Research and Development Strategies for Hybrid japonica Rice

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Abstract

The utilization of heterosis has resulted in significant breakthroughs in rice breeding. However, the development of hybrid japonica has been slow in comparison with that of hybrid indica. The present review explores the history and current status of hybrid japonica breeding. With the creation of japonica cytoplasmic male sterility and photo-thermo-sensitive genic male sterile lines, both three-line and two-line systems of hybrid rice have been created, and a series of hybrid japonica rice varieties have been developed and cultivated widely. At the same time, some progress has been made in genetic research of molecular mechanism for heterosis and QTL mapping for traits such as fertility, stigma exposure and flower time. In addition, genomics and transcriptome have been widely used in the research of hybrid rice, which provides a strong support for its development. Although the research on hybrid japonica has made many advances, there are still some restrictive problems. Based on the research and production of hybrid japonica rice, the prospect and development strategies of hybrid japonica rice are analyzed.

Keywords: Hybrid Japonica Rice, Three-line, Two-line, Heterosis

Introduction

Among more than 120 rice-producing countries, over 95% of them cultivate primarily indica varieties (Deng 2008; Fang 2005). Globally, only a few countries, such as China, Japan, South Korea, United States, Australia, and Egypt, produce and export japonica rice (Deng 2008). The japonica varieties occupy 8.8% of the rice farming area and are responsible for 14.2% of total rice production worldwide (Fang 2005). From 2007 to 2015, the total amount of rice traded on international markets increased from 32 million tons to 41.67 million tons, while the proportion of japonica rice trade decreased during the same time from 10.9% to 8.1%. This decrease corresponds to approximately 3.5 million tons, which is less than 5% of the amount of japonica rice consumed in China (Cao et al. 2018). China has the largest planting area and the highest total production of japonica rice in the world. Because the culinary quality of japonica is superior to that of the indica rice, the total production and demand for japonica rice has been increasing continuously in China, especial in Northeast China from 1990 to 2015 (Fig. 1, Fig. 2) (Tang et al. 2017). To meet the growing need, the share of the japonica in overall rice planting has been increasing recently, particularly in south China, the main indica producing area of the country.

The utilization of heterosis resulted in a major breakthrough in rice breeding, and the growing popularity of hybrid rice contributed significantly to world food production (Yuan 1987). In 1970, the wild abortive cytoplasm in rice was found in Hainan province, China, and in 1976, hybrid rice cultivars were released to farmers. In 1991, the area under hybrid rice was 17.6 million hectares, i.e., 55% of the total area occupied by hybrid rice in China. In particular, the current area of hybrid indica cultivation comprises more than 50% of the rice planting area (Pu et al. 2015). In contrast, the development of hybrid japonica was very slow, as it occupied...
less than 3% of the total planting area of japonica (Deng 2008). As the development of hybrids offers a great potential to increase the yield of rice, Yuan (2000) predicted that hybrid japonica is the most likely to make a breakthrough in the next 30 years, which will lead to a new growth point in China’s grain production. To further facilitate the development of the hybrid japonica rice, we have reviewed recent progress in research on the breeding of hybrid japonica and analyzed existing problems, thus providing a reference for the development of hybrid japonica rice.

The History of Research on Hybrid japonica Rice
The research on hybrid japonica rice was originated in Japan (Li and Wu 1991). In the 1950s, Weeraratne and Sampath first reported the phenomenon of cytoplasmic male sterility (CMS) in rice (Sampath and Mohauty, 1954). In 1958, CMS lines with the wild rice cytoplasm
were obtained for the first time by Katsuo and Mizushima by backcrossing Fujisaka 5 and Chinese red-awned wild rice; however, no restorer lines were found at that time (Deng 2008). In 1966, Shinjyo and O’mura developed the first CMS lines of Baotai (BT) type in the backcross of Chinsurah Bolo II indica rice from India and Taichung 65 from Taiwan and found a few conspecific restorer lines, but due to the inconspicuous heterosis, the three-line variety could not be widely promoted (Shinjyo C, O’ mura 1966; Shinjyo C 1969, 1972). Subsequently, Watanabe developed the CMS-Lead lines in the cross of Lead (Myanmar indica) and Fujisaka 5 (Deng 2008). American and Indian researchers developed japonica CMS lines with cytoplasm from Taiwan cultivars Birco and Oryza glaberrima (Deng 2008). The International Rice Research Institute (IRRI) launched the hybrid rice research program in 1977, and after more than 10 years of effort, they developed the first batch of hybrid rice parents and hybrid rice varieties in 1989. With the help of international organizations and China, the technology and the material were transferred to some rice-producing countries in Asia to develop the production of hybrid rice (Huang 2004).

At present, there are more than 120 rice-cultivating countries on five continents. Outside of China, 110 million ha of rice are cultivated worldwide, mostly in Asia, Africa, and the Americas (Deng 2008; Hu 2010), and the area occupied by hybrid rice reached 6.36 million ha in 2014. Of these, 5.91 million ha were in Asia, and 0.45 million ha were in South and North America. The countries growing hybrid rice included Bangladesh, Pakistan, India, Indonisia, the Philippines, Myanmar, Vietnam, Sri Lanka, Iran, United States, Brazil, Argentina and Uruguay. China, India, Bangladesh, Pakistan, Indonesia, the Philippines, Myanmar, Vietnam, and the United States are the major countries growing hybrid rice. Hybrid rice in the United States accounts for more than half of its total rice production area. However, as the indica hybrid was the dominant rice in these countries, the breeding and promotion of hybrid japonica rice were limited (Xie and Peng 2016).

Research Progress of Hybrid japonica Rice in China

Since the 1960s, breeders led by Li Z and Yang Z have been carrying out research on hybrid japonica rice (Li 1977, 2000; Li and Wu Jl. 1991; Yang 1994, 1998, 1999, 2005, 2016). Over the past 50 years, remarkable progress has been made in the breeding of hybrid japonica rice. By 2019, China has approved 396 hybrid japonica rice combinations, whose parents, variety types, and time of being certified are listed in Table 1. As can be seen from Table 1 and Fig. 3, most of the varieties were generated between 2000 and 2019, and the hybrid japonica rice accounts for 88.4% of the total number of cultivars, while indica-japonica varieties for only 11.6%. Among these hybrid japonica rice varieties, the majority (360) are three-line varieties, and only 36 are two-line varieties.

A Three-Line System for Hybrid japonica Rice

The three-line system is composed of sterile line, maintainer line, and restorer line. The discovery of sterile lines enabled large-scale production of hybrid rice. The key to the breeding of hybrid japonica rice is finding suitable restorer lines that can restore the male sterile lines and improve the heterosis.

Dian-Type Male Sterile Lines

The study of hybrid japonica rice in China began in 1965. A naturally sterile plant was found in the Taipei 8, and was used as a female to develop the CMS-Dian I via nuclear replacement from japonica cultivar Hongmaoying in 1969. CMS-Dian I was the first and the most significant japonica CMS line in China (Li 2000; Yang 2016). Subsequently, japonica CMS lines, such as Dian-II, Dian-III, Dian-IV, Dian-V, Dian-VI, Dian-VII, and Dian-VIII were generated in the same manner. Although the lack of restorer lines limited the application of these CMS-Dian lines in the three-line system, they formed the foundation for the development of japonica hybrid rice in southwest, northwest, and eastern provinces of China (Li 1977). With the breakthrough achievement of creating Dian-type hybrid japonica rice, a number of stable CMS lines (Dianyu 1A, Dianxun 1A, Liyu A, and Yumi 15A) were developed, which were further used to create other hybrid japonica varieties, such as Yuzu 29, Xunza 36, Dianza 32, Dianza 31, Yunguang 8, Yunguang 9, Yunguang 12, and Yunguang 14. These varieties not only exhibit a higher production of hybrid seeds but also display stronger heterosis and higher resistance to the blast disease in the F1 generation (Huang 2004; Yang 2016).

BT-Type Male Sterile Lines

In 1972, the CMS-BT line Taichung 65 was introduced from Japan by the Liaoning Academy of Agricultural Sciences (LAAS) and the Chinese Academy of Agricultural Sciences. This line was used as the female parent to develop several CMS-BT lines, such as Liming A, Xueling A, Akihikari A, Sasanishiki A, Liuqiangxin A, Sidao 8A, Wuyunjing 7A, Hanfeng A, Xiushui 4A, Zhong 7941A, 41A, Ning 67, and Yongjing 2A. However, all these lines lacked appropriate japonica restorer lines (Deng 2008). In 1975, using the “indica-japonica bridging technique”, LAAS introduced restorer genes from indica to japonica by backcross of IR8 / Keqing 3 // Keqing 3. As a result, the japonica restorer line C57 with...
Table 1 List of hybrid *japonica* rice varieties bred in China

