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Clonal Seeds from Hybrid Rice: A New Approach to Meet the Exceeding Hybrid Seed Demand of the Farming Community

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Abstract

Plant breeders exploit heterosis to produce high-yielding crop varieties over their pure line parents; however, genetic segregation in the advanced generations leads to losing economic traits. Therefore, clonal propagation through matured seeds would be good enough to self-propagate the F_1 hybrids. This approach would be rewarding to the farming community as they will not be forced to purchase fresh F_1 hybrids seeds every year as they can use their farm seeds for the next season.

Introduction

Heterosis or hybrid vigor has been used extensively in agriculture and allied sectors to increase the productivity and adaptability of F_1s over their parents. Although, its cost of production is too high and more challenging for self-pollinated crops than cross-pollinated crops. In plants, a flower is a modified form of shoot bud having different parts such as calyx, corolla, androecium, and gynoecium or their modifications. There are different types of genetic control of flower development in plants through mutations *viz.,* first-type affects floral development and petals, second for petals and stamens, and third for stamens and carpels. Gene *ap1* is needed to develop sepals and petals, *ap3* and *pi* both for petals and stamens, and *ag* for stamens and carpels. These genes encode transcription factors that belong to the *MADS*-box family of transcription factors. Obligate synthetic apomixis could help fix the heterosis of F_1 hybrids in crop cultivars, including hybrid rice. Apomixis is an asexual reproduction wherein descendants are produced through seeds without meiosis and fertilization.

Hybrid Rice

Hybrid rice is produced by crossing two inbred lines genetically fixed for the traits. Hybrids are mainly known for '*heterosis*' or hybrid vigor, and their performance is better than their parents. In rice, hybrid varieties produce up to a 30% yield advantage over their high-yielding pure lines under the same cultivation practices. Globally, rice plays a significant role in alleviating food and nutritional security as the crop is being cultivated in most agricultural lands. Although heterosis in first-generation seeds is well recognized in crop breeding, its application in rice has been limited due to the crop's self-pollination nature. Furthermore, Chinese scientists' introgressed the male sterility gene from wild rice to generate the CMS line in 1974, which was later employed in breeding operations to develop hybrid rice. In China alone, hybrid rice is estimated to be planted on >

50% of rice-growing land and has contributed significantly to increasing rice productivity, which is among the highest in Asia.

Constraints of Hybrid Rice

The concept of hybrid rice was just a daydream until 1974 and was never thought to commercialize the hybrid rice seed. However, the farmers cannot profitably save seeds obtained from hybrid varieties for replanting in the next season as hybrids segregate in next-generation, which leads to yield loss. Therefore, farmers must purchase new hybrid seeds every year from the seed companies if they want high yields, and this way, seed companies are assured of sales and profits (Virmani, 1996). Hence, private seed companies were not involved in hybrid rice seed production due to the high seed rate, input cost, and low profitability than vegetable crops. Nowadays, the scenario is changing, and it will gradually but confidently revolutionize rice farming, particularly in Asia. Hybrid seed production is labor-intensive, skill-oriented, costly, and less remunerative, and the yield of seed production is also low. The high cost of hybrid seeds prevents poor farmers from benefiting from hybrid technology as the price is higher, almost 10-15 times than the pure line rice variety. In addition, the increased cost of hybrid seed production at the initial level needs heavy public subsidies to reduce the hybrid seed price and make available the seed to its stakeholders. Since the introduction of hybrid rice, the price differential between farm gate and retail has widened. A report highlighted that more than 20 percent of the Chinese government's total revenue was spent overcoming the gap until the 1980s. Subsidies for hybrid rice seeds have also gone directly to the seed industry. Those subsidies were temporarily discontinued in the 1990s, and China's hybrid rice field swiftly shrank by 2 million hectares as China moved to meet its requirements for joining the World Trade Organization and dismantled state subsidies. Therefore, a change in the seed production technology can only solve the problems that arise due to conventional hybrid seed production practices and clonal seed production might be the solution in the recent future.

