HortScience 58(9):1005–1009. 2023. https://doi.org/10.21273/HORTSCI17047-22

New Germplasm for Breeding: Pink-flowered and White-fruited Strawberry

Ling Guan
Institute of Pomology, Jiangsu Academy of Agricultural Sciences, Jiangsu Key Laboratory for Horticultural Crop Genetic Improvement, Nanjing 210014, China

Zoe A. Wilson
Division of Plant and Crop Science, School of Biosciences, University of Nottingham, Sutton Bonington Campus, Sutton Bonington, Leicestershire LE12 5RD, UK

Mizhen Zhao, Yushan Qiao, Ejiao Wu, Qinglian Wang, Huazhao Yuan, Linlin Xu, Fuhua Pang, Weijian Cai, Xiaodong Chen, and Jin Xia
Institute of Pomology, Jiangsu Academy of Agricultural Sciences, Jiangsu Key Laboratory for Horticultural Crop Genetic Improvement, Nanjing 210014, China

Keywords. germplasm innovation, pink-flowered, strawberry breeding, white fruit

Abstract. **Most strawberry plants have white flowers and red fruit. We developed a new strawberry selection with pink flowers and white fruit, and named it G23. Basic phenotypic data were recorded over years of observation and experimentation with the flower crown diameter, petal color, and rate of fruit set, as well as fruit skin color, flesh color, seed color and attachment status, fruit weight and shape, soluble solids contents, and firmness. We found that G23 bloomed with a stable pink flower and produced white fruit consistently with a relatively high fruit-set rate compared with its female parent, 'Pink Panda'. G23 displayed high resistance to Fusarium wilt (*Fusarium oxysporum*) and anthracnose (*Colletotrichum* spp.). It is also tolerant of high temperatures (up to 40 °C) and long-term drought. The asexual propagation ability of G23 is high, with ~60 to 100 stolon ramets formed during the summer. In summary, this new pink-flowered and white-fruited strawberry germplasm is suitable for ornamental use, as a result of its remarkable flowering and fruiting characteristics. In addition, it provides opportunities for innovative strawberry germplasm for future breeding.**

Strawberry (*Fragaria* sp.) is a perennial herb in the Rosaceae family. The flower petals usually are white and the fruit color is mostly red, with only a small proportion of white or pink fruit for cultivation (Darrow 1966). Approximately 300 years ago, breeders in Europe used the wild octoploid strawberries *Fragaria chiloensis* and *Frugaria virginiana* to breed *Fragaria* ×*ananassa* Duch. with large fruit and white flowers for cultivation (Njuguna et al. 2013). The early strawberry fruit were mainly white, inherited from *F. chiloensis*, and widely cultivated in Chile (Dale and Sjulin 1990; Morales-Quintana and Ramos 2019). However, through the efforts of strawberry breeders worldwide, the bright-red cultivated strawberry rapidly became a mainstream global phenotype (Hardigan et al. 2021).

Strawberry flowers form in cyme inflorescence, which means that the flowers on the same inflorescence open in succession and have a long flowering period. During the past 20 years, many breeders have begun crossbreeding, selecting for ornamental, red-flowered strawberry varieties on a large scale (Bentvelsen and Bouw 2006; Mabberley 2002). The purple-flowered hexaploid marsh cinquefoil [*Potentilla palustris* (L.) Scop.] is closely related to the strawberry and was used as the red-flowered gene donor that was crossed with the cultivated strawberry (*Fragaria* ×*ananassa* Duch.). Thus, the first ornamental, red-flowered strawberry cultivar Pink Panda was produced (Asker 1971). However, the distant hybridization caused reproductive obstacles, such as a poor pollen–pistil compatibility, resulting in difficulty in bearing fruit or the tendency to produce deformed fruit. Therefore, the ornamental flowering and edible properties of the fruit could not be reproduced concomitantly (Gheorghe et al. 2012; Xue et al. 2019). This problem caused a bottleneck in the development of new varieties of ornamental strawberry.

