



# Current status of pineapple breeding, industrial development, and genetics in China

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Received: 7 June 2021 / Accepted: 22 April 2022 / Published online: 1 June 2022  
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**Abstract** Pineapple is the most important economic plant in the family Bromeliaceae and the third-most economically important tropical fruit in the world. It has become an important tropical fruit in Guangdong, Hainan, and Guangxi, which are suitable areas for its cultivation. However, modern and well-organized breeding systems have not yet been established for pineapple. In this review, we describe the current status of the geographical distribution, industrial development, and breeding of pineapple in China. The current status of pineapple breeding is introduced, including traditional breeding methods, such as crossbreeding, mutagenesis breeding, and biotechnology breeding, combining cell engineering and

gene engineering. In addition, the research progress on assisted breeding technology based on genetic map construction and molecular marker development is presented. New challenges and perspectives for obtaining high fruit quality are discussed in the context of breeding programs for pineapple.

**Keyword** Pineapple · Industry development · Germplasm resources · Breeding technology

## Introduction

Pineapple (*Ananas comosus* (L.) Merr.) is a perennial monocotyledonous herbaceous fruit tree that is found in almost all tropical and subtropical areas of the world, ranking third in terms of economic production behind banana and citrus. Pineapple originated in the region between 10 degrees north to 10° south and 55–75° west; this region includes northwestern and eastern Brazil, Colombia, Guyana, and Venezuela (Coppens d'Eeckenbrugge et al. 1997). Columbus was the first westerner to discover pineapple when he discovered it on the island of Guadeloupe in 1493. By then, however, pineapples were already widespread in tropical America, and several native varieties had been domesticated (Collin 1949). Pineapples were introduced into Europe in the 16th century and to the tropical and subtropical areas of Asia and Africa in the eighteenth century (Collins 1949).

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At present, there are about 90 countries and regions worldwide where pineapples are cultivated. The total global area of pineapple cultivation exceeds 400,000 hectares and is mainly distributed in Asia, America, and Africa. The top 10 pineapple producers are Thailand, the Philippines, China, Brazil, India, Nigeria, Costa Rica, Mexico, Indonesia, and Kenya, and their production accounts for approximately 73% of the global total pineapple output. In the global tropical fruit trade, pineapple is one of the most active varieties, with an annual trade volume of more than 2.5 billion US dollars.

The pineapple industry plays an important role in promoting the economy of tropical and subtropical areas in China, and so the demand for different pineapple varieties is becoming increasingly urgent. Breeding and genetic studies of tropical fruits are limited compared with those of temperate fruit crops, as most improvements have originated from the selection of chance seedlings, open-pollinated seedlings, or mutations, although crossbreeding by controlled pollination has been carried out in pineapple (Ogata et al. 2016). However, pineapple has a long breeding cycle due to its high heterozygosity and self-incompatibility, among other factors. We describe the current status of pineapple breeding and related research on pineapple cultivated and consumed in China. We focus on the following: (1) the current position of the pineapple industry in China, including the production area, distribution, and main cultivars; (2) the germplasm resource collection, varieties, and breeding methods of pineapple; and (3) aspects relating to the genetics, genomics, and biotechnology.

### Geographical distribution of pineapple in China

Pineapples were seen growing in China in 1594 (Joy and Anjana 2016) and were first introduced to Macao by the Portuguese, and then to Taiwan, Guangxi, Guangdong, Fujian, Hainan, and other southern regions of China. A small number of pineapples were also cultivated in southern Yunnan and Guizhou. With a history of nearly 400 years, pineapples have become one of the most distinctive and competitive tropical fruit varieties in the tropical and subtropical areas of China.

Pineapple is a typical tropical and subtropical fruit that requires a warm growth environment. It grows

best at an average temperature of 24–27 °C per year. It can grow in temperatures of 15–40 °C, but below 15 °C growth is slow, and it largely stops at temperatures below 10 °C. The critical temperature at which cold damage occurs is 5 °C. Deep soils with a light clay and sandy loam texture that are well drained and within a pH range of 5.0–5.5 are preferred. Pineapple production areas that meet the above natural ecological conditions constitute suitable areas for commercial pineapple production.

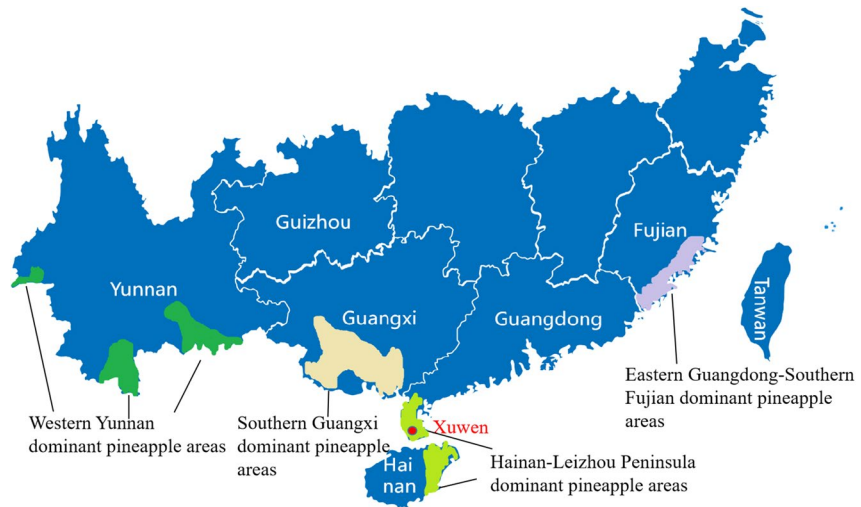
The pineapple production areas in China are mainly concentrated in Guangdong, Hainan, Yunnan, Guangxi, and Fujian, which are located on both sides of the Tropic of Cancer. There are four dominant pineapple cultivation areas: Hainan–Leizhou Peninsula, Southern Guangxi, Eastern Guangdong–Southern Fujian, and Western Yunnan (Fig. 1). The cultivation area is mainly concentrated in Guangdong and Hainan provinces, and Xuwen County in Guangdong Province is the largest pineapple planting area in China. The annual average temperature in Xuwen is 23 °C, and the winter temperature is 10–24 °C, which is suitable for pineapple production.

### Development status of the pineapple industry in China

In 2016, China ranked fourth in terms of pineapple cultivation area and sixth in terms of yield worldwide. According to statistics from the South Asia Office of the Ministry of Agriculture and Rural Affairs in 2017, there are approximately 670,000 hectares of pineapples in China, with a total annual output of 1.67 million tons and a total output value of \$456 million. The imported pineapple products in 2017 amounted to 168,500 tons, worth \$170 million, whereas 29,000 tons worth \$32.98 million were exported.

The proportion of provincial pineapple output relative to the national output for the five main provinces is 60.75% for Guangdong, 23.62% for Hainan, 7.63% for Guangxi, 4.40% for Fujian, and 3.60% for Yunnan. These data were obtained from the South Asia Office of the Ministry of Agriculture and Rural Affairs. ‘Comte de Paris’ (Philippine species) is the main cultivar planted in spring and summer, and the main fresh fruit production areas include the southeast, east and north of Hainan Island, the south of Leizhou Peninsula, and Hekou County in Yunnan

**Fig. 1** Schematic diagram of the layout of the dominant pineapple areas. Dark green areas represent Western Yunnan dominant pineapple cultivation areas, yellow areas represent Southern Guangxi dominant pineapple cultivation areas, light green areas represent Hainan–Leizhou Peninsula dominant pineapple cultivation areas, and purple areas represent Eastern Guangdong–Southern Fujian dominant pineapple cultivation areas.



Province. ‘Sarawak’, belonging to the Cayenne group, is the main fresh fruit pineapple planted in the autumn in southern Fujian, eastern Guangdong, southern Guangxi and Xishuangbanna, and Dehong in southwestern Yunnan. The main pineapple producing areas in China produce pineapple for canning, juicing, and other processing purposes using different varieties and planting methods, and the harvest period is from March to November.

Guangdong is the largest pineapple production province in China, with an area of more than 40,000 hectares. Xuwen County in Zhanjiang city is the leading county for pineapple production in China. Xuwen County alone cultivates more than 20,000 hectares of pineapple, with an annual output of more than 700,000 tons and an output value of \$210 million. The main cultivated pineapple varieties in Xuwen County are ‘Comte de Paris’ and ‘Cayenne’. In addition, Tainung No. 11, Tainung No. 17, and Yellow Mauritius are cultivated in Hainan–Leizhou Peninsula, southern Guangxi, and eastern and central Guangdong-south Fujian (Deng et al. 2018).

The main products of the pineapple trade in China are fresh or dried pineapple, preserved pineapple, canned pineapple, and pineapple juice (Jin 2016). However, pineapple is sold in the domestic market mainly as a fresh fruit, with fewer processed products sold locally. The pineapple industry in China has gone through five major stages: steady development, slow decline, rapid growth, fluctuating growth, and slow growth (Liu and Liu 2017).

### Collection and preservation of germplasm resources

In order to meet breeding and research requirements, many countries ascribe great importance to the collection of pineapple germplasm resources. The world’s leading research institutes for pineapple breeding include the Empresa Brasileira de Pesquisas Agropecuarias/Centro Nacional de Pesquisas de Mandioca e Fruticultura (EMBRAPA/CNPMF) in Cruz das Almas, Brazil, the Centro Internacional de la Recherche Agricole–Département Productions Fruitières et Horticoles (CIRAD–FLHOR) in Martinique, the Pineapple Research Institute (PRI) in Hawaii, and the Taiwan Agricultural Research Institute.