| Varieties       | Female     | Male        | Type          | Subspecies    | Year of release |
|-----------------|------------|-------------|---------------|---------------|-----------------|
| Li you 57       | Li ming A  | CS7         | Three-lines   | Japonica      | 1980            |
| Xiu you 57      | Xiu ling A | CS7         | Three-lines   | Japonica      | 1984            |
| Dang you C bao  | Dang xia nwan 3 A | C Bao | Three-lines   | Japonica      | 1985            |
| Di you 57       | D 57 A     | CS7-10      | Three-lines   | Japonica      | 1985            |
| Ji jing za 1    | Li ming A  | K55         | Three-lines   | Japonica      | 1986            |
| Qiu you 20      | Qiu guang A| F20         | Three-lines   | Japonica      | 1986            |
| Yan you 57      | Yan jing 903 A | CS7V       | Three-lines   | Japonica      | 1988            |
| Han you xiang qing | Han feng A | xiang qing | Three-lines   | Japonica      | 1989            |
| Liu you 3-2     | Liu qian xin A | ning hui 3-2 | Three-lines   | Japonica      | 1989            |
| Dang you 9      | Dang xuan wan 2 A | wan hui 9 | Three-lines   | Japonica      | 1989            |
| Feng you 9      | Feng jin A | C79-64      | Three-lines   | Japonica      | 1989            |
| 76 you 312      | 76-27 A    | pei C312    | Three-lines   | Japonica      | 1990            |
| Han you 1027    | Han feng A | T1027       | Three-lines   | Japonica      | 1990            |
| Ai you 82       | Dong jiu ai 4 A | hong yu 82 | Three-lines   | Japonica      | 1990            |
| Qi you 6        | 76-27A     | 2674        | Three-lines   | Japonica      | 1990            |
| Xun za 29       | Dian xun 1 A | nan 29      | Three-lines   | Japonica      | 1991            |
| Wan dao 16      | Liu qian xin A | Cbao       | Three-lines   | Japonica      | 1992            |
| Xin dao 4       | –          | –           | Three-lines   | Japonica      | 1992            |
| Xin dao 3       | Liao 10120A | hui 73-28   | Three-lines   | Japonica      | 1992            |
| Wan dao 18      | Liu qian xin A | 82,022     | Three-lines   | Japonica      | 1992            |
| Xu you 3-2      | Xu dao 2 A | ning hui 3-2 | Three-lines   | Japonica      | 1993            |
| Si you 422      | Si dao 8 A | lun hui 422 | Three-lines   | Japonica      | 1993            |
| Jing you 6      | Zhong zuo 59 A | jin 1244-2 | Three-lines   | Japonica      | 1993            |
| Wan dao 26      | 7001S      | xiu shui 04 | Two-lines     | Japonica      | 1994            |
| Wan dao 22      | 80-4 A     | wan hui 9   | Three-lines   | Japonica      | 1994            |
| 70 you 9        | 7001S      | wan hui 9   | Two-lines     | Japonica      | 1994            |
| Ning you 1      | 552 A      | FR-79       | Three-lines   | Japonica      | 1994            |
| Si you 9083     | Si dao 8 A | C9083       | Three-lines   | Japonica      | 1994            |
| E jing za 1     | N5088S     | R187        | Two-lines     | Japonica      | 1995            |
| 8 you 161       | 8204 A     | R161        | Three-lines   | Japonica      | 1995            |
| Hua jing za 1   | 7001S      | R1514       | Two-lines     | Japonica      | 1995            |
| Yu za 29        | Dian yu 1 A | nan 29-1    | Three-lines   | Japonica      | 1995            |
| Wan dao 34      | 80-4 A     | HP121       | Three-lines   | Japonica      | 1996            |
| 9 you 138       | Xu 9201 A  | N138        | Three-lines   | Japonica      | 1996            |
| Liu you 3       | Liu qian xin A | yin hui 3  | Three-lines   | Japonica      | 1996            |
| Qi you 7        | 76-27 A    | K1457       | Three-lines   | Japonica      | 1996            |
| Wan dao 48      | 7001S      | shuang jiu  | Two-lines     | Japonica      | 1997            |
| Si you 9022     | Sidao 8 A  | C9022       | Three-lines   | Japonica      | 1997            |
| Qiu you 62      | Qiu guang A| C9162       | Three-lines   | Japonica      | 1997            |
| Wan dao 46      | 80-4 A     | T1027       | Three-lines   | Japonica      | 1997            |
| Ti you 418      | Ti jin A   | C418        | Three-lines   | Japonica      | 1998            |
| Min you 128     | 83 A       | R128        | Three-lines   | Japonica      | 1998            |
| Liu you 121     | Liu qian xin A | HP121      | Three-lines   | Japonica      | 1998            |
| Si you 88       | Sidao 8 A  | hui 88      | Three-lines   | Japonica      | 1998            |
| Varieties     | Female       | Male            | Type      | Subspecies | Year of release |
|--------------|--------------|-----------------|-----------|------------|-----------------|
| Si you 418   | Sidao 8 A    | C418            | Three-lines| Japonica   | 1999            |
| Wan dao 50   | 4008S        | xiu shui 04    | Two-lines | Japonica   | 1999            |
| Si you 523   | Sidao 8 A    | R523            | Three-lines| Japonica   | 1999            |
| Jin jing za 1| LS2S         | zhong zuo93     | Two-lines | Japonica   | 1999            |
| 9 you 418    | Xu 9201 A    | C418            | Three-lines| Japonica   | 2000            |
| Yong you 1   | Ning 67 A    | K1722           | Three-lines| Japonica   | 2000            |
| Ning you 2   | 401 A        | R253            | Three-lines| Japonica   | 2000            |
| Yun guang 8  | N5088S       | yun hui 11      | Two-lines | Japonica   | 2000            |
| 8 you 682    | Xu 8908 A    | R37682          | Three-lines| Japonica   | 2000            |
| 8 6you 8     | 863 A        | ning hui 8     | Three-lines| Japonica   | 2000            |
| 3you 18      | Jin 3 A      | C418            | Three-lines| Japonica   | 2001            |
| Liao you 5218| Liao S216 A  | C418            | Three-lines| Japonica   | 2001            |
| Hua jing za 2| N5088S       | 41,678          | Two-lines | Japonica   | 2001            |
| Yong you 2   | Yongjing 2 A | K1722           | Three-lines| Japonica   | 2001            |
| Si you 3418  | Liao 326A    | C418            | Three-lines| Japonica   | 2001            |
| Jin jing za 3| Zao hua dong A| c you 1         | Three-lines| Japonica   | 2001            |
| 69 you 8     | Xu 69A       | R11238          | Three-lines| Japonica   | 2001            |
| Yan you 1    | Yan jing 5 A | yun hui 93,005 | Three-lines| Japonica   | 2001            |
| Liao you 4418| Xiu ling A   | C418            | Three-lines| Japonica   | 2001            |
| Liao you 5   | Liao yan 28 A| S04–6          | Three-lines| Japonica   | 2001            |
| Jin jing za 2| Jin 3 A      | C272            | Three-lines| Japonica   | 2001            |
| Lyyou 98     | MH2003 A     | R18             | Three-lines| Japonica   | 2002            |
| Chang you 1  | Wu yun jing 7 A| shen hui 254 | Three-lines| Japonica   | 2002            |
| Yong you 3   | Yongjing 2 A | K1863           | Three-lines| Japonica   | 2002            |
| Dian za 31   | Yu mi 15 A   | nan 34          | Three-lines| Japonica   | 2002            |
| Shen you 1   | 8204 A       | shen hui 1     | Three-lines| Japonica   | 2002            |
| Liu you 8    | Liu qian xin A| HP121–8        | Three-lines| Japonica   | 2002            |
| Dian za 32   | Li yu A      | nan 34          | Three-lines| Japonica   | 2002            |
| Min you 55   | 2615         | min55           | Two-lines | Japonica   | 2002            |
| Jin jing za 4| S02 A        | R411            | Three-lines| Japonica   | 2002            |
| Liao you 1518| Liao 151 A   | C418            | Three-lines| Japonica   | 2002            |
| Yun guang 9  | 7001 S       | yun hui 124    | Two-lines | Japonica   | 2002            |
| Liao you 2021| Liao 02 A    | C01             | Three-lines| Japonica   | 2002            |
| Pu you 801   | 69 A         | J60             | Three-lines| Japonica   | 2002            |
| 86 you 242   | 863 A        | R242            | Three-lines| Japonica   | 2002            |
| Ba you 8     | 8204 A       | R9525           | Three-lines| Japonica   | 2002            |
| Xin za jing 1| Pei ai 64S   | yu jing 3      | Two-lines | Japonica   | 2003            |
| Jin jing za 5| Zao hua dong A| 773             | Three-lines| Japonica   | 2003            |
| Xiang you 18 | Ai zhi xiang A| MR18           | Three-lines| Japonica   | 2003            |
| Liang you pei jing | Pei ai 64S | 94,205         | Two-lines | Japonica   | 2003            |
| Ning you 3   | Zhong zuo59 A| 1229            | Three-lines| Japonica   | 2003            |
| Wan dao 74   | 80–4 A       | wan hui 98     | Three-lines| Japonica   | 2003            |
| Yan you 2    | Yan 93,538 A | lun hui 422    | Three-lines| Japonica   | 2003            |
| Variety   | Female       | Male       | Type        | Subspecies | Year of release |
|-----------|--------------|------------|-------------|------------|-----------------|
| jing you 15 | Zhong zuo 59 A | Y772      | Three-lines | Japonica   | 2003            |
| shen you 4  | Shen 4 A      | xiang qing | Three-lines | Japonica   | 2003            |
| liao you 14 | Liao 30 A     | C4115      | Three-lines | Japonica   | 2003            |
| yun guang 12 | 95076S       | yun hui 124 | Two-lines   | Japonica   | 2003            |
| min you xiang jing | 261S | Wxiang 99,075 | Two-lines   | Japonica   | 2003            |
| yan liang you 2818 | GBO28S | C418      | Two-lines   | Japonica   | 2003            |
| jin you 2003 | 341 A         | 773        | Three-lines | Japonica   | 2003            |
| wan dao 72   | 80-4 A        | 2277       | Three-lines | Japonica   | 2003            |
| yong you 4    | Yong jing 2 A | K2001      | Three-lines | Japonica   | 2003            |
| wan dao 70    | 80-4 A        | MR19       | Three-lines | Japonica   | 2003            |
| dong jing za 3 | N5088S       | minhui 128 | Two-lines   | Japonica   | 2004            |
| liao you 16   | Liao 30 A     | C272       | Three-lines | Japonica   | 2004            |
| wan dao 80    | Shuang jiu A  | wan hui 3402 | Three-lines | Japonica   | 2004            |
| wan dao 78    | Y A           | 9 M059     | Three-lines | Japonica   | 2004            |
| yu za 34      | Dian yu 1 A   | nan 34     | Three-lines | Japonica   | 2004            |
| wan han you 1 | N4225         | R8272      | Two-lines   | Japonica   | 2004            |
| dian za 33    | Yu mi 15 A    | dian nong R-3 | Three-lines | Japonica   | 2004            |
| wan dao 76    | Ai zhi xiang A | MC20518   | Three-lines | Japonica   | 2004            |
| jing you 14   | Zhong zuo 59 A | jin dao 1229 | Three-lines | Japonica   | 2004            |
| shen you 254  | Shen 6 A      | shen hui 254 | Three-lines | Japonica   | 2004            |
| 10 you 18     | 10 A          | R148       | Three-lines | Japonica   | 2004            |
| yong you 6    | Yongjing 2 A  | K4806      | Three-lines | Japonica   | 2005            |
| xiu you 5     | Xiu shui 110 A | xi hui 69 | Three-lines | Japonica   | 2005            |
| jia you 1      | Jia 60 A      | jia hui 40 | Three-lines | Japonica   | 2005            |
| liao you 1052 | 105 A         | CS2        | Three-lines | Japonica   | 2005            |
| jia le you 2   | 151 A         | DH32       | Three-lines | Japonica   | 2005            |
| liao you 853  | Nong lin 150A | R853       | Three-lines | Japonica   | 2005            |
| chang you 3    | Wu yun jing 7 A | R192    | Three-lines | Japonica   | 2005            |
| yong you 5     | Yong nuo 2 A  | K6926      | Three-lines | Japonica   | 2005            |
| jing you 13    | Zhong zuo 59 A | lu hui 3  | Three-lines | Japonica   | 2005            |
| zhe you 9      | 5016 A        | zhe hui 9816 | Three-lines | Japonica   | 2005            |
| shen you 693   | Shen 6 A      | R693       | Three-lines | Japonica   | 2005            |
| xu you 201     | Xu 9320 A     | xu hui 201 | Three-lines | Japonica   | 2005            |
| su you 22      | Wu yun jing 7 A | R16189   | Three-lines | Japonica   | 2005            |
| zhong jing you 1 | Jin 6 A       | jin hui 1 | Three-lines | Japonica   | 2005            |
| chang you 2    | Wu yun jing 7 A | CS3      | Three-lines | Japonica   | 2005            |
| liao you 2006  | Liao 20 A     | C2106      | Three-lines | Japonica   | 2005            |
| yong you 8     | Yong jing 3 A | K6876      | Three-lines | Japonica   | 2006            |
| qiu you jin feng | Qiu feng A   | R44        | Three-lines | Japonica   | 2006            |
| ai you 39      | Ai zhi xiang A | MR39      | Three-lines | Japonica   | 2006            |
| shen you 8     | Shen 4 A      | R8         | Three-lines | Japonica   | 2006            |
| dian za 80     | Dian I-11A    | nan 34     | Three-lines | Japonica   | 2006            |
| ling xiang you 18 | Ling xiang A | YC418     | Three-lines | Japonica   | 2006            |
| jin jing you 68 | Jin 1007A     | jin hui 68 | Three-lines | Japonica   | 2006            |
Table 1 List of hybrid *japonica* rice varieties bred in China (Continued)

