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SUPER HYBRID RICE BREEDING TO BREAK THE YIELD PLATEAU: APPROACHES AND PROSPECTS

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ABSTRACT

Super hybrid rice breeding is an advanced approach aimed at significantly enhancing rice productivity by utilizing the phenomenon of heterosis, or hybrid vigor. This breeding strategy combines superior parental lines to create hybrids that exhibit higher yields, improved resistance to biotic and abiotic stresses, and enhanced grain quality. The development of super hybrid rice involves a combination of conventional breeding techniques such as new plant type breeding, inter sub-specific hybridization, molecular markers, and genomic selection to identify key traits such as increased biomass, improved harvest index, and enhanced resistance to lodging. By leveraging hybrid vigor, super hybrid rice varieties have shown yield advantages of 15-20% over conventional varieties. These hybrids are bred to optimize critical yield components, including panicle size, grain number, and tiller production, while ensuring adaptability to diverse environmental conditions. Integration of modern biotechnological tools, such as marker-assisted selection (MAS) and genomic prediction, accelerates the breeding process and increases the precision of trait selection. As a result, super hybrid rice breeding plays a pivotal role in addressing global food security challenges by meeting the growing demand for rice with higher productivity and sustainability. The current review discusses on super rice breeding history, approaches and future prospects.

***Key word*: NPT, Super rice, Harvest index, Molecular marker, Hybrid vigor, Heterosis**

Introduction

Rice (*Oryza sativa*) originated in Asia, with over 90% of the world's rice production coming from the region. Rice, being the primary cereal crop of Asia, serves as the main food source for Asia's population, with 205 of world production from India (Singh *et al*., 2022). To uphold rice's crucial role in Asian agriculture and global food security, Japan spearheaded research on super high-yielding rice in the early 1980s (Khush, 1987). The International Rice Research Institute (IRRI) initiated the New Plant Type rice (NPT) Breeding Project in 1989 to enhance yield by 20% compared to current high-yield varieties, which gained global attention as the "Super Rice" (Peng *et al*., 2008). The main focus of rice breeding and cultivation has always been achieving high yields. In 1981, Japan's Ministry of Agriculture, Forestry, and Fisheries initiated extensive collaborative research initiatives aimed at creating super-high-yield rice and enhancing cultivation methods. For more than 25 years, the plan resulted in the introduction of high-yield varieties that yielded 10 tons of brown rice per hectare, a 50% increase from the control variety Akihikari. In the late 1980s, certain types of grain like Chenxing, Aoyu 326, and Beilu 130 had a yield approaching 10 t/ha, but farmers didn't plant them much because of issues like low seed setting rate, poor quality, and limited adaptability (Priyadarshan and Priyadarshan, 2019). In 1994, during the CGIAR meeting, IRRI reported that its NPT rice achieved a yield of 12.5 t/ha, representing a 20% growth from the control variety (Khush, 1995). Nevertheless, the NPT rice displayed low seed setting, inadequate grain filling, and low resistance to brown planthopper. The negative characteristics limited the extensive growth of NPT rice. IRRI made efforts to enhance those drawbacks, but did not succeed in achieving significant advancement (Shidenur *et al.*, 2020). The current review covers the history of super rice breeding in the world, the targeted traits for enhancing the yield, current status and problems associated with the breeding for super hybrid rice.

History of Hybrid Rice Technology in China and India

In 1964, Yuan Long Ping first put forward the idea of utilizing the heterosis in rice and initiated the research on hybrid rice in China. In 1970, a pollen abortive wild rice plant (Wild Abortive; WA) was discovered among the plants of common wild rice at Nanhong Farm of Hainan Island of China and the available restorer genes in indica rice led the beginning of hybrid rice technology (Li *et al.*, 2024). In 1972, the first group of CMS lines such as Zhenshan 97A, V20A were developed by using WA as the donor of male sterile genes by way of successive backcrossing method. In 1976 First commercial three-line rice hybrid released in China. In 1994 first commercial two-line rice hybrid released in China (Mehandi *et al.*, 2021). To break the yield 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 13000-15000 kg/ha and increase of 20-30% than the control varieties. 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 (Parida *et al.*, 2022). The China's super rice project was started in 1996 by the cooperation of nationwide breeders and researchers of China. 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. The new hybrid rice combinations were also called 'super hybrid rice', which stood for the success of super rice breeding in China (Wang *et al.*, 2022).

