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REVIEW

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In 1996, a mega project that aimed to develop rice varieties with super-high yield potential (super rice) was launched by the Ministry of Agriculture (MOA) in China using a combination of the ideotype approach and intersubspecifc heterosis. Signifcant progress has been made in the last two decades, with a large number of super rice varieties being approved by the MOA and the national average grain yield being increased from 6.21 t $ha^{-1}$ in 1996 to 6.89 t $ha^{-1}$ in 2015. The increase in yield potential of super rice was mainly due to the larger sink size which resulted from larger panicles. Moreover, higher photosynthetic capacity and improved root physiological traits before heading contributed to the increase in sink size. However, the poor grain flling of the later-fowering inferior spikelets and the quickly decreased root activity of super rice during grain flling period restrict the achievement of high yield potential of super rice. Furthermore, it is widely accepted that the high yield potential of super rice requires a large amount of N fertilizer input, which has resulted in an increase in N consumption and a decrease in nitrogen use effciency (NUE), although it remains unclear whether super rice is responsible for the latter. In the present paper, we review the history and success of China's Super Rice Breeding Program, summarize the advances in agronomic and physiological mechanisms underlying the high yield potential of super rice, and examine NUE differences between super rice and ordinary rice varieties. We also provide a brief introduction to the Green Super Rice Project, which aims to diversify breeding targets beyond yield improvement alone to address global concerns around resource use and environmental change. It is hoped that this review will facilitate further improvement of rice production into the future.

super rice, yield potential, nitrogen use effciency, Green Super Rice

The global demand for crop production is expected to double by 2050 as a result of the increasing size of the human population, dietary shift that has resulted from greater levels of affuence and biofuel consumption (Tilman . 2011; Ray . 2015). Rather than clearing more land for food production, the augmentation of crop yields is the most promising approach for maintaining food security with the minimum environmental impacts (Foley . 2011; Tilman . 2011). Rice is a staple food crop for approximately

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half of the global population (Godfray . 2010), but its current rate of yield increase of 1.0% is less than the 2.4% per year that is required to double its production by 2050 (Ray . 2015). Therefore, it is necessary to develop new varieties that have a higher yield potential.

Yield potential is defined as the yield of a cultivar when it is grown in an environment to which it is adapted in the presence of nutrients and a non-limiting water supply, with the effective control of pests, diseases, weeds, lodging, and other stresses (Evans and Fischer 1999) or, alternately, the yield obtained when an adapted cultivar is grown with minimal possible stress, which is achieved with the best management practices (Cassman 1999). Over the last five decades, China has pioneered breeding techniques for increasing yield potential of rice. To improve the harvest index and nitrogen (N) responsiveness by increasing lodging resistance, breeding for semidwarf rice varieties was initiated in 1956, with the first semidwarf variety Guangchangai being developed in 1959 (Huang 2001). Rice yield potential was then further improved in the 1970s through the utilization of heterosis, which resulted in the hybrid rice having a yield potential that was approximately 20% higher than that of inbred rice (Yuan 1987). Finally, in the 1990s, super rice was developed in China through a combination of the ideotype approach and intersubspecific heterosis, allowing the yield ceiling to be broken (Cheng 2007).

The creation of genetically improved crop varieties combined with the application of improved agronomic practices led to the average rice grain yield in China being increased from 2.08 t $ha^{-1}$ in 1961 to 6.75 t $ha^{-1}$ in 2013 (Fig. 1). However, the improved N responsiveness and lodging resistance of these high-yielding rice varieties resulted in the overuse of fertilizers, particularly N fertilizers (Peng . 2002), as farmers tended to apply a higher amount of N fertilizer than required to realize the high yield potential of the super rice. Thus, global N consumption increased approximately 8-fold from 1961 to 2013, of which China accounted for approximately 8% in 1961 and 35% in 2013 (Fig. 2). These rice varieties also had a significantly lower N use efficiency (NUE), with a recovery efficiency ($RE_N$) of . 30–35% and an agronomic efficiency ($AE_N$) of <10 kg grain yield $kg^{-1}$ N in China (Zhu 1985; Lin 1991; Li 1997). The high N input has commonly been considered the reason for the low NUE in China's rice production (Peng . 2002). However, NUE differences between super rice, ordinary hybrid rice, and inbred rice have rarely been studied.