By 2005, CIRAD had collected more than 600 pineapple germplasm materials, each of which have data on their origin, plant traits, and agronomic traits (Harry et al. 2005). Five hundred germplasm materials were collected by the Pineapple Gene Bank of CNPMF in Brazil (Ferreira and Cabral 1993). These collections have been partially characterized with morphological descriptors (Coppens d’Eeckenbrugge et al. 1997; Ferreira and Cabral 1993; Horry et al. 2005; Paz et al. 2005). In addition, other countries, such as Mexico, Japan, and China, have collected germplasm resources. For example, the Pineapple Germplasm Bank in Mexico has a collection of all of the cultivated species in the country, as well as pineapple germplasm collections from Hawaii, Cote d’Ivoire, and Latin America (Paz et al. 2005).

The early introduction of pineapples into China was from Southeast Asia for sporadic cultivation. In the early twentieth century, enterprises, research institutions, and the government began to collect pineapples from abroad on a large scale. Taiwan has done the most systematic and continuous work in pineapple breeding, and its main research institutions include the Chiayi Agricultural Experiment Station, Taiwan Agricultural Research Institute, and the Taiwan Pineapple Association. On the mainland, in the 1950s, the South China Agricultural University (SCAU) and the Institute of Fruit Tree Research of Guangdong Academy of Agricultural Sciences (IFTR) began crossbreeding and introducing pineapple varieties. In recent years, the South Subtropical Crop Research Institute of the Chinese Academy of Tropical Agricultural Sciences (SSCRI, CATAS), FTRI, and Tropical Crops Genetic Resource of Chinese Academy of Tropical Agricultural Sciences (TCGR, CATAS) have introduced, collected, and preserved various pineapple germplasm resources. Among them, 130 pineapple germplasm resources were preserved in the National Field Genebank for Tropical Fruit (Zhanjiang) in the SSCRI. The South China Agricultural University collected and preserved all of the seven species of *Ananas* and 28 species of other genera of Bromeliaceae. Some pineapple germplasm resources in China have been screened and evaluated.

## Overview and trends of pineapple breeding technology

### Breeding history and major global cultivars

There are more than 100 cultivars of pineapple worldwide, which are divided into five categories according to their economic characters: the Cayenne group, Queen group, Spanish group, Abacaxi group, and Maipure group. The three most economically valuable traditional pineapple cultivars worldwide are ‘Cayenne’, ‘Singapore Spanish’ and ‘Queen’ (Coppens d’Eeckenbrugge et al. 1997), while three others (‘Red Spanish’, ‘Pérola’, and ‘Manzana’) are locally grown in their native markets (Coppens d’Eeckenbrugge et al. 1997). Smooth Cayenne has become the most important cultivar due to its high yield potential and good fresh fruit processing characteristics.

The first pineapple breeding program was launched in Florida, USA, with the aim of obtaining varieties more suitable for local conditions and with better fruit quality. Subsequently, pineapple breeding programs were launched in Hawaii (USA), South Africa, India, Malaysia, Cote d’Ivoire, Brazil, Japan, and other countries (Coppens d’Eeckenbrugge et al. 1997; Shoda 2011; Ogata et al. 2016; Joy and Anjana 2016). The primary objective of these breeding programs is the further breeding of ‘Smooth Cayenne’. However, the global progress on pineapple breeding programs has been very slow (Soneiji and Rao 2009). So far, no country has been able to breed a new processing-type variety with comprehensive traits beyond those of ‘Smooth Cayenne’, and the global pineapple processing industry still relies on ‘Smooth Cayenne’. With the development of the fresh fruit market, fruit quality has become an increasingly important feature. Therefore, the objectives of most pineapple breeding programs have gradually changed from high yield and easy processing to high-quality fresh fruit.

Self-incompatibility is one of the characteristics of pineapple cultivars. The main conventional breeding method of pineapple is hybridization to obtain hybrid offspring. The most successful pineapple breeding program was carried out by the Hawaiian Pineapple Research Institute (PRI), with the aim of developing alternative varieties of Smooth Cayenne for fresh food and processing (Williams and Fleisch 1992). MD-2 (PRI hybrid 73–114) with Smooth Cayenne as a parent, generated by hybrid breeding, is among the most important fresh pineapple varieties in the world and has a comparable yield and a good sugar profile to balance acid during the winter months (Joy and Anjana 2016). The hybrids ‘BRS Vitoria’ and ‘BRS Imperial’ bred by the EMBRAPA research center in Brazil have strong *Fusarium* resistance and fertility. ‘Josapind’, the parent of ‘Spain’ and ‘Smooth Cayenne’ in Malaysia, has good fresh characteristics and a strong resistance to black heart disease (Bartholomew et al. 2010; Paull et al. 2016). Several new varieties have also been developed in other countries with pineapple breeding programs, including Japan’s ‘Okinou P17’, ‘Soft Touch’, ‘Gold Barrel’ and ‘Julio Star’ (Ikemiya et al. 1984; Ogata et al. 2016), of which ‘Okinou P17’, the newest cultivar produced in 2015, is an excellent high-sugar variety (Ogata et al. 2016). In addition, new cultivars, including ‘Aus Jubilee’, ‘Aus Carnival’ and ‘Aus Festival’, were bred in

Australia (Bartholomew et al. 2010; Sanewski 2014), as well as ‘Imperial’ in Brazil (Bartholomew et al. 2010; Cabral and de Matos 2009).

#### The major cultivars grown in China

The pineapple industry in China was developed based on the introduction of foreign varietal resources. Five pineapple varieties, including Smooth Cayenne, Queen, Spain, Pernambuco, and Perolella, were introduced and are cultivated in mainland China. ‘Comte de Paris’ (Philippines) (mainly used for fresh fruit) comprises approximately 80% of the main pineapple varieties in China, and the remaining 20% includes Sarawak, mainly as a processing type of variety, ‘Yellow Mauritius’ (Taiwanese species), and other traditional varieties (Shi et al. 2011).

Although these varieties have the advantages of strong resistance and wide adaptability, long-term asexual reproduction and the application of scale have resulted in quality degradation and poor commodity value of the fruits relating to faults, quality, and appearance aspects, resulting in the lack of a competitive advantage compared with ‘MD-2’—a Tainung series that was the main cultivar in the international market in recent years. The Taiwan Agricultural Research Institute has made outstanding achievements in pineapple crossbreeding, successively breeding and popularizing the Tainung series: Tainung No. 1–8, No. 11, No. 13, and No. 16–19 (Xu and Yang 2007). The mainland has introduced a series of Taiwanese varieties, mainly including Tainung No. 11 (perfume pineapple), No. 16 (sweet honey), and No. 17 (gold diamond), among others (Table 1). After more than 10 years of domestication and breeding, these varieties have been promoted in the west of Hainan Province. In 2009, the SSCRI introduced ‘MD-2’ seedlings from the Philippines. After propagation by tissue culture, a large number of seedlings were planted starting in 2011–2013 (Sun et al. 2014). At present, ‘MD-2’ is widely cultivated in Guangdong and Hainan.

The breeding progress in mainland China is relatively slow and is carried out mainly with the support of government projects. Few new pineapple varieties are selected and bred, and local governments have cultivated their own varieties or excellent lines. In recent years, some pineapple varieties have passed examination and approval in mainland China. The

57–236 pineapple cultivated by the IFTR and SCAU and later approved as ‘Yue crispy’ pineapple is the first hybrid pineapple cultivar selected and bred in mainland China (Liu et al. 2006) (Table 1). Another new cultivar was crossbred and named ‘Yuetong’ by the IFTR, which has a large fruit, bright color, and sweet and juicy flesh and is an excellent variety with good fresh food and processing characteristics. The Horticultural Research Institute of Guangxi Academy of Agricultural Sciences (HRI, GAAS) found a single plant bud mutation of the pineapple variety ‘Comte de Paris’ with excellent variation (Table 1). After clonal breeding and systematic observation and evaluation, it obtained variety rights in 2014 and was named ‘Jin Xiang pineapple’; the fruit eye is large and flat, the conical protrusion is not as obvious as that in ‘Comte de Paris’, the mature fruit skin is dark yellow, the flesh is yellow, the texture is crisp, and there is little fiber (Wang et al. 2016).

In terms of introduction and breeding, Guangdong introduced and bred ‘Yue yin ao card’ in 2010. In 2013, the imported cultivars Tainung No. 11 and Tainung No. 16 were identified in Hainan Province, and in 2014, the imported cultivar Tainung No. 16 was approved in Guangxi. Other institutes have also selected and bred certain varieties, such as Minnung No. 1 bred by the Fujian Academy of Agricultural Sciences and 4312 bred by the GAAS; however, production eventually failed due to various reasons.

#### Breeding objectives in China

The objectives of pineapple breeding are to develop high-yielding and disease-resistant cultivars that are especially resistant to pests and diseases, heart rot, and root rot. For fresh fruits, the aim is to develop cultivars suitable for table purposes; that is, medium-sized fruits that are 1–2 kg, cylindrical, and sweeter in taste than existing varieties. For processing cultivars, the aim is to develop cultivars suitable for canning purposes: larger-sized fruits that are  $\geq 2$  kg, cylindrical, sweeter in taste, and with a higher juice content (Kumar 2006). The emphasis of breeding in China varies according to the geography, climate, and market demand.

