TYPE Original Research
PUBLISHED 12 October 2022
DOI 10.3389/fsufs.2022.986655

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Land, Livelihoods and Food Security, a section of the journal Frontiers in Sustainable Food Systems

RECEIVED 05 July 2022
ACCEPTED 18 August 2022
PUBLISHED 12 October 2022

CITATION
Wang H, Xiong R, Zhou Y, Tan X, Pan X, Zeng Y, Huang S, Shang Q, Xie X, Zhang J and Zeng Y (2022) Grain yield improvement in high-quality rice varieties released in southern China from 2007 to 2017. *Front. Sustain. Food Syst.* 6:986655. doi: 10.3389/fsufs.2022.986655

Grain yield improvement in high-quality rice varieties released in southern China from 2007 to 2017

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In recent years, high-quality rice varieties have been widely cultivated for food production in southern China. However, changes in the yield performance of different high-quality rice varieties are still unclear. In this study, the yield and yield components of 710 different types (hybrid or inbred rice and *japonica* or *indica*) of high-quality rice varieties were investigated in six provinces from 2007 to 2017. The results showed that, from 2007 to 2017, the grain yield and yield traits, including the number of spikelets per panicle and seed-set percentage, of high-quality *indica* rice varieties increased significantly, while the number of panicles decreased only in *indica* inbred rice. The grain yield of high-quality *japonica* rice also increased significantly, whereas *japonica* hybrid rice increased the number of spikelets per panicle and decreased the number of panicles. Compared with inbred rice, hybrid rice had a significant increase in grain yield due to a higher number of spikelets, rather than a lower number of panicles and seed-set percentage. Meanwhile, *japonica* rice showed higher grain yield than *indica* rice, which was attributed to seed-set percentage and an optimized structure between the number of panicles and the number of spikelets. In addition, the coefficient of variation of the grain yield of *japonica* rice decreased, whereas that of *indica* rice increased over time, and those of the number of panicles and seed-set percentage remained stable. Among the six provinces, Zhejiang had the highest grain yield because the number of spikelets per panicle and seed-set percentage increased over time. Our results suggested that, based on an increase in the yield potential of high-quality rice varieties over the past 11 years, future breeding of high-quality rice should be emphasized to improve the number of panicles and seed-set percentage for hybrid rice and the number of spikelets for inbred rice, especially the grain weight for *indica* inbred rice.

KEYWORDS

southern China, high-quality rice varieties, grain yield, yield traits, breeding target

Introduction

Rice (*Oryza sativa* L.) is a staple cereal crop. China is the world's largest producer of rice, and its annual rice production accounts for almost 30% of total world production (FAO, 2018; Zhang et al., 2019). Sufficient food production can satisfy the need to feed the Chinese population (Tester and Langridge, 2010). Improving rice yield potential has been a major breeding goal in many countries for decades (Peng S. B. et al., 2008). As rice breeding, especially rice crossbreeding, has made rapid progress, the grain yield potential of rice has enhanced significantly in the last three decades (Yuan, 2017). Since 1980, rice production has increased by 59% despite a decline in available arable land. This is mainly due to the development of crossbreeding (Peng et al., 2009). Meanwhile, consumer demand for better quality and taste is also increasing due to better living standards and, therefore, the planting of high grain quality rice varieties is becoming more and more popular in rice production (Zeng et al., 2019). The proportion of high-quality rice in the rice market has increased significantly, and the Ministry of Agriculture and Rural Affairs is actively implementing green and efficient campaigns to promote high-quality and high-yielding varieties (Xu et al., 2021). High-quality rice varieties can enhance the market status and increase rice production benefits (Yang et al., 2015).

It is encouraging that, in the last 10 years, China has made great progress in developing high-quality rice production. The quality parameters of *japonica* and *indica* rice are different. Compared to *japonica,* better quality was achieved in *indica* rice (Zeng et al., 2019). The quality rate of inbred rice is higher than that of hybrid rice, and hybrid rice, especially three-line *indica* hybrid rice and *japonica* hybrid rice, has much room for improvement (Mao et al., 2017; Zeng et al., 2019). At present, the majority of rice varieties planted in China are mainly high-quality rice varieties, with the northern region having more high-quality rice varieties than the southern region (Wang et al., 2018).

Rice, which contains *indica* (*O. sativa* L. subsp. *indica*) and *japonica* (*O. sativa* L. subsp. *japonica*) in both hybrid and inbred rice varieties (Tripp et al., 2010), is widely planted in China. In China, *japonica* rice is cultivated mainly in northeastern China and in the lower reaches of the Yangtze River Basin and consists mainly of inbred varieties (Peng J. H. et al., 2008). *Indica* rice is grown mainly in southern China and consists mainly of hybrid varieties (Deng et al., 2006). The southern rice region is an important rice-producing region in China, including Zhejiang, Jiangxi, Hunan, Guangxi, Guangdong, and Fujian provinces along the Yangtze River. The boundaries of rice cultivation in China have moved northward due to the rising temperatures since the 1980s, and rice acreage is shrinking in southeast China (Yang et al., 2010; Liu et al., 2013).

The success of hybrid rice breeding greatly increases rice grain yield and has far-reaching significance in the developmental history of modern agriculture. Our previous studies (Zeng et al., 2019) elucidated the changing trend of rice quality of 710 high-quality rice varieties in the past 11 years, from 2007 to 2017, and analyzed rice quality change characteristics in different types of high-quality *indica* and *japonica* rice, as well as rice quality change characteristics in different provinces of the southern rice region. However, the yield characteristics of different types of high-quality rice released in southern China in the last few decades are not clear.

Continuous breeding of new high-yielding, good quality varieties is undoubtedly the most effective and economical means of increasing rice grain yield, and clarifying the formation rules of high-yielding rice varieties or types is an important goal of cultivation research. In addition, the grain yield of high-quality rice varieties is susceptible to environmental impacts and varies between specific years (Yoshida et al., 2006; Chen et al., 2008). We hypothesize that there are differences in rice grain yield traits from 2007 to 2017 among high-quality rice types from all the provinces in southern China. Therefore, the objectives of this study are to (1) compare the changes and status of major yield formation traits in 710 high-quality rice varieties; (2) explore differences in the yield characteristics of high-quality rice varieties in six provinces; and (3) ascertain strategies to improve high-quality rice in the future for southern China.

