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Domestication History and Adaptive Genomic Variations of Pineapple: From Wild to Cultivated Varieties

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Abstract This time, we studied the domestication process of pineapple (*Ananas comosus*) and the changes in its genes. This information helps us understand how it evolved step by step and can also help improve the quality of pineapples in the future. In the study, we focused on the changes that occurred in the genes of pineapples during domestication, especially some key mutations that can distinguish wild species from artificial species (that is, varieties grown by humans). We analyzed genomic data from different pineapple species and found signals related to domestication, such as larger fruits, more sugars, and enhanced stress resistance. We also found some interesting phenomena, such as some differences in the genetic composition between cultivated varieties, and introgression between genes. These make them more diverse. At the same time, we also found several genes that may be related to adaptability, such as those that can help pineapples resist drought or saline-alkali environments. Comparative analysis also made us see some things clearly, such as gene duplication and the disappearance of some specific genes, which may be the reasons for helping pineapples become more delicious or more resistant to the environment. Overall, our research reveals how pineapples have adapted to the environment step by step and become as delicious and easy to grow as they are now. These findings will be very helpful for future breeding and improving fruit quality and yield.

Keywords Pineapple; Domestication; Genomic variations; Adaptive evolution; Genetic diversity

1 Introduction

Pineapple (*Ananas comosus*) is one of the most important fruits in the world. Among tropical fruits, it ranks second only to bananas and mangoes (Zhou et al., 2015). Because it is grown and eaten in large quantities, especially in tropical regions, pineapple has high economic value (Ming et al., 2015). People have been growing pineapples for more than 6 000 years. There are many varieties on the market, such as "Smooth Cayenne", which is currently one of the most widely grown varieties in the world (Sanewski, 2018). However, wild genes are rarely introduced during modern breeding, so the genetic diversity of cultivated varieties is mostly accumulated through somatic mutations (Zhou et al., 2015; Sanewski, 2018).

Why do we want to study the domestication of pineapples and the changes in their genes ? There are several reasons. For example, if we can understand the genetic basis of traits such as fiber content, sugar accumulation, and fruit ripening, we can breed higher-yield and better-quality varieties (Chen et al., 2019). For another example, in-depth research on pineapple's crassulacean acid metabolism (CAM) will help us understand how plants adapt to arid or semi-arid environments, which is very important for saving agricultural water (Ming et al., 2015; Zhu and Ming, 2019).

In addition, genomic research also tells us that sexual reproduction and asexual reproduction actually coexist during the domestication of pineapples. In other words, pineapples are not domesticated in one step like some clonal crops, but have undergone a more complex process (VanBuren, 2018; Chen et al., 2019).

The goal of this study is to understand how pineapples were domesticated step by step. We are particularly interested in the genetic differences between wild and artificial species. Next, we will analyze the possible effects of these genetic changes. The article first briefly reviews the domestication history of pineapples, then discusses some of the key genetic variations and adaptation mechanisms currently known, and finally sees whether these findings can help with future breeding and how to use them in practice to make breeding more efficient.

2 Origin and Early Domestication of Pineapple

2.1 Wild ancestors and their geographical distribution

It is now generally believed that the genus Ananas, including the cultivated pineapples we eat, originated from South America. Wild species such as *Ananas comosus* var. *microstachys* and *Ananas parguazensis* are mainly distributed in the northern Amazon region (d'Eeckenbrugge et al., 2018; VanBuren, 2018). These wild pineapples help us better understand the genetic characteristics of pineapples and how they evolved. Based on the distribution of these ancestral species, Guyana is likely to be the first place where pineapples were domesticated. The western Amazon may be another center, where pineapples have undergone genetic recombination brought about by sexual reproduction (d'Eeckenbrugge et al., 2018).

2.2 History of early cultivation by indigenous peoples

Indigenous peoples in South America actually started to grow pineapples very early. According to archaeological and linguistic studies, they have been growing and eating pineapples in the Amazon basin and the coast of Peru for more than 3 000 years. In Central America, there is also a history of cultivation of about 2 500 years (d'Eeckenbrugge et al., 2018). These early cultivation activities show that pineapple was an important crop in the community at that time.