China is on the northern edge of the pineapple production area (especially the continent, the cultivation area of which accounts for more than 85%). Low temperature and cold injury seriously affect the yield,

**Table 1** Cultivars that have been bred and that have obtained variety rights in China

| Cultivar name                 | The institute of breeding  | The institute of introduction and domestication                                      | The methods of breeding                              | The time of introduction          | The major characters of the fruit in the cultivated area  |
|-------------------------------|--|--|--|-----------------------------------|---|
| Yue crispy                    | Institute of Fruit Tree Research of Guangdong Academy of Agricultural Sciences | Institute of Fruit Tree Research of Guangdong Academy of Agricultural Sciences       | Hybridization, 'Smooth Cayenne' x 'Yellow Mauritius' | Breeding in Guangzhou in 2005     | The fruit is long and conical in shape, with yellow skin and yellow flesh at maturity. The average fruit weight is 1500 kg, and the soluble solid content is 15.2%–23.0%. The quality of fresh fruits was better than that of Comte de Paris, and the processing characters were better than that of Cayenne. (Guangzhou) |
| Jin xiang pineapple           | Horticultural Research Institute of Guangxi Academy of Agricultural Sciences   | Horticultural Research Institute of Guangxi Academy of Agricultural Sciences         | Bud mutation from 'Comte de Paris'                   | Breeding in Guangxi in 2014       | The fruit is cylindrical, golden yellow in mature skin and yellow in flesh, with an average single fruit weight of 1150 g. The eye of the fruit is full, large and flat, and the cone-shaped protuberance is not as obvious as 'Comte de Paris'. The soluble solid content is 15.2%. (Guangxi)                            |
| Yue yin ao ka                 | Institute of Fruit Tree Research of Guangdong Academy of Agricultural Sciences | Institute of Fruit Tree Research of Guangdong Academy of Agricultural Sciences       | Introduction and domestication of Cayenne            | Introduced from Australia in 1979 | Fruit long tubular, yellow skin at maturity, yellow flesh, single fruit weight 1445–2025 g, soluble solid 15.4%–18.6%. (Guangzhou)  |
| Tainung No. 17 (gold diamond) | Chiayi Agricultural Experiment Station, Taiwan Agricultural Research Institute | Tropical Crops Genetic Resource of Chinese Academy of Tropical Agricultural Sciences | Hybridization, 'Smooth Cayenne' x 'Rough'            | Introduced from Taiwan in 2003    | The fruit is cylindrical, with yellow skin and yellow flesh at maturity. The average weight of each fruit is 1.45 kg. The soluble solid content is 15.8% and the titratable acid content is 0.28%. (Hainan)   |



**Table 1** (continued)

| Cultivar name                      | The institute of breeding  | The institute of introduction and domestication                                      | The methods of breeding                   | The time of introduction       | The major characters of the fruit in the cultivated area  |
|------------------------------------|--|--|---|--------------------------------|---|
| Tainung No. 16 (sweet honey)       | Chiayi Agricultural Experiment Station, Taiwan Agricultural Research Institute | Institute of Tropical Fruit trees, Hainan Academy of Agricultural Sciences           | hybridization, Smooth Cayenne × Rough     | Introduced from Taiwan in 2000 | The fruit is conical or elliptic in shape, yellow to bright yellow in skin and yellow in flesh at maturity. The average weight of each fruit is 1230 g, and the soluble solid substance is 17.5%. (Hainan, Guangxi)         |
| Tainung No. 11 (perfume pineapple) | Chiayi Agricultural Experiment Station, Taiwan Agricultural Research Institute | Tropical Crops Genetic Resource of Chinese Academy of Tropical Agricultural Sciences | Hybridization, 'Smooth Cayenne' × 'Rough' | Introduced from Taiwan in 2003 | The fruit is oblong, with yellow skin and pale yellow flesh at maturity. The average weight of a single fruit is 1371.5 g. The eye size is medium and slightly protruding, and the soluble solid content is 14.6%. (Hainan) |

production cycle, and fruit quality of pineapples, and have become important factors restricting the development of the pineapple industry in China. Although the current production employs bagging, film covering, and other pineapple cold-resistant measures, in most cases, the effect is limited. Therefore, the creation of resistant germplasm and breeding of new varieties with good quality and strong cold resistance are important directions for pineapple production.

Pineapple is a perennial herbaceous plant, and the period from planting to fruit growth is 18 months. Shortening the growth period, achieving early flowering and fruiting, and improving the associated economic benefits are thus urgent production objectives. In addition to obtaining varieties with cold resistance, a short nutritional period, and a high sugar–acid ratio, pineapple breeding aims to develop spineless, large-shaped, and vitamin C-rich varieties. The specific requirements include a fruit that is cylindrical in shape, a bright color, and with orange flesh, with plants that flower easily and are easy to manage.

### Pineapple breeding methods

Crossbreeding is the main technique used in the history of pineapple breeding. In addition to crossbreeding, introduction, selection breeding, clonal selection, and mutation breeding (including radiation mutagenesis, chemical mutagenesis, and the combination of mutagenesis with in vitro techniques) are traditional breeding methods. However, traditional breeding methods are hindered by their significant time consumption, heavy workload, and low breeding efficiency. At present, the breeding of new pineapple varieties based on traditional breeding methods has reached a bottleneck, and it is urgent that traditional approaches are combined with new biotechnology methods to accelerate the breeding process. Currently, these novel breeding methods include genetic engineering, the development of molecular markers, evaluation of genetic diversity, and the development of DNA markers linked to traits of interest and their use in marker-assisted selection (MAS).

### Crossbreeding

Most cultivated pineapples are diploid ( $x=25$ ,  $2n=50$ ) in nature and have a high heterozygosity rate. For instance, 'F153', 'MD2', and *A. bracteatus*

CB5 have a combined heterozygosity rate of 1.89%, 1.98%, and 2.93%, respectively (Ming et al. 2015). In addition, pineapple is self-incompatible, and hybridization among similar groups does not result in seed production (Brewbaker and Gorrez 1967).

Artificial breeding of pineapples was first carried out by the PRI in the early twentieth century. This institute obtained a series of new varieties through interspecific hybridization and intergeneric hybridization; these new varieties were modified for resistance, nutrition, seasonality, acidity, and flavor. The commercial ‘MD-2’ and ‘CO-2’ were two successful varieties (Bartholomew et al. 2009, 2010; Joy and Anjana 2016). Both ‘MD-2’ and ‘CO-2’ have a slightly higher brix value than ‘Smooth Cayenne’. However, it took a long time to release new cultivars from traditional breeding programs; for example, ‘MD-2’ was released 23 years after its initial selection (Yabor et al. 2020). The Taiwan Agricultural Research Institute bred ‘Tainung No. 22’ (mother ‘Smooth Cayenne’ and father ‘Tainung No. 8’), which was hybridized in 1976, and the variety rights were obtained in 2012 (Kuan et al. 2018). The breeding system designed by OPARC evaluates accession characteristics in three steps: primary selection, secondary and tertiary selection, and adaptability and regional tests (Ogata et al. 2016). In mainland China, the first hybrid pineapple variety ‘Yue crispy’ was bred by the FTRI, which began hybrid breeding in 1957 using ‘Smooth Cayenne’ and ‘Yellow Mauritius’ (Queen group). Variety rights were obtained in 2015; that is, more than 50 years later (Liu et al. 2006).

### *Introduction and selection*

By directly utilizing germplasm resources imported from abroad or other places, germplasm with excellent performance in a local area can be identified and evaluated through strict breeding procedures and then commercialized and applied. American companies in Costa Rica introduced some hybrid lines from the Pineapple Institute of Hawaii when they planted ‘Smooth Cayenne’. ‘Smooth Cayenne’ was not successfully tested in Costa Rica, but the hybrid ‘MD-2’ performed well, and the original variety was later replaced and planted over a large area.

The hybrid pineapple strain 73–50 developed by the Pineapple Institute of Hawaii was successfully introduced in Australia and has since become a major

fresh food species in Australia (Sanewski 2007). Brazil introduced ‘Pérola’, a variety grown in the mountains of Colombia and Venezuela, and also introduced and successfully commercialized the hybrid Gomo-de-Mel (peeled pineapple, Tainung 4) from Taiwan, China (Cabral et al. 2009). The main cultivars in China, ‘Comte de Paris’, ‘Yellow Mauritius’, and ‘Smooth Cayenne’, have been introduced and successfully commercialized by Chinese growers. In recent years, domestic scientific research institutions and enterprises have introduced overseas varieties in succession. After years of trial breeding, ‘Australian Cayenne’, ‘Tainung No. 11’, ‘Tainung No. 16’, ‘Tainung No. 17’, and ‘MD-2’ have passed provincial identification (examination).

### *Clonal selection*

The long-term use of asexual reproduction in pineapple has resulted in a high frequency of variation and more adverse variations. The beneficial bud changes of pineapple include spine to spine-free variation, large fruit variation, flavor enhancement variation, and resistance enhancement variation, among others.

Varieties continue to mutate during cultivation, and the Queensland Agricultural Centre, Department of Economic Development, has identified at least 30 mutants resulting from lidocaine. Up to 20% of the genomic marker variants were found in the Smooth Cayenne mutants (Smith et al. 2005). A natural mutant line PQM-1 (Prakash et al. 2009) was selected and bred from the Queen groups in India with the characteristics of late ripening, high quality, and dual fresh food processing use (Prakash et al. 2009). Australia selected and bred ‘magligo’ and ‘Alexander’ from ‘Queen’. The red fruit mutant was selected from Spain in Malaysia. Two tissue culture mutants were selected from Pinar (red Spanish) in Cuba (Pérez et al. 2012, 2011, 2009). In Taiwan, ‘Tainung No. 1’, ‘Tainung No. 2’ and ‘Tainung No. 3’ were selected and bred from Smooth Cayenne, and ‘Smooth Cayenne red skin’ was selected and bred from ‘Smooth Cayenne red skin’ (Guan 2008). ‘Jin Xiang pineapple’ was selected from the variable bud of ‘Comte de Paris’ transformed by HRI, GAAS (Wang et al. 2016).