Materials and methods

Data collection and yield trait description

Between 2007 and 2017, we collated the major yield traits of 710 high-quality rice varieties selected from 1,797 rice varieties released in Jiangxi, Zhejiang, Fujian, Hunan, Guangxi, and Guangdong provinces. These traits were examined and approved by the provincial crop variety assessment committee (PCVAC) at the China Rice Data Center (2018). The high-quality rice varieties released did not include glutinous rice and sterile lines. Here, they were divided into four types, namely, 25 *japonica* inbred rice varieties, 25 *japonica* hybrid rice varieties, 138 *indica* inbred rice varieties, and 522 *indica* hybrid rice varieties, according to subspecies (*japonica* and *indica*) and breeding type (hybrid, inbred).

The yield traits of the collected data primarily include the number of panicles, the number of spikelets per panicle, seed-set percentage, grain weight, and grain yield. Data on the yield traits of the 710 rice varieties were measured by the Inspection and Testing Center of the Ministry of Agriculture's Rice and Product Quality Supervision Group according to the method of Peng et al. (2010). In this study, *japonica* rice varieties are primarily planted in Zhejiang province, and *indica* rice varieties are widely planted in the southern region of China, including the aforementioned six provinces, which have adequate temperature, light, and water resources. The annual average temperature is 15–24°C. The annual average rainfall is 950–2,500 mm. The number of sunshine hours ranges from 1,200 to 2,500 h, and the active accumulated temperature above 10°C (AAT) is 5,000–9,000°C (AAT= {mean daily temperature − 10} ×number of days). The soils are primarily red and paddy soils.

Statistical analysis

Means of yield traits and variation coefficients were performed with SPSS 22.0 statistical software (SPSS, Inc., Chicago, USA) to determine the least significant difference (LSD) at a p-value <0.05. The variation coefficient for each yield trait in every year of release was calculated as the ratio of the standard deviation (SD) to the average value of yield traits. A multivariate analysis of variance (ANOVA) was conducted to determine the effects of the subspecies (*indica* and *japonica*), the type of breeding (hybrid and inbred rice), and the year of release (as independent variables), as well as their levels of interaction in the yield traits of rice varieties (as dependent variables) at significance levels of 0.05, 0.01, and 0.001. The relative (%) genetic gain of the yield traits of high-quality rice varieties released annually was calculated by single linear regression, according to the methods of Feng et al. (2017).

$$\mathrm{Yi} = \mathrm{a} + \mathrm{b} \cdot \mathrm{Xi},$$

where *Yi* is the value for each grain yield trait, *Xi* is the year of release for the cultivar *i*, *a* is the intercept of the equations, and *b* is the absolute slope. According to the release years for the six provinces, rice varieties could be divided into three stages, 2007–2010, 2011–2015, and 2016–2017.

Results

ANOVA for the yield traits of high grain quality rice types

Breeding type, subspecies, the year of release, and their interactions differed according to yield traits (Table 1). Breeding type was significant in relation to the number of panicles, the number of spikelets per panicle, seed-set percentage, and grain yield. Seed-set percentage and grain yield were also significantly affected by subspecies and the year of release. The number of spikelets per panicle was also significantly affected by subspecies. A significant interaction between the year of release and breeding type was observed for the number of panicles and seed-set percentage. For grain yield, a significant interaction between the year of release and subspecies was observed. A significant interaction between breeding type and subspecies was observed for the number of spikelets per panicle. A significant interaction between the year of release, breeding type, and subspecies was observed only for the number of panicles.

Differences in the yield performance between *japonica* and *indica* rice types

Compared with *indica* rice and *japonica* inbred rice, the number of panicles of *japonica* hybrid rice was lower by 18.7–28.6 and 34.9%, respectively (Table 2). However, the number of spikelets per panicle of *japonica* hybrid rice was higher by 33.2–39.6 and 43.3%, and significantly opposite trends were observed between inbred and hybrid varieties for both the number of panicles and the number of spikelets per panicle (p < 0.05). *Japonica* rice had a significantly higher seed-set percentage than *indica* rice, from 4.9 to 8.9%, and the same trends were observed between inbred and hybrid varieties. The grain weight of *indica* inbred rice was significantly lower than that of *japonica* rice and *indica* hybrid rice varieties by 14.7–17.1 and 17.7%, respectively, but no differences were found between the different types of *japonica* rice. *Japonica* rice had significantly higher grain yield than *indica* rice by 10.6–40.7%, and a significant inverse trend was shown between inbred and hybrid rice varieties.

Differences in the genetic gain of yield performance from 2007 to 2017

Genetic gains in the grain yield of both *japonica* and *indica* rice showed significantly increasing trends between 2007 and 2017 for both inbred and hybrid rice varieties (Table 3), suggesting that these high grain quality rice varieties had a high yield potential. Rice varieties between *indica* and *japonica* varied significantly in grain yield traits in the last 11 years. For *japonica* inbred rice, no significant changes in grain yield traits were observed. In contrast, *japonica* hybrid rice showed a significant decline in the number of panicles but a significant increase in the number of spikelets per panicle. Similarly, *indica* inbred rice showed a significant decline in the number of panicles but finally also increased yield with a significant increase in the number of spikelets per panicle and seed-set percentage. A significant increase in the number of spikelets per panicle and seed-set percentage in *indica* hybrid rice contributed to yield improvement.

Variation coefficient for different yield performance in high grain quality rice varieties

In three stages of high grain quality rice released during the study periods (2007–2010, 2011–2015, and 2016–2017), the subspecies also showed reduced variation coefficients in the number of panicles and seed-set percentage. *Japonica* inbred rice and *indica* varieties showed decreased variation coefficients in the number of spikelets per panicle but increased in grain weight. In contrast, *japonica* hybrid rice had increased variation

TABLE 1 Analysis of variance (ANOVA) of yield traits in rice.

Factors	Panicle number	Spikelet number per panicle	Seed-set percentage	Grain weight	Grain yield
Breeding type (hybrid, inbred)	16.40***	18.64***	15.74***	0.56^{ns}	20.93***
Subspecies (*japonica*, *indica*)	0.16^{ns}	4.01*	48.81***	0.74^{ns}	143.36***
Year released	1.08^{ns}	1.21^{ns}	2.80**	0.11^{ns}	8.93***
Year released × Breeding type	2.77**	0.64^{ns}	1.85*	0.15^{ns}	0.61^{ns}
Year released × Subspecies	1.11^{ns}	0.90^{ns}	1.50^{ns}	0.17^{ns}	2.18*
Breeding type × Subspecies	2.07^{ns}	8.96**	2.22^{ns}	1.68^{ns}	3.08^{ns}
Year released × Breeding type × Subspecies	3.19*	1.41^{ns}	0.54^{ns}	0.03^{ns}	0.65^{ns}

*, **, and ***Indicate significant differences at the probability levels of 0.05, 0.01, and 0.001, respectively; ns, indicate non-significant.

TABLE 2 Differences in the mean yield traits between *japonica* and *indica* types of high-quality rice.