In India, the Indian Council of Agricultural Research (ICAR) launched a project on hybrid rice in December 1989, marking a significant step in the country's agricultural development (Chakraborti *et al.*, 2021). The International Rice Research Institute (IRRI), Philippines, collaborated with the project by providing the needed germplasm and technical support (Rahman and Zhang., 2023). This project was further strengthened with financial support from the United Nations Development Programme (UNDP) and technical support from the Food and Agriculture Organization (FAO) from September 1991 to 1996. The Mahyco Research Foundation (MRF), now known as the Barwale Foundation, provided financial assistance to the hybrid rice project during 1996-2002 to fill critical gaps, exemplifying how a private foundation supported public sector research. In 1994, India released its first hybrid rice varieties: APHR1, APHR2, MGR1, and KRH1 (Krishnan *et al.*, 2022).

Theory of super rice breeding

Raising the level of heterosis in rice breeding is a multifaceted challenge that requires careful consideration of genetic compatibility, plant architecture, and environmental adaptability. By focusing on hybrid combinations that maximize heterosis, particularly indica/japonica hybrids, and by strategically increasing biomass through plant height and stem thickness, rice breeders can develop super hybrid rice varieties with significantly higher yield potential. These efforts are essential to meeting the growing global demand for rice while ensuring that crops are resilient, productive, and sustainable (Zhang, 2022).

Key Morphological Features

1. Tall Erect-Leaf Canopy

The ideal super-high-yielding rice plant has upper leaves that are long, erect, narrow, V-shaped, and thick. Each of these characteristics plays a vital role in maximizing the plant's photosynthetic efficiency and structural integrity (Nandakumar *et al.*, 2024). The leaves ensure a larger leaf area that is capable of capturing more sunlight. The erect nature of the leaves allows sunlight to penetrate deeper into the canopy, thus optimizing light interception across the entire plant. The narrow leaves minimize shading of lower leaves, allowing a higher effective leaf area index. This means that more leaf area is available for photosynthesis without overcrowding. The V-shape contributes to the stiffness of the leaf blade, reducing the likelihood of drooping (Hidayah, 2022). This structural feature is crucial for maintaining the upright posture of the leaves, even under heavy load from grains or strong winds. Thicker leaves are associated with higher chlorophyll content and photosynthetic activity, which enhances the plant's ability to produce assimilates (sugars and other compounds) necessary for grain filling and overall growth (Archana *et al.*, 2023). Additionally, thicker leaves are less prone to senescence, meaning they stay green and functional longer, contributing to sustained photosynthesis throughout the growing season.

2. Lower Panicle Position

The panicle, which is the flowering head of the rice plant where grains are produced, should ideally be positioned only 70 cm above the ground at the ripening stage. This lower position is strategically advantageous for several reasons. It reduces the risk of lodging, or the bending over of plants, which is a significant issue in rice cultivation as it can lead to yield loss, especially in high-yielding varieties with heavy grain loads. By keeping the panicle close to the ground, the plant's center of gravity is lowered, making it less susceptible to lodging due to wind or rain. A lower panicle position can also contribute to more uniform grain maturation and filling, as the plant's energy is more efficiently directed towards the grains (Yuan, 2017).

3. Greater Panicle Size

An ideotype for super-high yield in rice aims for a panicle that can produce around 7 grams of grain. This significant grain weight per panicle is achieved by optimizing both the number of spikelets and the filling rate of these spikelets (Peng *et al*., 2008). The target is approximately 250 panicles per square meter, which, when combined with the ideal grain weight per panicle, provides a theoretical yield potential of about 15 tons per hectare (Wang *et al*., 2021). This high panicle density, when managed correctly, maximizes the yield per unit area by ensuring that each panicle contributes significantly to the overall yield (Mai *et al*., 2021).