2.3 Archaeological and historical evidence of pineapple domestication

Many archaeological discoveries and literature have proved that the domestication process of pineapple began as early as 6 000 years ago. Varieties such as "Smooth Cayenne", which are still common today, were slowly cultivated at that time (Sanewski, 2018). In the process of pineapple domestication, sexual reproduction and asexual reproduction actually work together. This is different from our general view that clonal crops are "domesticated in one step" (VanBuren, 2018; Chen et al., 2019). In addition, historical data also mentioned that in the 16th century, Portuguese merchants brought pineapples from Brazil to tropical regions in Asia and Africa. This further shows that pineapples were widely planted and had a great influence at that time (d'Eeckenbrugge et al., 2018).

3 Morphological and Physiological Changes During Domestication

3.1 Key phenotypic differences between wild and cultivated varieties

During the process of being domesticated by humans, the appearance and characteristics of pineapples have changed a lot. Compared with wild species, cultivated pineapples are usually larger, sweeter, and have fewer seeds. These characteristics were deliberately selected to make pineapples more delicious and easier to sell (Figure 1) (d'Eeckenbrugge et al., 2018; Chen et al., 2019). Most cultivated pineapples are now grown asexually. This ensures that good characteristics are passed down from generation to generation and are not easy to change (d'Eeckenbrugge et al., 2018).

3.2 Adaptability to different environments

The reason why pineapples can grow in various environments, especially in arid areas, is mainly because of its special photosynthesis method. It uses a method called "crassulacean acid metabolism" (CAM). This method can save more water, so pineapples can grow well in semi-arid areas (Ming et al., 2015; Zhu and Ming, 2019). CAM photosynthesis is a "transformation" of the original C3 mode, which helps pineapples continue to grow even when water is scarce (Ming et al., 2015). In addition, in cultivated pineapples, the expression of some genes that control water transport (such as aquaporin genes) is different from that of wild species. These genes not only affect fruit development, but also allow pineapples to better adapt to different climates (Zhu and Ming, 2019).

4 Genomic Insights into Pineapple Domestication

4.1 Overview of genomic studies on pineapple

Recently, scientists have done a lot of research on the pineapple genome. These studies have given us a better understanding of how pineapples were "domesticated" by humans. They measured the genes of several pineapple varieties, including *Ananas comosus* var. *bracteatus* and other common cultivated varieties. The study found that some traits, such as pineapple fiber, sweetness, and ripening, are related to specific genes (Figure 1) (Chen et al., 2019). The study also pointed out that when people select seeds, whether through sexual reproduction or asexual reproduction, they have a great influence on pineapple traits. This also shows that the domestication process of pineapples cannot be completed in one step (VanBuren, 2018).

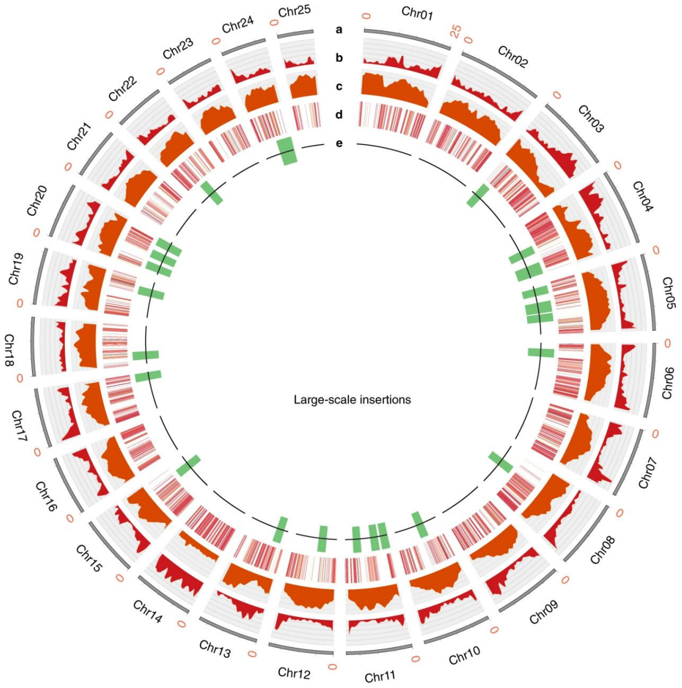

Figure 1 Distribution of genomic features along the pineapple CB5 genome (Adopted from Chen et al., 2019)

4.2 Important genetic markers in domestication

Researchers have found many single nucleotide polymorphism (SNP) markers. They are particularly useful in understanding the genetic diversity and domestication process of pineapples. These markers show that there are many duplications in the genes of cultivated varieties, as well as many somatic mutations. This shows that many changes in the appearance or traits of pineapples are actually due to these mutations, rather than complex breeding work (Zhou et al., 2015). In addition, scientists have also found genes related to “self-incompatibility”, which may also be selected during the domestication process (Chen et al., 2019).