Rice type	n	Panicle number (m^{-2})	Spikelet number per panicle	Seed-set percentage (%)	Grain weight (mg)	Grain yield (t hm^{-2})
Japonica inbred	25	305.2a	130.9c	88.6a	25.8a	8.43b
Japonica hybrid	25	226.2c	230.8a	84.9b	25.1a	9.34a
mean		265.7	180.9	86.7	25.5	8.89
Indica inbred	138	291.0a	139.5c	82.9c	21.4b	6.64d
Indica hybrid	522	268.6b	154.2b	80.7d	26.0a	7.62c
mean		279.8	146.9	81.8	23.7	7.13

Different lowercase letters between different rice types in the same column are significant at a p-value < 0.05.

TABLE 3 Genetic gain (%) of yield traits in high grain quality rice varieties.

Rice type	*n*	Panicle number (m^{-2})	Spikelet number per panicle	Seed-set percentage (%)	Grain weight (mg)	Grain yield (t hm^{-2})
Japonica inbred	25	Ns	ns	Ns	ns	12.40***
Japonica hybrid	25	−0.74***	13.02***	Ns	ns	11.43***
Indica inbred	138	−0.24***	1.37***	0.30**	ns	5.06***
Indica hybrid	522	Ns	1.52*	0.41***	ns	6.13***

*, **, and ***Indicate significant differences at the probability levels of 0.05, 0.01, and 0.001, respectively; ns, indicate non-significant.

coefficients in the number of spikelets per panicle but decreased grain weight. In addition, variation coefficients of grain yield decreased in *japonica* rice but increased in *indica* rice (Table 4).

For *indica* inbred rice, variation coefficients of the number of panicles and grain yield were the lowest in Guangxi province among the six provinces. Relatively low variation coefficients of the number of spikelets per panicle and grain weight were observed in Hunan province, and those of the seed set were found in Zhejiang province. In contrast, variation coefficients of each yield component trait in Fujian province were relatively high. For *indica* hybrid rice, variation coefficients of the number of panicles, the number of spikelets per panicle, and grain yield were lower in Guangdong province than in the other provinces, while those of the seed-set percentage and grain weight decreased in Hunan province. In contrast, variation coefficients of each yield component trait in Jiangxi province were high (Table 5).

Yield performance of high grain quality rice for each variety type in six provinces

From 2007 to 2017, the grain yield of high-quality rice varieties showed an increasing trend in all six provinces except Fujian, with the largest increases of 22.5%, 22.0%, and 25.3% in Zhejiang, Hunan, and Jiangxi provinces, respectively (Figure 1A). Of the three stages (2007–2010, 2011–2015, and 2016–2017), Fujian province had relatively high grain yield

TABLE 4 Variation coefficients for the yield traits of the released inbred and hybrid rice varieties.

Rice type	Year	Panicle number (m^{-2})	Spikelets number per panicle	Seed-set percentage (%)	Grain weight (mg)	Grain yield (t hm^{-2})
Japonica inbred	2007–2010	10.21	14.25	4.94	5.33	6.56
	2011–2015	19.05	9.69	5.55	3.26	9.83
	2016–2017	6.61	4.25	2.62	6.69	3.48
	Mean	11.96ab	9.40b	4.37ab	5.09*c*	6.62b
Japonica hybrid	2007–2010	9.11	9.47	5.76	6.97	3.62
	2011–2015	21.31	10.82	8.10	11.65	8.78
	2016–2017	12.72	15.48	4.65	6.68	5.98
	Mean	14.38ab	11.92b	6.17a	8.43b	6.13b
Indica inbred	2007–2010	12.24	11.87	4.10	12.43	6.83
	2011–2015	6.73	9.97	4.75	11.42	5.75
	2016–2017	8.82	8.47	3.59	14.46	8.97
	Mean	9.26b	10.10b	4.15b	12.77a	7.18b
Indica hybrid	2007–2010	15.36	59.44	6.19	9.07	8.66
	2011–2015	14.79	17.04	4.70	10.07	9.58
	2016–2017	14.78	14.85	4.05	79.80	10.56
	Mean	14.98a	30.44a	4.98ab	32.98a	9.60a

Different lowercase letters between different rice types in the same column are significant at a p-value < 0.05.

TABLE 5 Changes in variation coefficients for the yield traits of high grain quality rice varieties in different provinces.

Rice type	Province	Panicle number (m^{-2})	Spikelet number per panicle	Seed-set percentage (%)	Grain weight (mg)	Grain yield (t hm^{-2})
Japonica inbred	Zhejiang	12.72	11.27	4.54	5.23	10.31
Japonica hybrid	Zhejiang	18.90	21.07	5.11	7.28	7.50
Indica inbred	Zhejiang	8.71	15.48	1.99	6.77	3.94
	Jiangxi	10.49	17.90	5.74	10.46	15.48
	Hunan	18.06	3.56	5.14	4.01	11.21
	Guangxi	5.01	11.68	7.34	9.81	1.93
	Guangdong	9.23	8.10	3.84	12.03	6.53
	Fujian	29.23	53.07	6.54	8.86	19.27
Indica hybrid	Zhejiang	11.66	18.52	5.14	7.97	9.03
	Jiangxi	12.19	60.68	5.81	67.83	10.14
	Hunan	9.16	9.17	3.30	5.17	11.15
	Guangxi	8.74	10.89	4.53	9.96	5.89
	Guangdong	8.01	7.57	4.21	8.99	5.13
	Fujian	11.36	17.24	4.66	6.30	10.65

in both the first and second stages, followed by Zhejiang province in the third stage. In the other provinces except Jiangxi, the number of panicles of high-quality rice varieties showed decreasing trends, with a relatively larger number in Hunan in the first stage and in Jiangxi in the next two stages (Figure 1B). The number of spikelets per panicle of those decreased in Guangxi but increased in other provinces, especially Zhejiang in the third stage, and was relatively high in Guangxi province in the first stage (Figure 1C). The seed-set percentage in all provinces except Guangxi showed an increasing trend, and the growth rate was relatively stable (Figure 1D). Zhejiang province had a higher seed-set percentage in all three stages. Grain weight in all provinces except Zhejiang showed an increasing trend, with Fujian province showing a high value in the previous two stages and Jiangxi province showing a rapid increase in the third stage (Figure 1E).

