

Practices and Prospects of Super Hybrid Rice Breeding

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Abstract: The great progress in super rice breeding both in China and other countries has been made in recent years. However, there were three main problems in super rice breeding: 1) the super rice varieties were still rare; 2) most super rice varieties exhibited narrow adaptability; and 3) current breeding theories emphasized too much on the rice growth model, but they were unpractical in guidance for rice breeding. According to the authors' experience on the rice breeding, the breeding strategies including three steps (super parent breeding, super hybrid rice breeding and super hybrid rice seed production) were proposed, and the objectives of each step and the key technologies to achieve the goals were elucidated in detail. The super parent of hybrid rice should exhibit excellent performance in all agronomic traits, with the yield or sink capacity reached the level of the hybrid rice control in regional trials. The super hybrid rice combination should meet the following criteria: good rice quality, wide adaptation, lodging resistance, resistance to main insects and diseases, and the yield exceeded above 8% over the control varieties in the national and provincial regional trials. To achieve the goal, the technical strategies, such as selecting optimal combination of the parents, increasing selection pressure, paying more attention to harmony of ideal plant type, excellent physiological traits and all the agronomic traits, should be emphasized. The yield of seed production should reach 3.75 t/ha and 5.25 t/ha for the super hybrid rice combinations derived from early-season and middle-season types of male sterile lines, respectively. The main technologies for raising seed production yield included selecting optimum seed production site, using the male sterile line with large sink capacity and good outcrossing characteristics, and improving the amount of the pollen by intensive cultivation of the male parent. According to the technologies of the three-step breeding on super hybrid rice, two super rice parents, including a male parent 996 and a thermo(photo)-genic male sterile [T(P)GMS] line C815S, were bred. Furthermore, a super early hybrid rice combination, Luliangyou 996, which could be used as a double-season early rice variety in middle and lower reaches of the Yangtze River, China, was bred by using the super rice variety 996 as the male parent, and several hybrid rice combinations with higher yield than control variety in regional trials both of Hunan Province and state were bred with the T(P)GMS line C815S as the female parent.

Key words: super hybrid rice; breeding strategy; super parent; hybrid rice seed production

The issue of food security will become a more challenging problem and need to be resolved firstly in the world. China is a developing and agricultural country with a population of 1.3 billion, and food security is an important strategic problem at any time. To meet the need of the food consumption for both urban and rural residents is the most important event that related to people's livelihood, economic and social development and political stability. Food security is also the foundation of comprehensive, harmonious and sustainable development of economics and society for China.

Rice, as the largest crop in terms of planted area

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and yield in China, plays a pivotal role in the country's food security. However, rice planted area has shown an irreversible decreasing trend because of the continuing reduction of cultivated land area and the serious lack of water resource during the past three decades. Therefore, it seems that at present the most effective and economic way is to develop and extend super rice varieties or hybrids with wide adaptation and super high yielding potential, which is also a fundamental solution to China's food security problem and an important way to maintain social stability.

The history of super-high yielding rice breeding

China and some other countries have paid great attention to super high-yielding rice breeding. In 1982,

the Japanese government initiated the super highyielding rice breeding program [1]. The target was to achieve the yield of the brown rice output to 7 500 -9 800 kg/ha in the medium and low yield areas, and over 10 000 kg/ha in the high yield areas, to increase rice yield by 50% than control varieties in 15 years, by breeding high-yielding potential rice varieties and developing the corresponding cultivation technology. Five rice varieties such as Akenohoshi and Akichikara, which achieved nearly 10 000 kg/ha in the high yield areas, were developed at several breeding stations in Japan in the later eight years. However, these varieties were not being extended in large areas due to the lack of cold resistance, poor grain quality and low seed setting rate [2]. To break the yield potential barrier, scientists at the International Rice Research Institute (IRRI) proposed the plan of breeding 'new plant type rice' (also called 'super rice') in 1989. The goal was to breed new rice varieties with the yield potential of 13 000 - 15 000 kg/ha and increase by 20-30% than the control varieties by the year 2005. The bred lines have low tillering ability (3 to 4 tillers per plant when direct seeded), few unproductive tillers, 200 to 250 grains per panicle, a plant height of 90 to 100 cm, thick and sturdy stems, dark green, thick and erect leaves, a vigorous root system, 100 to 130 days growth duration, and increased harvest index. However, due to low biomass production, poor grain filling, low seed setting rate and susceptibility to diseases and insects, the new varieties have not been released for rice production in farmers' fields yet [3].