4. Disease and Pest Resistance

Resistance breeding is a crucial aspect of plant breeding as it imparts inherent resistance to a hybrid or variety against various pests and diseases (Mbinda and Masaki 2021). Super-high-yielding varieties must also be bred for resistance to diseases and pests to ensure sustainable productivity. The dense canopy and large panicles of these high-yielding varieties can create microenvironments conducive to the spread of pathogens and pests, making the incorporation of resistance traits into the ideotype essential for maintaining high yields Increasing Biomass and plant height (He *et al*., 2022)

In rice breeding, yield is a function of the harvest index (HI) and biomass. The harvest index, which is the ratio of grain yield to total above-ground biomass, has already reached high levels (above 0.5) in modern rice varieties (Yan *et al*., 2022). As a result, further increases in rice yield potential are more likely to come from increasing biomass rather than further improving HI (Khush, 1995). One of the most effective ways to increase biomass is by increasing plant height. However, biomass of the cultivar often decreases due to nutrient stress in the field, such as Fe toxicity, which negatively impacts plant growth and yield (Sonu *et al*., 2024). Taller plants generally produce more biomass because they have more extensive vegetative structures, such as leaves and stems, which can support greater photosynthetic activity and nutrient accumulation. However, increasing plant height must be done cautiously. While taller plants can potentially yield more, but they are also more susceptible to lodging, which can severely reduce yield (Zhang *et al*., 2017). Therefore, maintaining a high harvest index (above 0.5) and ensuring that plants are resistant to lodging are critical considerations in breeding taller rice varieties (Akita, 1989). Another approach to increasing biomass without significantly increasing plant height is to enhance stem thickness. Thicker stems provide greater structural support, making plants more resistant to lodging, especially under the weight of large panicles filled with grain (Kashiwagi *et al*., 2008).

5. Nutrient and water management

The ideotype's success is also dependent on optimal nutrient management, particularly nitrogen, which is crucial for sustaining the growth of large, productive canopies and panicles. Ensuring balanced nutrition that supports both vegetative growth and reproductive development is essential. Efficient water management practices are required to maintain the ideal plant architecture (Dobermann and White, 1999). Both under-irrigation and over-irrigation can negatively affect the development of the desired traits, such as panicle size and leaf morphology. The ideal plant type must be adaptable to varying environmental conditions, including temperature fluctuations, varying sunlight intensities, and soil types. This adaptability ensures that the plant can express its high-yield potential across different growing regions.

Key Genetic Features

Heterosis, or hybrid vigor, is a fundamental concept in plant breeding that refers to the phenomenon where hybrid offspring exhibit superior qualities compared to their parents. In rice breeding, heterosis is a critical factor for developing high-yielding varieties, especially in the context of super hybrid rice. Research has shown that the level of heterosis in rice hybrids follows a specific trend based on the genetic background of the parent varieties.

1. Enhancing heterosis through inter-specific hybridization

Indica/Japonica Hybrids: These hybrids demonstrate the highest level of heterosis, with yield potential up to 30% higher than the commonly used *indica/indica* hybrids. The combination of *indica's* vigor and *japonica's* superior grain quality results in hybrids with a large "sink" (capacity for grain production) and a rich "source" (capacity for photosynthesis and nutrient acquisition) (Kallugudi *et al*., 2022). *Indica/Javanica*

Table 1: Genes and QTLs with targeted traits for breeding programs aimed to enhancing rice yield.

QTL/Gene	Chromosome	Affected Trait	Reference
Hd3a	6	Flowering Time, Grain Yield	Kojima *et al.*, 2002
TAC1	9	Plant Architecture, Grain Yield	Yu *et al.*, 2007
NOG1	11	Fatty Acid β-Oxidation, Grain Yield	Huo *et al.*, 2017
qGN4.1	4	Grain Number Per Panicle	Deshmukh *et al.*, 2010
Gn1a	1	Grain Number Per Panicle	Ashikari *et al.*, 2005
qSW5/GW5	5	Grain Width, Weight	Shomura *et al.*, 2008
qGL3	3	Grain Length	Zhang *et al.*, 2012
qTGW3	3	Thousand-Grain Weight	Li *et al.*, 2018
GS3	3	Grain Size	Fan *et al.*, 2006
qGL7/GW7	7	Grain Length, Width, Weight	Wang *et al.*, 2015

hybrids also show strong heterosis, though not as pronounced as the *indica/japonica* combination. *Japonica/Javanica* hybrids exhibit moderate heterosis, often less than that observed in indica/javanica hybrids. *Indica/Indica* and *Japonica/Japonica* hybrids combination tend to show the lowest levels of heterosis, as they are intra-subspecies crosses, which typically do not generate the same level of genetic diversity or vigor. While *indica/japonica* hybrids have great potential due to their high heterosis, they also present significant challenges, particularly in achieving a high seed set. The primary challenge arises from genetic in compatibilities between the indica and japonica subspecies, which often lead to reduced fertility and lower seed set (Zhang, 2020).