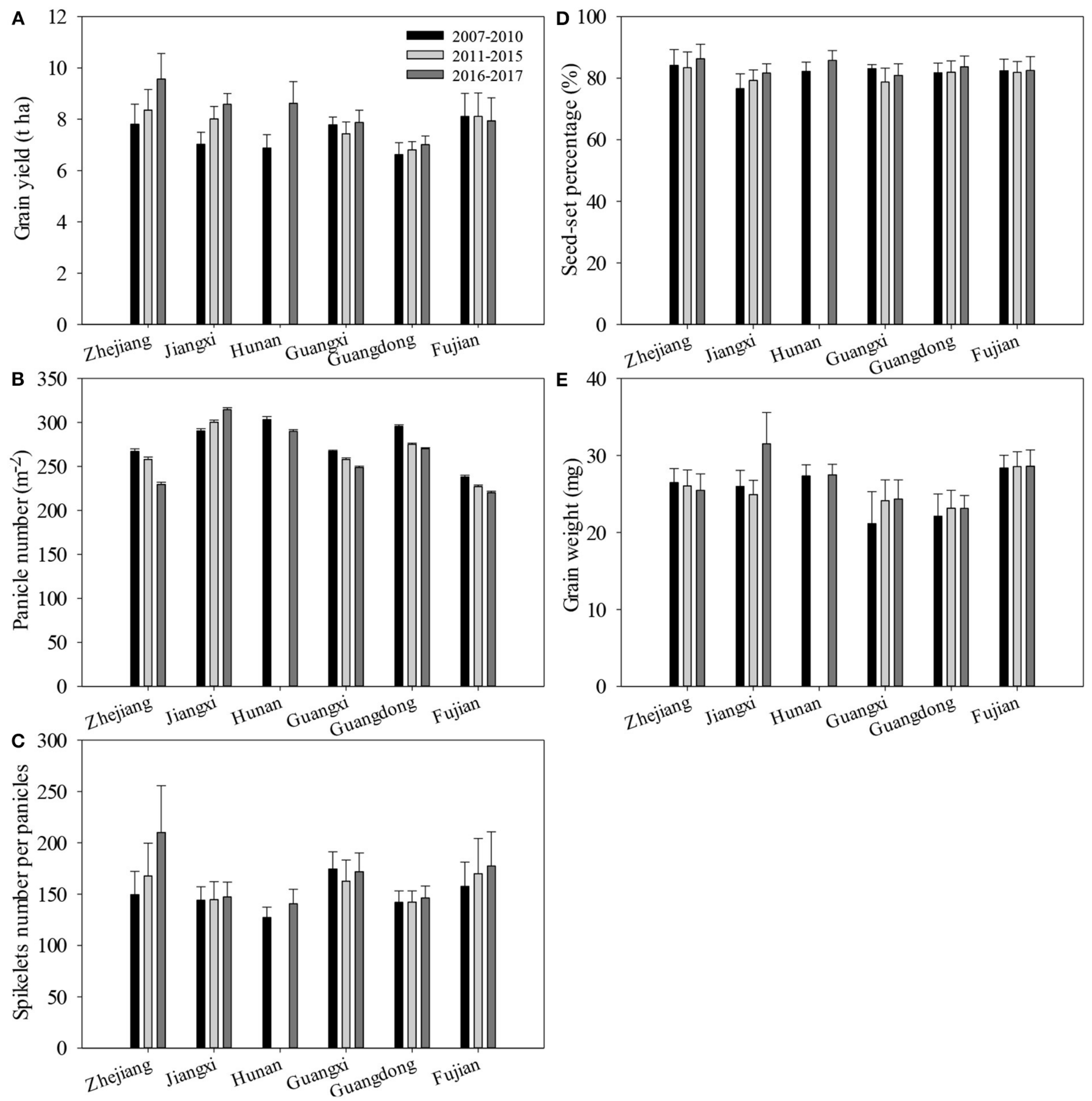

FIGURE 1
Grain yield **(A)**, the number of panicles **(B)**, the number of spikelets per panicles **(C)**, seed-set percentage **(D)**, and grain weight **(E)** of high grain quality rice varieties in six provinces.

Relationships between grain quality and yield in high-quality rice varieties

The number of panicles and seed-set percentage and grain weight were positively and negatively correlated with the head rice rate, respectively (Figure 2). The chalkiness rate and chalkiness degree were negatively and positively associated with the number of panicles and seed-set percentage, while grain weight and grain yield were positively associated with the chalkiness rate (Figure 2). There were negative relationships between amylose content, the number of spikelets, seed-set percentage, and grain yield (Figure 2). The number of panicles and the number of spikelets per panicle were negatively and positively correlated with gel consistency, respectively (Figure 2).

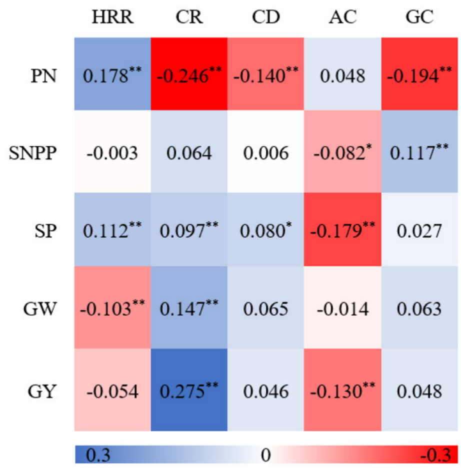

FIGURE 2
Correlation coefficient between grain yield and quality of high-quality rice from 2007 to 2017 ($n = 710$). *Correlation is significant at the 0.05 level, while ** correlation is significant at the 0.01 level (two-tailed). PN, panicle number; SNPP, spikelet number per panicles; SP, seed-set percentage; GW, grain weight; GY, grain yield; HRR, head rice rate; CR, chalkiness rate; CD, chalkiness degree; AC, amylose content; GC, gel consistency.

Discussion

Changes in grain yield and yield traits for selected high-quality rice varieties

In the present study, the grain yield of high-quality rice varieties *indica* or *japonica* rice and hybrid or inbred rice continued to increase between 2007 and 2017 (Table 3). These were mainly due to the increase in grain yield per unit rather than the rice planting area, so the yield per unit was the deciding factor for the increase in China's total grain yield (Chen et al., 2012). Zhejiang, Jiangxi, and Hunan provinces are mainly located in the rice preponderance area of the Yangtze River Basin, while Guangdong, Guangxi, and Fujian provinces are mainly located in the rice preponderance area of the southeast coast of China (Peng, 2014). In this study, for these three stages, grain yield increased in most provinces except Fujian, and Guangxi and Guangdong provinces had a small increase in grain yield trends from 2007 to 2017 (Figure 2). The concentration degree of rice production and background soil fertility of rice fields are higher in the rice preponderance area of the Yangtze River Basin than in the rice preponderance area of the southeast coast of China (Li J. J. et al., 2016). Second, the plantation area of single crop rice in the rice preponderance area in the Yangtze River Basin has increased year by year, which is the main reason for the large increase in yield per unit area in Hunan and Jiangxi provinces (Chen et al., 2012).