Recently, however, progress has been made in the improvement of ornamental, red-flowered strawberry varieties. In China, many new varieties of ornamental strawberry have been bred with various flower colors and diverse petal types. Varieties with the same color, but considerable differences in color chromaticity were bred by Jiajun Lei and Li Xue, such as the red- or pink-flowered strawberry 'Pink Beauty', 'Pretty Beauty', 'Pink Princess', 'Sijihong', and 'Xiaotaohong' (Lei et al. 2015; Xue 2016; Xue et al. 2015, 2017). In addition, the Jiangsu Academy of Agricultural Sciences in China has bred ornamental strawberry cultivars with red or pink flowers and edible high-quality red fruit, such as 'Zijinhong' and 'Zijin Fenyu' (Wang et al. 2017, 2021). This study reports on the breeding processes and characteristics of a new strawberry cultivar that has pink flowers and white fruit, and provides a novel approach to creating and enriching strawberry germplasm resources.

Materials and Methods

The female parent 'Pink Panda' grows close to the ground and is cultivated in Nanjing, China. The stolons are mostly red, with the first node typically remaining dormant, whereas the second node can be grown and developed as an independent ramet. The flowering characteristics include a short peduncle, red flower (the red color becomes darker with colder winter temperatures), an average flower crown diameter of 1.82 cm, and typically five to seven petals on the flower (rarely eight or more). In open-field cultivation conditions, there are no or very few flowers in winter; however, many flowers blossom in the spring. The rate of fruit set reached the maximum in May in Nanjing; however, very few fruit are produced, and those that are produced are generally deformed (Fig. 1). The fruit size is tiny (average fruit transverse diameter, 0.82 cm), and the flavor is unfavorable and slightly sour, with little strawberry aroma. It is difficult to find the fruit in Nanjing in any month other than in May.

The male parent 'Hatsukoi', which produces white flowers with an average diameter of 1.43 cm, and white fruit with an average diameter of 2.21 cm, is suitable for cultivation in plastic tunnels (Fig. 1). The initial ripening period of the fruit of 'Hatsukoi' in Nanjing is in January, which is about 1 month later than that of conventional, red-fruited varieties such as 'Benihoppe' under the same cultivation conditions.

We adopted conventional breeding protocols. Configuration of cross combinations started in Spring 2016. We collected the 'Hatsukoi' mature flower buds, removed the petals, moved the

Received for publication 23 Dec 2022. Accepted for publication 13 Jun 2023.
Published online 11 Aug 2023.
We sincerely thank Xianfeng Meng, Longjing Wang, Jiaquan Liu, and Jinhong Yang, who are the technical staff at Jiangsu Academy of Agricultural Sciences, for nursing the strawberry germplasm accessions kindly and carefully.
This work was supported by funding from the National Key Research and Development Program of China (2019YFD1000800), the Xuzhou Science and Technology Planning Project (KC 21332), and the Jiangsu Seed Industry Revitalization "Unveiling and Commanding" Project [JBGS(2021)016].
M.Z. is the corresponding author. E-mail: njzhaomz@163.com.

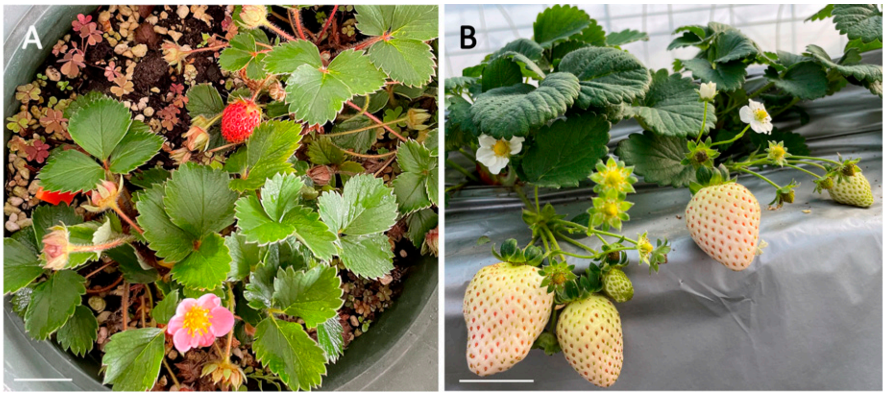

Fig. 1. Flowering and fruiting status of the female parent 'Pink Panda' (**A**) and male parent 'Hatsukoi' (**B**), separately. Scale bars in **A** and **B** are 1.0 and 2.0 cm, respectively.