| Varieties          | Female    | Male       | Type      | Subspecies | Year of release |
|-------------------|-----------|------------|-----------|------------|-----------------|
| yongyou 1460      | Yongjing 2 A | T1460      | Three-lines | Japonica   | 2006            |
| wan dao 88        | 9201 A    | R-8        | Three-lines | Japonica   | 2006            |
| jin jing you 88   | Jin 1007 A | jinhui 88  | Three-lines | Japonica   | 2006            |
| ba you 52         | 8204 A    | Z052       | Three-lines | Japonica   | 2006            |
| liao you 2016     | Liao 20 A  | C216       | Three-lines | Japonica   | 2006            |
| liao you 2015     | Liao 20 A  | C4115      | Three-lines | Japonica   | 2006            |
| dian za 36        | He x 42-7 A | nan 36     | Three-lines | Japonica   | 2006            |
| jin jing you 28   | Jin 1007 A | jinhui 28  | Three-lines | Japonica   | 2006            |
| jin jing you 9    | Jin 341 A  | C4115      | Three-lines | Japonica   | 2006            |
| jin jing you 10   | Yong jing 2 A | K6093     | Three-lines | Japonica   | 2006            |
| jia you 2         | Jia 60 A   | jiahui 30  | Three-lines | Japonica   | 2006            |
| xu you 733        | Xu 364 A   | xuhui 11,733 | Three-lines | Japonica   | 2006            |
| dian you 34       | Dian jing you 1 A | nan 34 | Three-lines | Japonica   | 2006            |
| chun you 58       | Chun jiang 12 A | CH58   | Three-lines | Japonica   | 2006            |
| jing za you 1     | 80-4 A    | jinhui 1   | Three-lines | Japonica   | 2006            |
| chang you 4       | Wu yun jing 7 A | CR-25   | Three-lines | Japonica   | 2006            |
| shuang you 3404   | Shuang jiu A | wan hui 3404 | Three-lines | Japonica   | 2006            |
| tian xie 13       | Xu 9320 A  | xuhui 11,733 | Three-lines | Japonica   | 2006            |
| shen you 9723     | Shen 97 A  | R4023      | Three-lines | Japonica   | 2006            |
| jin jing you 180  | Jin 5 A    | R180       | Three-lines | Japonica   | 2006            |
| su jing you 3      | 9703 A    | xiangqing  | Three-lines | Japonica   | 2006            |
| yong you 11       | Yong jing 2 A | K216211 | Three-lines | Japonica   | 2006            |
| liao you 5273     | Liao 5216 A | C73       | Three-lines | Japonica   | 2006            |
| zhong jing you 470 | Zhong zuo 59 A | C470   | Three-lines | Japonica   | 2006            |
| xu you 169        | jia hua 1 A | XB69      | Three-lines | Japonica   | 2006            |
| T you 5           | 951 A      | R981       | Three-lines | Japonica   | 2006            |
| 5 you 135         | jin 5 A    | C135       | Three-lines | Japonica   | 2006            |
| jin jing you 116  | jin 6 A    | R116       | Three-lines | Japonica   | 2006            |
| hua you 14        | shen 9 A   | fan 14     | Three-lines | Japonica   | 2006            |
| xin dao 22        | LA3        | LC64       | Three-lines | Japonica   | 2006            |
| ti you 267        | ti jin A   | C267       | Three-lines | Japonica   | 2006            |
| 5 you 280         | jin 5 A    | R280       | Three-lines | Japonica   | 2006            |
| qiu you 118       | qiu feng A | R118       | Three-lines | Japonica   | 2006            |
| 5 you 190         | jin 5 A    | R190       | Three-lines | Japonica   | 2006            |
| zhong jing you 8  | jin jing 12 A | jinhui 3 | Three-lines | Japonica   | 2006            |
| fu you 135        | fu A       | C135       | Three-lines | Japonica   | 2006            |
| xu 2you 1         | xu 20,111 A | xuhui 201 | Three-lines | Japonica   | 2006            |
Table 1 List of hybrid *japonica* rice varieties bred in China (Continued)

