THE SCIENCE WORLD
A Monthly e Magazine
ISSN:2583-2212
March, 2023; 3(03), 328-333

Popular Article

Polyploid rice: new resources for future rice breeding

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https://doi.org/10.5281/zenodo.7702040

Introduction

Asian cultivated rice (*Oryza sativa* L.) is a diploid species with two sets of 12 chromosomes (2n= 24). Despite the fact that Asian cultivated rice may have experienced whole genome duplication more than 96 million years ago, this species is regarded as diploid, as it did not experience a recent polyploidization. A polyploid individual is an individual with more than two sets of chromosomes in somatic cells. Polyploidization is one of the important ways of plant evolution. Polyploid plants are characterized by large size, high nutrient and secondary metabolite content. They also show strong vitality and adaptability, drought and cold resistance and other advantages. Therefore, polyploid technology has been widely used in plant breeding, especially for the purpose of increasing the mass of vegetative organs or total biomass. In addition, polyploids can be used to breed varieties directly and can also serve as a bridge to overcome the barriers to distant hybridization and transfer foreign genes, thereby promoting gene exchange between species or populations. At present, the most widely cultivated rice is diploid. Compared with polyploid crops (such as wheat), rice has a smaller genome and lower DNA content. The genetic resources of cultivated diploid rice are limited. Therefore, further development of rice breeding is hindered. Polyploid rice was first discovered and

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Published 06.3.2023

reported by Nakamori in 1933. A surge in polyploid rice breeding and research followed this discovery.

1. Diploid vs Polyploid rice

Compared with diploid rice, polyploid rice has advantageous agronomic traits like large grain size, high 1000 - grain weight, strong stem, strong stress tolerance and high adaptability which attracted the attention of rice researchers. In general, polyploidization confers greater stress tolerance by fostering slower development, delayed reproduction, longer life span, improved defence against pathogens and herbivores, larger seeds, and lower reproductive effort with greater emphasis on vegetative reproduction. In rice, large grain and leaf size are often observed in autotetraploid plants. These studies suggest the potential usefulness of tetraploid rice for breeding. Low numbers of spikelets per panicle and low fertility have frequently observed in tetraploid rice throughout its known existence. This low seed set rate has been the main barrier preventing use of autotetraploid for rice breeding. However, the bottleneck problem of low seed setting rate of autotetraploid rice had not been solved, which made it difficult to translate research results to production.

2. Methods of induction of polyploid in rice

Artificial induction of polyploidy is divided into physical, biological and chemical induction. In physical induction, temperature shocks, ionizing radiation, grafting, etc., can lead to the formation of polyploids. The chemical mutagens are colchicine, naphthalene pentane, naphthalene ethane, colchicine being the most commonly used. Colchicine inhibits the spindle formation as a result, chromosomes fail to separate. Thus, cells with increased ploidy are produced. However, the efficiency of doubling with seedlings, buds or anthers is very low and chimeras are often formed. With the development of tissue culture technology, colchicine has been used to treat plant tissues or cells (such as callus, embryoids, protoplasts, etc.) in vitro. Other researchers have attempted to induce polyploidy by plant regeneration. Compared with traditional methods, plant regeneration methods lead to more efficiency and less chimerism.

3. Kinds of polyploid rice

3.1. Autotetraploid rice

Auto polyploidy, in which the extra copies genomes come from the same species, is produced by direct doubling of diploid chromosomes. It is common in plants. The grain size of autotetraploid rice is larger and heavier than that of diploid rice. At the same time, grain bulk density is stable and

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has great potential to increase yield. However, compared with diploid rice, autotetraploid rice has weaker sexual reproduction ability and lower seed setting rate. This problem has been perplexing breeders, resulting in the slow progress of polyploid rice breeding research. The light compensation point of diploid rice was about 2.5 Klux, and that of tetraploid rice was about 4 Klux. Net photosynthetic rates fluctuated with the light intensity, but their fluctuation amplitude was different from each other. The obvious characteristics of tetraploid rice were a decrease in panicle number, grain number per panicle, seed setting rate and plant height, but an increase in 1000-grain weight, thicker stem, and higher lodging resistance.

3.2. Indica-Japonica tetraploid hybrid rice

Asian cultivated rice is divided into three subspecies, indica, japonica and javanica. There are differences in morphological, physiological, and biochemical characteristics between them. Studies have shown that the heterosis between indica and japonica is much greater than that within indica or japonica. The utilization of heterosis between indica and japonica is an important new approach for rice breeding. There are significant differences in genome sizes, gene number and gene categories between indica and japonica. Under diploid condition, this not only affects the normal chromosome pairing during meiosis, but also the gene expression at each developmental stage, which makes indica-japonica hybrids difficult to use. However, under tetraploid conditions, this imbalance can be overcome, which is conducive to the utilization of the heterosis of indica and japonica rice. The plant height, growth period, panicle length, effective panicles per plant, spikelets per panicle and 1000-grain weight of indica-japonica tetraploid hybrid rice was significantly higher. The hybrids of typical indica and typical japonica usually show obvious biological yield heterosis effect. Using tetraploid indica-japonica hybrid as a bridge is a way to tap into the greater yield potential of rice.

3.3. Polyploid male sterile rice lines

In the utilization of plant heterosis, sterile lines are the key germplasms. In rice production, the use of heterosis to improve rice yield largely depends on the breeding of male sterile lines. Search for natural male sterile mutants of rice marked the beginning of the research on male sterile lines in rice. The tetraploid restorer line was characterized by large pollen grains and a large amount of pollen. Tetraploid male sterile lines were characterized by stable pollen sterility. These characteristics are helpful to utilize the heterosis of polyploid rice.