Increasing the yield potential of super rice employed involves a combination of ideotype breeding, heterosis utilization, and the goal of modifying plant architecture, and heterosis is a time tested strategy to achieve increased yield potential (Khush, 2005). These approaches result in the adoption of semi-dwarf cultivars for better lodging resistance and the exploitation of heterosis, which is known to substantially increase rice yields over the last half century (Lei et al., 2010; Wing et al., 2018). The number of panicles and the number of spikelets per panicle are important components of ideotype in super rice (Deng et al., 2004). In this study, the number of panicles in the *japonica* hybrid and *indica* inbred rice decreased significantly over time, but no change was observed in the *japonica* inbred and *indica* hybrid rice (Table 3), while the number of panicles in the hybrid rice largely varied over time (Table 4). Thus, improving the number of panicles for high-quality hybrid rice might be another breeding target. Previous studies showed that the breeding approach of a high number of panicles in rice production was feasible because the *MOC1* gene (the first cloned gene related to rice tillering) on chromosome 6 was mapped, and the functional analysis proved that this gene was a key regulatory gene in regulating rice tillering (Li X. Y. et al., 2003). Subsequently, the following genes related to rice tillering, such as *OsTB1, D14, MT1,* and *HTD2,* were discovered by other researchers, supporting our results (Li et al., 2003; Arite et al., 2009; Liu et al., 2009; Zhou et al., 2009). In addition, in this study, high-quality *indica* hybrid rice showed large variation coefficients in the number of spikelets per panicle over time (Table 4), suggesting that it should also be improved. As genes that regulate tillers and spikelets tend to be highly pleiotropic and affect many different traits, this study on obtaining high yield potential might involve balancing the different traits (Xing and Zhang, 2010). When considering the improvement of rice yield, it is important to characterize the entire regulatory network rather than component traits or individual genes. As a result, this can verify the breeding achievements related to the high yield of high-quality rice varieties. In fact, a proposal for ideotype breeding is to improve the efficiency of canopy radiation use (Guo et al., 2020). Hence, a perfect physiological function (such as photosynthesis capacity, biomass accumulation, and translation ability) of tillering could achieve ideotype breeding of high-quality varieties because of their high yield potential (Xiao F. et al., 2021).

The seed-set percentage of rice was mainly determined by flowering fertilization and grain filling (Deng et al., 2021). Previous studies demonstrated that spikelet fertility is one of the most environmentally sensitive components of rice grain production (Suzuki et al., 2015). Our research indicated that the seed-set percentage in *indica* rice increased significantly over time, but no change was observed in *japonica* rice. In the context of global warming, the process of improving high-quality *japonica* rice is continuously developing because *japonica* rice is relatively weak in heat resistance (Wang et al., 2019). Meanwhile, the subspecies showed a small difference in seed-set percentage, and high-quality *indica* rice showed large variation coefficients in grain weight in three stages (Table 4), implying that they should be improved in future breeding. However, there were no significant changes in grain weight, indicating that grain weight is not the main factor affecting grain yield over time. An increase in the grain yield of *japonic*a hybrid rice was mainly due to the number of spikelets per panicle rather than the number of panicles; an increase in the grain yield of *indica* rice was mainly related to the number of spikelets per panicle and seed-set percentage in the last 11 years.

Differences in grain yield traits between high-quality rice types in southern China

Zhang et al. (2013) reported that the grain yield of *japonica* rice was significantly higher than that of *indica* rice when comparing local representative *indica* and *japonica* rice varieties in the lower reaches of the Yangtze River in China. In Liaonig province, the yield of northeast *japonica* rice increased by 13.48% compared with control *indica* rice (Gao et al., 2013). We also saw similar yield results in the subspecies. The reason might be that the storage substance of *japonica* rice before the heading stage was higher than that of *indica* rice, and the amount of nutrients transported to grains was larger (Xu et al., 2018). *Indica* rice showed a quicker senescence degree of leaves and roots than *japonica* rice at the grain filling stage (Gong et al., 2014). In addition, in the late growth stage, *japonica* rice could adapt to low temperatures and was still well filled in the glumes, even though the number of spikelets in *japonica* rice was equal to or slightly less than that in *indica* rice (Zhang et al., 2013). Meanwhile, the results showed that the yield of hybrid rice was significantly higher than that of inbred rice in the same subspecies, indicating that the breeding work of hybrid rice had made great progress in the past 11 years (Table 2).

In this study, the number of panicles of hybrid rice was significantly decreased compared with inbred rice (Tables 2, 3). In contrast, hybrid rice significantly increased the number of spikelets per panicle in the same subspecies (Tables 2, 3). Hybrid rice with a large heavy panicle type showed relatively high yield (Sheehy et al., 2001), and our results were similar to those of Lin (2008). The reason might be that a decrease in the number of panicles and an increase in the number of spikelets per panicle could significantly improve the grain–panicle structure, rationally use light conditions, and enlarge the sink capacity to promote the coordinated development of grain yield and quality (Chen et al., 2018). However, the opposite trends of the number of panicles and the number of spikelets per panicle in breeding type and subspecies rice varieties could not be solved with ideal plant type alone because it involves population effects, which can also be verified by the results mentioned above. Although single trait enhancement increased yield in our study, it was always difficult to coordinate the factors of population structure. Therefore, the optimization of the contradiction between the number of panicles and the number of spikelets will be of great significance through agricultural measures such as water and fertilizer management or genetic improvement for the use of yield potential and the coordination of high-quality rice varieties, especially varieties of different subspecies and types of breeding. In addition, high variation coefficients were found for yield traits in both the number of panicles and the number of spikelets per panicle in six provinces, especially Fujian, possibly suggesting a worse climatic environment to influence rice growth (Table 5).

Grain weight per panicle (GWPP) is determined by the number of spikelets per panicle and grain weight (Chen et al., 2007), and increased GWPP can achieve super high yield (Yang et al., 2006). On the other hand, an increase in the number of spikelets per panicle is accompanied by a decrease in seed-set percentage (Wu et al., 2010). Similar results were obtained in the present study (Table 2). Xu et al. (2006) reported that secondary panicle branches usually had a lower seed-set percentage. On the contrary, in breeding varieties with vascular bundles developed at the panicle neck, a large number of primary branches and secondary branches on the upper panicle could effectively solve the contradiction between the number of spikelets per panicle and seed-set percentage (Xu et al., 1998; Xu et al., 2006). In the present study, *japonica* rice had a significantly higher seed-set percentage than *indica* rice for high-quality rice breeding types in the last 11 years. The grain filling time of *japonica* rice was longer and more stable, especially in the late filling stage and even when the filling of inferior grain was also better (Gong et al., 2014). Therefore, the optimized yield components of high-quality *indica* rice should possess a high number of spikelets and seed-set percentage, whereas the relatively lower tillers of inbred *indica* rice should be optimized for this study. Due to complex and negative relationships between yield and quality traits, the breeding of high-yielding, high-quality varieties is difficult (Xiao N. et al., 2021). However, the breeding of high-yielding, high-quality rice varieties may be promising, due to recent technological advances in genome biology such as genome editing and molecular breeding (Wing et al., 2018).