| Varieties         | Female     | Male             | Type       | Subspecies | Year of release |
|-------------------|------------|------------------|------------|------------|-----------------|
| 6you 160          | jin 6 A    | R160             | Three-lines| Japonica   | 2008            |
| zhe jing you 1    | zhe jing 2 A | zhe jing hui 04-02 | Three-lines | Japonica   | 2008            |
| zhe you 10        | 8204 A     | zhe hui 9816     | Three-lines| Japonica   | 2008            |
| xin 8 you 122     | xin 8 A    | GR03122          | Three-lines| Japonica   | 2008            |
| zhe you 12        | zhe 04 A   | zhe hui H414     | Three-lines| Japonica   | 2008            |
| chun you 59       | chun jiang 16 A | CH59            | Three-lines| Japonica   | 2009            |
| yun liang you 144 | 23015      | yun R144         | Two-lines  | Japonica   | 2009            |
| jin 7 you 18      | jin feng 7 A | jin hui 18      | Three-lines| Japonica   | 2009            |
| xiu you 378       | xiu shui 3 A | XR78            | Three-lines| Japonica   | 2009            |
| zhe jing you 2    | zhe jing 3 A | zhe jing hui 04-02 | Three-lines | Japonica   | 2009            |
| shen you fan 15   | shen 10 A  | shen fan 15     | Three-lines| Japonica   | 2009            |
| chun you 172      | chun jiang 12 A | C172          | Three-lines| Japonica   | 2009            |
| liao you 9573     | liao 95 A  | C73              | Three-lines| Japonica   | 2009            |
| jin 7 you 58      | jin feng 7 A | jin hui 58      | Three-lines| Japonica   | 2009            |
| 95 you 161        | 95,122 A   | R161             | Three-lines| Japonica   | 2009            |
| chun you 658      | chun jiang 16 A | CH58          | Three-lines| Japonica   | 2009            |
| dian za 86        | D5 A       | nan 34           | Three-lines| Japonica   | 2009            |
| xu you 502        | xu 8908 A  | xu hui 502       | Three-lines| Japonica   | 2009            |
| zhong jing you 13 | jin jing 13 A | jin hui 3       | Three-lines| Japonica   | 2009            |
| yong you 14       | yong jing 3 A | F5006          | Three-lines| Japonica   | 2009            |
| 5 you 360         | jin 5 A    | R360             | Three-lines| Japonica   | 2009            |
| dian za 40        | chu jing 23 A | nan 34         | Three-lines| Japonica   | 2009            |
| jia you 608       | jia 60 A   | jia hui 82       | Three-lines| Japonica   | 2009            |
| 3 you 88          | jin 3 A    | LC50–88          | Three-lines| Japonica   | 2009            |
| xin han you 26    | pei ai 64S | 99,026           | Two-lines  | Japonica   | 2009            |
| liao you 1498     | 14 A       | C198             | Three-lines| Japonica   | 2009            |
| yun you 948       | G2480 A    | yun R948         | Three-lines| Japonica   | 2009            |
| dian za 501       | D5 A       | Y-11             | Three-lines| Japonica   | 2009            |
| ji liao you 1     | liao 99 A  | C746             | Three-lines| Japonica   | 2009            |
| xin dao 25        | LA3        | LC109            | Three-lines| Japonica   | 2009            |
| jia you 3         | jia 335 A  | jia hui 32       | Three-lines| Japonica   | 2009            |
| xu 68 you 201     | xu 91,068 A | xu hui 201     | Three-lines| Japonica   | 2009            |
| jin 9 you 78      | jin feng 9 A | jin hui 78      | Three-lines| Japonica   | 2009            |
| dian za 41        | he xi 42–7 A | nan 43         | Three-lines| Japonica   | 2009            |
| ba you 315        | 8204 A     | zhe hui H315     | Three-lines| Japonica   | 2009            |
| zhong zhong you 2005 | 25 A  | R18             | Three-lines| Japonica   | 2009            |
| yong you 12       | yong jing 2 A | F5032         | Three-lines| Japonica   | 2010            |
| yun guang 101     | N950765    | yun jing hui 1  | Two-lines  | Japonica   | 2010            |
| jia le you 100    | 151 A      | GR100            | Three-lines| Japonica   | 2010            |
| su you 72         | su 77 A    | su hui 162       | Three-lines| Japonica   | 2010            |
| jin jing you 132  | jin jing 13 A | jin hui 2     | Three-lines| Japonica   | 2010            |
| chang you 5       | chang 01–11 A | CR-27         | Three-lines| Japonica   | 2010            |
| jing liang you 5975 | 02595  | gr75             | Two-lines  | Japonica   | 2010            |
| han you 8         | hu han 2 A  | xiang qing      | Three-lines| Japonica   | 2010            |
| Varieties       | Female            | Male            | Type       | Subspecies | Year of release |
|----------------|-------------------|-----------------|------------|------------|-----------------|
| zhong jing you 15 | jin jing 12 A      | jin hui 5       | Three-lines | Japonica   | 2010            |
| yong you 13      | yong jing 3 A      | F5032           | Three-lines | Japonica   | 2010            |
| dian za 37       | he xi 42–7 A       | yin hui 1       | Three-lines | Japonica   | 2010            |
| liao you 9906    | liao 99 A          | C2106           | Three-lines | Japonica   | 2010            |
| yong you 7       | yong jing 3 A      | K6262           | Three-lines | Japonica   | 2010            |
| long you 1715    | long 17 A          | R1415           | Three-lines | Japonica   | 2010            |
| jia pu you 608   | jia 335 A          | jia hui 52      | Three-lines | Japonica   | 2010            |
| bi jia za 2035   | BI-1 A             | ZC2035          | Three-lines | Japonica   | 2010            |
| shen you 1       | S A                | C3              | Three-lines | Japonica   | 2010            |
| jing liang you 2847 | NC228S            | R4769           | Two-lines   | Japonica   | 2010            |
| jia you 5        | jia 335 A          | jia hui 125     | Three-lines | Japonica   | 2010            |
| dian you 35      | DHC-10 A           | nan 34          | Three-lines | Japonica   | 2010            |
| dan jia you 8    | dan jia 4 A        | dan hui 8       | Three-lines | Japonica   | 2011            |
| dian za 46       | he xi 42–7 A       | nan 46          | Three-lines | Japonica   | 2011            |
| jing you 558     | jing 139 A         | R558            | Three-lines | Japonica   | 2011            |
| shen you 16      | shen 46 A          | shen fan 16     | Three-lines | Japonica   | 2011            |
| yun guang 109    | N95076S            | yun jia hui 7   | Two-lines   | Japonica   | 2011            |
| yun guang 104    | N95076S            | yun jia hui 4   | Two-lines   | Japonica   | 2011            |
| xin jing you 1   | xin dao 97,200 A   | xin hui 3       | Three-lines | Japonica   | 2011            |
| xin dao 38       | LA28               | LC109           | Three-lines | Japonica   | 2011            |
| yun guang 107    | yun jia 202 s      | yun jia hui 7   | Two-lines   | Japonica   | 2011            |
| jiao jia 1       | jiao 31 A          | jiao hui 2      | Three-lines | Japonica   | 2011            |
| dong jing you 775 | dong wan 17 A      | jing xiang 75   | Three-lines | Japonica   | 2011            |
| dian za 94       | D5A                | Y-16            | Three-lines | Japonica   | 2011            |
| yong you 17      | yong jia 4 A       | yonghui 12      | Three-lines | Japonica   | 2012            |
| zhe you 18       | zhe 04 A           | zhe hui 818     | Three-lines | Japonica-indica | 2012 |
| dian you 38      | DHC-10 A           | dian hui 8 R-5  | Three-lines | Japonica   | 2012            |
| chun you 618     | chun jia 16 A      | C18             | Three-lines | Japonica   | 2012            |
| shuang you 18    | shuang jia A       | C418            | Three-lines | Japonica   | 2012            |
| shen you 99      | shen wu 1 A        | shen fan 16     | Three-lines | Japonica   | 2012            |
| 6you 33          | 1586S              | xin jia 5003    | Two-lines   | Japonica   | 2012            |
| bao jia za 2     | N95076S            | BR-4            | Two-lines   | Japonica   | 2012            |
| xin dao 40       | LRA3               | LRC64           | Three-lines | Japonica   | 2012            |
| dian za 701      | D5 A               | dian kun xiang 4| Three-lines | Japonica   | 2012            |
| jia he you 555   | jia he 212 A       | jia he hui 555  | Three-lines | Japonica   | 2012            |
| jin hui you 50   | jin hui A          | JP15            | Three-lines | Japonica   | 2012            |
| qin na 1         | yan nong S         | hun fu ben      | Two-lines   | Japonica   | 2012            |
| dong jia you 763 | dong wan 17 A      | xiang hui 63   | Three-lines | Japonica   | 2012            |
| dian za 49       | he xi 42–7 A       | nan 50          | Three-lines | Japonica   | 2012            |
| yong you 16      | yong jia 8 A       | yonghui 12      | Three-lines | Japonica   | 2012            |
| jia you 6        | jia 335 A          | jia hui 69      | Three-lines | Japonica   | 2012            |
| dian you 37      | DHC-10 A           | dian hui R-3    | Three-lines | Japonica   | 2012            |
| jia chang you 7   | qiao feng A        | hui 135         | Three-lines | Japonica   | 2012            |
| yong you 538     | yong jia 3 A       | F7538           | Three-lines | Japonica-indica | 2013 |
| Varieties       | Female          | Male            | Type     | Subspecies          | Year of release |
|-----------------|-----------------|-----------------|----------|---------------------|-----------------|
| chun you 84     | chun jiang 16 A | C84             | Three-lines | Japonica             | 2013            |
| yong you 2640   | yong jing 26 A  | F7540           | Three-lines | Japonica-indica     | 2013            |
| gang you 1      | 071 A           | C419            | Three-lines | Japonica             | 2013            |
| long jing 1550  | yan feng 475    | liaoxing 1      | Two-lines | Japonica             | 2013            |
| wu you 17       | wu A            | C17             | Three-lines | Japonica             | 2013            |
| yong you 1640   | yong jing 16 A  | F7540           | Three-lines | Japonica             | 2013            |
| dian he you 34  | H479A           | nan 34          | Three-lines | Japonica             | 2013            |
| yong you 720    | yong jing 7 A   | yong hui 20     | Three-lines | Japonica             | 2013            |
| chang you jing 6| chang 119 A     | CR-312          | Three-lines | Japonica             | 2013            |
| zhe nuo you 1   | zhe nuo 1 A     | zhe nuo hui 04-01 | Three-lines | Japonica             | 2013            |
| T12you 66       | T4012 A         | R7066           | Three-lines | Japonica             | 2013            |
| jing liang you S519 | N55s         | R19             | Two-lines | Japonica             | 2013            |
| 18 you 75       | 18 A            | R1575           | Three-lines | Japonica             | 2013            |
| pu you 22       | ai jing 15 S    | pu hui 22       | Two-lines | Japonica             | 2013            |
| jin jing you 11 | jinjing 11 A    | jinhui 1        | Three-lines | Japonica             | 2013            |
| ji you 1769     | T176 A          | C269            | Three-lines | Japonica             | 2013            |
| tong you jing 1  | yang fu jing 7 A| R98             | Three-lines | Japonica-indica     | 2013            |
| yong you 1540   | yong jing 15 A  | F7540           | Three-lines | Japonica-indica     | 2014            |
| zhe you 13      | zhe 04 A        | zhe hui 813     | Three-lines | Japonica             | 2014            |
| ji you 3985     | 639 A           | jijing 85       | Three-lines | Japonica             | 2014            |
| yong you 1109   | yong jing 11 A  | F7509           | Three-lines | Japonica             | 2014            |
| shen you 17     | shenwu 1 A      | shenfan 17      | Three-lines | Japonica             | 2014            |
| Illyou 304      | 2003 A          | XH04            | Three-lines | Japonica             | 2014            |
| long you 467    | long 3 A        | R467            | Three-lines | Japonica             | 2014            |
| dan jing you 1  | danjing 4 A     | danhui 1        | Three-lines | Japonica             | 2014            |
| jing you 106    | jing 139 A      | C2106           | Three-lines | Japonica             | 2014            |
| re jing you 35  | rejing 1A       | jinghui 35     | Three-lines | Japonica             | 2014            |
| jiao yuan you 69| jiaoyuan 5A     | JP69            | Three-lines | Japonica             | 2014            |
| dian kun you 8  | KS A            | S8              | Three-lines | Japonica             | 2014            |
| yong you 362    | yong jing 5 A   | F7562           | Three-lines | Japonica             | 2014            |
| chun you 149    | chunjiang 19 A  | CH149           | Three-lines | Japonica             | 2014            |
| liao 16you 06   | liao 5216 A     | C2106           | Three-lines | Japonica             | 2014            |
| liao 73you 62   | liao 73 A       | C62             | Three-lines | Japonica             | 2014            |
| yong you 1538   | yong jing 15 A  | F7538           | Three-lines | Japonica-indica     | 2015            |
| shen you 24     | shen 01 A       | shenfan 24     | Three-lines | Japonica             | 2015            |
| dian he you 56  | yumi 15 A       | nan 56          | Three-lines | Japonica             | 2015            |
| 5 you 68        | S A             | R68             | Three-lines | Japonica             | 2015            |
| dong you 91     | dongnuo 19 A    | nuohui 11      | Three-lines | Japonica             | 2015            |
| yong you 4949   | yong jing 49 A  | F9249           | Three-lines | Japonica-indica     | 2015            |
| 76 liang you 5  | 950765          | bao hui 5       | Two-lines | Japonica             | 2015            |
| qiu you 336     | qiu 15 A        | R336            | Three-lines | Japonica             | 2015            |
| dian he you 4106| he xi 42-7 A    | yinhui 106      | Three-lines | Japonica             | 2015            |
| yong you 1140   | yong jing 6 A   | F7540           | Three-lines | Japonica-indica     | 2015            |
| tian long you 619| L6 A           | R19             | Three-lines | Japonica             | 2015            |
Table 1 List of hybrid *japonica* rice varieties bred in China (Continued)