anthers to the transfer-paper box, and dried them in cool conditions. When the release of anther pollen was complete, we collected the pollen and dried it at a low temperature (4 °C) for subsequent use. About 20 'Pink Panda' plants with good growth and sufficient flowers to be pollinated were selected as female parent plants for cross-pollination. We ensured there were more than 50 female parent plant flowers for cross-pollination to guarantee producing a sufficient number of progeny seedlings (> 2000 seedlings expected). Thirty days after cross-pollination, the mature fruit could be harvested, and the hybrid seeds collected. The seeds were dried and maintained at 4 °C for nearly 1 month for stratification and were then sown when the weather conditions were suitable.

In late Spring 2016, the hybrid seeds were sown in the substrate (peat, perlite, and vermiculite; 3:1:1, v/v), and the germinated seedlings were transferred into a plug tray where they underwent vegetative growth through the summer until they had grown into mature strawberry plants. In autumn, they were moved into the field for clonal propagation. Under the cultivation conditions of the polytunnel, the botanical characteristics, phenological observations, flower ornamental descriptions, fruit characteristics, and other indicators of these hybrid seedlings were recorded in detail. After a series of comprehensive investigations and evaluations, the best individual seedlings were selected. In Spring 2017, the selected seedlings were moved into the open field for asexual propagation. The phenotypes and relative values compared with parental selections were measured. In particular, ramet formation ability, disease resistance, and flowering and fruiting characteristics were recorded in 2017 and 2018. After 2 years of systematic phenotyping, analyses, and observations on their botanical, resistance, phenological, flowering, and fruiting characteristics, the new selections with bright and stable pink-colored flowers and relatively high-quality white fruit were selected, and a regional-level test was conducted in 2019 and 2020.

Results

Botanical records. We found that the new strawberry selection, which we named G23, had the ornamental characteristic of stable pink flowers and the quality characteristic of white fruit. This new germplasm of pink-flowered and white-fruited strawberry, G23, has a plant height of 7.0 to 10.0 cm, which is equal to or less than half of the height of normal cultivated strawberry (*Fragaria ×ananassa* Duch.); however, the root system is robust and shows a strong similarity to the cultivated strawberry. The morphological characteristics of the leaf are mostly inherited from the female parent 'Pink Panda', presenting a dark-green color and a leathery surface with medium-length trichomes. The first node of the stolon in G23 is mostly dormant; the second node can be grown and developed as an independent ramet. When there is sufficient sunlight, the stolon color is red. Color measurements for flower petals, fruit skin, fruit flesh, and any other color listed here were evaluated based on the Royal Horticultural Society Colour Chart (Royal Horticultural Society 2007). In Nanjing, stolons of G23 can be initiated from the crown axillary buds from May to October, with an average of 10 stolons per plant; approximately 60 to 100 stolon ramets can be formed from each mother-plant during the summer.

Resistance, phenological, and flowering observations. G23 is highly resistant to the prevalent and serious diseases of Fusarium wilt (*Fusarium oxysporum*) and anthracnose (*Colletotrichum* spp.) when compared with other main cultivated strawberry varieties, such as 'Benihoppe', 'Akihime', and 'Sweet Charlie', under the same cultivated conditions in Nanjing, China. It also demonstrates a strong tolerance to higher temperatures (up to 40 °C in the summer), with a good survival rate (up to 90%), even in the open field. It continues to flower and bear fruit from July to August (in temperatures ranging between 35.0 and 40.0 °C) in Nanjing in the summer. In open-field cultivation, the peak blossoming dates are from March to May; however, flowers and fruit can be seen at any time except during the extremely low temperatures experienced in winter. Under cultivation in the plastic tunnel, G23 initially entered the flowering period in October. In general, the initial ripening stage of G23 fruit is from the end of November to the beginning of December, which—based on our current knowledge—is earlier than most of the red- or pink-flowered strawberry cultivars. The low temperatures and deficiency of sunlight in winter causes the first crop of white fruit of G23 to be stable and uniform (Fig. 2). The color of the G23 flower petals ranges from pink to red, with the darker colors occurring at lower temperatures. The color of the base of the petals is darker compared with the distal portions of the petal. The stamens and pistils are typically yellow (Fig. 3). The crown diameter of the G23 flower is moderate compared with its parents (Table 1), which is attractive and suitable for ornamental use.