Synergistic improvement strategy of high-quality rice yield and quality

The super high yield of rice remains the eternal direction of research objectives in China. However, with the improvement of people's living standards, the demand for rice has diversified (Zhang et al., 2021). High yield and high quality are urgent problems that must be solved in high-quality rice. Correlation analysis showed that grain yield was positively correlated with the chalkiness rate and negatively correlated with amylose, which were beneficial to the synergistic improvement of rice eating quality and grain yield, but was not conducive to the improvement of rice appearance quality (Figure 2). During carbon and nitrogen metabolism at the filling stage of rice grain, protein synthesis increases, resulting in improved rice yield (Xiong et al., 2021). Reduced amylose content resulted in an uneven arrangement of rice starch granules, loose tissues in the endosperm, and finally increased the chalkiness rate (Yang et al., 2019). Unlike the number of spikelets per panicle, seed-set percentage, and grain weight, an inverse correlation was observed between the panicle number with appearance (chalkiness rate and chalkiness degree) and eating quality (amylose content and gel consistency) (Figure 2). Attention should be paid to the breeding goal of ensuring rice with high yield and high quality. In addition, grain weight is also different from the number of spikelets per panicle and seed-set percentage. The former has a negative correlation with the head rice rate, while the latter has a positive correlation with the head rice rate (Figure 2). The results showed that an adequate reduction of grain weight and the increase in the number of panicles and seed-set percentage were beneficial to improve the processing quality.

Conclusions

Grain yield increased significantly in each subspecies (*japonica* and *indica*) and breeding type (hybrid, inbred) of high-quality rice varieties from 2007 to 2017. The number of spikelets per panicle, instead of the number of panicles, contributed to the grain yield of *japonic*a hybrid rice, but both the number of spikelets per panicle and seed-set percentage could contribute to the grain yield of *indica* rice over time. *Japonica* rice showed significantly higher grain yield than *indica* rice due to the higher seed-set percentage and better optimized yield trait structure such as the number of panicles and the number of spikelets per panicle and the hybrid rice achieved high grain yield compared with the inbred rice, which was mainly attributed to the higher number of spikelets per panicle. Additionally, variation coefficients of grain yield showed a decreasing trend in *japonica* rice in the past 11 years but had an increasing trend in *indica* rice, and variation coefficients for both the number of panicles and seed-set percentage were also reduced in the subspecies, suggesting that *japonica* rice varieties had stable grain yields. For the past 11 years, the grain yield of high-quality rice varieties had a higher increase in Zhejiang, Hunan, and Jiangxi provinces than in other provinces, especially in Zhejiang province, which was supported by reasonable yield components, such as the highest number of spikelets per panicle and seed-set percentage. Future high-quality rice breeding should focus on the optimized yield components, with hybrid rice focusing on improving the number of panicles and seed-set percentage and inbred rice improving the number of spikelets, especially the grain weight for *indica* inbred rice.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

HW, RX, and YZh: investigation, data curation, and writing—original draft. XT: software, methodology, and visualization. XP, YoZ, SH, QS, and XX: writing—review and editing. JZ: validation and project administration. YaZ: writing—review and editing and conceptualization. All authors contributed to the article and approved the submitted version.

Funding

The study was supported by the Key Project of Jiangxi Provincial Natural Science Foundation (20202ACBL215004), the National Natural Science Foundation of China (32071950 and 32272212), the Earmarked Fund for Jiangxi Agriculture Research System (JXARS-19-02 and JXARS-02-03), the National Key Research & Development Project of China (2016YFD0300501), and the Key Research & Development Project Jiangxi Province, China (20171BBF60030).

Acknowledgments

We would like to thank those at the forefront of the fight against the COVID-19 epidemic for allowing us to focus on writing this paper safely.

Conflict of interest

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.

Publisher's note

References

Arite, T., Umehara, M., Ishikawa, S., Hanada, A., Maekawa, M., Yamaguchi, S., et al. (2009). D14, a strigolactone-insenstive mutant of rice, shows an accelerated outgrowth of tillers. *Plant Cell Physiol.* 50, 1416–1424. doi: 10.1093/pcp/pcp091

Chen, S., Zeng, F. R., Pao, Z. Z., and Zhang, G. P. (2008). Characterization of high-yield performance as affected by genotype and environment in rice. *J. Zhejiang Univ. (Sci. B: Int. Biomed. Biotechnol. J.).* 5, 363–370. doi: 10.1631/jzus.B0710603

Chen, W. F., Xu, Z. J., and Zhang, W. Z. (2007). Advances and prospects in breeding japonica rice for super high yield in the Northern China. *Agric. Sci. China* 6, 1157–1165. doi: 10.1016/S1671-2927(07)60159-X

Chen, X. B., Rao, M. D., Su, R. L., and Le, K. F. (2018). Breeding and yield structure analysis of blast-resistant hybrid rice 'Guyou 168'. *Chin. Agric. Sci. Bull.* 34, 7–12. Available online at: https://kns.cnki.net/kcms/detail/detail.aspx?FileName=ZNTB201836002&DbName=CJFQ2018

Chen, Y. X., Wang, X. Z., Guo, J. P., Zhao, Y. X., and Huang, J. F. (2012). The temporal-spatial dynamic analysis of China rice production. *Scientia Agricultura Sinica* 45, 3473–3485. doi: 10.3864/j.issn.0578-1752.2012.17.003

China Rice Data Center. (2018). *Database of Rice Varieties and their Genealogies in China*. Available online at: https://www.ricedata.cn/variety/index.htm

Deng, F., Zeng, Y. L., Li, Q. P., He, C. Y., Li, B., Zhu, Y. Y., et al. (2021). Decreased anther dehiscence contributes to a lower fertilization rate of rice subjected to shading stress. *Field Crops Res.* 273, 108291. doi: 10.1016/j.fcr.2021.108291

Deng, H. F., He, Q., Shu, F., Zhang, W. H., Yang, F., Jing, Y. H., et al. (2006). Status and technical strategy on development of *japonica* hybrid rice in China. *Hybrid Rice* 21, 1–6. doi: 10.16267/j.cnki.1005-3956.2006.01.001

Deng, Q. Y., Yang, L. P., Liang, F. S., Li, J. M., Li, X. Q., Wang, L. G., et al. (2004). Studies on yield-enhancing genes from wild rice and their marker-assisted selection in hybrid rice. *Hybrid Rice* 19, 6–10. doi: 10.16267/j.cnki.1005-3956.2004.01.002

FAO (2018). *Food and Agric. Organization of the United Nations, in Agric. Producer Price Indices.* FAO, Rome.