2. Use of the Wide Compatibility (WC) Gene ($S5^n$)

The $S5^n$ gene plays a crucial role in overcoming the fertility barriers between *indica* and *japonica* varieties. It helps in stabilizing the seed set in hybrids, allowing for normal development of seeds. The introduction of this gene into breeding programs has been instrumental in creating viable *indica/japonica* hybrids (Chen *et al*., 2008).

3. Intermediate-type parents

Instead of using typical *japonica* varieties as male parents, breeders have found success by using intermediate type male parents that possess traits of both *indica* and *japonica*. This strategy helps bridge the genetic gap between the two subspecies, resulting in hybrids with strong heterosis and normal seed set (Sun *et al*., 2002).

QTLs identified for higher yield in Rice

Rice yield improvement has been significantly advanced through the identification and utilization of key quantitative trait loci (QTLs) and genes associated with grain yield, flowering time, and plant architecture. The QTL *Hd3a*, which is linked to heterosis, plays a pivotal role in delaying flowering under long-day conditions while having a considerable impact on grain yield (Zhang *et al*., 2019). Studies have shown that the heterozygous state of *Hd3a* (*Hd3a/hd3a*) offers a balanced advantage by slightly delaying flowering compared to the wild-type *Hd3a/Hd3a*, but not to the extent that it hampers agricultural productivity. Moreover, this heterozygous genotype contributes to a 9.9% increase in grain yield per plant and a 7.4% enhancement in seed-setting rate compared to the homozygous state, making it a favourable genotype for maximizing yield while maintaining appropriate flowering timing.

Another critical gene, *TAC1*, which regulates plant architecture, has shown potential in increasing grain yield per unit area (Yu *et al*., 2007; Gao *et al*., 2021). The heterozygous genotype (*TAC1/tac1*) results in a beneficial modification of tiller angle, enhancing planting density by approximately 15%. Although the *tac1* allele reduces tiller number slightly, the improved architecture and light capture efficiency associated with the heterozygous state led to a significant yield advantage in dense planting systems. Additionally, the *NOG1* gene, which regulates fatty acid β-oxidation and jasmonic acid levels, has been shown to enhance grain yield by 25.8% when overexpressed in transgenic plants, highlighting its potential for yield improvement through metabolic regulation (Huo *et al*., 2017, Huo *et al*., 2022). Collectively, these genes and QTLs represent promising targets for breeding programs aimed at enhancing rice yield tabulated in Table 1.

Problems and Prospects in Super Hybrid Rice Breeding

Since launching the project of 'super rice breeding' in China in 1996, great achievements in super rice breeding have been acquired in ten years. However, we should be well aware of the super rice varieties which are still rare, especially for growing in double-cropping rice regions in southern China (Chen *et al*., 2007). 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 (Zheng *et al*., 2020). 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. Exploitation of *indica/japonica* heterosis can heighten the level of yield. With the development of molecular marker technology in rice, the subspecies differentiation of parents can be determined and the proper contribution of *indica* and *japonica* genes in hybrids can be established for high yields in combination with harmonious plant types. Molecular marker-assisted selection has provided an approach to pyramid beneficial alleles of QTLs for improving yield and other important traits (Singh *et al*., 2021). Recently, some restorer lines carrying beneficial alleles of yield QTLs and major genes for disease resistance are under evaluation in the super hybrid rice breeding program. Incorporation of the characteristics of high photosynthetic rate from other species into rice plants is of importance for future super hybrid rice breeding.