The China's super rice project was started in 1996 [4]. The goal of the plan was that the yield in large areas reached 9.0-10.5 t/ha in 2000 and 12 t/ha in 2005, and should be increased by at least 15% over control varieties in 1996. Furthermore, it was also proposed by Prof. Yuan Longping that the yield criterion of super rice should be modified according to the ecological areas and planting seasons. In his opinion, it is more reasonable taking the yield per day as the yield index. Therefore, he suggested the daily yield of 100 kg/(ha · d), the milled rice quality of the second class of the national standard of China and high resistance to two or more of the main diseases and insects as the breeding goal for the super rice during 'the Ninth Five-Year Plan' (1996-2000) to 'the

Tenth Five-Year Plan' (2001-2005) [4]. By the cooperation of nationwide breeders and researchers, more than 20 super rice varieties or hybrid rice combinations such as Liangyoupeijiu and Xieyou 9308 were bred. The yields of these varieties or hybrids were higher than 10.5 t/ha in larger planted areas, and increased by 15% comparing to the hybrid rice combinations widely planted at present in China [5-6]. The new hybrid rice combinations were also called 'super hybrid rice', which stood for the success of super rice breeding in China.

Accordingly, Chinese rice breeders developed some theories and technologies of super high-yielding rice breeding. Among them, the most representative models were 'the model of super high-yielding hybrid rice breeding by combining the ideal plant type and the improved utilization of heterosis, with complemented by the use of favorable genes from wild rice' proposed by Yuan [4], the 'erect and large panicle' model for japonica rice in northern China by Yang et al [7], the 'bushy type and early rapid growing' model for indica rice in southern China by Huang [8], the 'heavy panicle' model by Zhou et al [9] and the 'late-stage vigor super hybrid rice' model by Cheng et al [10] and so on. These models had played or are playing important roles in guiding super high-yielding hybrid rice breeding in China.

The difficulties and the main existing problems in super high-yielding rice breeding

Since launching the project of 'super rice breeding' in China in 1996, great achievements in super rice breeding have been acquired in the ten years. However, we should be well aware of that the super rice varieties are still rare, especially for growing in double-cropping rice regions in southern China [11]. In addition, most of the currently super hybrid rice combinations have low seed setting rate, poor yield stability and weak adaptability, caused by their genetic disharmonies. These problems have been the factors inhibiting extension of these super rice varieties to the large area.

On the other hand, with the increasing in yield of

the new rice varieties and level of breeding strategy, the theories of super high-yielding breeding have to be further improved. There are three main shortcomings in current breeding theories. The first one is that most of the theories based on the plant traits of F₁, and ignored the importance of parent selection for hybrid rice, resulting in the difficulties of further raising the breeding level ^[4, 7-9]. The second one is that the current breeding theory emphasized too much on partial characters of rice, and neglected the overall harmony of the rice growth. The third one is that most breeders only take the super rice itself into account, rather than the safe and efficient production of commercial hybrid rice seed with lower cost.

The strategy of super hybrid rice breeding

The new breeding strategy for super hybrid rice including three steps were proposed, according to the authors' experience in rice breeding of the dual-purpose genic male sterile lines, the restorer line and super hybrid rice combinations in recent years.

The first step: super parent breeding

The concept of super parent

There have been three main theories to explain the cause of heterosis, including dominance hypothesis ^[12], overdominance hypothesis ^[13] and consanguinity hypothesis, since Shull proposed the concept of 'heterosis' in 1908 ^[12]. In the breeding practice, we are often guided by the principle: the farther the genetic distance between the parents is, the more powerful the heterosis will be. However, the relationship between the parents with farther distances often results in worse stability of seed setting rate in hybrid rice ^[14-15].

Generally, the concept of heterosis elucidates the genetic basis, emphasizes particularly on the relationship between the parents and F_1 , tending to ignore the utilization of hybrid rice combination in practice. The indexes of heterobeltiosis, mid-parent heterosis and standard heterosis are often used to evaluate the heterosis. However, in the practice of breeding, the heterobeltiosis and mid-parent heterosis

can not substitute the standard heterosis. A cross with heterobeltiosis or mid-parent heterosis may have no standard heterosis. Only when the parents' yields reach the level of control varieties, the stronger the heterobeltiosis is, the greater the standard heterosis will be.