Feng, F., Li, Y. J., Qin, X. L., Liao, Y. C., and Siddique, K. H. M. (2017). Changes in rice grain quality of indica and japonica type varieties released in China from 2000 to 2014. *Front. Plant Sci.* 8, 1863. doi: 10.3389/fpls.2017.01863

Gao, H., Li, F. F., Lu, G. Y., Xia, Y. J., Wang, J. Y., Sun, J., et al. (2013). Effect of *indica-japonica* hybridization on grain quality of rice cultivars in Northeast China. *Acta Agronomica Sinica* 39, 1806–1813. doi: 10.3724/SP.J.1006.2013.01806

Gong, J. L., Xing, Z. P., Hu, Y. J., Zhang, H. C., Dai, Q. G., Huo, Z. Y., et al. (2014). Studies on the difference of yield components characteristics between *indica* and *japonica* super rice. *J. Nuclear Agric. Sci.* 28, 0500–0511. |doi: 10.11869/j.issn.100- 8551.2014.03.0500

Guo, W., Chen, L. M., Herrera, E. L., Gao, D., and Tran, L. S. P. (2020). Altering plant architectureto improve performance and resistance. *Trends plant Sci.* 25, 1154–1170. doi: 10.1016/j.tplants.2020.05.009

Khush, G. S. (2005). What it will take to feed 5.0 billion rice consumers in 2030. *Plant Mol. Biol.* 59, 1–6. doi: 10.1007/s11103-005-2159-5

Lei, J. G., Wang, X. L., Xiao, Y. L., Li, M. Z., and Yu, C. Y. (2010). Analysis on main characters and discussion on high-yielding breeding of late-season indica hybrid rice. *Acta Agriculturae Jiangxi* 22, 11–13. doi: 10.19386/j.cnki.jxnyxb.2010.06.004

Li, J. J., Xu, M. G., Duan, J. J., Ren, Y., Li, D. C., Huang, J., et al. (2016). Spatial and temporal characteristics of basic soil productivity in China. *Scientia Agricultura Sinica* 49, 1510–1519. doi: 10.3864/j.issn.0578-1752.2016.08.008

Li, X. Y., Qian, Q., Fu, Z. M., Wang, Y. H., Xiong, G. S., Zeng, D. L., et al. (2003). Control of tillering in rice. *Nat.* 422, 618–621. doi: 10.1038/nature01518

Li, X. Y., Qian, Q., and Li, J. Y. (2003). Progress in elucidating the Mol. mechanism of rice tillering. *Bull. of Chin. Acad. Sci.* 4, 274–276. doi: 10.16418/j.issn. 1000-3045.2003.04.009

Lin, Q. (2008). Statistical analysis of main characteristics and yield of early hybrid rice in Fujian Province. *Seed* 27, 72–74. doi: 10.16590/J.CNKI.1001-4705.2008. 04.055

Liu, W., Wu, C., Fu, Y., Hu, G., Si, H., Zhu, L., et al. (2009). Identification and characterization of *HTD2*: a novel gene negatively regulating tiller bud outgrowth in rice. *Planta* 230, 649–658. doi: 10.1007/s00425-009-0975-6

Liu, Z. H., Li, Z. G., Tang, P. Q., Li, Z. P., Wu, W. B., Yang, P., et al. (2013). Change analysis of rice area and production in China during the past three decades. *J. Geogr. Sci.* 23, 1005–1018. doi: 10.1007/s11442-013-1059-x

Mao, T., Li, X., Jiang, S. K., Tang, L., Wang, J. Y., Xu, H., et al. (2017). Discussion on strategy of grain quality improvement for super high yielding japonica rice in Northeast China. *J. Integr. Agric.* 16, 1075–1083. doi: 10.1016/S2095-3119(16)61563-0

Peng, J. H., Isii, K., and Ukai, Y. (2008). Response of genetic variability of quantitative characters to nitrogen levels in rice. *Breed. Sci.* 41, 255–264. doi: 10.1270/jsbbs1951.41.255

Peng, S. B. (2014). Reflection on China's rice production strategies during the transition period. *Scientia Sinica Vitae* 44, 845. doi: 10.1360/052014-98

Peng, S. B., Huang, J. L., Cassman, K., Laza, M. R. C., Visperas, R. M., Khush, G. S., et al. (2010). The importance of maintenance breeding: A case study of the first miracle rice variety-IR8. *Field Crops Res.* 119, 342–347. doi: 10.1016/j.fcr.2010.08.003

Peng, S. B., Khush, G. S., Virk, P., Tang, Q. Y., and Zou, Y. B. (2008). Progress in ideotype breeding to increase rice yield potential. *Field Crops Res.* 108, 32–38. doi: 10.1016/j.fcr.2008.04.001

Peng, S. B., Tang, Q. Y., and Zou, Y. B. (2009). Current status and challenges of rice production in China. *Plant Prod. Sci.* 12, 3–8. doi: 10.1626/pps.12.3

Sheehy, J. E., Dionora, M. J. A., and Mitchell, P. L. (2001). Spikelet numbers, sink size and potential yield in rice. *Field Crops Res.* 7, 77–85. doi: 10.1016/S0378-4290(01)00145-9

Suzuki, K., Aoki, N., Matsumura, H., Okamura, M., Ohsugi, R., Shimoni, H., et al. (2015). Cooling water before panicle initiation increases chilling-induced male sterility and disables chilling-induced expression of genes encoding OsFKBP65 and heat shock proteins in rice spikelets. *Plant Cell Environ.* 38, 1255–1274. doi: 10.1111/pce.12498

Tester, M., and Langridge, P. (2010). Breeding technologies to increase crop production in a changing world. *Sci.* 327, 818–822. doi: 10.1126/science.1183700

Tripp, R., Hu, R., and Pal, S. (2010). "Rice seed provision and the evolution of seed markets," in *Rice in the Global Economy: Strategic Res. and Policy Issues for Food Security*, eds S. Pandey, D. Byerlee, D Dawe, A. Dobermann, S. Mohanty, S Rozelle et al. Los Baños. International Rice Res. Institute, Manila, 213–228.

