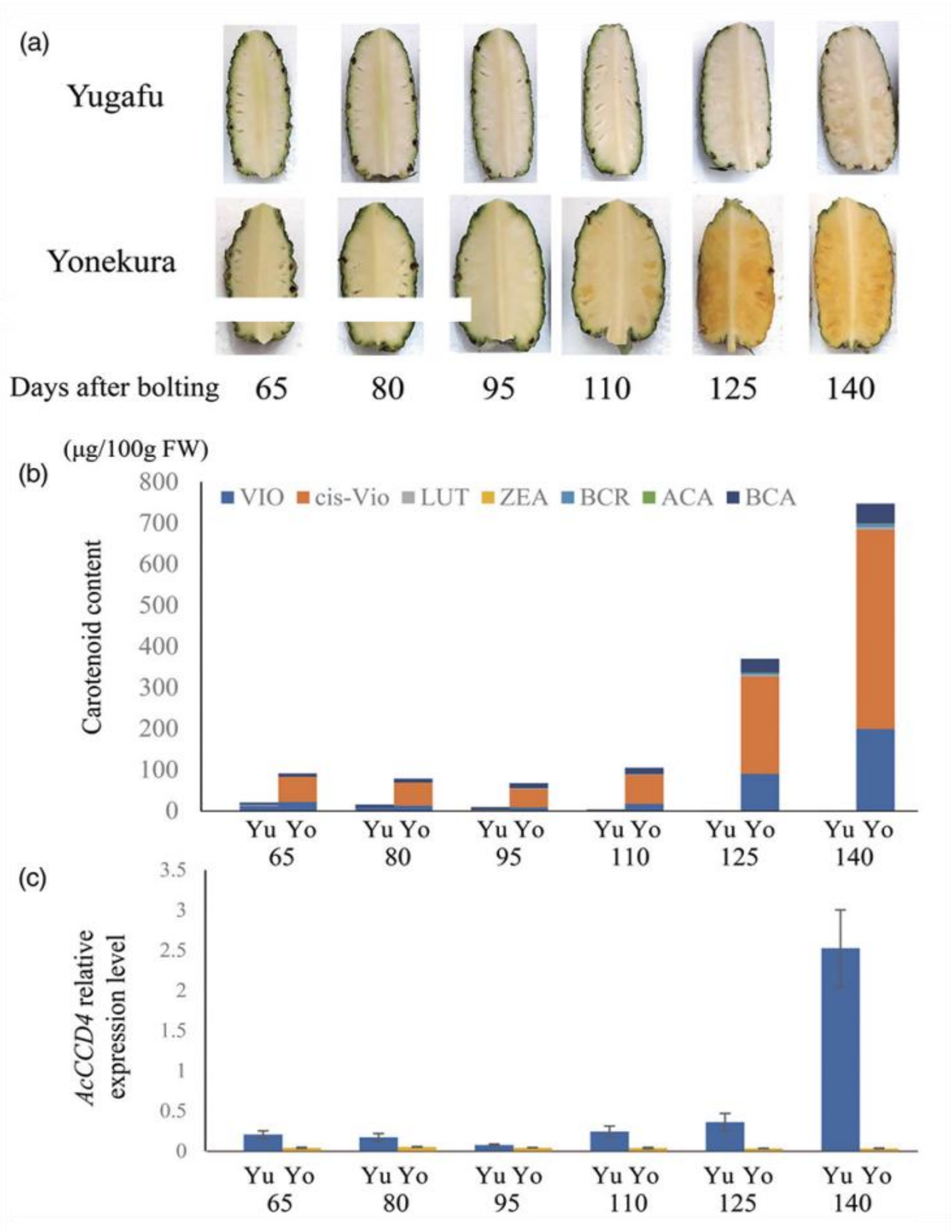

Figure 3 Carotenoid accumulation and *AcCCD4* expression during fruit ripening in ‘Yugafu’, (Yu) and ‘Yonekura’ (Yo) (Adopted from Nashima et al., 2022)