Fruiting characteristics. Open-field cultivation of G23 in Nanjing displays the best fruit-bearing capability in May. The rate of fruit set is much higher in G23 than in any other currently known red- or pink-flowered strawberry cultivars (Xue 2016). The fruit color of G23 is white, and under sufficient sunlight becomes slightly pink (Fig. 4C). During this period, the fruit size also reaches a maximum, with an average single fruit weight of 10.21 g (Table 2). The fruit shape of G23 is roughly conical (Fig. 4C), particularly in ideal conditions with a temperature of ∼25 °C and sufficient sunlight. The side of the fruit exposed to the sunlight is slightly pink, whereas the side of the fruit that is in the shade retains its original white color, which is similar to the color found in the male parent 'Hatsukoi'. The sepals of G23 grow close to the fruit, and the fruit neck is in close proximity to the sepals. The mature

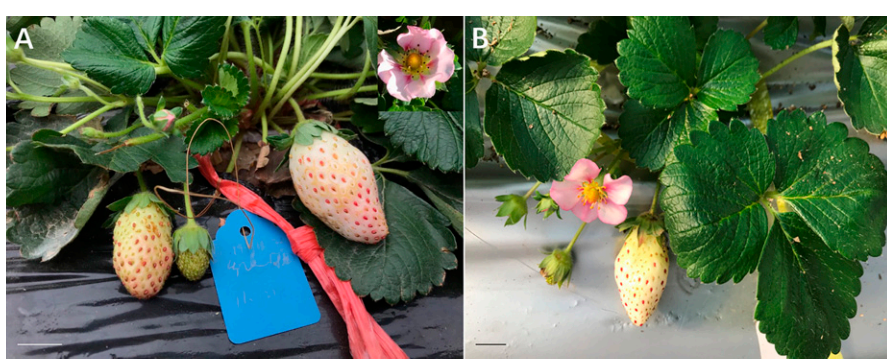

Fig. 2. Status of flowering and fruit bearing of G23 under the cultivation of ridge planting (**A**) and high bench (**B**) in the polytunnel, respectively. Scale bars are 1.0 cm.

Fig. 3. Flower presentation of the female parent 'Pink Panda' (**A**), male parent 'Hatsukoi' (**B**), and pink-flowered and white-fruited selection G23 (**C**), respectively. Scale bar is 1.0 cm.

Table 1. Flowering characteristics of G23 and its parent plants.[i]

Material	Petal color	Flower crown diam (cm)[ii]	Peak blossoming dates	Rate of fruit set (%)
Pink Panda	Red	1.82 ± 0.03	March to May	10.54 ± 0.51
Hatsukoi	White	1.43 ± 0.04	March to May	92.11 ± 0.78
G23	Pink	1.53 ± 0.05	March to May	70.65 ± 0.32

[i] The cultivation condition is in the open field.

[ii] Flower crown diameter means the diameter of the corolla. Data are the mean ± *SE* (n = 6). More than 100 plants of each material were planted for testing; six were selected as the typical representatives for acquiring statistics, the same as in Table 2.

seeds of G23 are red and embedded under the fruit surface. The flavor of the fruit is sweet and slightly sour; the average soluble solids content value is ~7.0° Brix, and the fruit has medium firmness (Table 2).

Discussion

Effects of temperature and light on strawberry coloration. Several studies have reported that environmental factors, especially temperature and light, affect the coloration of flowers and fruit of horticultural crops at different levels (Gruda 2005; Muhammad et al. 2022; Wang et al. 2022). Similarly, temperature and light have a significant effect on the flower and fruit coloring of strawberries (Khammayom et al. 2022; Zhang et al. 2018a, 2018b). In our study, the flower color of G23 in the colder winter is significantly darker than in the warmer spring in Nanjing. In contrast, G23 fruit maturation occurs in a period of low temperatures coupled with cloudy days, and the fruit color is almost white. However, when the temperature and sunlight increase in spring, G23 fruit have a light-pink coloring on the fruit surface exposed to light. The shaded side of G23 fruit, despite being exposed to the same warmer spring temperatures, retains the original white coloring. This indicates that G23 fruit coloration is more dependent on light intensity than temperature.