### Polyploid breeding

Most of the existing cultivated and wild varieties of pineapple are diploid. The generation of polyploid varieties mainly depends on natural mutation, hybridization, and artificial mutagenesis (using colchicine to mutagenize diploid plants into homologous tetraploids). Polyploid breeding of pineapple is regarded as an important research direction.

In the 1940s, the PRI carried out polyploid research and cultivated tetraploids and found that the autotetraploid of Smooth Cayenne was more vigorous than the diploid, but the fruit quality was poor (Sanewski et al. 2011). In the hybridization between *A. comosus* and the tetraploid strain *A. macrodontes* (the most resistant to root rot disease), 5–10% of the seeds had high vigor, high fertility, self-fertile tetraploids, and a few sterile triploids (Sanewski et al. 2011), but no commercial variety has been developed.

In China, Xu (2006) treated ‘Comte de Paris’ and ‘Yellow Mauritius’ pineapples with colchicine and obtained some homozygous tetraploids, and there were significant differences in leaf thickness, leaf length, stomatal density, guard cell size, and chloroplast number between tetraploid plants and diploid plants. Based on a comparison of the electrolyte exosmosis rate and catalase activity at  $-5\text{ }^{\circ}\text{C}$ , the results showed that the tetraploids had stronger cold resistance than the diploids.

### Radiation breeding

Radiation mutagenesis breeding is a method of breeding mutants with excellent traits by treating the vegetative organs, tissues, callus, and other materials of pineapple with radiation and causing mutations. Researchers at the Institute of Agricultural Research and Development of Malaysia radiated the apical meristem of the pineapple variety ‘Jospine’ (Chan 2008), and 16 individual plants resistant to bacterial black heart rot was screened from 20,000 radiating seedlings (Ibrahim et al. 2009). Researchers in the Philippines used  $\gamma$ -rays to irradiate Queen species to develop spiny or spine-free materials and ornamental materials of the chlorophyll mutant type (Lapade et al. 1995). Researchers in Ghana mutated Smooth Cayenne and Sugar Loaf by means of  $\gamma$ -rays and tissue culture technology, with a view to cultivating a drought-resistant and heat-resistant variety, and

determined the LD50 to be 45 Gy (Osei-Kofi et al. 1997; Lokko and Amoatey 2001). In Kerala, India, irradiation of plants of the cultivars Kew and Mauritius led to growth retardation, and in one plant, premature suckers (Anonymous 1964). Marz (1964) reported the induction of self-fertile mutants by X-raying pollen during meiosis.

In China, radiation breeding of pineapple began in the 1960s. Since 1972, the pineapple collaborative research group in Guangxi has used  $\text{Co}^{60}$  gamma irradiation to irradiate seedlings of Cayenne and hybrid seeds of Philippines  $\times$  Cayenne, producing a batch of variant offspring, and selected some good strains from it. The suggested dose appropriate for the irradiation of Cayenne seedlings is 50,000 r/min (Zhao and Shen 1978). Huang (2011) used  $\text{NaN}_3$  and  $\gamma$ -radiation to treat ornamental bromeliad callus and a truncated stem to obtain the mutant character of mosaic stripes on the leaves. In 1987, the Institute of Fruit Tree Research of Guangdong Academy of Agricultural Sciences used 10.32 C/Kg (40,000 R)  $\gamma$ -ray irradiation to treat the ‘Comte de Paris’ crown bud, and the mutation rate reached 8% after transplanting. However, most of the irradiated mutants were chimeras, and no mutant with particularly excellent traits was found among more than 10,000 radiation-treated plants.

### Chemical mutagenesis breeding

Chemical mutagenesis breeding is a breeding method that uses chemical substances to mutate pineapple cells, tissues, organs, and plants to improve genetic material variation. Ethyl methanesulphonate (EMS), a common chemical mutagen that can induce point mutations (Paull et al. 2016), is used to induce pineapple shoots in vitro (Mhatre and Rao 2002), crown axillary buds (Chen and Chen 2012), and even seeds. Koh and Davies (2001) treated *Tillandsia fasciculata* var. *fasciculata* Sw. seeds with gamma rays or EMS. The results showed that the effect of a 27 kR radiation dose on the induction of chlorophyll-deficient mutants was better than other radiation doses, with an induction rate of 8.4%, while that of 1.2% EMS treatment for 3 h was 15.8%.

In China, Huang et al. (1995) treated callus of pineapple with EMS mutagenesis, which resulted in a large number of variations. Some mutated cells could grow on selective medium containing hydroxyproline,

and the content of free proline in the surviving callus was 1.6–2.8 times higher than that of the control group, indicating that EMS mutagenesis treatment was effective. Peng et al. (2017) obtained a batch of cold-resistant mutants from sterile test tube seedlings of an ornamental bromeliad treated by EMS. The sterile test tube seedlings of pink leaf coral pineapple were treated with 0.5% EMS for 6 h. The survival rate of the seedlings was 48.4% and the differentiation rate of the adventitious buds was 34.4%. Chen (2012) treated ‘Tainung No. 17’ pineapple tissue culture seedlings with EMS to explore the optimal condition for EMS mutagenesis, and after 0.4% EMS treatment for 12 h, the plant survival rate was 97.5%. In addition to EMS, He’s team from Southern China Agricultural University processed somatic embryos using 5-azac, a methylation inhibitor, and obtained a mutant library. Related work is still in progress, and no further research has been reported (He et al. 2018).

#### *Cell-engineering breeding technology*

When mutagenesis is carried out with multi-cellular materials such as vegetative organs, tissues, and callus, chimeras generally exist. The mutagenic cells or tissues are often unable to compete with normal cells and tissues and gradually disappear in the process of individual growth or vegetative reproduction. It is difficult to isolate and purify chimeras. Through single cell pathways, and with the help of protoplast single cell culture technology, single cell mutagenesis can be carried out, and then a whole plant can be developed through the somatic embryo pathway, which can reduce the occurrence of chimeras.

As a good material for mutagenesis breeding and transgene formation, somatic embryos can reduce the generation of chimeras, and somaclonal variation is considered a promising improvement strategy in pineapple (Dhurve et al. 2021). Researchers have studied the occurrence of somatic embryos in pineapple and have successfully established a regeneration system for pineapple through somatic embryogenesis (Sripaoraya et al. 2003; Firoozabady et al. 2004; Yapo et al. 2011).

In China, Liang et al. (2009) directly induced somatic embryos from pineapple slices. He et al. (2007, 2009) successfully induced somatic embryos with callus from the base of pineapple leaves and established an embryonic cell suspension system of

pineapple. He’s team found that *AcSERK1* plays an important role in the induction and development of somatic embryos in pineapple (Ma et al. 2012b; Luan et al. 2019) and that *AcSERK2* is highly expressed only in embryogenic cells before the pro-embryonic pineapple stage (Ma et al. 2012a). *AcSERK3* plays an important role in callus proliferation and root development (Ma et al. 2014). Zhang et al. (2022) screened and obtained a cold-tolerant variant that could withstand 0 °C for 72 h by combining cell culture with low temperature stress. Guedes et al. (1997) from Brazil and Zhao et al. (2011) from China carried out research on pineapple protoplast separation technology, which provided a preliminary basis for the further application of protoplast fusion technology in the somatic hybridization breeding of pineapple.

#### *Genetic engineering breeding*

Compared with conventional hybridization, genetic engineering breeding has a broad prospect because of its high efficiency, directionality, and short cycle (Mathiazhagan et al. 2021). However, consumer resistance to genetically modified fruit is one of the main reasons limiting the large-scale use of the technology (Sanewski et al. 2011). Pineapple transformation offers the possibility of making small targeted changes to the recipient plant’s genome and is seen as an excellent strategy for genetic improvement.

*Agrobacterium tumefaciens*-mediated transformation and direct gene transfer through microprojectile bombardment are the main methods for the introduction of recombinant DNA to pineapple cells and tissues. Efficient procedures for genetic transformation (Sripaoraya et al. 2001; Espinosa et al. 2002) and in vitro regeneration and propagation (Firoozabady and Gutterson 2003; Sripaoraya et al. 2003) have already been established. However, the genetic transformation system still has low transformation efficiency, and the transformation of different cultivars is difficult and varies greatly. At present, pineapple genetic engineering breeding has been widely used in disease and insect resistance, flowering time control, and fruit quality improvement.

Sripaoraya et al. (2001) first reported a transgenic plant with bialaphos resistance (bar) by bombing pineapple leaves with particles; this was published as a new strain in 2005 that not only maintained the sweetness and high yield of the original Phuket

strain, but also reduced the production cost by 50% (Sripaoraya et al. 2001, 2006). Espinosa et al. (2002) transferred the chitinase gene and an anti-phytophthora protein gene AP24 into ‘Smooth Cayenne’ by *Agrobacterium*-mediated biological reaction with the help of temporary infiltration, with a conversion rate of 6.6% and a series of biochemical evaluations (Yabor et al. 2006, 2008, 2010, 2016, 2017). A detailed histological analysis was conducted on the roots and leaves of transgenic pineapple plants grown in the field for 8 years (fourth-generation tissue culture seedlings). It was found that although there were some histological differences between the transgenic plants and control plants, these differences did not affect the final fruit yield (Yabor et al. 2020). In Australia, the particle bombardment transformation system was used to obtain an anti-dark heart strain with the PPO gene (Ko et al. 2006). Through down-regulation of the expression of the PPO gene in pineapple, the incidence of black heart disease was reduced (Ko et al., 2013). Pérez et al. (2006) from the Hawaii Agricultural Research Institute transformed the coat protein (CP) gene of the pineapple powder pest wilt virus associated-2 (PMWa V-2) into pineapple leaf and protocorm, obtaining seven strains of pineapple resistant to powder pest wilt disease and successfully reducing the incidence of pineapple powder pest by inhibiting *PMWaV-2* gene expression (Pérez et al. 2006).