Image caption: (a) Flesh appearance. (b) Carotenoid content. (c) *AcCCD4* relative gene expression. Three biological replicates for each sample were examined to determine carotenoid quantities and conduct gene expression analysis. Error bars indicate SE. VIO, violaxanthin; cis-VIO, 9-cis-violaxanthin; LUT, lutein; ZEA, zeaxanthin; BCR, b-cryptoxanthin; ACA, acarotene; BCA, b-carotene (Adopted from Nashima et al., 2022)

This work provides practical molecular markers for modern pineapple breeding and accelerates the breeding of high-quality new varieties. More importantly, the discovery of RNAi controlling leaf shape has opened up a new path for regulating plant structural traits, which is not only applicable to pineapples, but also provides theoretical support and technical inspiration for the morphological improvement of other crops. It can be seen that the flow and cooperation of global germplasm resources are constantly driving the pineapple industry to develop in a precise, efficient and diversified direction.

8 Conservation and Sustainable Utilization of Pineapple Germplasm

8.1 In situ and ex situ conservation strategies

In situ conservation, refers to maintaining the genetic diversity of plants in their native habitats or traditional cultivation environments. However, this approach faces increasing challenges due to increasing environmental pressures and human development. To address this problem, some regions have proposed more community-participatory solutions. For example, in Cabaceiras do Paraguaçu in Bahia, Brazil, local residents have successfully achieved the goal of in situ conservation by planting traditional pineapple varieties in their own yards (Da Silva et al., 2018). This approach reduces dependence on traditional agricultural environments and also enables urban or rural residents to actively participate in the protection of germplasm diversity.

In contrast, ex situ conservation emphasizes the systematic preservation of germplasm outside its native environment. The Active Germplasm Bank (AGB), managed by the Embrapa Cassava and Fruit Research Center, a tropical crop research institution in Brazil, collects and maintains a rich variety of pineapple genetic materials (Souza et al., 2019). Ex situ conservation also includes a series of laboratory techniques, such as in vitro preservation and cryopreservation.

Da Silva et al. (2016; 2021) showed that in vitro preservation can effectively maintain the genetic stability and morphological characteristics of pineapple materials and is suitable for long-term preservation. Cryopreservation is the storage of plant materials (such as stem tips and pollen) at extremely low temperatures to achieve longer-term maintenance of biological activity. Experiments have shown that pineapple stem tips and pollen stored under ultra-low temperature conditions still have good activity and genetic stability, providing strong technical support for future germplasm utilization and recovery (Da Silva et al., 2017; Villalobos-Olivera et al., 2019).

8.2 Biotechnological approaches in germplasm conservation

Biotechnology plays an important role in the conservation of pineapple germplasm. For example, in vitro conservation technology maintains the survival rate and stability of pineapple tissue culture seedlings by optimizing culture medium conditions. Studies have found that M2 medium is the best choice for long-term preservation of pineapple germplasm resources. It can maintain high survival rate and inhibit growth rate, which is conducive to long-term storage). The application of inhibitors (such as paclobutrazol) in in vitro tissue culture can reduce the number of subcultures, thereby improving the efficiency of germplasm conservation (Canto et al., 2004).

Another important biotechnology is cryopreservation, which achieves long-term storage by freezing plant tissues to extremely low temperatures (usually liquid nitrogen temperature -196 °C). For pineapples, researchers have developed a technique called droplet-vitrification to preserve shoot apical tissues of cultivated and wild types. This method has good preservation effects and is more efficient than traditional preservation methods. It is easy to operate and has a very good survival rate after recovery (Souza et al., 2015).

More importantly, Villalobos-Olivera et al. (2021) found that pineapple plants that were cryopreserved and revived in the field performed basically the same as the untreated control group, with no significant differences in growth rate, yield or morphological characteristics. This fully verifies the safety and reliability of this method in terms of genetic stability and agricultural adaptability. Therefore, cryopreservation technology is particularly suitable for rare, endangered or genetically valuable pineapple germplasm resources, providing a solid technical guarantee for the construction and future use of the global pineapple gene bank.

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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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