We speculate that the different responses of flower and fruit coloration in strawberries to environmental factors may be attributable to the different temperature response mechanisms in anthocyanin synthesis and accumulation during flowering and fruiting. For example, low temperature can be a stress factor in either flowering or fruiting. The darker color during strawberry flowering in response to a low temperature attracts insects more effectively for pollination, thus providing an advantage in genetic transmission. A low temperature during fruiting decreases the secondary metabolism rate of the strawberry fruit. We suggest that this may be because the synthesis and accumulation of anthocyanin-related substances, which are key for fruit coloration, are affected by low temperatures (Zhang et al. 2018b). However, heredity is the final determinant. Environmental factors such as temperature and light can only affect the change in chromaticity within a very limited range. Although a low temperature produces a darker petal in the red- or pink-flowered strawberry, and a low temperature coupled with a shortage of sunlight hinders fruit coloring, these environmental factors cannot make a white flower become red or pink, nor can a red-fruited strawberry produce white fruit.

Development of an ornamental flowered and edible-fruit strawberry germplasm will help meet diversified consumption and promote horticultural applications. With the gradual increase in demand of balcony gardening, there is a great market potential for ornamental flower and edible-fruit horticultural plants, particularly in the current pandemic situation, where the opportunity for people to walk freely outdoors is greatly reduced. Therefore, a novel direction for future breeding is to develop new horticultural germplasms with ornamental flowers and edible fruit, especially in perennial herbaceous plants such as strawberries. In our study, a new strawberry germplasm, G23, was established successfully over years of breeding. The G23 strawberry has pink flowers and white fruit, which is contrary to the traditional understanding that strawberries almost exclusively produce white flowers and red fruit, and—to a certain extent—it has shown potential market appeal.

Through a series of selections and improvements, the flower color of G23 is stable in pink, the fruit surface is white to slightly pink, and the red seeds are embedded in the fruit surface. According to our observations, G23 has high environmental adaptability; high resistance to Fusarium wilt (*Fusarium oxysporum*), anthracnose (*Colletotrichum* spp.), and *Tetranychus urticae* Koch, when compared with other main varieties or red-flowered

Fig. 4. Fruit surface, seed attachment status (left three), and flesh presentation (right three with longitudinal cutting) of female parent 'Pink Panda' (**A**), the male parent 'Hatsukoi' (**B**), and the pink-flowered and white-fruited selection G23 (**C**), respectively. Scale bar is 1.0 cm.

Table 2. Fruit quality of G23 and its parents.

Material	Peel color	Flesh color	Seed color and attachment status	Fruit transverse diam (cm)	Fruit wt (g)	Fruit shape	Soluble solids content (%)	Firmness (kg/cm^2)
Pink Panda	Red	Red	Red and surface	0.82 ± 0.02	4.85 ± 0.03	Globose	4.5 ± 0.3	0.30 ± 0.01
Hatsukoi	White	White	Red and surface	2.21 ± 0.06	13.64 ± 0.10	Conical	10.5 ± 0.4	0.52 ± 0.02
G23	White	White	Red and embedded	1.83 ± 0.04	10.21 ± 0.06	Conical	7.0 ± 0.2	0.38 ± 0.03

strawberry, which means it can produce flowers and fruit continuously; and displays a high ornamental value. In addition, the fruit of G23 has a similar aroma to commercial strawberry, with a pleasant sour–sweet flavor. G23 ramets present a high survival rate for transplanting and display strong adaptability in conditions of open-field, potting, or plastic tunnel cultivation. Suitable for most strawberry growers, this new strawberry germplasm has ornamental flowers and edible fruit.