In addition, breeders emphasized traditionally too much on the general combining ability (GCA) but not the traits of the parents, according to the gene additive effect from the dominance hypothesis or gene heterozygosity from the overdominance hypothesis. In other words, it means that the parents without excellent traits can also breed elite hybrid rice, which only depended on the utilization of the heterosis in the past. However, as for the super high-yielding hybrid rice breeding, apart from taking advantage of the heterosis reasonably, we should pay more attention on the selection of the parents with comprehensive improved agronomic traits, namely super parent.

The criteria of super parent

The super parent should have good performance in all the agronomic traits. The detailed criteria are summarized as follows:

- 1) Outstanding agronomic traits. The female parent exhibiting dwarf plant, lodging resistance, good plant type, powerful tillering ability and high biological yield is emphasized.
- 2) Outstanding yield traits. The yield or the sink capacity reaches the level of the control varieties in regional yield trials both for the male and female parents.
- 3) Good general combining ability. The genetic differences between the parents must be moderate.
- 4) Stable fertility, security for hybrid seed production, high-yielding seed propagation are required for male sterile lines. As for the thermo-sensitive genic male sterile lines (TGMS), the critical sterility-inducing temperature should be lower than 22.5°C. As for the photo-(thermo-) sensitive genic male sterile lines [P(T)GMS], the critical sterility-inducing temperature should be 21-22°C under long-day and 23-24°C under short-day conditions, with narrow range of the critical sterility-inducing temperatures and longer duration (over 5 d) for sterility-inducing. The yield of seed propagation for P(T)GMS or TGMS will be high

when irrigated with low-temperature water. The sterility not be affected easily by climatic factors, is also required for cytoplasmic male sterile (CMS) lines.

- 5) Excellent outcrossing characters. High exsertion rate (over 70%) and powerful viability of stigma, good outcrossing affinity, early and synchronous flowering and the post fertilization closure of lemmas are required for the female parent. Luxuriant plant growth, well-developed anthers, large quantity and strong vigor of pollen are required for the male parents.
- 6) Good rice quality. Both female and male parents should exhibit high head rice rate (female over 50% and male over 60%), low chalky rice rate (lower than 20%), moderate amylose content (16-24%) and good palatability.
- 7) Multiple resistances to diseases, insects and environmental stresses. The super parents should be moderately or highly resistant to rice blast, resistant to the higher and lower temperatures, sheath blight and the kernel smut to a certain extent.

Successful examples of super parent breeding

The super parents provide a genetic basis for super hybrid rice breeding. The rice variety 996 is an example, which yielded 4.3% higher than the control variety (hybrid rice Jinyou 402) in the regional yield trials of Hunan Province in 2003, with excellent performances in all of the agronomic traits. Another example is a TGMS line, C815S, with a large sink capacity equal to hybrid rice Shanyou 63, which was bred by the authors too [16]. The crosses derived from the C815S showed higher yield than the control variety, which was attributed to the large sink capacity of C815S. C815S also had low critical sterilityinducing temperature (below 22°C), good agronomic traits, high outcrossing rate, good rice quality, and strong combining ability and so on. By using another TGMS line, Zhu 1S, which has outstanding comprehensive traits, many hybrid rice combinations were bred, with higher yield in double-cropping early rice regional yield trials of many provinces and the nation of China. The rice variety 93-11 (also called Yangdao 6), which is the male parent of the first super rice variety Liangyoupeijiu, yielded no less than hybrid rice Shanyou 63 and was widely planted as a conventional

variety ^[17]. By using rice variety Shuhui 527 with excellent plant traits as male parent, more than 20 released hybrid rice combinations were bred ^[18]. The yield and agronomic traits of the varieties mentioned above basically reached the demand for super rice parent.

The second step: super hybrid rice breeding

The standard of super hybrid rice

- 1) High yield. The current yield standard in China, which depends on the ecological conditions and cultivation techniques to a great extent, cannot reflect accurately the yield potential of super rice. Therefore, the authors suggest that yield around 8% higher than the control should be taken as the standard of the super rice.
- 2) Wide adaptability. The super rice varieties should exhibit wide adaptation to different types of paddy fields, ecological regions and farming systems. Especially, the tolerance or resistance to abnormal climate such as higher or lower temperatures cannot be weaker than those of the control.
- 3) Good rice quality. The rice quality should reach the second class of national standard of China or better.
 - 4) Moderate resistance or better to the rice blast.
 - 5) Strong resistance to lodging.