Clonal Seeds Production from Hybrid Rice

Synthetic apomixis has been considered a method of resolving F_1 hybrid heterosis in crop varieties. Apomixis is an asexual reproduction method that produces progeny without meiosis or fertilization through seeds. Despite that apomixis has been identified in a variety of flowering plant taxa, it has not been reported in agricultural crops. Combined mutations in three genes (*REC8*, *PAIR1*, and *OSD1*), that play a crucial role in the meiotic division develop a genotype, *i.e.,* MiMe (Mitosis instead of meiosis) in which meiosis type of cell division is replaced by a mitotic like-division, resulting in the production of male and female clonal diploid gametes in *Arabidopsis* and rice. Despite this, self-fertilization doubles the ploidy level of these plants every generation. A mechanism for fixing heterosis in self-pollinated F_1 hybrids should be developed. Further, MiMe technology's feasibility was tested in hybrid rice variety, *i.e.,* Chunyou84 (CY84) an advanced inter-sub specific hybrid rice developed by crossing between *japonica* type male sterile line Chunjiang 16A (16A) and an *indica-japonica* intermediate type line C84 (Wang *et al.*, 2019). Multiplex CRISPR-Cas9 system was used to edit the three genes (*REC8*, *PAIR1*, and *OSD1*) concurrently to confirm the speedy generation of MiMe in the CY84 background. Interestingly, triple mutant type MiMe plants could not be separated from the wild-type CY84 plants based on their phenology or growth. In addition, flow cytometric analysis revealed that the progeny of the MiMe plant had tetraploid type ploidy. Furthermore, these progeny plants completely retained the heterozygosity of the CY84 parent for ten tested insertion-deletion (indel) markers. In comparison to wild type, the progeny of self-fertilized MiMe plants had increased grain size, reduced fertility, and elongated awn length, and these traits show much resemblance to tetraploid rice. It highlights that the CRISPR-Cas9 system could be efficiently used to introgress the MiMe phenotype into hybrid varieties. Gametes from MiMe clonal participate in normal self-fertilization and seed development and double the ploidy level of progeny. However, doubling of ploidy levels in progenies must be prevented to achieve desirable apomixis. A few years ago, it was reported that mutation of the MATRILINEAL (*MTL*) gene, which encodes a sperm-specific phospholipase, activates haploid induction in maize. To know the effect of the *MTL* gene in rice, scientists edited or mutated the *MTL* gene. The *mtl* mutants revealed typical vegetative growth; however, the seed-set was reduced by 11.50%. Further, haploid plants displayed reduced glume size and plant height and complete loss of fertility; however, doubled haploid plants had normal vegetative growth and panicle size. The findings highlighted that self-fertilization could produce recombinant haploid plants from hybrid varieties. Since omitting the meiosis and promoting mitosis in the F_1 hybrid may lead to fixation of heterozygosity. Therefore, heterozygosity could be fixed by manipulating the four genes (*REC8*, *PAIR1*, *MLT*, and *OSD1*) in the CY84 rice hybrid, and the seed set rate was only 4.5%, which was lower than the *mtl* mutant. By considering the above results, it can be concluded that diploid progeny of Fixed plants (having all four mutant alleles) has the same level of heterozygosity, ploidy, and phenotype as that of the Fixed parents, which are able to produce clonal seeds and fix the heterozygosity of F_1 hybrid rice. When the four genes were altered in hybrid rice at the same time *via* genome editing, fixed plants exhibited a similar type of reduced fertility. Despite the fact that the fixed plant's fertility was reduced due to the *MTL* mutation, it was still able to generate clonal seeds with the same ploidy and heterozygous genotype.

Conclusion

The findings showed that by altering four endogenous genes in a rice F^1 hybrid variety, hybrids can be fixed through self-pollination, and true-breeding type progeny can be obtained through seeds. Concurrent editing of three genes, including *REC8*, *PAIR1*, and *OSD1*, had no influence on the hybrid's plant growth or reproduction; however, the *MTL* gene, which was utilized to eliminate the paternal genome, had a negative impact on hybrid fertility and seed set. Conventional hybrid seed production technology is impractical for most tropical counties in Asia. So, the Fixed strategy could be immediately applied to crop varieties in which fertility and seed production are less important, such as pasture and forage crops.

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