Creation of a new strawberry germplasm via distant hybridization requires the joint effort of horticultural breeders worldwide. Strawberry plants have rich resources with diversified ploidy variations worldwide. There is strawberry germplasm with different ploidy, fruit aroma, fruit color, phenotype, and other characteristics. China is known as an important location in global horticulture, with the largest number of native wild strawberry species in the world (Lei et al. 2006). Currently, 14 of the known wild strawberry (*Fragaria*) species are native to China (Qiao et al. 2016, 2021; Sun et al. 2021). However, wild strawberry germplasm innovation and utilization status require further improvement. At present, only one interspecific hybrid cultivar, Tokun, has been commercialized successfully, by Japanese strawberry breeders. The breeders used the diploid wild strawberry (*Fragaria nilgerrensis* Schlecht.) and hybridized it with octoploid cultivated strawberry (*Fragaria* ×*ananassa* Duch.) to create 'Tokun' (Noguchi 2011; Ruan et al. 2020). This process involved initially obtaining pentaploid interspecific hybrids, then using colchicine to double the chromosome sets, which resulted in decaploid materials that were subsequently and continuously improved and bred selectively over a couple of years to obtain the Tokun cultivar. 'Tokun' inherited a unique peach aroma and white fruit color from the diploid wild strawberry (*F. nilgerrensis*). A few studies have used other wild strawberry germplasm, such as crossing the diploid strawberry *Fragaria viridis* Duch., which has a melon flavor and high resistance to biotic and abiotic stresses, with the cultivated strawberry (Shi et al. 2016, 2017; Su et al. 2018). In addition, the fruit of the European wild germplasm of hexaploid wild strawberry *Fragaria moschata* Duch. has a unique musky aroma, and the plant has a strong tolerance to stress and a robust plant morphology. Breeders have exerted considerable efforts into the applications of breeding this germplasm resource (Dávalos-González et al. 2022; Horvath et al. 2011; Marta et al. 2004; Olbricht et al. 2021); however, further improvements are required for commercialization. Additional studies on hybridization can be conducted on other related species.

The first use of the purple-flowered *Potentilla palustris* (L.) Scop. crossed with the cultivated strawberry to create the red-flowered strawberry is a good example. The yellow-flowered *Duchesnea*, which is widely distributed in China, is similar to strawberry phenotypically and has a strong adaptability to various environmental conditions. This is a close genus germplasm and may potentially develop colorful-flowered strawberry varieties (Marta et al. 2004). We speculate that a further possibility is the raspberry (such as *Rubus dianchuanensis* sp. nov., native to China), which belongs to the Rosaceae family and, similar to the strawberry, is an aggregate-fruit type. To ascertain whether it can be used successfully to crossbreed with the strawberry will require further study and experimentation. The creation of new strawberry germplasms necessitates a global effort involving horticultural breeders to diversify strawberry germplasm resources to offer colorful, diverse options for people to admire and consume worldwide.

References Cited

Asker S. 1971. Some viewpoints on *Fragaria* × *Potentilla* intergeneric hybridization. Hereditas. 67:181–190. https://doi.org/10.1111/j.1601-5223.1971.tb02372.x.

Bentvelsen G, Bouw B. 2006. Breeding ornamental strawberries. Acta Hortic. 708:455–458. https://doi.org/10.17660/ActaHortic.2006.708.80.

Dale A, Sjulin TM. 1990. Few cytoplasm contribute to North American strawberry cultivars. HortScience. 25:1341–1342. https://doi.org/10.21273/HORTSCI.25.11.1341.

Darrow GM. 1966. The strawberry: History, breeding and physiology. Holt, Rinehart and Winston, New York, NY, USA.

Dávalos-González PA, Aguilar-García R, Rodríguez-Guillén A, Jofre-y-Garfias AE. 2022. The genetic diversity of strawberry species, the underutilized gene pool and the need for cultivars with new quality and agronomic attributes. In: Kafkas NEY (ed). Recent studies on strawberries. IntechOpen Limited, London, UK. https://doi.org/10.5772/intechopen.102962.

Gheorghe RN, Popescu A, Popescu C, Deliu I. 2012. Assessment of genetic stability in micropropagated plants of some ornamental strawberry varieties. J Exp Mol Biol. 13:1. https://www.researchgate.net/publication/321062054.

Gruda N. 2005. Impact of environmental factors on product quality of greenhouse vegetables for fresh consumption. Crit Rev Plant Sci. 24:227–247. https://doi.org/10.1080/07352680591008628.