In terms of regulation of the flowering period, Trusov and Botella (2006) reduced the expression of the *AcACS2* gene through gene silencing, inhibited the natural flowering of pineapple, and improved the consistency of flowering and harvesting of pineapple in the field.

In China, He’s team in SCAU has been working on the tissue culture and genetic transformation of pineapple and has established pineapple transgenic technology and methods (He et al. 2010a, b), He’s team transformed the *CYP1A1* gene into Yellow Mauritius pineapple, mediated by *A. tumefaciens*, with a conversion rate ranging from 0.12 to 2.69% and with high randomness (He et al. 2010b). In addition, the *Ac CBL* genes strongly associated with pineapple fruit eye development were transformed into Yellow Mauritius, and two green seedlings were obtained after three rounds of screening; the transformation efficiency was 3.51% (Wu et al. 2019). Through the use of CRISPR/Cas9 technology, the *PDS* gene of

pineapple was knocked out by *Agrobacterium*-mediated transformation. After three successive rounds of screening, a total of four white transformation buds were obtained with a cumulative transformation efficiency of 0.54%. The above-mentioned transgenic plants have not yet been reported. Jiang (2007) transformed the resveratrol synthase gene (RS) into Tainung No. 16 pineapple by particle bombardment, and six positive plants were detected by PCR. Real-time PCR analysis showed that the RS gene was expressed in two transgenic lines. Other institutions, such as the SSCRI, are engaged in research on pineapple transgenes, but no associated papers have been published.

### *MAS breeding*

With the development of DNA fingerprinting, a variety of DNA marker-assisted breeding techniques have been developed. For example, randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), restriction fragment length polymorphism (RFLP), simple sequence repeat (SSR), and ISSR system (ISSR) markers have been successfully applied in the evaluation of germplasm resources and the analysis of genetic diversity in pineapple (Kato et al. 2005; Liu et al. 2008; Tong et al. 2010; Zhang et al. 2014; Wang et al. 2015a,b; Silva et al. 2019; Villalobos-Olivera et al. 2022). In recent years, with the development of genomic sequencing technology, molecular markers for Indel and single nucleotide polymorphism (SNP) sites have been applied to the molecular breeding of rice, maize, and other crops, while Indel and SNP markers remain to be developed in pineapple (Chen et al. 2016; Yang et al. 2019).

Kato et al. (2004) evaluated 162 accessions, including 148 of *A. comosus* and 14 of related species, using AFLP markers and found abundant genetic variation among them. However, the major cultivar groups of the 148 *A. comosus* accessions of pineapple, such as ‘Cayenne’, ‘Spanish’ and ‘Queen’, could not be distinctively separated by AFLP (Kato et al. 2005). Vanijajiva (2012) screened nine pairs of primers to perform ISSR analysis on 15 Thai pineapple cultivars and obtained 56 bands, 27 of which exhibited polymorphisms. The similarity coefficient was 0.316–0.968, and the genetic diversity level was high. Thirty-one pineapple accessions could be

differentiated by 18 SSR markers but could not be clustered into distinct groups through morphological classification (Shoda et al. 2012). Similar results were reported for 48 pineapple cultivars that were clustered into four subgroups using SSR markers (Feng et al. 2013). Wohrmann and Weising (2011) identified 696 SSRs among 3389 expressed sequence tag (EST) uni-genes and developed primer sequences and described the locus characteristics for 18 selected EST-SSR markers.

In China, Chinese scholars used RAPD, AFLP, RFLP, ISSR, and SSR to develop molecular markers that could be used for the identification of resources. Wang et al. (2015a) used RAPD molecular markers to analyze the genetic diversity of 47 types of pineapple germplasm from nine different countries or regions. The germplasm was divided into four groups. In addition, 26 pineapple germplasms from nine countries or regions were used to construct DNA fingerprints using SSR markers. A total of 35 polymorphic sites were detected among eight pairs of SSR primers with high polymorphism and good stability (Wang et al. 2015b).

Chen et al. (2017) obtained 617 pineapple ESTs containing SSR through electronic screening, information analysis, and development of the published 5659 ESTs of *A. comosus*. According to the searched EST sequence, a total of 30 pairs were designed, of which 27 pairs of primers were polymorphic. Zhang et al. (2013) used ISSRs to analyze the phylogenetic relationship of 40 Bromeliaceae plants from four different genera, and the results were consistent with the botanical classification. Lin et al. (2015) used 16 SSR markers to study the genetic relationships between 27 cultivars and lines of pineapple, and the number of alleles of each locus ranged from 2 to 6 (3.19 on average), with a total of 51 alleles.

The first genetic maps of pineapple were constructed using 46 F1 plants (Carlier et al. 2004); later, a large number of improvements were made. In 2012, Carlier et al. (2012) drew a relatively complete genetic linkage map of pineapple with 33 linkage groups and 492 DNA markers (348 AFLP, 57 RAPD, 22 ISSR, 20 SSR, 12 EST-SSR, 25 Sequence Characterized Amplified Regions (SCARs), 8 cleaved amplified polymorphism sequences (CAPS), and several loci involved in the determination of morphological characteristics. Sousa and Carlier et al. (2013) further improved the previous linkage map, covering 741

loci, including 739 DNA sites, 1 isozyme locus, and 1 locus coding for spineless leaves; that is, the ‘piping’ locus.

In China, Ming’s team from Fujian Agriculture and Forestry University published pineapple genome information in 2015 (Ming et al. 2015), and in 2019, they assembled the bracteatus CB5 genome to the chromosome level (Chen et al. 2019) and then further revised the two mistakes published in the pineapple F153 genome assembly. They developed a pineapple genomics database (PGD, <http://pineapple.angiosperms.org/pineapple/html/index.html>) as a central online platform for storing and integrating genomic, transcriptomic, function annotation, and genetic marker data for *A. comosus*. SSR markers for 4629 gene-coding sequences and 46,860 genome-level SSR markers are listed in the database, totaling 7,252,423 SNPs and 17,540 intron polymorphic (IP) markers. The disclosure of these marker data will greatly facilitate the development and utilization of molecular markers (Xu et al. 2019).

In addition to the use of molecular markers for resource identification and genetic diversity analysis, the development of genetic markers for screening agronomic and other traits of interest is important for breeding. DNA markers related to leaf margin phenotypes and fruit characteristics (pulp color, sugar content, and maturation stage) are being developed in Japan (Urasaki et al. 2015). The leaf margin phenotype is controlled by two genes, the P gene and the S gene, and researchers have successfully converted five RAD-seq markers for the P gene and two Rad-seq markers for the S gene into CAPS or SSR markers (Urasaki et al. 2015). Molecular markers involving a specific trait have not been developed in China.

### Future prospects of the pineapple industry in China

Chinese mainland pineapple breeding in the 1990s experienced a long interval characterized by little progress. Most of the main cultivars were introduced in the last century; the Queen group accounts for more than 85% and includes Comte de Paris, which accounts for about 95%, and Yellow Mauritius accounts for about 5%. New cultivars introduced for yield, regulated fruit maturation, and fruit quality, among other characteristics, need to be adapted

to local production conditions. At present, pineapple breeding in China is faced with the following problems:

- 1) The low diversity of cultivars, especially the lack of stress-resistant cultivars, has greatly limited the development of the pineapple industry. In recent years, many unsellable pineapples have appeared in major pineapple producing areas in China, which has had a serious impact on the development of the pineapple industry. This phenomenon, to a large extent, was directly correlated with the extreme low temperatures in that year. In addition, the use of a single cultivar and the centralized marketing of products has hindered the sale of fruits.
- 2) Self-incompatibility makes it difficult to back-cross species, which limits the creation of inbred lines and increases breeding difficulties. A highly heterozygous nature and unclear parental genetic background make breeding difficult, resulting in a long breeding cycle and slow cultivar renewal.
- 3) Compared with model plants, the genetic transformation efficiency of pineapple is still low, and chimeras are likely, which limits the scale and efficiency of the genetically engineered breeding of pineapple.
- 4) Different cultivars have different flowering periods and different sensitivities to ethylene. The conversion between the vegetative growth period and the reproductive growth stage, as well as the mechanism of flowering regulation, is not yet clear.

In order to solve the above breeding problems, the first step is to collect, introduce, and create germplasm resources for pineapple breeding; to clarify the genetic background and laws; and to lay a foundation for breeding. Breeding materials, including the establishment of a variety of mutagenic germplasm banks, should be created, and chemical and physical mutagenesis as well as seed and tissue mutagenesis should be conducted.

Second, the self-incompatibility mechanism should be explored to create self-incompatible materials, to carry out genotype identification, and to provide a theoretical basis for hybridization.

Third, the latest molecular technology should be used to transform flower genes and cold resistance,

disease resistance, and other genes by transgenic technology. The gene editing technology should be implemented to obtain a short vegetative growth period and stress-resistant materials.

Fourth, the regulatory mechanism of the flowering period of pineapple should be explored and production should be conducted according to the different ripening stages of different cultivars.