4.3 Genetic comparison of wild species and cultivated species

By comparing different genomes, the study found that the genetic diversity of cultivated pineapples is actually quite rich. This is because their ancestors came from different wild species and also experienced hybridization (VanBuren, 2018). However, although there are many types of cultivated pineapples, the genetic differences between them are not large. In other words, domestication has not reduced their genetic diversity too much (Gaut et al., 2018). This diversity may be related to the mixing of genes from wild species and the history of pineapple spread in different places (d’Eeckenbrugge et al., 2018).

5 Adaptive Genomic Variations in Pineapple

5.1 Key genes involved in stress tolerance

Pineapple can adapt to drought, saline-alkali land and pests and diseases, which is related to some of its special gene mutations. Studies have found that there are 54 genes called WRKY in the pineapple genome. These genes will behave differently when facing various environmental pressures (Xie et al., 2018). They play a big role in improving pineapple's ability to adapt to difficult environments. Therefore, these genes are critical when breeding stress-resistant pineapple varieties.

5.2 Genetic basis of CAM photosynthesis

Pineapple is a plant that uses CAM photosynthesis. Unlike ordinary C3 photosynthesis, CAM photosynthesis allows pineapples to live well in places with little water. Scientists have found that pineapples do not change the way of photosynthesis by adding new genes, but by changing the use of existing genes, that is, changing their functions (Ming et al., 2015). This method allows pineapples to save water, which is very important for arid areas (Ming et al., 2015; Zhu and Ming, 2019).

5.3 How did pineapple’s disease resistance evolve?

Pineapple's disease resistance also evolved over a long period of time. Some genes were gradually “eliminated” because they were not helpful in fighting diseases, and some repeated gene structures also appeared. For example, someone found a repeated “protease inhibitor” gene that may help pineapples resist pests (Chen et al., 2019). In addition, there are many types of genes such as WRKY, and there are complex interactions between them, which may also be one of the reasons why pineapples have enhanced disease resistance (Xie et al., 2018).

6 Population Genomics and Phylogenetics of Pineapple Varieties

6.1 Genetic relationships among different pineapple cultivars

The genes of different pineapple varieties are quite different. Studies have found that there are two species and five variants in the genus Anine, and there is a clear genetic separation between them. But in many cultivated varieties, most of the differences in appearance and traits are due to somatic mutations, not the result of long-term breeding (VanBuren, 2018). Common varieties such as “Smooth Cayenne” and “Queen” have traces of ancient genes in their genes, as well as new genes that have been mixed in recently. This shows that the evolution and domestication process of pineapples is quite complicated (Chen et al., 2019).

6.2 New discoveries brought by whole genome research

By measuring the whole genome of pineapples, such as the two varieties “F153” and “MD2”, scientists found that they did not experience ancient whole genome duplication events like some plants (Ming et al., 2015). In other words, the genes of pineapples are not changed through large-scale duplication. These studies also found many changes in gene structure that are useful for domestication, as well as some genes that may have been “selected”, which played a significant role in pineapple's adaptation to the environment (Figure 2) (Chen et al., 2019; Feng et al., 2024).