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3.4. Allopolyploid rice

Allopolyploidy is a kind of polyploidy produced by chromosome doubling of hybrids between different species. Allopolyploidization leads to heterozygosity between genomes, which can increase the genome capacities, widen the ranges of genetic variation, and enhance tolerance to adverse environmental factors. It has obvious advantages in genetic evolution. After allopolyploidization, fertility can often be restored completely or partially, which plays an important role in overcoming the sterility of distant hybridization. Therefore, allopolyploidy as a genetic medium has become an effective means for gene transfer. Most of the natural polyploid species that appear between related species are allopolyploid. There are many varieties of heteropolyploid rice in nature, such as Oryza minuta (BBCC), Oryza latifolia (CCDD), Oryza coarctata (HHLL), Oryza longiglumis Jansen (HHJJ), Oryza schlechteri Pilger (HHKK), etc. Allopolyploid rice is important resource for biological research and rice breeding. Artificial allopolyploids can be obtained by crossing cultivated rice with wild rice and doubling their chromosomes. The combination of distant hybridization and polyploidization is promising for rice breeding.

4. Low seed fertility: a barrier preventing tetraploid rice use

Low fertility of polyploid is due to abnormal behaviour of the chromosomes during meiosis. In the first division of meiosis, a pair of homologous chromosomes forms a bivalent, which later segregates. However, in polyploids, especially autopolyploid, the formation of bivalents is often inhibited, because homology among three or more chromosomes. In autotetraploid rice, chromosomal behaviour at meiosis displays abnormal meiotic behaviours including a higher rate of multivalent, univalent, and trivalent during prophase, lagging chromosomes during metaphase, and micronuclei during anaphase and telophase. In addition to such abnormalities, asynchrony of chromosomes and abnormal cell shape are also observed in meiosis in pollen mother cells in tetraploids with low fertility. Recent studies have revealed the differences of epigenetic state and transcriptomes between the diploid and tetraploid rice suggested that the increased methylation level of transposable elements (TE) alters the expression of genes near by the TE in autotetraploid rice. Transcriptomic differences, including the expression of small RNAs, long non-coding RNAs, meiosis-related genes, and carbohydrate metabolism related genes have been suggested to be related to meiotic abnormalities and the subsequent reduction of pollen fertility in autotetraploid rice.

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5. Emerging fertile autotetraploid rice

Low seed fertility has been a barrier preventing the use of autotetraploid rice in breeding, two new autotetraploid rice series with high seed and pollen fertilities, identified herein as the PMeS and Neo-Tetraploid lines.

5.1. PMeS (Polyploid Meiosis Stability)

The PMeS lines have been developed and analysed by Cai et al. (2007). They derive from the progenies of crosses between indica and japonica rice subspecies. Unlike other autotetraploid rice lines, PMeS lines do not show abnormal chromosomal behaviour during meiosis. In addition, their pollen development pattern appears normal at all stages, lacking the many abnormalities seen in other autotetraploid rice lines. These results suggest that stable meiosis, timely tapetum degradation, and normal mitochondrial development were the critical factors ensuring the high pollen fertility of PMeS lines.

5.2. Neo-tetra ploidy:

These lines derived from the progenies of crosses between T44 (96025) and T45 (Jackson-4X) and showed a seed set rate of more than 80%, while their parents (T44 and T45) showed less than 32%. Cytological observation of the meiotic stages in Neo-Tetraploid rice lines showed that fewer abnormalities in these lines than their autotetraploid parents, which displayed different chromosomal configurations at diakinesis. Surprisingly, a total of 324 genes including Os01g0716200, Os05g0527700, Os06g0556300 and Os11g0513900 in the Neo-Tetraploid rice genome showed new mutations, which do not exist in its parents' genomes. Transcriptome analysis suggested that genomic structural reprogramming such as neo-functionalization, sub-functionalization or loss of duplicated segments, recombination, transposable elements and genetic drift cause differences between formerly homologous chromosomes. DNA variations and differential expression of some important meiosis- and epigenetics-related genes might be associated with the high fertility of Neo-Tetraploid lines.

Conclusion

Rice (*Oryza sativa* L.) is one of the world's three major food crops. It is important to boost rice yields in order to meet the demands of a growing global population and shrinking arable land. Due to rapid climate change, which has already become a major threat to agriculture and food security, this problem has grown considerably more challenging. Therefore, we need to develop new high yielding rice varieties that are more resilient to climate variability and disasters. Distant hybridization and polyploidization are important trends in plant evolution, as well as important directions in crop evolution. Polyploid plants often have advantages in genome buffering, vigorousness, and robust adaptation to environmental changes. The genome of rice is small and its DNA content is low. However, the genetic resources of Oryza genus are very rich. Therefore, increasing the ploidy levels, increasing the genome capacities, and expanding the range of genetic variations are beneficial explorations for the basic theory and practical application of rice breeding. Since the first report of tetraploid rice in 1933, great achievements have been made in research on polyploid rice. In particular, the breeding of high-fertility PMeS tetraploid rice lines and neo-tetraploid rice lines broke through the bottleneck of low seed setting rate of polyploid rice, which made polyploid rice research enter a new stage of development. With the deepening of our understanding, we believe that polyploid rice breeding as a new way of breeding will show attractive prospects.

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