Fifth, genetic markers should be developed that can be used to screen agronomic characteristics and other interesting traits. DNA markers related to a short vegetative period, leaf margin phenotype, fruit characteristics (pulp color, white sugar content, and maturity stage), disease resistance, and cold resistance should be developed. It is necessary to initiate the use of these and other markers in MAS, as this will shorten the breeding time and will improve the detection of promising germplasm, thereby reducing the production time and costs.

In order to achieve a breakthrough in the breeding of new pineapple varieties, it is necessary to further promote the innovation of breeding methods and technologies. Therefore, the future trend of pineapple breeding is to develop and establish advanced molecular breeding techniques based on the genome, such as the development of genetic markers that can be used to screen for agronomic and other traits of interest. In order to meet this demand, it is necessary to launch research projects that utilize new-generation sequencing platforms and technology for a comprehensive analysis of DNA polymorphism and development of DNA molecular markers.

**Acknowledgements** This work was supported by a research grant from the National Key Research and Development Program of China (No. 2019YFD1001104) and Conservation Fee Project of Species Resources in Ministry of Agriculture and Rural Affairs (No.125163006000160001). We thank Accdon ([www.accdon.com](http://www.accdon.com)) for its linguistic assistance during the preparation of this manuscript.

**Funding** The authors have not disclosed any funding. Key Research and Development Program, No. 2019YFD1001104, Jingjing Chen, Conservation Fee Project of Species Resources, No.125163006000160001, Jingjing Chen

**Declarations**

**Conflict of interest** The authors have not disclosed any competing interests.



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## References

- Anonymous (1964) Pineapple research station, Kannara, Kerala Agric. Res Indian Counc Agric Res 4:141–142
- Bartholomew DP (2009) ‘MD-2’ pineapple transforms the world’s pineapple fresh fruit export industry. Pine News No 16:2–5
- Bartholomew DP, Coppens d’Eeckenbrugge G, Chen CC (2010) Register of new fruit and nut cultivars list, pineapple. HortScience 45:740–742
- Brewbaker JL, Gorrez DD (1967) Genetics of self-incompatibility in the monocot genera, *Ananas* (pineapple) and *Gasteria*. Am J Bot 54:611–616
- Cabral JRS, de Matos AP (2009) Imperial, a new pineapple cultivar resistant to fusariosis. Acta Hort 822:47–50
- Cabral JRS, de Matos AP, Junghans DT, Souza F (2009) Pineapple genetic improvement in Brazil. Acta Hort 822:39–46
- Carlier JD, Reis A, Duval MF, Coppens d’Eeckenbrugge G, Leitao JM (2004) Genetic maps of RAPD, AFLP and ISSR markers in *Ananas bracteatus* and *A. comosus* using the pseudo-testcross strategy. Plant Breed 123:186–192
- Carlier JD, Sousa NH, Santo TE, Coppens d’Eeckenbrugge G, Leitao JM (2012) A genetic map of pineapple (*Ananas comosus* (L.) Merr.) including SCAR, CAPS. SSR EST-SSR Mark Mol Breed 29:245–260
- Chan YK (2008) Breeding of seed and vegetatively propagated tropical fruits using papaya and pineapple as examples. Acta Hort 787:69–76
- Chen JH (2012) Studies on mutation breeding of “Tainung No.17” pineapple by ethyl methanesulfonate. Chung hsing university, Taiwan (**In Chinese with English abstract**)
- Chen CH, Chen CC (2012) Establishment of EMS mutagenesis and proliferation system of etiolated pineapple shoots. Horticulture 37:27–37 (**In Chinese with English abstract**)
- Chen LK, Gao WW, Guo T (2016) A genotyping platform assembled with high-throughput DNA extraction, codominant functional markers, and automated CE system to accelerate marker-assisted improvement of rice. Mol Breed 36(9):123
- Chen JH, Lu Y, Ni YJ, Zhang ZJ, Zhong YP, Bao JJ, Luo SP (2017) Development of novel EST-SSR markers in pineapple (*Ananas comosus*) by data mining from public EST sequences. J Zhejiang Agric Forest Univ 34(2):332–339 (**In Chinese with English abstract**)
- Chen LY, VanBuren R, Paris M, Zhou H, Zhang X, Wai CM, Yan H, Chen S, Alonge M, Ramakrishnan S, Liao Z, Liu J, Lin J, Yue J, Fatima M, Lin Z, Zhang J, Huang L, Wang H, Hwa TY, Kao SM, Choi JY, Sharma A, Song J, Wang L, Yim WC, Cushman JC, Paull RE, Matsumoto T, Qin Y, Wu Q, Wang J, Yu Q, Wu J, Zhang S, Boches P, Tung CW, Wang ML, Coppens d’Eeckenbrugge G, Sanewski GM, Purugganan MD, Schatz MC, Bennetzen JL, Lexer C, Ming R (2019) The bracteatus pineapple genome and domestication of clonally propagated crops. Nat Genet 51:1549–1558
- Collins JL (1949) History, taxonomy and culture of the pineapple. Econ Bot 3:335–359
- Coppens d’Eeckenbrugge G, Leal F, Duval MF (1997) Germplasm resources of pineapple. Horticult Rev 21:133–175
- de Sousa N, Carlier J, Santo T, Leitão J (2013) An integrated genetic map of pineapple (*Ananas comosus* (L.) Merr.). Sci Hort 157:113–118
- Deng CM, Li YP, Liang WH, Ye L (2018) Present situation and countermeasures of pineapple industry in China. J Shanxi Agric Sci 46(6):1031–1034 (**In Chinese with English abstract**)
- Dhurve L, Ajith Kumar K, Bhaskar J, Sobhana A, Francies RM, Mathew D (2021) Wide variability among the ‘Mauritius’ somaclones demonstrates somaclonal variation as a promising improvement strategy in pineapple (*Ananas comosus* L.). Plant Cell Tiss Org 145:701–705
- Espinosa P, Lorenzo JC, Iglesias A, Yabor L, Menéndez E, Borroto J, Hernández L, Arencibia AD (2002) Production of pineapple transgenic plants assisted by temporary immersion bioreactors. Plant Cell Rep 21(2):136–140
- Feng S, Tong H, Chen Y, Wang J, Chen Y, Sun G, He J, Yaoting W (2013) Development of pineapple microsatellite markers and germplasm genetic diversity analysis. BioMed Res Int 2013:1–11. <https://doi.org/10.1155/2013/317912>
- Ferreira FR, Cabral JRS (1993) Pineapple germplasm in Brazil. Acta Hort 334(334):23–26
- Firoozabady E, Gutterson N (2003) Cost effective in vitro propagation methods for pineapple. Plant Cell Rep 21:844–850
- Firoozabady E, Moy Y (2004) Regeneration of pineapple plants via somatic embryogenesis anorganogenesis. In Vitro Cell Dev Biol Plant 40(1):67–74
- Guan QS (2018) Pineapple varieties from Taiwan in China. World Trop Agric Inf 12:27–28 (**In Chinese with English abstract**)
- Guedes NM, Maria J, Zambolim L, Ventura J (1997) Protoplast isolation of *Ananas comosus*(L) Merr Cv “perolera.” Acta Hort 452:259–265
- Harry JP, Lenoir H, Perrier X, Perrier X, Teisson C (2005). The CIRAD pineapple germplasm database. Acta Horticulturae, (666):73–76.
- He YH, Luo J, Wu HT, Wang RX, Gao AP, Zhao CX, Yu XL, Ye ZX, Wang ZH, Han JZ, Liu HP (2007) Somatic