The strategies for super hybrid rice breeding

The main strategies for breeding super hybrid rice combinations with wide adaptability, high yielding potential, good rice quality and multiple disease and insect resistances are to combine the ideal plant type with physiological vigor and to harmonize all the growth traits, by improving the selective pressure on the basis of crosses from the super parents.

Firstly, optimal combination of the parents is one of the key strategies for hybrid rice breeding. Optimal combination means that the hybrid rice combination derived from the parents with a reasonable genetic difference, such as from 1) lowland rice and upland rice varieties, 2) different varieties with geographically remote distance, 3) different ecological types, 4) different dominant varieties, and 5) indica and japonica

subspecies. However, what needs to be emphasized in particular is that we can exploit only part of the heterosis between the indica and japonica subspecies, but not the heterosis between the typical indica and japonica rice or the one including excessive indica and japonica ingredients. Lots of examples show that it is hard to succeed in breeding an elite hybrid rice combination derived from the typical indica and japonica rice, even with the wide compatibility variety as a parent. Generally, the hybrid rice crossed from the typical indica and japonica rice would result in the poor adaptability and stability of seed setting rate.

Secondly, maintaining high harmony in a great degree of plant type, leaf shape, yield components and physiological function is another key strategy of super hybrid rice breeding. Undoubtedly, the fine plant type is the foundation of a high yielding variety. However, in the past, the breeders emphasized too much on plant model, which was an exclusive index for super rice breeding. As for the super high-vielding rice breeding, on the contrary, comprehensive harmonies including plant type, leaf shape and yield components should be emphasized according to the different ecological conditions, cropping systems and plant growth characteristics. Meanwhile, excellent physiological function, including long functional duration and high photosynthetic rate of leaves, late senescence of shoots and high vigor of roots at the ripening stage should also be emphasized. Moreover, the comprehensive harmony should also be present in the plant type, leaf shape, physiological traits and yield components. Therefore, in the authors' opinion, there are not fixed model in super rice breeding. A suitable model with ideal plant type and yield components, which is variably depended on the growth region and yield potential, need to follow the principles: maximizing the utilization of the sunlight and keeping sink-source balance on the base of large panicle.

Increasing selection pressure is the third important strategy for breeding super hybrid rice with wide adaptability. For some important traits, such as resistance to higher or lower temperatures and rice blast, and the sterility of T(P)GMS and CMS lines, we usually grow the candidate plants in the conditions where it is easy to identify these traits. The super hybrid rice will be more vigorous and competitive

only be bred under the conditions with added selection pressure. However, the breeding efficiency will be improved greatly after pyramiding multi-resistance and other favorable genes into the super hybrid rice parents by using the molecular breeding technology.

Successful examples of super hybrid rice breeding

Take the hybrid rice Luliangyou 996 as the first example, which was bred by crossing the super parent 996 with the TGMS line Lu 18S, and released by the Hunan Province and National Crops Variety Approval Committee in 2005 and 2006, respectively. The yields of Luliangyou 996 increased 7.6% and 7.9% compared to Jinyou 402 in the regional yield trials of Hunan Province in 2003 and 2004, respectively, and 7.2% over the control in the national regional yield trials in 2005. With the average yield per day being 9% over that of the control hybrid rice Jinyou 402, a new yield increasing record was set in the regional yield trial both of Hunan Province and the nation of China.

For another example, C-liangyou 396, whose yield was 10 023 kg/ha and 12.5% higher than the control Liangyoupeijiu in the regional yield trials of Hunan Province in 2005, was bred with the super parent TGMS line C815S. The other hybrid rice C-liangyou 87, which was also derived from C815S, yielded the highest in the regional yield trials for single-season late rice in Hunan Province, and it also set a new yield record of single-season rice in Hunan Province, with the yield of 13 547.25 kg/ha. C-liangyou 343 was also bred by using C815S, its yield increased 14.5% than the control Shanyou 63 in the preliminary regional yield trails for single-season late rice in Hunan Province. The fact of the successful breeding of the above hybrid rice combinations illustrated that the super rice will be bred with the guidance of the above breeding strategies.