| Varieties | Female | Male | Type | Subspecies | Year of release |
|-----------|--------|------|------|------------|-----------------|
| yong you 7850 | yong jing 78 A | F9250 | Three-lines | Japonica-indica | 2015 |
| dian he you 55 | yu mi 15 A | nan 55 | Three-lines | Japonica | 2015 |
| jing you 586 | jing 139 A | CS86 | Three-lines | Japonica | 2015 |
| yong you 4350 | yong jing 43 A | F9250 | Three-lines | Japonica-indica | 2015 |
| bi jing you 210 | bi jing 2 A | NR210 | Three-lines | Japonica | 2015 |
| yong you 4550 | yong jing 45 A | F9250 | Three-lines | Japonica-indica | 2015 |
| yong you 150 | yong jing 2 A | F9250 | Three-lines | Japonica-indica | 2016 |
| bi jing you 3 | bi jing 2A | bi jing hui 3 | Three-lines | Japonica | 2016 |
| yong you 4901 | A49 | F8001 | Three-lines | Japonica-indica | 2016 |
| jia you zhong ke 3 | jia 66 A | zhong ke jia hui 1293 | Three-lines | Japonica-indica | 2016 |
| zhe you 21 | zhe 04 A | zhe hui F1121 | Three-lines | Japonica | 2016 |
| dian he you 6612 | yu mi 15 A | nan 6612 | Three-lines | Japonica | 2016 |
| jiao yuan you 1 | jiao yuan 3 A | jiao hui 1 | Three-lines | Japonica | 2016 |
| yongyou 4149 | yong jing 41 A | F9249 | Three-lines | Japonica-indica | 2016 |
| yongyou 4912 | yong jing 49 A | F7512 | Three-lines | Japonica-indica | 2016 |
| pu you 201 | pu jing 06 A | T201 | Three-lines | Japonica-indica | 2016 |
| jia he you 1 | jia he 212 A | hui SC01–1 | Three-lines | Japonica-indica | 2016 |
| yong you 540 | yong jing 3 A | F7540 | Three-lines | Japonica-indica | 2016 |
| yong you 7050 | A70 | F9250 | Three-lines | Japonica-indica | 2016 |
| yong you 8050 | yong jing 80 A | F9250 | Three-lines | Japonica-indica | 2016 |
| jia you zhong ke 1 | jia 66 A | zhong ke jia hui 1 | Three-lines | Japonica-indica | 2016 |
| zi xiang you 24 | zi xiang A | shen fan 24 | Three-lines | Japonica | 2016 |
| zhe you 19 | zhe 04 A | zhe hui F1015 | Three-lines | Japonica-indica | 2016 |
| dian he you 6611 | yu mi 15 A | nan 6611 | Three-lines | Japonica | 2016 |
| yong you 493 | yong jing 49 A | F6853 | Three-lines | Japonica-indica | 2016 |
| zhong jia you 6 | jia he 316 A | zhong hui 7206 | Three-lines | Japonica-indica | 2016 |
| jin jing you 2018 | jin 20 A | jin hui 18 | Three-lines | Japonica | 2016 |
| jia he you 7245 | jia he 212 A | zhong hui 7245 | Three-lines | Japonica | 2016 |
| chun you 115 | chun jiang 16 A | CH115 | Three-lines | Japonica-indica | 2016 |
| shen you 26 | shen 9 A | shen hui 26 | Three-lines | Japonica | 2016 |
| qian jing you 57 | 163 A | NR210 | Three-lines | Japonica | 2016 |
| jing you 165 | jing 139 A | C165 | Three-lines | Japonica | 2016 |
| jia you zhong ke 6 | jia 66 A | zhong ke 6 | Three-lines | Japonica | 2016 |
| qiu you 122 | qiu 9 A | R122 | Three-lines | Japonica | 2016 |
| chang you 2 | chang jing 1 A | hui KF2 | Three-lines | Japonica-indica | 2016 |
| chang you 312 | chang 132 A | CR-312 | Three-lines | Japonica | 2016 |
| yong you 7860 | yong jing 78 A | F6860 | Three-lines | Japonica-indica | 2016 |
| yong you 5552 | yong jing 55 A | F6852 | Three-lines | Japonica-indica | 2016 |
| chun you 984 | chun jiang 99 A | C84 | Three-lines | Japonica-indica | 2016 |
| tian long you 518 | long 5 A | C818 | Three-lines | Japonica | 2016 |
| jin jing you 1918 | jin 19 A | jin hui 18 | Three-lines | Japonica | 2016 |
| yong you 4543 | yong jing 45 A | F7543 | Three-lines | Japonica-indica | 2016 |
| shen you 415 | shen 9 A | C415 | Three-lines | Japonica | 2016 |
| lian 8 you 3 | lian 8 A | yun R3 | Three-lines | Japonica | 2016 |
| Varieties          | Female      | Male        | Type         | Subspecies     | Year of release |
|-------------------|-------------|-------------|--------------|----------------|-----------------|
| zhe jing you 1578 | zhe jing 7 A| zhe hui 1578| Three-lines  | Japonica       | 2017            |
| yong you 7861     | yong jing 78 A| F6861       | Three-lines  | Japonica-indica| 2017            |
| yong you 1662     | yong jing 16 A| F6862       | Three-lines  | Japonica-indica| 2017            |
| jing you 1        | jing 1 A     | guang hui 1 | Three-lines  | Japonica       | 2017            |
| hua zhong you 1   | hua zhong 1 A| hui 16      | Three-lines  | Japonica-indica| 2017            |
| jiao yuan you 5   | jiao yuan 3 A| jiao hui 5  | Three-lines  | Japonica       | 2017            |
| yong you 5550     | yong jing 55 A| F9250       | Three-lines  | Japonica-indica| 2017            |
| 7you 1            | 7 A          | yun R1      | Three-lines  | Japonica       | 2017            |
| chun you 927      | chun jiang 16 A| C927       | Three-lines  | Japonica-indica| 2017            |
| jiao yuan you 6   | jiao yuan 2 A| jiao hui 6  | Three-lines  | Japonica-indica| 2018            |
| chun you 284      | chun jiang 23 A| C84        | Three-lines  | Japonica       | 2018            |
| shen you 114      | shen 01 A    | C14         | Three-lines  | Japonica-indica| 2018            |
| yong you 7753     | yong jing 77 A| F6853       | Three-lines  | Japonica-indica| 2018            |
| xiu you 7113      | xiu 71 A     | XR13        | Three-lines  | Japonica-indica| 2018            |
| yong you 6760     | yong jing 67 A| F6860       | Three-lines  | Japonica-indica| 2018            |
| jiang liang you 7901| jiang 79S  | jiang hui 1501| Two-lines  | Japonica       | 2018            |
| qiu you 23        | qiu 23 A     | R23         | Three-lines  | Japonica       | 2018            |
| qian jing you 2   | 163 A        | qian jing hui 2 | Three-lines  | Japonica       | 2018            |
| shen wu you 26    | shen wu 1A   | shen hui 26 | Three-lines  | Japonica       | 2018            |
| shen 9you 09      | shen 9 A     | shen hui 9  | Three-lines  | Japonica       | 2018            |
| zhong he you 1    | jia he 212 A | NP001       | Three-lines  | Japonica       | 2018            |
| jing you 653      | jing 65 A    | C315        | Three-lines  | Japonica       | 2018            |
| xiu you 207       | xiu shui 134 A| R207       | Three-lines  | Japonica       | 2018            |
| zi xiang you 26   | zi xiang A   | shen hui 26 | Three-lines  | Japonica       | 2018            |
| bi jing you 5     | 67 A         | NR210       | Three-lines  | Japonica       | 2018            |
| shu you 9         | jia 81 A     | zhong ke jia hui 1308 | Three-lines  | Japonica       | 2019            |
| pu jing you 701   | pu jing 06 A | PR701       | Three-lines  | Japonica       | 2019            |
| chun you 584      | chun jiang 25 A| C84        | Three-lines  | Japonica       | 2019            |
| chang you 998     | chang 386 A  | CR998       | Three-lines  | Japonica       | 2019            |
| yong you 6711     | yong jing 67 A| F5711       | Three-lines  | Japonica-indica| 2019            |
| jin liang you 852 | jin rui 85   | yun hui 503 | Two-lines    | Japonica       | 2019            |
| yong you 1526     | yong jing 15 A| F4926       | Three-lines  | Japonica-indica| 2019            |
| shen you 27       | shen 10 A    | shen hui 26 | Three-lines  | Japonica       | 2019            |
| zhe jing you 16153| zhe jing 7 A | zhe jing hui 6153 | Three-lines  | Japonica       | 2019            |
| yong you 7053     | yong jing 70 A| F6853       | Three-lines  | Japonica-indica| 2019            |
| yong you 6763     | yong jing 67 A| F6863       | Three-lines  | Japonica-indica| 2019            |
| yun liang you 504 | yun jing 2085| yun hui 504 | Two-lines    | Japonica       | 2019            |
| pu jing you 201   | pu jing 06 A | PR201       | Three-lines  | Japonica       | 2019            |
| liao 99you 30     | liao 99 A    | C30         | Three-lines  | Japonica       | 2019            |
| jia you 8         | jia 74 A     | jia hui 8   | Three-lines  | Japonica       | 2019            |
| yong you 5526     | yong jing 55 A| F4926       | Three-lines  | Japonica-indica| 2019            |
| chang you jing 7  | chang 410-2 A| CR-928      | Three-lines  | Japonica       | 2019            |
| liao 99you 15     | liao 99 A    | C415        | Three-lines  | Japonica       | 2019            |
| yong you 5518     | yong jing 55 A| F4918       | Three-lines  | Japonica-indica| 2019            |
strong combining ability was developed, and the first hybrid _japonica_ rice variety, Liyou 57, was successfully bred and was widely cultivated in China. This progress greatly promoted the research on hybrid _japonica_ rice and its and utilization in northern China (Yang 1994). Many _japonica_ restorer lines and their combinations were developed from C57 and its offspring for application in Beijing, Anhui, Zhejiang, Jiangsu, Hebei, Tianjin, and other provinces of China. This achievement resulted in a remarkable increase in the yield per unit area in northern China (Yang 2005). After the creation of the C57 line, the _japonica_ restorer line C418 was developed by introducing wide-compatible genes, allowing to generate a series of hybrid rice combinations, such as Tiyou 418, Siyou 418, 9 You 418, and 3 You 18, and further promoting the development of hybrid rice (Yang 1998, 1999). The introduction of super-hybrid rice breeding project in 1998 drove continuous development in super-hybrid _japonica_ rice research (Hua et al. 2002, 2006). The seed production of _japonica_ hybrid rice has been a difficult problem due to the delayed flowering time and low stigma exposure of _japonica_ CMS lines. LAAS and National _Japonica_ Research Center (NJRC) improved genetically the stigma exposure rate in sterile lines by introducing _indica_ genes responsible for the high rate of stigma exertion. Using this strategy, a number of _japonica_ CMS lines with high stigma exposure rates have been bred, which include Liao 105A, Liao 30A, Liao 02A, Liao 5216A, Liao 99A, Liao 60A, Liao 166A, Liao 11A, Liao 73A, and Liao 143A (Li 1987; Ling 1989; Shen et al. 1994; Wang et al. 2008). The National _Japonica_ Engineering Technology Center (NJETC), China Rice Research Institute, and Jiangsu Academy of Agricultural Sciences have also developed _japonica_ CMS lines with high stigma exposure rates, such as L6A, 18A, and Chunjiang 99A (Chen et al. 2011a; Dong et al. 2016). The genetic improvement of _japonica_ CMS lines increased the stigma exposure rate from less than 30% to more than 60%, reaching as high as 80% in some CMS lines (Wang et al. 2008). Further, the seed setting rate in natural outcrossings reached 40–60%, and the seed production yield was markedly increased, from 1.5–2 t/ha to 3.5–4.5 t/ha. Additionally, the flowering time of sterile lines started 30–60 min earlier, and the difference of flowering time between the parents shortened, so the problem of low seed production in hybrid _japonica_ rice was solved (Wang et al. 2008). After the development of C418, a series of restorer lines with high quality, wide-compatibility, and good combining ability were created by crossing early maturity _japonica_ with ideotype in north China and tropical _japonica_ in Southeast Asia. Examples of these lines are C2106, C787, C419, C315, C62,
These restorer parents with tropical *japonica* background are characterized not only by wide restoring spectrum but also strong restoring ability. These restorer parents exhibit several features of the ideal plant type, such as compact plant architecture, short flag leaf, and semi-dense or dense panicle type. In addition, quality, resistance, and maturity were also improved (Zhang et al. 1999). A series of high-quality super-hybrid *japonica* varieties developed using the newly developed CMS and restorer lines were released. For instance, the hybrid *japonica* varieties include the Liaoyou 5218, Liaoyou 1518, Liaoyou 16, Liaoyou 14, Liaoyou 5273, Liaoyou 0201, Liaoyou 1052, Liaoyou 9573, Liaoyou 1498, Liaoyou 20, Liaoyou 2006, Liaoyou 2015, Liaoyou 2106, Liaoyou 5206, Liaoyou 9906, Liaoyou 1518, Liaoyou 27, Liaoyou 30, Liaoyou 06, Liaoyou 62, Liaoyou 106, Liaoyou 165 and Liaoyou 653 released by LAAS (Wang 2008), Jinjingza 2 and Jinjingza 4 released by the Tianjin Academy of Agricultural Science, Gangyou 1 released by the Donggang Farm in Liaoning province, and the high-quality fragrant hybrid *japonica* rice Tianlongyou 619 released by the National *japonica* rice Engineering Technology Center (NJETC). In addition, a series of hybrid *japonica* rice, such as Younong 3, Younong 538, Younong 12, Younong 2640, Chunyou 84, Chunyou 927, Changyou 1, and Shenyou 1 were also released in the southern rice-growing regions. These new hybrid *japonica* varieties have significant advantages in grain number per panicle, yield potential, quality, plant architecture, and resistance to blast, rice bacterial blight, and rice stripe disease (Dong et al. 2016).