In this paper, we review the development of China's super rice, beginning with the history and success of the breeding program. We then summarize the agronomic and physiological basis for its high yield potential, and examine whether super rice is responsible for the low NUE in rice production in China. We end with a brief introduction to the Green Super Rice Project. We hope that this information will help to further progress rice improvement and to identify additional suitable targets in the future.

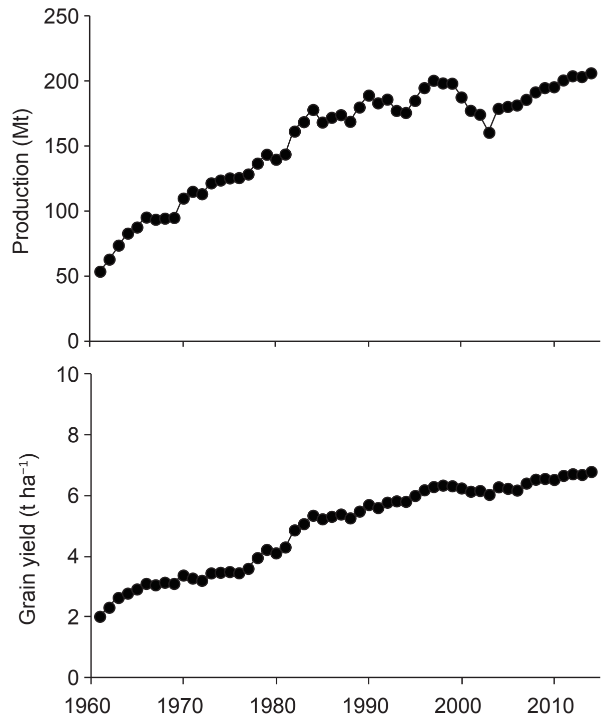
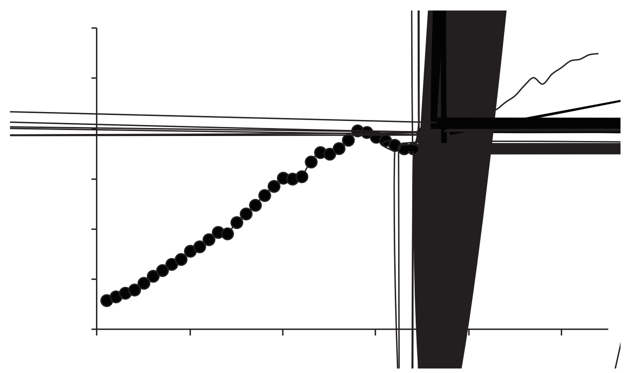



**Fig. 1** Trends in rice production and grain yield in China from 1961 to 2013 (FAO 2016).



Breeding for super rice was initiated in Korea and Japan in the 1970s–1980s by crossing with rice (Peng . 2008), which led to the development of several intersubspecific hybrid varieties with high yield potential (Chung and Heu 1980; Nagari . 2001). In Korea, the high-yielding varieties from × hybridizations were designated as “Tongil-type” and exhibited a high lodging resistance and N responsiveness (Choi . 1974). By contrast, super rice varieties in Japan, such as Takanari, were characterized by a large number of spikelets per panicle (Nagari . 2001). In China, × hybridization attempts were made in the 1950s (Cheng . 1998).

In 1989, new plant type (NPT) breeding began at the International Rice Research Institute (IRRI), based on simulation modeling predictions that modifcations to the high-yielding rice plant type could lead to a 25% increase in yield potential (Dingkuhn . 1991; Khush 1995). The frst generation NPT rice was characterized by a lower tillering capacity, no unproductive tillers, 200–250 grains per panicle, a height of 90–100 cm, a very sturdy stem, dark green, thick, and erect leaves, a vigorous root system, a growth duration of 100–130 days, and multiple disease and insect resistance (Khush 1995). However, grain yield was disappointing due to low biomass production and poor grain flling (Peng . 2008). Therefore, biomass production was signifcantly increased in the second-generation NPT rice; however, yield potential was still not improved mainly due to the low grain flling percentage (Fu . 2011).

China’s super rice program was established in 1996 by the Ministry of Agriculture (MOA), China, based on a combination of intersubspecifc heterosis and harmonious plant types (Cheng 2007). Super rice breeding in Japan aimed to increase the yield potential of rice by 50%, while NPT breeding at IRRI aimed to develop varieties with a yield potential of 15 t $ha^{-1}$ (Khush 1995). By contrast, the objectives of China’s Super Rice Breeding Program were the following (Cheng . 1998):

(1) Develop super rice varieties with a maximum yield of 9–10.5 t $ha^{-1}$ by 2000, 12 t $ha^{-1}$ by 2005 and 13.5 t $ha^{-1}$ by 2015 measured over a large planting area of at least 6.7 ha.