- embryogenesis from leaf base callus of *Ananas comosus*. *J Fruit S* 24(1):59–63 **(In Chinese with English abstract)**
- He YH, Fang SQ, Lu M, Ma J, Hu ZY, Peng B, Cao L, Xia JX (2009) Establishment of embryogenic cell suspension line in pineapple. *Acta Horti Sinica* 36(S):1938
- He YH, Fang SQ, Ma J, Hu ZY, Peng B (2010a) Histocytology observation on the somatic embryogenesis in *Ananas comosus* callus. *Acta Horti Sinica* 37(5):689–696 **(In Chinese with English abstract)**
- He YH, Wu HT, Luo J, Fang SQ, Ma J, Lu M, Peng B, Wu CH (2010b) Agrobacterium-mediated transformation of *Ananas comosus* with *CYP1A1*. *J Hunan Agric Univ (Natural Sciences)* 36(01):34–38 **(In Chinese with English abstract)**
- He JH, Luan AP, He YH, Zhang W (2018) Construction of a 'red pineapple' mutant library induced by DNA methylation inhibition. *Acta Horticulturae Sinica*, 45 (S1): 2568. **(In Chinese)**
- Horry JP, Lenoir H, Perrier X, Teisson C (2005) The CIRAD pineapple germplasm database. *Acta Horti* 666:73–76
- Huang BL (2011) Studies on the micropropagation and somaclonal variation induction of ornamental bromeliads. National Sun Yat-sen University, Taiwan **(In Chinese with English abstract)**
- Huang JH, Kong DQ, Huang F (1995) Callus induction and antimetabolite mutant selection for pineapple. *Chin J Trop Crops* 16(S):1–6 **(In Chinese with English abstract)**
- Ibrahim R, Hamzah A, Jam ZJ, Bahagia M, Joyo M (2009) Gamma irradiation-induced mutation for the improvement of Josapine pineapple against bacterial heart rot disease and improved fruit quality. An International Joint FAO/IAEA Symposium
- Ikemiya H, Onaha A, Nakasone H (1984) Excellent strain N67–10 in pineapple. *Kyushu Agric Res* 46:268
- Jiang LM (2007) Study on establishment of genetic transformation system of pineapple (*Ananas Comosus* (L.) Merr) tainong-16 and gene transfer of resveratrol synthase into pineapple. Chinese Academy of Agricultural Sciences, Beijing **(In Chinese with English)**
- Jin Y (2016) The pineapple industry of China development report and situation forecast in 2015. *World Trop Agric Inf* 9:16–24 **(In Chinese with English abstract)**
- Joy PP, Anjana R (2016) Evolution of Pineapple. In: Peter KV(ed) *Genesis and Evolution of Horticultural Crops*, 1st edn. Astral International Pvt. Ltd., New Delhi, pp 1–39
- Kato CY, Nagai C, Moore PH, Zee F, Kim MS, Steiger DL, Ming R (2004) Intra-specific DNA polymorphism in pineapple (*Ananas comosus* (L.) Merr.) assessed by AFLP markers. *Genet Resour Crop Evol* 51:815–825
- Kato CY, Nagai C, Moore PH, Zee F, Kim MS, Steiger DL, Ming R (2005) Intra-specific DNA polymorphism in pineapple (*Ananas comosus* (L.) Merr.) assessed by AFLP markers. *Genet Resour Crop Evol* 51(8):815–825
- Ko HL, Campbell PR, Jobin-De´cor MP, Eccleston KL, Graham MW, Smith MK (2006) The introduction of transgenes to control blackheart in pineapple (*Ananas comosus* L.) cv. smooth cayenne microprojectile bombardment. *Euphytica* 150:387–395
- Ko L, Eccleston K, O'Hare T, Wong L, Giles J, Smith M (2013) Field evaluation of transgenic pineapple (*Ananas comosus* (L.) Merr.) cv. 'Smooth Cayenne' for resistance to blackheart under subtropical conditions. *Sci Horti* 159:103–108
- Koh YC, Davies FT (2001) Mutagenesis and in vitro culture of *Tillandsia fasciculata* Swartz var. *Fasciculata* (*Bromeliaceae*). *Sci Horti* 87(3):225–240
- Kuan CS, Lee TC, Tsai MS, Tsai HW, Tang CH (2018) A new pineapple cultivar *Ananas comosus* (L.) Merr. ('Tainung No. 22'). *Hortscience* 53(4):578–581
- Kumar N (2006) *Breeding of horticultural crops: principles and practices*. New India Publishing Agency, Delhi, pp 118–120
- Lapade AG, Veluz AMS, Santos IS (1995) Genetic improvement of the Queen variety of pineapple through induced mutation and in vitro culture techniques. In: Conference on the international symposium IAEA and food agric Org of the UN IAEA. Proceedings induced mutations and molecular techniques for improvement. Vienna
- Liang XL, Chen XL, Cheah K, Sether DM, Qi L, Hu J (2009) Establishment of direct somatic embryogenesis system through transverse thin cell layer culture in pineapple (*Ananas comosus* L. Merrill). *Acta Horticulturae Sinica* 36(11):1597–1602 **(In Chinese with English abstract)**
- Lin YS, Kuan CS, Weng IS, Tsai CC (2015) Cultivar identification and genetic relationship of pineapple (*Ananas comosus*) cultivars using SSR markers. *Genet Mol Res* 14(4):15035–15043. <https://doi.org/10.4238/2015.November.24.11>
- Liu HQ, Liu ZY (2017) Analysis on international competitiveness of China's pineapple fresh fruit industry. *Jiangsu Agric ences* 45(17):334–337 **(In Chinese)**
- Liu Y, Zhong YMXC, Xu SQ, Liu PZ (2006) A new variety for Pineapple 'Yuecui'. *Acta Horticulturae Sinica* 33:214 **(In Chinese with English abstract)**
- Liu WG, Yi GJ, Liu Y, Zhang QM, Zeng JW (2008) Identification of pineapple germplasm and relationship analysis with AFLP. *J Fruit Sci* 25:516–520 **(In Chinese with English abstract)**
- Lokko Y, Amoatey H (2001) Improvement of pineapple using in vitro and mutation breeding techniques [C]/ M.SR, Asad S, Zafar Y, et al. In vitro techniques for selection of radiation induced mutations adapted to adverse environmental conditions 5–29.
- Luan A, He Y, Xie T, Chen CJ, Mao Q, Wang X, Li C, Ding Y, Lin W, Liu C, Xia J, He J (2019) Identification of an embryonic cell-specific region within the pineapple *SERK1* promoter. *Genes* 10:883
- Ma J, He YH, Hu ZY, Xu WT, Xia JX, Guo CH, Lin SQ, Cao L, Chen CJ, Wu CH, Zhang JL (2012a) Characterization and expression analysis of *AcSERK2*, a somatic embryogenesis and stress resistance related gene in pineapple. *Gene* 500:115–123
- Ma J, He YH, Wu CH, Liu HP, Hu ZY, Shun GM (2012b) Cloning and molecular characterization of a *SERK* gene transcriptionally induced during somatic embryogenesis in *Ananas comosus*. cv Shenwan. *Plant Mol Biol Rep* 30:195–203

- Ma J, He Y, Hu Z, Xu W, Xia J, Guo C, Lin S, Chen C, Wu C, Zhang J (2014) Characterization of the third SERK gene in pineapple (*Ananas comosus*) and analysis of its expression and autophosphorylation activity in vitro. *Genet Mol Biol* 37(3):530–539
- Marz GS (1964) Study of self-incompatibility in the Pineapple. *Agric res pretoria* 2–6: 561–562.
- Mathiazhagan M, Bhavya Chidambara B, Hunashikatti LR, Ravishankar KV (2021) Genomic approaches for improvement of tropical fruits: fruit quality shelf life and nutrient content. *Genes* 12(1881):1–41
- Mhatre M, Rao PS (2002) Influence of physical and chemical mutagens on pineapple shoot cultures. *Pineapple News* 9:11–12
- Ming R, VanBuren R, Wai CM, Tang H, Schatz MC, Bowers JE, Lyons E, Wang ML, Chen J, Biggers E, Zhang J, Huang L, Zhang L, Miao W, Zhang J, Ye Z, Miao C, Lin Z, Wang H, Zhou H, Yim WC, Priest HD, Zheng C, Woodhouse M, Edger PP, Guyot R, Guo HB, Guo H, Zheng G, Singh R, Sharma A, Min X, Zheng Y, Lee H, Gurtowski J, Sedlazeck FJ, Harkess A, McKain MR, Liao Z, Fang J, Liu J, Zhang X, Zhang Q, Hu W, Qin Y, Wang K, Chen LY, Shirley N, Lin YR, Liu LY, Hernandez AG, Wright CL, Bulone V, Tuskan GA, Heath K, Zee F, Moore PH, Sunkar R, Leebens-Mack JH, Mockler T, Bennetzen JL, Freeling M, Sankoff D, Paterson AH, Zhu X, Yang X, Smith JA, Cushman JC, Paull RE, Yu Q (2015) The pineapple genome and the evolution of CAM photosynthesis. *Nat Genet* 47:1435–1442
- Nath V, Kumar G, Pandey S, Pandey S (2019) Impact of climate change on tropical fruit production systems and its mitigation strategies. In: Sheraz Mahdi S (ed) *Climate change and agriculture in India: impact and adaptation*. Springer, Berlin, pp 129–146
- Ogata T, Yamanaka S, Shoda M, Urasaki N, Yamamoto T (2016) Current status of tropical fruit breeding and genetics for three tropical fruit species cultivated in Japan: pineapple, mango, and papaya. *Breed Sci* 66(1):69–81
- Osei-Kofi F, Amoatey HM, Lokko Y (1997) Improvement of pineapple using biotechnology and mutation breeding techniques. In: Report of 2 FAO/IAEA Research coordination meeting on invitro techniques for selection of radiation-induced mutant adapted to adverse environmental conditions, pp 23–27
- Paull RE, Bartholomew DP, Chen CC (2016) Pineapple breeding and production practices. In: Lobo MG and Paull RE (ed) *Handbook of Pineapple Technology: Production, Postharvest Science, Processing and Nutrition*, 1rd edn. Wiley, New York, pp.16–38.
- Paz EY, Gil K, Rebolledo L, Rebolledo A, Simpson J (2005) AFLP characterization of the Mexican pineapple germplasm collection. *J Am Soc Hortic Scie* 130(4):575–579
- Peng XN (2017) Optimization of *Bromeliaceae* culture in vitro and its cold-tolerant mutants induction. Hunan Agricultural, Changsha (**In Chinese with English abstract**)
- Pérez EP, Sether DM, Melzer MJ, Subere CV, Cheah K, Chen Y, Qi L, Borth W, Wang IC, Nagai C (2006) Characterization and control of pineapple mealybug wilt associated ampeloviruses. *Acta Hortic* 702(702):702
- Pérez G, Yanes E, Isidron M, Lorenzo JC (2009) Phenotypic and AFLP characterization of two new pineapple somaclones derived from in vitro culture. *Plant Cell Tiss Org* 96(1):113–116
- Pérez G, Mboghli A, Sagarra F, Aragón C, González J (2011) Morphological and physiological characterization of two new pineapple somaclones derived from in vitro culture. *In Vitro Cell Dev Biol Plant* 47(3):428–433
- Pérez G, Yanez E, Mboghli A, Valle B, Sagarra F, Yabor L, Aragón C, González J, Isidron M, Lorenzo JC (2012) New pineapple somaclonal variants: P3R5 and Dwarf. *Am J Plant Sci* 3(1):1–11
- Prakash J, Bhattacharyya S, Chattopadhyay K, Roy S, Dasa SP, Singh NP (2009) PQM-1: a new developed superior clone of pineapple for northeastern India as evident through phenotype, fruit quality and DNA polymorphism. *Sci Hortic* 120(2):228–291
- Sanewski GM (2007) Skin russetting in the pineapple variety 73–50. *Pineapple News* 14:9–12
- Sanewski GM (2014) Aus-Festival. *Plant Var J* 27:275–278
- Sanewski GM, Smith MK, Pepper PM, Giles JE (2011) Review of genetic improvement of pineapple. *Acta Hortic* 902:95–108
- Shi WQ, Sun WS, Xi JG, Chen J, Zuo XD (2011) Present situation and development countermeasure of pineapple industry in China. *Guangdong Agric Sci* 3:181–186 (**In Chinese with English abstract**)
- Shoda M (2011) Pineapple: Introduction, industry and current domestic production. *Food Pre Sci* 3:249–255
- Shoda M, Urasaki N, Sakiyama S, Terakami S, Hosaka F, Shigeta N, Nishitani C, Yamamoto T (2012) DNA profiling of pineapple cultivars in Japan discriminated by SSR markers. *Breed Sci* 62:352–359
- Silva JM, Lima PR, Souza FV, Ledo CA, Souza EH, Pestana KN, Ferreira CF (2019) Genetic diversity and nonparametric statistics to identify possible ISSR marker association with fiber quality of pineapple. *An Acad Bras Ciênc* 91:144–154
- Smith MK, Ko HL, Sanewski GM, Botella JR (2005) *Ananas comosus* pineapple. In: Litz RE (ed) *Biotechnology of fruit and nut crops*. CABI, Wallingford, pp 158–172
- Soneiji JR, Rao MN (2009) Genetic engineering of pineapple. *Transgenic plant J* 3(1):47–56
- Sripaoraya S, Marchant R, Power JB, Davey MR (2001) Herbicidetolerant transgenic pineapple (*Ananas comosus*) produced by microprojectile bombardment. *Ann Bot* 88(4):597–603
- Sripaoraya S, Marchant R, Power JB, Davey M (2003) Plant regeneration by somatic embryo- genesis and organogenesis in commercial pineapple (*Ananas comosus* L.). *In Vitro Cell Dev Biol Plant* 39(5):450–454
- Sripaoraya S, Keawsompong S, Insupa P, Power JB, Davey MR, Srinives P (2006) Genetically manipulated pineapple: transgene stability, gene expression and herbicide tolerance under field conditions. *Plant Breed* 125:411–413
- Sun WS, Liu SH, Wu QS, Wang J (2014) Introduction of a new pineapple variety, MD-2 in Zhanjian Guangdong. *Fruit Sci South China* 43(2):103–104 (**In Chinese with English abstract**)