**WA-Type and Yinshui-Type Male Sterile Lines**

In the 1970s, several research institutes in China bred WA-type *japonica* using the three-line system (Yang and Zhu 2009). However, large-scale breeding and cultivating WA-type hybrid *japonica* rice was once considered impossible due to the unavailability of restorer lines. Nevertheless, some progress has been made in recent years, such as breeding *japonica* CMS lines Nongku 26A and Zhen 5A, and identifying corresponding restorer lines (Zhang et al. 2003). However, the WA-type CMS lines were seldom used in agriculture because of their poor restorability, poor flowering, and pollenation characteristics.

In recent years, the Chinese Rice Research Institute and LAAS have studied the Yinshui-type hybrid *japonica* rice, and developed three-line varieties. Importantly, heterosis and seed production technology of Yinshui-type hybrid *japonica* continues to be investigated.

**The Two-Line System for Hybrid Japonica Rice**

Studies on breeding the two-line system of hybrid *japonica* rice in China began in 1973 (Shi 1981). In 1985, the first *japonica* photo-sensitive genic male sterile (PGMS) line was generated (Luo et al. 1992). Since then, more than 20 years of research by Chinese scientists produced significant improvements in the two-line system of hybrid rice. Nuclear sterile genes of *japonica* lines currently available in China are mostly derived from Nongken 58S. The two-line system of hybrid *japonica* rice was developed rapidly in both Taihu and Yangtze valleys. Since the creation of the *japonica* male sterile line N5088S (used for both sterile and maintainer lines) in Hubei Province in the late 1990s, a series of similar lines, such as 7001S, has been developed and is now used for breeding. Trials and subsequent production in the Yangtze valley demonstrated that these derived cultivars have the advantages of high yield, high quality, and multi-resistance (Wang et al. 1994; Wang et al. 1995). Recently, the Northern Hybrid *japonica* Research Center successfully overcame the problem of low seed setting rate of subspecies hybrids by using the two-line system. During the Chinese “Tenth Five-Year-Plan”, the Anhui Academy of Agricultural Sciences used the BT-type CMS lines as the cytoplasm donor, and the *japonica* PGMS lines as the male maintainer to create a new SA-type sterile line. This approach not only eliminated self-fertilization of BT-type CMS lines under high-temperature conditions but also effectively prevented self-fertilization of PGMS lines under low-temperature conditions (Li et al. 1997; Mou T 2016; Wang et al. 2005; Yang et al. 2008).

In northern China, GB028S was the first reported *japonica* PGMS line. It had the starting temperature for fertility conversion of approximately 22 °C (Li 1997). During the mid-1990s, *japonica* PGMS line 108S was developed to be used as sterile and maintainer lines in northern China (Wei et al. 2000).

*Japonica* photo-thermo-sensitive genic male sterile (PTGMS) lines were developed rapidly in the Yangtze valleys. For example, the N5088S, 31111S, and 31301S were generated in Hubei Province (Dong et al. 2016), Peiai 64S in Jiangsu Province (Yuan et al. 2012), 7001S, 2304S, 8087S, and 3502S in Anhui Province (Li et al. 1994; Wang et al. 2005). These PTGMS lines were used in the two-line system breeding to create a number of hybrid *japonica* varieties, such as 70You9, 70You4, 70Youhuangjiu, Eijingza 1, Eijingza 2, Liangyou 8828, Liangyou 122, Liangyou 276, Liangyouxinxing 1, and Liangyouxinxing 2 (Yang et al. 2009a, 2009b). The new varieties of Peiai 64S/C8420 and Peiai 64S/C418, obtained by crossing the indica PTGMS lines and *japonica* restorer lines with wide-compatibility genes, exhibited great potential for increasing the yield in northern China (Si et al. 2011).

**Progress in Genetic Studies on Traits Related to Heterosis Utilization**

**Yield and Hybrid Vigor**

Increasing grain yield is a long-term goal in rice breeding dictated by the need to meet the demand for global...
food security. Heterosis, i.e., higher performance for a trait in the hybrid than in both parents, offers an important strategy for rice breeding. Over the years, numerous studies have focused on the biological basis of heterosis in hybrid *indica* rice. It is generally believed that yield heterosis is mediated by many mechanisms, such as genetic distance (Saghai et al. 1997; Xiao et al. 1996), dominant complementary (Xiao et al. 1995), additive by additive epistatic effects (Zhuang et al. 2002), overdominance and pseudo-overdominance (Zhou et al. 2012), allele-specific expression (Lin et al. 2019), and accumulation of excellent alleles (Huang et al. 2015). Gene mapping of yield and yield-related heterosis parameters was performed in various populations, and hundreds of heterotic agronomical traits quantitative trait loci have been mapped on almost all rice chromosomes. Many QTLs contribute to heterosis, with some exhibiting strong heterotic effects on essential agronomical traits such as grain yield, flowering time, panicle grain number, seed setting rate, growth period, and photosynthetic efficiency (Chen et al. 2010; Huang et al. 2015; Huang et al. 2016; Li et al. 2016; Xin et al. 2014). Thus far, significant progress has been made in breeding hybrid *japonica* varieties. However, the yield of hybrid *japonica* has been low and was unstable in comparison with the hybrid *indica*. To improve hybrid vigor and combining ability (CA) between hybrid *japonica* parents, 81 hybrids were created, and the CA of 18 hybrids *japonica* parents was calculated. Associated loci residing on chromosomes 2, 5, 7, 9, and 11 that recorded maximum positive values for the CA of traits were identified. It was concluded that the strategy to improve the heterosis of hybrid *japonica* rice involved pyramiding favorable SNP loci of CA and eliminating the unfavorable loci from parental genomes (Zaid et al. 2017).

**Flowering Time**
The yield of seed production in hybrid *japonica* is affected by several factors, such as physiological characteristics of parents, the technology of chemical control, cultivation methods, climate, and flowering time. For sterile lines characterized by low stigma exposure, the synchronization of flowering time with restorer lines is critical for seed production (Tong et al. 2002). The genetic factors that influence flowering time include, among others, the characteristics of the flower organ, the difference of variety type, the length and width of grain. The flowering speed of sterile lines is slower, while the flowering time occurs later than in restorer lines. Additionally, a difference in the flowering time exists between the *indica* and *japonica* varieties (Zhang et al. 2016). Typically, *indica* rice blooms early, reaching full flowering at about 11:00 am, while *japonica* rice blooms later, reaching full flowering at about 12:30 pm. Grain properties are closely related to the flowering characteristics of rice. The rounder the grain, the later it blossoms, and the longer the grain, the earlier it blossoms (Zhang et al. 2016). Due to the complexity of factors affecting the time of flowering, the research on its genetic mechanism began relatively late. Since 2010, different groups have been used to map QTLs for flower time. Using the Chuanxiang 29B/Lemont reconstituted inbred line population, three early flowering QTLs were mapped, two of them located on chromosome 10, and one on chromosome 5. The contribution rate of a major QTL reached 73.72% (Zhang et al. 2016). Another RIL population derived from Qishanzhan/Qiuguang was used in the studies on the genetic control of flowering time. The blooming time was found to be a quantitative trait controlled by multiple genes. Six QTLs located on chromosomes 1, 2, 7, 8, 10, and 12 were identified, with a contribution rate of 7.08% to 26.95% (Ma et al. 2011). Using the F₂ population derived from WAB368-B-2-H2-HB (9:31–10:00)/Liuqianxin (11:01–11:30), 4 QTLs were mapped to chromosomes 1, 1, 10, and 12, respectively, and the contribution rate of each QTL ranged from 5.8% to 11.3% (Wan et al. 2013). Recently, the CRISPR/Cas9 technique has been introduced to breed early flowering rice lines. By editing the grain length gene GS3, long-grain *japonica* rice was created, which had an earlier flowering time than the short-grain *japonica* rice. In addition, when the flowering time of the sterile line and restorer line do not coincide, hormone spraying can also provide satisfactory results. It has been demonstrated that a methyl jasmonate (MeJA) spray effectively promotes rice flowering, and *indica* rice is more sensitive than *japonica* to the treatment with MeJA, and the response of *indica* rice is faster than that of *japonica* rice. High concentration (4 mmol/L) of MeJA applied late in the afternoon, at 5:00 pm, is the optimal treatment to promote the flowering of *japonica* rice (Zhang et al. 2016).