(2) Develop super rice varieties with a yield potential of 12 t $ha^{-1}$ by 2000, 13.5 t $ha^{-1}$ by 2005 and 15 t $ha^{-1}$ by 2015 in both experimental and demonstration plots.

(3) Raise the national average rice yield to 6.9 t $ha^{-1}$ by 2010 and 7.5 t $ha^{-1}$ by 2030 by developing super rice varieties.

To achieve these goals, a set of plant types were formulated according to the ecological and cropping conditions of different rice growing regions in China; for example, an erect panicle type for Northeast China (Xu . 2004), an early vigor type for South China (Huang and Lin 1994), a heavy panicle type for Southwest China (Zhou . 1995), and a late-stage vigor type for the middle reaches of the Yangtze River (Cheng . 2005). The characteristics for each plant type were summarized in Cheng (2007). The ideotype in the Yangzte River Valley was conceived with the following attributes (Cheng . 2007):

(1) Medium tillering capacity with 12–15 panicles per plant

(2) Plant height of 115–125 cm

(3) Droopy panicle with erect, longer and slightly rolling fag leaf

(4) Yield of 190–220 grains per panicle

(5) Multiple resistance to diseases and insects

(6) Growth duration of 135–140 days

(7) Harvest index of 0.55

Over the last two decades, 146 super rice varieties have been developed in China, including 95 varieties and 51 varieties, which cover an accumulative planting area of more than 47 million ha. Their development increased the national average yield from 6.21 t $ha^{-1}$ in 1996 to 6.89 t $ha^{-1}$ in 2015 (Cheng 2016). In the frst and second phases, the representative super rice varieties included Xieliangyou 9308 and Liangyoupeijiu, which had a maximum grain yield of 11.84 and 12.11 t $ha^{-1}$, respectively, in 2000 (Yu and Lei 2001; Cheng . 2005). This maximum yield was further increased in the third phase to >15 t $ha^{-1}$ for Yongyou 12 in Zhejiang Province, China in 2012 (Sun . 2013) and 15.4 t $ha^{-1}$ for Yliangyou 900 in Hunan Province, China in 2014 (Li . 2014).

The physiological traits underlying the high yield potential of Xieliangyou 9308 and Liangyoupeijiu have previously been summarized in Peng . (2008). In general, the yield advantage of Xieliangyou 9308 resulted from a high rate of fag-leaf photosynthesis, slow leaf senescence, effcient remobilization of carbohydrates, and high root activity (Wang . 2002; Zhai . 2002); while the high yield of Liangyoupeijiu resulted from effcient remobilization of carbohydrates from straw to grain during the grain flling period, slower leaf senescence, higher leaf area density (LAD) and greater specifc leaf weight (Yao . 2000; Zong . 2000; Katsura . 2007).

Fu . (2012) found that the average grain yield of four super rice varieties was 16.1% higher than that of two high-yielding control varieties due to signifcantly larger sink size that mainly resulted from the larger panicle size rather than panicle number, which in turn was partly due to the larger number of primary and secondary branches (Wu . 2007, 2010). They also demonstrated that the increased differentiation and survival of spikelets in super rice resulted from its higher photosynthetic capacity and improved root physiological traits before heading (Fu . 2012). Chang . (2016) also characterized and compared following features contributed to the high yield potential of Yliangyou 900:

(1) The superior leaf physiology and canopy architectural parameters, which facilitate the increased canopy photosynthetic rate

(2) Improved lodging resistance

(3) Delayed senescence, which increases biomass production after heading

(4) Higher pre-anthesis carbohydrate accumulation in the sheath, leaf and stem, which helps to maintain the activity of the spikelets for longer