The third step: super hybrid rice seed production

As we know, the CMS line II-32A is an important female parent for most of hybrid rice combinations, and the planted area of hybrid rice combinations derived from II-32A was the largest in China currently ^[19]. The reason that II-32A has become the 'largest' CMS line in China, to a large extent, attributes to its high outcrossing rate and low cost of seed production. As for a

hybrid rice combination, even if it possesses all other traits reached the standard of super hybrid rice, but produces seed without security, or with the low reproduction output, or with the high cost of seed production, then it cannot be utilized commercially.

Yield standard of super hybrid seed production

The yield standard of seed production for super hybrid rice should be established according to the female growth duration. As for the early-season male sterile line, which exhibits shorter growth duration and lower yield potential, the yield of its hybrid rice seed production should reach 3.75 t/ha in large areas. Comparatively, as for the middle-season type male sterile line, which has longer growth duration and higher yield potential, the yield standard of the seed production should reach 5.25 t/ha, even reach 6.75 t/ha for the highest.

The strategies of super hybrid rice seed production

Super parents provided the prerequisite for the super hybrid rice seed production

Taking C815 for an example, we demonstrated the feasibility that the highest yield of super hybrid rice seed production might reach 6.75 t/ha. In 2005, the hybrid rice seed production was conducted by using C815S as a female parent and the variety 838 as a male parent in Changsha, Hunan Province. The field investigation showed that the number of spikelets was 468 million per hectare, the sink capacity of sterile line reached 11.2 t/ha according to 1000-grain weight of 24 g, the yield reached 6.75 t/ha on the base of the outcrossing rate of 60%. In fact, if the field of the hybrid rice seed production was arranged in the area where the ecological conditions is better than Changsha, the outcrossing rate of C815S should be over 65%, then it would be much easy that the yield of the hybrid rice seed production exceed 6.75 t/ha.

The key technique of super hybrid seed production: selecting the optimum ecological site

To select a suitable site is vital to the success of hybrid rice seed production for two-line or three-line hybrid rice seed production. Besides the higher yield, the security periods for fertility sensitivity, flowering and harvesting in the two-line hybrid seed production system should be considered ^[20]. Although great progress on breeding of two-line male sterile line and its hybrid rice have been made in China, however, the breeders pay too less attention to the research on the selection of the suitable ecological region for two-line hybrid rice seed production.

To choose the best site plays an important role in ensuring the safety and high purity of hybrid seed production. Usually, breeders determined the critical sterility-inducing temperature of TGMS lines according to the weather conditions, and also arranged for hybrid rice seed production at local site once the hybrid rice combinations were bred. In fact, this way is not rather reasonable. If the place for two-line hybrid rice seed production was arranged in Guangdong, Guangxi, Fujian and the south of Hunan and Jiangxi Provinces, where the average temperature is usually higher than 23.5°C in summer and autumn, then the security of hybrid seed production will be greatly enhanced. In addition, it is also requested that the unusual high temperature, continuously low temperature and rainy do not occur in the place of super hybrid rice seed production during the flowering period.

The selection of ecological region for hybrid rice seed production is also important for three-line hybrid rice, particularly for the sterile lines with the fertility sensitive to high or low temperatures.

The extraordinarily technical measures of super hybrid rice seed production

Large amount of spikelets and high outcrossing rate are required in high-yielding hybrid rice seed production. Therefore, several extraordinarily technical measures may be taken as follows:

1) Combining extraordinary cultivation of the male parent with the large ratios of row numbers of the female parent to male parent. In order to increase the number of female parent plants and get more spikelets, we need increasing the row ratio of parents, e.g. 2:16-22 or 1:14-18 for male and female parents, according to the growth duration, tillering ability, and the amount of pollen of the male parent. Meanwhile, in order to guarantee the pistil of sterile line could get enough pollen under the conditions with large row ratio, we should apply more fertilizer to the male parent at the tillering stage and early stage of young

panicle differentiation.

- 2) Extraordinary fertilizer and water managements. The rice plants should grow as rapidly as possible at the early stage by applying much basal fertilizer and quick-acting nitrogen fertilizer. The total number of the tillers was controlled by regulating the irrigation. Topdressing fertilizer was applied at the booting stage in order to enlarge the panicle. It is feasible to develop a kind of compound fertilizer suitable for plant growth and development of hybrid rice parents.
- 3) Developing a set of systems for hybrid rice seed production with high yield and high purity by improving and ameliorating the current high-yielding hybrid seed production technologies. It is also important to enhance the outcrossing rate and reduce the losses by lodging and preharvest sprouting via applying a series of physical and chemical products.

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