**Stigma Exposure Rate**
The degree of stigma exsertion is an important feature determining the seed setting rate. Increasing the seed setting rate in male sterile lines is important to achieve a high yield of hybrid seeds, and the stigma exposure rate is the main factor affecting this parameter (Dang et al. 2016). The stigma exsertion rate correlates positively with the yield of seeds; the seed setting rate in sterile lines increases by 0.74–0.92 percentage points for every 1% increase in stigma exposure rate, equivalent to an increase of at least 47 to 68 kg per hectare (Yang 2016). Stigma exposure in rice is generally considered to be a quantitative trait controlled by multiple genes, with dominant inheritance, lower epistasis effect, and greater environmental influence (Li et al. 2014a, 2014b; Ma...
et al. 2018). At present, nearly 60 QTLs related to stigma exposure rate have been identified (Li et al. 2014a, 2014b; Ma et al. 2018; Miyata et al. 2007; Yan et al. 2009), and are distributed throughout the 12 chromosomes of rice. Liu et al. (2015) mapped a main gene controlling the length of stigma in rice, qSTL3, to the 19.8 kb interval in the center of the short arm of chromosome 3 and verified the gene function. Using 227 rice germplasm as the material in the genome-wide association study, Dang et al. (2016) detected 6 QTLs regulating stigma length. Most of the stigma exertion genes were derived from wild rice and indica subspecies, and prevalently had a low contribution rate, small additive effect, and were sensitive to the environmental conditions. In addition, the stigma exertion rate was higher in varieties with longer spikelets and longer stigma. Grain length, grain aspect ratio, stigma span, and ovary length were all positively correlated with stigma exposure rate.

**CMS and Fertility Restoration**

CMS, a maternally inherited inability to produce functional pollen, has been observed in more than 200 species of higher plants, and this defect is dependent on cytoplasmic genes (Hu et al. 2012). Recent studies have shown male sterility caused by CMS genes are genetically bound to mitochondria. Accordingly, a protein that restores pollen sterility is encoded by nuclear genes, known as fertility restorer genes (Rf genes) (Budar et al. 2003). Thus far, five rice CMS genes and eight Rf genes have been cloned (Table 2 and Table 3). As indicated in Table 2, all rice CMS genes are derived by the recombination process of the mitochondrial genome and are frequently coupled with the functional genes of mitochondrial respiratory chain to form a co-transcribed transcript of infertility genes (Liu et al. 2018). Among the five types of sterile lines, BT-CMS is the one most widely used in hybrid japonica rice. The BT-CMS gene orf79 was discovered in 1994 using Southern hybridization during the analysis of mitochondrial gene recombination events. The orf79 gene is located downstream of the mitochondrial Atp6 gene and encodes a protein containing 79 amino acids (Akagi et al. 2004), and its effect on fertility can be reversed by restorer lines carrying the Rf1a and Rf1b genes. Rf1 is the first known restorer gene for gametophytic male sterility. The BT-CMS restorer genes Rf1a and Rf1b encode pentatrico-peptide (PPR) proteins with the length of 791 and 506 amino acids, respectively. Rf1a and Rf1b contain, respectively, 18 and 11 PPR domains, and are candidate proteins for targeting mitochondria (Wang et al. 2006).

**Breeding Strategies**

**High Yield Breeding**

The utilization of interspecific heterosis is an effective strategy to obtain super-high yield hybrid japonica rice. In the 1960s, strong heterosis was reported in interspecies hybrids of indica-japonica, manifested mostly by tall plant height, large panicle size, large grain number, strong tillering power, strong stem strength, highly developed root system, and strong disease resistance (Yang et al. 1962). In the 1980s, breeding of indica-japonica interspecific hybrid combinations was conducted in China, resulting in the development of certain hybrid combinations, e.g., chengte232/erliuzhai and 3037/02428, which increased the yield by more than 20% when compared with indica rice combination Xian you 63 in the same period (Deng 2008). In recent years, a series of new high-yield indica-japonica hybrid rice combinations, such as Yongyou and Chunyou, have been bred by combining sterile lines of japonica with indica restorer lines. Ningbo seed co. LTD developed Yongyou 538, which has high and stable yield. In the provincial production test, the average yield of Yongyou 538 was 11.3 t/ha, 29.6% higher than the control. Chunyou 84 was obtained by crossing the japonica sterile line Chunjiang 16A and indica-japonica restorer line C84; it provided an average yield of 10.3 t/ha, 22.9% higher than the control. Nevertheless, due to significant genetic differences between the parent lines, the hybrid varieties often exhibit certain undesirable traits, such as overhigh plant (Dai et al. 1991), low seed setting rate (Zhu and Liao 1990), long growth period (Yuan 2002), and poor grain filling degree (Yuan 2002). These problems can be solved to some extent by the introduction of a wide-compatibility gene or the aggregation of the specific compatibility gene Sg in japonica rice (Chen et al. 2011b; Mi et al. 2016; Shahid et al. 2013; Wan 2010). In northern China, in addition to using the heterosis of indica-japonica, the emphasis is placed on the introduction of the dep1 gene in the cultivation of many hybrid species.

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**Table 2** CMS types and related genes in rice

| Type       | Related gene | Protein characteristics | Reference        |
|------------|--------------|-------------------------|-----------------|
| BT-CMS (G) | B-atp6-orf79 | Membrane protein        | Akagi 2004      |
| HL-CMS (G) | atp6-orfH79  | Membrane protein        | Peng et al. 2010|
| WA-CMS (S) | rpl5-WA352   | Membrane protein        | Luo et al. 2013 |
| LD-CMS (G) | L-atp6-orf79 | –                       | Etsuko et al. 2011|
| CW-CMS (G) | orf307       | –                       | Fujii and Toriyama 20
Table 3: Restorers of fertility for CMS in rice

| Type          | Related genes | Protein characteristics                                      | Reference          |
|---------------|---------------|-----------------------------------------------------------|-------------------|
| BT-CMS (G)    | Rf1a, Rf1b    | Triangular pentapeptide repeat structural protein (PPR)   | Wang et al. 2006   |
| HL-CMS (G)    | Rf5, Rf6     | Triangular pentapeptide repeat structural protein (PPR)   | Hu et al. 2012     |
| WA-CMS (S)    | Rf3, Rf4     | Triangular pentapeptide repeat structural protein (PPR)   | Cai et al. 2012    |
| LD-CMS (G)    | Rf2          | glycine-rich protein                                      | Etsuko et al. 2011 |
| CW-CMS (G)    | Rf17         | Acyl transporter synthetase                               | Fujii and Toriyama 2009 |

**japonica** rice varieties with upright and semi-upright panicles, such as Liaoyou 9906 and Gangyou 1. These varieties have a higher yield, denser grain, and are less lodging than the loose panicle hybrid **japonica** rice (Gao et al. 2012).

**Quality**

Hybrid rice is produced by cross-breeding of two parents with different genotypes, the genetic mechanism of quality is very complex. It was repeatedly demonstrated that the phenotypes of the majority of quality traits in hybrid F1 tend to be of the middle parent type (Deng 2008). Therefore, when breeding high-quality **japonica** combinations, the selection of quality traits of both parents is essential. Choosing good quality traits of both parents can effectively prevent negative separation of hybrid rice quality (Yang 2016). For example, Jingyou 653, developed by the Liaoning Rice Research Institute, is a high-quality hybrid **japonica** rice variety, whose parent 65A and C315 are both high-quality lines. The Jingyou 653 hybrid won the first prize in the Japan-China rice tasting contest activity held in Japan in 2016.

**Disease Resistance**

Rice blast is a major disease in Zhejiang, Shanghai, Tianjin, Liaoning, and other regions with large planting areas of hybrid **japonica** rice, and has a great negative impact on rice production. Prolonged rainfall during the heading stage of rice results in the frequent occurrence of rice blast causes serious losses in rice production. The most economical and effective way to control this disease is the breeding and cultivation of blast-resistant rice varieties. To date, 36 rice blast resistance genes have been cloned. Thirty-four of these genes are dominant (Yang et al. 2019), enabling the improvement of the disease resistance of rice by gene pyramiding. The hybrid combination with strong disease resistance and broad resistance spectrum can be created by breeding and aggregating multiple **japonica** hybrid parents resistant to rice blast or by combining sterile lines and restorer lines with different genes. By this approach, a large number of hybrid **japonica** rice varieties with strong resistance and broad resistance spectrum were obtained (Chu et al. 2018). For example, the hybrid **japonica** rice varieties Liao73You62 carrying the Pid2 and Pid3 genes exhibited resistance to rice blast in Liaoning province for many years. Additionally, the genes of resistance to bacterial blight and rice blast were combined in the same hybrid to enhance broad resistance to various diseases (Abhilash et al. 2016; Dash et al. 2016).

**Combination Strategies**

The hybrid combination model plays a particularly important role in the breeding of hybrid **japonica** rice. During many years of breeding, the combination model of **indica-japonica** complementation, tiller angle complementation, yield components, morphological structure complementation, and photo/temperature complementation has been developed in China (Huang et al. 2016; Yang 2016; Yu et al. 2008). However, differences in the adopted strategies continue to be present among different regions. In the southern rice-growing regions, such as the middle and lower reaches of the Yangtze River, breeders take advantage mostly of the **indica-japonica** hybrid, introducing the wide-compatibility genes, and selecting the hybrid varieties with big panicles, such as the Yongyou and Chunyou series. In the Huang-Huai region in central China, breeders rely mostly on the combination of photosensitive **japonica** male sterile lines and temperature-sensitive restorer lines to breed two-line hybrid **japonica** rice varieties. In the northeast rice-cultivating region, where the temperature is lower and the frost-free period is shorter, the hybrid **japonica** hybrid rice combinations with medium panicle grain number, more tillers, higher seed setting rate, and good synchronicity of filling are generally hybridized with multi-branched sterile lines and rice restorer lines with large panicles (Leng and Wang 2019; Yang 2016; Wang et al. 2011).

**Cultivation of Hybrid **japonica** Rice in China**

Since the approval of the first **japonica** hybrid rice Liyou 57 in 1980, 396 varieties have been approved until 2019 (Table 1). Although the number of approved varieties is large, only some of them can be widely cultivated due to their unstable performance or the difficulty in seed production. According to the data obtained from the National Agro-Tech Extension and Service Center (http://www.natesc.org.cn), by 2018, a total of 17 varieties have been cultivated to an area of more than 10,000 ha in 9 provinces in China (Table 4), among which Zhejiang
province has the largest area, followed by Liaoning province (Fig. 4).

In the mid-1980s, the total area of japonica hybrid rice cultivation was only about 133,000 ha and accounted for just 2% of the total area of japonica rice. Even in northern China, the land used for growing hybrid japonica rice accounted for only approximately 6% of the total area of japonica rice (Xie et al. 2007). By the early 1990s, as studies on hybrid japonica rice began to decline, the planting area decreased to 80,000 ha, constituting only about 1% of the japonica rice area. However, in recent years, the area used for growing hybrid japonica rice has increased and is distributed throughout Liaoning, Jiangsu, Shanghai, Zhejiang, Yunnan, and other provinces (Jiang et al. 2014; Kang 2013; Ma et al. 1998; Ni et al. 2001; Quan et al. 2000). For example, Tianlongyou 619, released by Liaoning Province Crop Variety Approval Committee in 2016, developed by a cross of a sterile line and a restorer line, has increased and is widely planted in Southern Jilin, Liaoning, Tianjin, Ningxia, Jiangsu, Hainan, and other provinces. The Jiangsu Academy of Agricultural Sciences has developed a hybrid japonica variety Tianlongyou 95You161 by a cross between the early-blooming, sterile, dwarf japonica line Chunjiang 16A and a restorer line C84 with wide-compatibility. From 2014 to 2015, Zhongchunyou 84 was grown on an area of 46,700 ha (Dong et al. 2016). Although the planting area of hybrid japonica varieties has increased in recent years, it still accounts for less than 5% of the total japonica planting area (Pu et al. 2015). Due to certain key technical barriers that remain to be solved, the difference in the planting area between hybrid japonica and indica is still significant.