- Tong HL, Feng SP, Chen Y, Chen YY, Sun GM, Wu YT (2010) Development of molecular markers from genomic SSR of pineapple (*Ananas comosus*). *J Fruit Sci* 27:551–555 **(In Chinese with English abstract)**
- Trusov Y, Botella JR (2006) Silencing of the ACC synthase gene *AcACS2* causes delayed flowering in pineapple [*Ananas comosus* (L.) Merr.]. *J Exp Bot* 57:3953–3960
- Urasaki N, Goeku S, Kaneshima R, Takamine T, Tarora K, Takeuchi M, Moromizato C, Yonamine K, Hosaka F, Terakami MH, Yamamoto T, Shoda M (2015) Leaf margin phenotype-specific restriction-site-associated DNA derived markers for pineapple (*Ananas comosus* L.). *Breeding Sci* 65:276–284
- Vanijajiva O (2012) Assessment of genetic diversity and relationships in pineapple cultivars from Thailand using ISSR marker. *J Agri Tech* 8(5):1829–1838
- Villalobos-Olivera A, Ferreira CF, Yanes-Paz E, Gustavo Y, Lorente GY, Souza FV, Engelmann F, Martínez-Montero ME, Lorenzo JC (2022) Inter simple sequence repeat (ISSR) markers reveal DNA stability in pineapple plantlets after shoot tip cryopreservation. *Vegetos*. <https://doi.org/10.1007/s42535-021-00327-6>
- Wang JS, He JH, Chen HR, Chen YY (2015a) Construction of DNA fingerprint for pineapple germplasm based on SSR marker. *Chin J Trop Crops* 36(7):1274–1279 **(In Chinese with English abstract)**
- Wang JH, He JH, Chen HR, Chen YY (2015b) Genetic diversity analysis of forty seven pineapple (*Ananas comosus* (L.) Merr.) germplasm with RAPD marker. *Chin J Trop Crops* 36:1392–1397 **(In Chinese with English abstract)**
- Wang XM, Ren H, Liu YQ, Su WQ, Li Z, Huang HY, Fang WK, Lu GF (2016) Breeding report of a new pineapple variety 'Jinxiang Boluo.' *J Fruit Sci* 33(04):509–512 **(In Chinese with English abstract)**
- Williams DDF, Fleisch H (1992) History of plant breeding in Hawaii. In: Bartholomew DP, Rohrbach KG (eds) First international pineapple symposium. Honolulu, USA, pp 2–6
- Wohrmann T, Weising K (2011) In silico mining for simple sequence repeat loci in a pineapple expressed sequence tag database and cross-species amplification of EST-SSR markers across Bromeliaceae. *Theor Appl Genet* 123:635–647
- Wu J, He YH, Xie T, Ding YQ, Luan AP, Xue B, Zhang W, Li JJ, Liu CY (2019) Studies on the construction and transformation of *AcCBL* overexpression vector related to fruit eye development in pineapple. Chinese Society of Horticulture. Collection of abstracts of papers from the 2019. In: Annual conference and 90th anniversary conference of the Chinese society of horticulture. Chinese Society of Horticulture: Chinese Society of Horticulture, **(In Chinese)**
- Xu Y (2006) Studies on rapid propagation and polyploid breeding of *Ananas comosus* (L.) Merrill. Southwest University, Chongqing **(In Chinese with English abstract)**
- Xu HM (2019) Comparative analysis of transcriptomes of sugarcane cultivar hybrids and two *Saccharum* founding species obtained by single-molecule sequencing and pineapple genomics database. Dissertation, Fujian Agriculture and Forestry University. **(In Chinese with English abstract)**
- Xu CM, Yang LZ (2007) Advancement in technology research of pineapple. *J South China Univ Trop Culture* 13(3):24–29 **(In Chinese with English abstract)**
- Yabor L, Arzola M, Aragón C, Hernández M, Arencibia A, Lorenzo JC (2006) Biochemical side effects of genetic transformation of pineapple. *Plant Cell, Tiss Organ Cult* 86(1):63–67
- Yabor L, Aragón C, Hernández M, Arencibia A, Lorenzo JC (2008) Biochemical side effects of the herbicide FINALE on bar gene-containing transgenic pineapple plantlets. *Euphytica* 164:515–520
- Yabor L, Valle B, Carvajal C, Aragón C, Hernández M, González J, Daquinta M, Arencibia A, Lorenzo JC (2010) Characterization of a field-grown transgenic pineapple clone containing the genes chitinase, AP24, and bar. *In Vitro Cell Dev Biol Plant* 46:1–7
- Yabor L, Valle B, Rodríguez RC, Aragón C, Papenbrock J, Tebbe CC, Lorenzo JC (2016) The third vegetative generation of a field-grown transgenic pineapple clone shows minor side effects of transformation on plant physiological parameters. *Plant Cell Tiss Organ Cult (PCTOC)* 125(2):303–308
- Yabor L, Rumlow A, Gómez D, Tebbe CC, Papenbrock J (2017) Lorenzo JC (2017) Mineral composition of a transgenic pineapple clone grown in the field for 8 yr. *In Vitro Cell Dev Biol Plant* 53:489–493
- Yabor L, Pérez L, Gómez D, Villalobos-Olivera A, Lorenzo JC (2020) Histological evaluation of pineapple transgenic plants following 8 years of field growth. *Euphytica* 216:23
- Yang GL, Chen SP, Chen LK, Sun K, Huang CH, Zhou DH, Huang YT, Wang JF, Liu YZ, Wang H, Chen ZQ, Guo T (2019) Development of a core SNP arrays based on the KASP method for molecular breeding of rice. *Rice* 12:21
- Yapo ES, Kouakou TH, Kone M, Kouadio JY, Kouame P, Merillon JM (2011) Regeneration of pineapple (*Ananas comosus* L.) plant through somatic embryogenesis. *J Plant Biochem Biot* 20(2):196–204
- Zhang F, Ge YY, Wang WY, Yu XY, Shen XL, Liu JX, Liu XJ, Tian DQ, Shen FQ, Yu YM (2013) Molecular characterization of cultivated bromeliad accessions with inter-simple sequence repeat (ISSR) markers. *Int J Mol Sci* 13:6040–6052
- Zhang JS, Liu J, Ming R (2014) Genomic analyses of the CAM plant pineapple. *J Exp Bot* 65(13):3395–3404
- Zhang YF, Xu ZQ, Xie T, Zhang W, He YH, Liu CY (2022) In vitro selection and identification of a cold-tolerant variant in pineapple (*Ananas comosus*). *Hortic Environ Biotechnol* 63:275–286
- Zhao WZ, Shen XY (1978) Pineapple cultivation. Agriculture Press, Beijing
- Zhao WF, Yang WX, Wei CB, Sun GM (2011) A simple and efficient method for isolation of pineapple protoplasts. *Biotechnol Biotechnol Eq* 25(3):2464

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