(5) A high sink capacity as a result of the large panicle

However, the high yield potential of super rice varieties often fail to be achieved due to the poor grain filling of later-flowering inferior spikelets in contrast to the earlier-flowering superior spikelets (Yang and Zhang 2010; Wei . 2016). It has been found that the low activities of key enzymes in carbon assimilation, rather than assimilate supply, is the main factor leading to poor grain filling in inferior spikelets (Yang and Zhang 2010). Zhang H . (2009) further demonstrated that higher root oxidation activity (ROA) and root zeatin (Z) +zeatin riboside (ZR) content per plant at early and mid-growth stages resulted in the increase in sink size, while the lower ROA and root Z+ZR content during the grain filling period was responsible for the poor grain filling of super rice varieties. Recent studies have revealed new mechanisms underlying the poor grain filling of super rice, and provided possible traits that could be used to improve grain filling percentage of super rice. Starch accumulation is regarded as the main process of grain filling, and five enzymes including sucrose synthase (SuSase, EC 2.4.1.13), invertase (β-fructofuranosidase, EC 3.2.2.26), adenosine iphosphate-glucose pyrophosphorylase (AGPase, EC 2.7.7.27), starch synthase (StSase, EC 2.4.1.21), and starch branching enzyme (SBE, EC 2.4.1.18) play a key role in the metabolism of carbohydrates in developing rice endosperm (Yang and Zhang 2010). Zhu . (2011) performed DNA microarray and real-time PCR analysis for the superior and inferior spikelets, and concluded that the relatively high concentrations of ethylene and abscisic acid (ABA) in inferior spikelets suppress the expression of starch synthesis genes and their enzyme activities and consequently lead to a low grain-filling rate. Wang . (2015) found that moderate soil drying could increase the ABA content in inferior spikelets, which increased grain filling through regulating the activities of these key enzymes. Moreover, ABA functions in a dose-dependent manner in regulating grain filling (Wang . 2015). Comparative proteomics revealed that importin-α, elongation factor 1-β and cell division control protein 48, which are essential for cell cycle progression and cell division, were downregulated in inferior spikelets compared to superior spikelets (Das . 2016). Through analyzing two large panicle varieties with high grain filling percentage, Meng . (2016) found that a high leaf photosynthetic rate and root activity during filling phase, grater biomass accumulation and assimilate transport after heading, longer, thicker, and more erect upper three leaves were important morphological and physiological traits for improving grain filling. Furthermore, Jiang . (2016) demonstrated that rational application of panicle N in the right stage of grain filling was important for increasing grain filling percentage.

Root morphology and physiology are closely associated with the growth and development of above-ground part of plant, however, there have been relatively less study focusing on it (Yang . 2012). For a super rice variety Xieyou 9308, the agronomic traits including heading date, plant height, panicle length, grain yield per plant, number of spikelets per panicle, and grain setting density showed a significantly positive correlation with the root traits including root length, total root length, dry root weight, root surface area, root volume and number of root tip (Liang . 2011). Compared with the inbred high-yielding varieties, super rice varieties had greater ROA, total root absorbing surface area, active absorbing surface area, and Z+ZR content, on a single plant basis at early growth stages (Fu . 2012; Chu . 2014; Gong . 2014; Shen . 2014). However, the quickly decreased root activity of super rice during grain filling period resulted in the lower percentage of filled grains (Zhang H . 2009; Chu . 2014). The ultra-structure of root tip cells plays an important role in yield formation in rice, and it was observed that at the panicle initiation, a super hybrid rice variety Liangyoupeijiu with more spikelets (>200) per panicle had more amyloplasts and mitochondria in root tip cells than an inbred cultivar Xudao 2 with fewer spikelets (<130) per panicle (Yang . 2012). More efforts should focus on the causes for faster root senescence of super rice during grain filling period, and management practices that could delay the decrease in root activity.

It is widely accepted that a large amount of N fertilizer input is required to produce a high yield with super rice. For example, when the super rice varieties Yliangyou 900 and Yongyou 12 produced record yields of more than 15 t $ha^{-1}$, the N inputs were >350 kg $ha^{-1}$ (Sun . 2013; Li . 2014). In a summary of the key management practices for the super rice Yongyou 12, Wei . (2016) concluded that 330 kg $ha^{-1}$ N input was required for a super high yield greater than 13.5 t $ha^{-1}$. However, in a survey of super rice production in five regions of Jiangsu Province, Fu and Yang (2011) found that when the average yield was 11% higher (9.62 t $ha^{-1}$) than that of ordinary varieties, the average N input was 12% higher (284 kg $ha^{-1}$), representing only a 1.5% reduction in NUE for the super rice varieties.