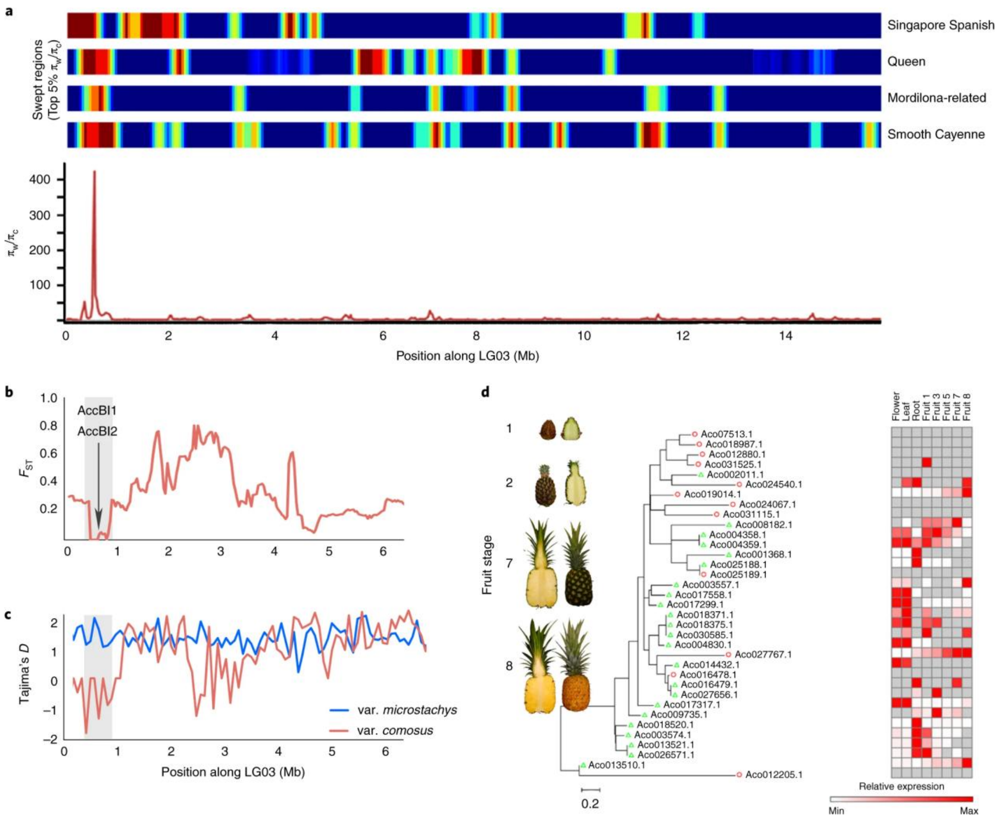

Figure 2 Putative domestication sweep around a bromelain inhibitor gene that helps control fruit ripening (Adopted from Chen et al., 2019)

6.3 Gene exchange and hybridization in pineapple domestication

Gene flow and hybridization are common in the evolution of pineapples. There have been a lot of mixing and hybridization between different pineapple species (VanBuren, 2018). Wild pineapples like *A. macrodontes* have also flowed into current cultivated varieties. This “hybridization” makes pineapple genes richer (d’Eeckenbrugge et al., 2018). These hybridization processes have helped people breed better pineapples, such as varieties with sweeter fruits and fewer diseases and pests.

7 Impact of Domestication on Pineapple Metabolomics and Flavor Compounds

7.1 Changes in sugar metabolism and fruit sweetness

Domestication has caused significant changes in the sugar metabolism of pineapples. Simply put, the fruit has become sweeter, and sweetness is the key to whether people buy it or not. Researchers analyzed the genes of different pineapple varieties and found that the fruit becomes sweeter because sugar accumulates in the fruit. This sugar accumulation is related to the fruit ripening process and directly affects the sweetness (Chen et al., 2019; Feng et al., 2024). However, the genetic combination of pineapples is very complex, and its “heterozygosity” is very high. This brings diversity, but also brings a lot of difficulties to breeding work, such as it is not easy to control the sugar content (Sanewski, 2018).

7.2 Genetic basis of aroma

The aroma is also very important for whether pineapples are delicious. These aromas come from a class of things called “volatile compounds”. Studies have found that the production of these compounds is related to certain specific genes. Scientists have found these key genes through genomic research (VanBuren, 2018; Chen et al., 2019). If you want to make pineapples more fragrant, these studies are particularly helpful for breeding.

7.3 The balance between flavor and nutrition

Although domestication has made pineapples sweeter and more fragrant, it has also brought some “side effects”. When people choose sweet and fragrant varieties, they may ignore other nutrients that are good for the body. As a result, some originally beneficial substances have become less in the newly cultivated varieties (d’Eeckenbrugge et al., 2018; VanBuren, 2018). Therefore, when breeding in the future, we must consider not only the taste, but also pay attention to retaining the nutrition.

8 Case Study: Genomic and Agronomic Improvement of a Pineapple Cultivar

Pineapple (*Ananas comosus*) is one of the common tropical fruits, and humans have been cultivating it for a long time. It originally came from South America and was domesticated about 6,000 years ago. Old varieties such as "Smooth Cayenne" are still widely planted in many countries (Sanewski, 2018). In the process of domesticating it, people used both sexual and asexual reproduction. And studies have found that the changes in pineapple traits are mainly the result of genetic diversity and somatic mutations (Zhou et al., 2015; VanBuren, 2018).

Later, scientists began to study the genome of pineapples. They measured the genes of many varieties, such as “MD2” and “Queen”, and found that there are many important differences in the genes of these pineapples. These differences affect the sugar content, ripening speed, and fiber content of the fruit (Ming et al., 2015; Chen et al., 2019). In addition, these genetic studies have helped us understand an interesting phenomenon: pineapples have switched from C3 photosynthesis to CAM photosynthesis. This transformation makes it more water-efficient and easier to grow in dry areas (Ming et al., 2015; Zhu and Ming, 2019).