Hardigan MA, Lorant A, Pincot DDA, Feldmann MJ, Famula RA, Acharya CB, Lee S, Verma S, Whitaker VM, Bassil N. 2021. Unraveling the complex hybrid ancestry and domestication history of cultivated strawberry. Mol Biol Evol. 38:2285–2305. https://doi.org/10.1093/molbev/msab024.

Horvath A, Sánchez-Sevilla JF, Punelli F, Richard L, Sesmero Carrasco R, Leone A, Höefer M, Chartier P, Balsemin E, Barreneche T. 2011. Structured diversity in octoploid strawberry cultivars: Importance of the old European germplasm. Ann Appl Biol. 159:358–371. https://doi.org/10.1111/j.1744-7348.2011.00503.x.

Khammayom N, Maruyama N, Chaichana C. 2022. The effect of climatic parameters on strawberry production in a small walk-in greenhouse. AgriEngineering. 4:104–121. https://doi.org/10.3390/agriengineering4010007.

Lei J, Dai H, Tan C, Deang M, Zhao M, Qian Y. 2006. Studies on the taxonomy of the strawberry (*Fragaria*) species distributed in China. Acta Horticulturae Sinica. 33(1):1–5. https://www.cnki.net/kcms/doi/10.16420/j.issn.0513-353x.2006.01.001.html.

Lei J, Xue L, Dai H, Deng M. 2015. Two new pink-flowered strawberry cultivars 'Pink Beauty' and 'Pretty Beauty'. Acta Horticulturae Sinica. 42:599–600. https://www.cnki.net/kcms/doi/10.16420/j.issn.0513-353x.2014-0188.html.

Mabberley DJ. 2002. *Potentilla* and *Fragaria* (Rosaceae) reunited. Telopea (Syd). 9:793–801. https://doi.org/10.7751/telopea20024018.

Marta AE, Camadro EL, Díaz-Ricci JC, Castagnaro AP. 2004. Breeding barriers between the cultivated strawberry, *Fragaria* ×*ananassa*, and related wild germplasm. Euphytica. 136:139–150. https://doi.org/10.1023/B:EUPH.0000030665.95757.76.

Morales-Quintana L, Ramos P. 2019. Chilean strawberry (*Fragaria chiloensis*): An integrative and comprehensive review. Food Res Int. 119:769–776. https://doi.org/10.1016/j.foodres.2018.10.059.

Muhammad N, Luo Z, Yang M, Li X, Liu Z, Liu M. 2022. The joint role of the late anthocyanin biosynthetic UFGT-encoding genes in the flowers and fruits coloration of horticultural plants. Sci. Hortic. 301:111110. https://doi.org/10.1016/j.scienta.2022.111110.

Njuguna W, Liston A, Cronn R, Ashman T-L, Bassil N. 2013. Insights into phylogeny, sex function and age of *Fragaria* based on whole chloroplast genome sequencing. Mol Phylogenet Evol. 66:17–29. https://doi.org/10.1016/j.ympev.2012.08.026.

Noguchi Y. 2011. 'Tokun': A new decaploid interspecific hybrid strawberry having the aroma of the wild strawberry. J Japan Assoc Odor Environ. 42(2):122–128. https://doi.org/10.2171/jao.42.122.

Olbricht K, Ulrich D, Waurich V, Wagner H, Bicking D, Gerischer U, Drewes-Alvarez R, Gong X, Parniske M, Gompel N. 2021. Breeding potential of underutilized *Fragaria* species. Acta Hortic. 1309:139–146. https://doi.org/10.17660/ActaHortic.2021.1309.20.

Qiao Q, Edger PP, Xue L, Qiong L, Lu J, Zhang Y, Cao Q, Yocca AE, Platts AE, Knapp SJ. 2021. Evolutionary history and pan-genome dynamics of strawberry (*Fragaria* spp.). Proc Natl Acad Sci USA. 118:e2105431118. https://doi.org/10.1073/pnas.2105431118.

Qiao Q, Xue L, Wang Q, Sun H, Zhong Y, Huang J, Lei J, Zhang T. 2016. Comparative transcriptomics of strawberries (*Fragaria* spp.)

provides insights into evolutionary patterns. Front Plant Sci. 7:1839. https://doi.org/10.3389/fpls.2016.01839.