Since super rice is better adapted to high N fertilizer conditions, farmers tend to apply a larger amount of N fertilizer to harvest a higher grain yield. Such high N fertilizer inputs often lead to low NUEs due to rapid losses from ammonia for GSR variety approval, and to develop agronomic and physiological parameters for evaluating each of these traits. To achieve this, rice germplasms that possessed potential green traits were collected, and their growth, nutrient uptake and utilization, and yield production under different water, N and phosphorus (P) input conditions were investigated. Parameters that were associated with resource use efficiency were then evaluated in terms of genotypic variation.

• Topic 2: To disclose the physiological mechanisms underlying the high N and P use efficiency of candidate GSR varieties through the Metabolomics, Proteomics, Transcriptomics, and measurement of enzyme activity and content of plant hormones.

• Topic 3: To develop crop management practices that are resource efficient and environmentally friendly. Several optimized crop management practices have been developed in Jiangsu and Guangdong provinces, China based on improved N management and alternate wetting and drying irrigation; and a range of simplified and mechanized crop management practices have been widely used by farmers, such as the completely mechanized ratoon rice production technology in Hubei Province, no tillage cultivation in Hunan Province, and mechanized rice transplanting technology in Jiangsu Province.

• Topic 4: To examine the occurrence and behavior patterns of rice pests, and to develop integrated pest management practices. To date, the characteristics of the major pest populations for different GSR candidate varieties under different N input conditions have been investigated.

• Topic 5: To conduct an economic and social evaluation of the GSR cropping system. This involved a survey from the farmers' perspective to better understand the requirements for variety properties and management techniques in rice cropping, as well as a survey from the scientists' perspective to examine trends in the development of rice breeding and management practices.

The advances made in the GSR project are comprised of the following sections:

• Topic 1: The Measures for Approval of GSR Variety was drafted. NUE of candidate GSR varieties provided by the breeding institutes within the GSR Project was evaluated. We determined variations in the grain yield and NUE of elite candidate GSR rice varieties and provided plant traits that could be used as selection criteria in breeding N-efficient rice varieties (Wu . 2016).

• Topic 2: A comparison between two N-efficient varieties and two controls under four N treatments (0, 100, 200, and 300 kg N ha$^{-1}$) showed that deeper roots, greater root oxidation activity, and higher photosynthetic NUE could be used to select for N-efficient rice varieties (Ju . 2015).

• Topic 3: The optimized management practices for GSR varieties was developed in different provinces aiming to increase nutrient use efficiency and protect the environment. For example in Guangdong Province, through application of the optimized management practice, N fertilizer rate and water input were reduced by 9.5 and 25.6%, respectively compared to that in farmer's practice.

• Topic 4: The occurrence of leaffolder and planthopper was significantly reduced without application of N fertilizer, compared to a N rate of 90 and 180 kg ha$^{-1}$. Moreover, pheromones and host plant volatiles affecting the behavior of leaffolder and planthopper were identified. It was also found that pv. infection significantly influenced the interactions of rice plants, BPH and its predator (Sun . 2016).

• Topic 5: Through the survey of farmers and scientists, it is found that reduction in the application of chemical fertilizers and pesticides and water-saving technology is pressingly needed in rice production. Moreover, the simplified and mechanized crop management practices should be one important area in the GSR project. However, the improvement in nutrient use efficiency and grain quality should not be achieved at the cost of a reduction in grain yield.

The combined results of each of these topics will help to direct this GSR research into the future.

The yield potential of rice has been greatly improved through the development of super rice varieties in China. The enlarged panicle size and improved N responsiveness of these varieties have contributed to their increased yield potential, together with changes in other agronomic and physiological traits such as canopy architecture, leaf photosynthetic physiology, and translocation of pre-anthesis carbohydrates. Furthermore, although super rice tends to require higher N inputs to realize its high yield potential, it is possible to achieve high yield and high NUE using appropriate N management during planting. However, despite these yield improvements, rice cropping is facing a series of challenges, such as resource exhaustion, climate change, and the frequent occurrence of both biotic and abiotic stresses, and so it is necessary to diversify the breeding targets beyond the improvement of yield potential. To this end, the GSR Project aims to develop varieties that have improved resistance to major diseases and insects; high nutrient use efficiency; resistance to major abiotic stresses such as drought, salinity, and abnormal temperatures; high grain yield; and good grain quality. Several GSR candidate varieties have been identified that have a high grain yield and NUE at a low N rate, indicating that it is possible to produce a high grain yield while reducing the resource inputs and environmental costs in a world with a changeable environment.

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