“MD2” is a typical example of improved pineapple varieties. It is sweet and low in acid, and its taste is very popular. In order to make it better, scientists have made many breeding and genetic improvements to it (Chen et al., 2019; Feng et al., 2024). During the breeding process of this variety, many different gene backgrounds were added. The main method is breeding through somatic mutation and selection of good traits. This is done to cope with its complex gene combination and some repeated genetic content (Zhou et al., 2015; Sanewski, 2018).

These research results are very helpful for future pineapple breeding. Now we have more comprehensive genetic data, as well as new breeding technologies such as marker-assisted selection and gene editing (Dhurve et al., 2021;

Feng et al., 2024). These tools can enable us to breed better pineapples that not only taste good, but are also more disease-resistant and adaptable to more complex weather. This way, pineapples can be grown more stably, profitably, and sustainably around the world.

9 Challenges and Future Directions in Pineapple Breeding

9.1 Genetic bottlenecks and loss of diversity

During the domestication and breeding process of pineapples, a lot of “heterozygosity” has emerged, that is, the genes are very inconsistent. Although this situation can bring some diversity, it also makes breeding more difficult (Sanewski, 2018; VanBuren, 2018). At present, there are very few wild genes introduced into modern pineapple varieties, which makes its genetic base very narrow. It becomes difficult to add new traits or improve existing characteristics. This problem is called "genetic bottleneck", which is a major obstacle in breeding work.

9.2 Improving pineapple traits with CRISPR and other tools

Now there are some new technologies, such as CRISPR and molecular marker-assisted breeding, which can help us solve the genetic problems mentioned above. These tools can directly modify the genes of pineapples and accurately add desired traits, such as making the fruit sweeter or enhancing disease resistance. Moreover, these methods do not require repeated hybridization and are much more efficient (Zhou et al., 2015; Sanewski, 2018). At the same time, scientists have also established a complete reference genome, which is like a “gene map” that can help us find the areas that need to be modified more accurately (Feng et al., 2024).

9.3 Breeding strategies for climate change and disease

Now, climate change has affected agriculture. In order to make pineapples grow well in various climates, breeding goals have also begun to focus on “climate adaptability” and “disease resistance”. One way is to find good genes that can still be used from wild pineapples and old varieties. Another way is to use genomic technology to screen out disease-resistant traits and then use them in new varieties (Ming et al., 2015; Zhu and Ming, 2019). In addition, pineapples themselves have a special photosynthesis method called CAM, which can save more water. Scientists hope to make this ability work better through genetic adjustment (Ming et al., 2015).

10 Conclusion and Perspectives

We are now learning more and more about the pineapple genome. These studies tell us one thing: the domestication process of pineapple is much more complicated than we originally thought. It not only relies on sexual reproduction (that is, breeding in the traditional sense), but also makes extensive use of asexual reproduction (such as propagation by rhizomes or cuttings). These two methods together determine the appearance of pineapples today.

By analyzing genes, scientists have discovered some particularly important variations. These variations may be related to the sweetness, fragrance, ripening time, fiber content, and heat and drought resistance of the fruit. In other words, when people grow pineapples, they inadvertently “select” these good traits. Through genome research, we can look back and see: which genes have changed, why they have changed, and what results these changes have brought.

Next, the research on the pineapple genome can be further deepened. For example, we still need to figure out which genes control fruit quality and which are related to disease and insect resistance, high temperature resistance, and water conservation. These are all of particular concern in breeding. At the same time, gene editing technologies such as CRISPR are also developing rapidly, which allows us to modify genes more accurately without spending many years on generation after generation. This could greatly speed up the process of breeding new varieties.

However, to breed better, we need a larger genetic database. Although there is genetic data for some common varieties, such as “MD2” and “Queen”, it is still not enough. If more wild species and local varieties can be sequenced, more useful genetic information can be found. This will not only help us breed, but also help protect the diversity of varieties.

Finally, the results of these genetic studies are not just to make pineapples sweeter and more delicious. They can also help us solve bigger problems, such as challenges such as climate change, water shortages and increased pests and diseases. We can use this knowledge to breed stronger and more adaptable varieties to new environments. For example, improving water use efficiency can make pineapples grow in arid areas; enhancing disease resistance can reduce the use of pesticides. Doing so will not only benefit agricultural production itself, but also promote more environmentally friendly and sustainable agricultural development.

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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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