Wang, J., Zeng, B., Lei, C. L., Zhao, Z. C., Wang, J. L., Cheng, Z. J., et al. (2018). Variety analysis of Northern rice regional trials in recent 15 years. *Crops* 1, 71–76. doi: 10.16035/j.issn.1001-7283.2018.01.011

Wang, Y. L., Wang, L., Zhou, J. X., Hu, S. B., Chen, H. Z., Xiang, J., et al. (2019). Research progress on heat stress of rice at flowering stage. *Rice Sci.* 26, 1–10. doi: 10.1016/j.rsci.2018.06.009

Wing, R. A., Purugganan, M. D., and Zhang, Q. F. (2018). The rice genome revolution: from an ancient grain to green super rice. *Nat. Rev. Genet.* 19, 505–517. 018-0024-z doi: 10.1038/s41576-018-0024-z

Wu, G. C., Zhang, H. C., Qian, Y. F., Li, D. J., Zhou, Y. Y., Xu, J., et al. (2010). Rule of grain yield components from high yield to super high yield and the characters of super-high yielding japonica super rice. *Scientia Agricultura Sinica* 43, 266–276. doi: 10.3864/j.issn.0578-1752.2010. 02.006

Xiao, F., Li, W. W., Xiao, M. H., Yang, Z. F., Cheng, W. D., Gao, S., et al. (2021). A novel light interception trait of a hybrid rice ideotype indicative of leaf to panicle ratio. *Field Crops Res.* 274, 108338. doi: 10.1016/j.fcr.2021.108338

Xiao, N., Pan, C. H., Li, Y. H., Wu, Y. Y., Cai, Y., Lu, Y., et al. (2021). Genomic insight into balancing high yield, good quality, and blast resistance of japonica rice. *Genome Biol.* 22, 283. doi: 10.1186/s13059-021-02488-8

Xing, Y., and Zhang, Q. (2010). Genetic and Mol. bases of rice yield. *Ann. Rev. Plant Biol.* 61, 421–442. doi: 10.1146/annurev-arplant-042809-112209

Xiong, R. Y., Xie, J. X., Tan, X. M., Yang, T. T., Pan, X. H., Zeng, Y. J., et al. (2021). Effects of irrigation management on grain yield and quality of high-quality eating late-season *indica* rice in South China. *Scientia Agricultura Sinica* 54, 1512–1524. doi: 10.3864/j.issn.0578-1752.2021.07.015

Xu, C. C., Ji, L., Chen, Z. D., and Fang, F. P. (2021). Analysis of China's rice industry in 2020 and the outlook for 2021. *China Rice* 27, 1–4. doi: 10.3969/j.issn.1006-8082. 2021.02.001

Xu, D., Zhu, Y., Zhou, L., Han, C., Zhen, L. M., Zhang, H. C., et al. (2018). Differences in yield and grain quality among various types of indica/japonica hybrid rice and correlation between quality and climatic factors during grain filling period. *Acta Agronomica Sinica* 44, 1548–1559. doi: 10.3724/SP.J.1006.2018.01548

Xu, Z. J., Chen, W. F., Cao, H. R., Zhang, L. B., and Yang, S. R. (1998). Relation between the characters of panicle and vascular bundle in neck-panicle of rice. *Acta Agronomica Sinica* 24, 47–54.

Xu, Z. J., Chen, W. F., Shun, Z. H., Zhang, S. L., Liu, L. X., and Zhou, S. Q. (2006). Distribution of rice grains on panicle axis and its relationship with seed-setting ability in Liaoning, China. *Rice Sci.* 3, 202–208. doi: 10.1016/S1671-2927(06)60039-4

Yang, H., Wen, Z. R., Huang, T. Q., Lu, W. P., and Lu, D. L. (2019). Effects of waterlogging at grain formation stage on starch structure and functionality of waxy maize. *Food Chem.* 294, 187–193. doi: 10.1016/j.foodchem.2019.05.072

Yang, J. C., Du, Y., Wu, C. F., Liu, L. J., Wang, Z. Q., Zhu, Q. S., et al. (2006). Growth and development characteristics of super-high-yielding mid-season japonica rice. *Scientia Agricultura Sinica* 39, 1336–1345.

Yang, X. G., Chen, F., Lin, X. M., Liu, Z. J., Zhang, H. L., Zhao, J., et al. (2015). Potential benefits of climate change for crop productivity in China. *Agric. For. Meteorol.* 208, 76–84. doi: 10.1016/j.agrformet.2015.04.024

Yang, X. G., Liu, Z. J., and Chen, F. (2010). The possible effects of global warming on cropping systems in China I. The possible effects of climate warming on northern limits of cropping systems and crop yields in China. *Scientia Agricultura Sinica* 43, 329–336. doi: 10.3864/j.issn.0578-1752.2010.02.013

Yoshida, H., Horie, T., and Shiraiwa, T. (2006). A model explaining genotypic and environmental variation of rice spikelet number per unit area measured by cross-locational experiments in Asia. *Field Crops Res.* 97, 337–343. doi: 10.1016/j.fcr.2005.11.004

Yuan, L. P. (2017). Progress in super-hybrid rice breeding. *Crop J.* 5, 100–102. doi: 10.1016/j.cj.2017.02.001

Zeng, Y. H., Tan, X. M., Zeng, Y. J., Xie, X. B., Pan, X. H., Shi, Q. H., et al. (2019). Changes in the rice grain quality of different high-quality rice varieties released in southern China from 2007 to 2017. *J. Cereal Sci.* 87, 111–116. doi: 10.1016/j.jcs.2019.03.015

Zhang, H., Zhou, G. S., Liu, D. L., Wan, B., Xiao, D. P., He, L., et al. (2019). Climate-associated rice yield change in the northeast China plain: a simulation analysis based on CMIP5 multi-model ensemble projection. *Sci. Total Environ.* 666, 126–138. doi: 10.1016/j.scitotenv.2019.01.415

Zhang, H. C., Hu, Y. J., Yang, J. C., Dai, Q. G., Huo, Z. Y., Xu, K., et al. (2021). Development and prospect of rice cultivation in China. *Scientia Agricultura Sinica* 54, 1301–1321. doi: 10.3864/j.issn.0578-1752.2021.07.001

Zhang, H. C., Zhang, J., Gong, J. L., Chang, Y., Li, M., Gao, H., et al. (2013). The productive advantages and formation mechanisms of "*indica* rice to *japonica* rice". *Scientia Agricultura Sinica* 46, 686–704. doi: 10.3864/j.issn.0578-1752.2013.04.004

Zhou, Y., Zhu, J. Y., Li, Z. Y., Gu, F., Zhang, H. G., Tang, S. Z., et al. (2009). Fine mapping and cloning of *MT*1, a novel allele of *D*10. *Progr. Nat. Sci.* 19, 1683–1689. doi: 10.1016/j.pnsc.2009.05.006