Royal Horticultural Society (RHS). 2007. RHS colour chart. London, UK: Royal Horticultural Society. https://www.rhs.org.uk/.

Ruan J, Wang G, Ning G, Yang C, Li F, Tian L, Wu L. 2020. Longer duration of short-day treatment is required to advance flowering and fruiting of decaploid strawberry 'Tokun'. HortScience. 55:30–34. https://doi.org/10.21273/HORTSCI14507-19.

Shi F, Pang F, Wang Q. 2016. Study on pollen viability of later generation of distant hybridization in strawberry. Modern Agric Sci Technol. 11:84–85. https://doi.org/10.3969/j.issn.1007-5739.2016.11.049.

Shi FQ, Wang Q, Zhao M, Wang J, Guan L. 2017. Identification of interspecific hybrids derived from *Fragaria ×ananassa × F. viridis* by morphological features and SSR markers. Guoshu Xuebao. 34:175–185. https://doi.org/10.13925/j.cnki.gsxb.20160201.

Su D, Tong J, Yang J, Chen S, Luo Z, Shen X, Lai Y, Arslan J, Wei S, Cui X. 2018. Advances in research, exploitation and utilization of *Fragaria* spp. germplasm resources in China. J Yunnan Univ Natural Sci Ed. 40:1261–1276. https://doi.org/10.7540/j.ynu.20180613.

Sun J, Sun R, Liu H, Chang L, Li S, Zhao M, Shennan C, Lei J, Dong J, Zhong C. 2021. Complete chloroplast genome sequencing of ten wild *Fragaria* species in China provides evidence for phylogenetic evolution of *Fragaria.* Genomics. 113:1170–1179. https://doi.org/10.1007/s12686-017-0713-5.

Wang Y, Zhang C, Xu B, Fu J, Du Y, Fang Q, Dong B, Zhao H. 2022. Temperature regulation of carotenoid accumulation in the petals of sweet *Osmanthus* via modulating expression of carotenoid biosynthesis and degradation genes. BMC Genomics. 23:418. https://doi.org/10.1186/s12864-022-08643-0.

Wang Q, Zhao M, Wang Z, Guan L, Liu J, Cai W, Xia J, Chen Z. 2021. Breeding report of a new strawberry cultivar with red flower Zijin Fenyu. Guoshu Xuebao. 07:1214–1216. https://doi.org/10.13925/j.cnki.gsxb.20210099.

Wang Q, Zhao M, Wang Z, Wu W, Qian Y. 2017. 'Zijinhong', a new red-flowered strawberry cultivar. Yuan Yi Xue Bao. 44:2425–2426. https://doi.org/10.16420/j.issn.0513-353x.2017-0211.

Xue L. 2016. Study on germplasm innovation and molecular mechanism of flower color formation in red-flowered strawberry. Shenyang Agricultural University, Shenyang, Liao Ning, China.

Xue L, Dai H, Lei J. 2015. Creating high polyploidy pink-flowered strawberries with improved cold tolerance. Euphytica. 206:417–426. https://doi.org/10.1007/s10681-015-1499-8.

Xue L, Lei J, Dai HP. 2017. Two new pink-flowered strawberry cultivars 'Sijihong' and 'Xiaotaohong'. Acta Hortic. 1156:141–144. http://doi.org/10.17660/ActaHortic.2017.1156.20.

Xue L, Liu Y, Wu X, Wang C, He J, Yue J, Lei J. 2019. Investigation on the flower and fruit characters of hybrids from the cross of red-flowered strawberry cvs Pink Beauty and Pretty Beauty. Shenyang Nongye Daxue Xuebao. 50:197–202.

Zhang Y, Hu W, Peng X, Sun B, Wang X, Tang H. 2018a. Characterization of anthocyanin and proanthocyanidin biosynthesis in two strawberry genotypes during fruit development in response to different light qualities. J Photochem Photobiol B Biology. 186:225–231. https://doi.org/10.1016/j.jphotobiol.2018.07.024.

Zhang Y, Liu Y, Hu W, Sun B, Chen Q, Tang H. 2018b. Anthocyanin accumulation and related gene expression affected by low temperature during strawberry coloration. Acta Physiol Plant. 40:192. https://doi.org/10.1007/s11738-018-2767-8.