**Current Status of Genomics in Hybrid japonica**

With the development of high-throughput sequencing technology, hundreds of agronomically relevant heterotic QTLs affecting the performance of heterozygous genotypes have been mapped. Many QTLs contribute to heterosis by dominant or overdominant effects, and some exhibit strong heterotic effects on important genes affecting yield, quality, and adaptability. The following table lists the varieties with an area of more than 100,000 ha.

| Varieties | Female | CMS type | Male | Area(10^4 ha) | Type | Subspecies | Year of released |
|-----------|--------|----------|------|--------------|------|------------|-----------------|
| Yongyou9  | Yongjing2 | BT       | K6093 | 71.5         | Three-lines | Japonica       | 2007            |
| E jing za 1 | N5088S | BT       | R187  | 61.3         | Two-lines   | Japonica       | 1995            |
| Li you 57 | LimingA | BT       | C57   | 59.9         | Three-lines | Japonica       | 1980            |
| 9 you 418 | Xu9201A | BT       | C418  | 40.8         | Three-lines | Japonica       | 2000            |
| Yong you 6 | Yongjing2A | BT     | K4806 | 28.9         | Three-lines | Japonica       | 2005            |
| Han you xiang qing | HanfengA | BT | Xiangqing | 25.7 | Three-lines | Japonica       | 1989            |
| Yong you 12 | Yongjing2A | BT | F5032 | 25.7 | Three-lines | Japonica       | 2010            |
| Yong you 1 | Ning67A | BT       | K1722 | 20.7         | Three-lines | Japonica       | 2000            |
| Xi you 57 | XiulingA | BT       | C57   | 20.4         | Three-lines | Japonica       | 1984            |
| Wan dao 26 | 7001S | BT       | Xiushui04 | 19.3 | Two-lines   | Japonica       | 1994            |
| Wan dao 34 | 80-4A | BT       | HP121 | 13.9         | Three-lines | Japonica       | 1996            |
| Yong you 538 | Yongjing3A | BT | F7538 | 13.7 | Three-lines | Indica-japonica | 2013            |
| Ill you98 | MH2003A | BT       | R18   | 13.4         | Three-lines | Japonica       | 2002            |
| E jing za 3 | N5088S | BT       | Minhui128 | 13.3 | Three-lines | Japonica       | 2004            |
| Yong you 17 | Yongjing4A | BT | Yonghui12 | 11.1 | Three-lines | Indica-japonica | 2012            |
| Chun you 59 | Chunjiang16A | BT | CH59   | 10.7         | Three-lines | Japonica       | 2009            |

Huayou 14, which was being used as a typical high-yield variety for the past 3 yrs. Huayou 14 exhibits high “Grade I” quality and is cultivated on an area of 80,000 ha. In the middle-lower Yangtze region, a number of hybrid japonica rice varieties with super-high yield and strong heterosis have been developed using indica-japonica complementation. Since 2011, a series of new indica-japonica hybrid rice varieties, including Yongyou and Chunyou, have shown high yield potential by reaching yield levels similar to those of super-high-yielding varieties (Jiang et al. 2014; Kang 2013). Zhongchunyou 84, a subspecies hybrid rice variety with a super-high yield, was developed by a cross between the early-blooming, sterile japonica line Chunjiang 16A and an indica-japonica restorer line C84 with wide-compatibility. From 2014 to 2015, Zhongchunyou 84 was the dominant rice variety in Zhejiang Province and was grown on an area of 46,700 ha (Dong et al. 2016).
agronomical characteristics such as grain yield and flowering time (Huang 2015; Huang 2016; Li et al. 2016; Lin et al. 2019). At the same time, the molecular mechanism of heterosis was gradually elucidated by transcriptome sequencing and genome resequencing technique. In 2015, DNA sequencing of 1495 elite hybrid rice varieties and their inbred parental lines was performed. Comprehensive analyses of heterozygous genotypes revealed that heterosis results mostly from the accumulation of numerous superior alleles with positive dominant effects (Huang et al. 2015). Huang et al. (2016) generated the sequences and recorded the phenotypes of 10,074 F2 lines from 17 representative hybrid rice crosses. They documented that a small number of genomic loci from female parents are responsible for a large part of the yield advantage that hybrids have over their male parents. For some of those loci, they found support for partial dominance of heterozygous locus for yield-related traits when all grain-yield traits were considered together. In the process of hybrid rice breeding, breeders tend to introduce different introgressed exogenous genomes unconsciously to shaped heterotic loci in the hybrid rice. Lin et al. (2020) generated two populations of rice F1 hybrids using commercial hybrid parents and genotyped the parents by a 50 k SNP chip and genome resequencing, the results from the analysis revealed that the male and female parents have different levels of genome introgressions from other rice subpopulations, including indica, aus, and japonica, therefore shaping heterotic loci in the hybrids. Among the introgressed exogenous genome, heterotic loci, including Ghd8/DTH8, Gn1a, and IPA1 existed in wild rice, but were significantly divergently selected among the rice subpopulations, suggesting these loci were subject to environmental adaptation. During modern rice hybrid breeding, heterotic loci were further selected by removing loci with negative effect and fixing loci with positive effect and pyramid breeding. These findings may facilitate future breeding of improved varieties of hybrid rice (Lin et al. 2020). However, these experimental studies

![Production map of hybrid japonica rice of China.](image)

**Fig. 4** Production map of hybrid japonica rice of China. The provinces marked green are those with a cumulative promotion area of more than 10,000 ha from 1981 to 2018. The deeper the green degree, the larger the cumulative promotion area.
utilized mostly *indica* hybrid rice or their parents, while the understanding of the genomics of hybrid *japonica* rice is still lagging behind.

**Problems and Prospects**

Under the leadership of Academician Longping Yuan and the joint efforts of several rice-breeding institutes in China, remarkable progress was made in the development of hybrid *japonica* rice. However, some problems restricting further improvements remain in place, necessitating collaborative research. First, the yield advantage of hybrid *japonica* rice is not high enough in comparison with traditional *japonica* rice. On the one hand, due to the limited knowledge of the genetic background of the parents of *japonica* hybrid rice, the genetic distance between the parents of *japonica* hybrid rice is not sufficiently large, leading to a weak yield heterosis. On the other hand, the introduction of the *indica* genome into hybrid *japonica* rice was typically considered as a strategy to enhance the heterosis. However, under the influence of the *indica* genetic background, hybrid *japonica* rice often exhibit premature senescence and differentiation between strong and weak (filled and partially-filled) grains. In addition, with low temperature present during the later growth stages, the weak grains are not sufficiently filled and do not mature fully, reducing the yield potential. Therefore, to avoid the negative effects of the introduction of *indica* rice genetic background, further research should focus on the mechanism of the formation of filled and partially-filled grains and the inheritance of cold tolerance. Second, despite the important breakthroughs and developments in mechanized seed production accomplished by the NJETC and the Shanghai Academy of Agricultural Sciences, the low yield of hybrid *japonica* seeds is the key limiting factor in the applications of hybrid *japonica*. Due to the fact that the restore genes were derived mostly from *indica* rice, the restorer lines with some *indica* background have early blooming time. However, most *japonica* sterile lines exhibit late blooming time and low percent of stigma exposure. Moreover, with the development of directly seeded rice, the need for an increased amount of seeds created a new challenge for the production of hybrid *japonica* rice seeds. Therefore, it is necessary to accelerate germplasm screening and gene mining, and utilize these data to achieve early blooming time, high stigma exposure rate, large stigma size, and strong stigma vigor.

It should also be noted that the growth and development of hybrid *japonica* rice are different from conventional *japonica* rice. Cultivation techniques should be developed according to the characteristics of hybrid *japonica* rice. The hybrid *japonica* rice possesses larger panicles and more grains, and it was usually faced with large sink but small source. In terms of cultivation, an adequate population structure should be established in the early and middle stages of growth to ensure sufficient and effective number of panicles and spikelets, and to avoid the overgrowth of plants. Attention should be given to ensuring grain filling and preventing premature senescence by postponing panicle fertilizer. To fully utilize the yield potential of hybrid *japonica* rice, early sowing and transplanting should be implemented to ensure that the heading and grain-filling occur at the most opportune period.

Finally, the cooperation between scientific research institutions and seed enterprises should be enhanced to jointly promote the commercial operation and industrial development of hybrid *japonica* rice, accelerate the expansion and application of new hybrid *japonica* rice varieties, and seize the advantages of hybrid *japonica* rice such as reduced use of fertilizer and water, strong resistance, and high yield. These steps will improve the utilization of middle- and low-yield fields and ensure food security.

**Conclusions**

With the increasing demand for high-quality *japonica* rice, the prospects for the development of hybrid *japonica* rice are increasingly better, particularly in China. Although the number and the spread area of hybrid *japonica* rice varieties lag behind hybrid *indica*, the research on hybrid *japonica* rice progressed remarkably over the past 70 years. Several male sterile lines (e.g., Dian-type, BT-type, WA-type, and Yinshui-type) with their corresponding restorer and maintainer lines have been used in the three-line system of growing *japonica* hybrid rice. The development of photo-thermo-sensitive genic male sterile lines for the two-line system also promises great potential for improving grain yield in hybrid *japonica* rice. Meanwhile, remarkable progress has been made in research on molecular mechanisms for heterosis, stigma exposure rate, flowering time, and male sterility in hybrid *japonica*. In future, exploiting and pyramiding the superiority genes with yield-related genes by MAS will have an important role in increasing grain yield of hybrid *japonica*. Given the present limitations, we have proposed four effective strategies to develop hybrid *japonica*: (1) increasing parental genetic distance and introducing the wide-compatibility genes; (2) accelerating germplasm screening, gene mining, and utilizing the data to achieve early blooming time, high stigma exposure rate, large stigma size, and strong stigma vigor; (3) using new cultivation techniques specific for hybrid *japonica*; and (4) enhancing cooperation with extension departments and cooperatives.
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Availability of Data and Materials

Not applicable.

Ethics Approval and Consent to Participate

Not applicable.

Consent for Publication

The manuscript has been approved by all authors.

Competing Interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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