Future strategies to make hybrid rice technology more popular and economical

To address the challenges limiting hybrid rice acreage in India, the following solutions can be implemented:

1. **Reduce Seed Costs:** Governments and private companies can collaborate to subsidize hybrid rice seeds, making them more affordable for small and marginal farmers. Bulk procurement and distribution through cooperatives can also help reduce costs.
2. **Improve Seed Availability and Quality:** Establish a robust and efficient seed production and distribution system to ensure the timely availability of high-quality hybrid seeds. Certification programs can be introduced to guarantee seed quality, building farmer trust. To improve hybrid rice production in India, the row ratio in the three-line system should be optimized by adopting techniques for better pollen dispersal, potentially increasing the ratio up to 2:16 as in China, which could boost seed productivity to 2.5-3.0 tonnes per hectare, making hybrid seeds more affordable (Verma *et al*., 2021). Adopting a two-line system, which eliminates the need for a maintainer line, reduces labor and costs while enhancing heterosis by 5-10% due to the absence of cytoplasmic penalties (Ali *et al*., 2021). Additionally, focusing on inter-sub-specific hybrids and utilizing wide compatible varieties (WCVs) can significantly increase heterosis, making hybrid rice cultivation more economical and productive.
3. **Simplify Cultivation Practices:** Develop and promote hybrid rice varieties that are more resilient and easier to manage under diverse conditions. Extension services should provide tailored, easy-to-follow guidelines on hybrid rice cultivation, focusing on accessible techniques for all farmers.
4. **Mitigate Yield Uncertainty:** Enhance R&D efforts to develop hybrid rice varieties that are consistent in performance even under suboptimal conditions. Insurance schemes can be introduced to protect farmers against yield losses, reducing the perceived risk of adopting hybrid rice.
5. **Promote Traditional Variety Qualities in Hybrids:** Breeding programs should aim to incorporate desirable traits from traditional varieties, such as grain quality and taste, into hybrid rice, making it more appealing to farmers and consumers alike.
6. **Enhance Awareness and Training:** Expand farmer education and training programs through government extension services, NGOs, and private companies. Use ICT tools like mobile apps, videos, and social media to reach a broader audience and provide ongoing support.
7. **Ensure Market and Price Stability:** Establish assured market linkages for hybrid rice, possibly through government procurement programs or partnerships with agro-businesses. Promote value addition and branding of hybrid rice to improve marketability and ensure better prices for farmers.

Popularizing hybrid rice in India requires a combination of demonstration trials, farmer training programs, efficient seed distribution networks, and awareness campaigns. On-farm demonstrations and field days can showcase the benefits of hybrid rice, while farmer training, supported by ICT tools, ensures proper cultivation practices. A robust seed supply chain, bolstered by public-private partnerships, ensures accessibility, and government incentives, including subsidies and crop insurance, make hybrid rice more affordable. Mass media campaigns and success stories can raise awareness, while assured market access and value addition enhance its appeal. R&D efforts should focus on locally adapted, stress-tolerant varieties, supported by a favorable regulatory environment and investment in hybrid rice research. Collaboration with NGOs and international organizations, along with state-level pilot programs and ongoing evaluation, can drive widespread adoption and improve farmer livelihoods.

Conclusion

Rice is one of the most important staple foods. Hybrid rice exploits the phenomenon of heterosis which increases yield about 15-25% over HYVs. In case of rapidly increasing population and decreasing natural resources, hybrid rice is one of the most important and practically feasible technologies to achieve the targeted food grain production (Rout *et al.*, 2020). Fast advances in molecular biology and biotechnology offer new hopes to design hybrid rice plants with higher yielding potential, better nutritional quality, resistance to biotic and abiotic stresses with higher nutrient and water use efficiency. Three types of male sterility (CGMS, EGMS, CHA's induced) have been used in hybrid rice seed production (Tien *et al.*, 2013). India is using CGMS system (3-line system) for hybrid rice seed production. Improvement in hybrid rice seed production technology will further reduce the cost of hybrid rice seed. Hybrid rice seed production technology is both labour and knowledge intensive. This will also generate more and more employment. The available hybrids are popular in the irrigated upland to medium lands. However, there is need to develop hybrids suited to rainfed lowlands as well as of longer duration to replace longer duration mega inbred varieties. Hybrids for meeting specific cooking qualities should also be developed to enhance the hybrid rice area in the country.

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