Longping Yuan

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Basic Information



Name: Longping Yuan (Sep 1930–May 2021)

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Honor:	Father of Hybrid Rice

1. Introduction

The father of hybrid rice, academician Longping Yuan, passed away on 22 May 2021, in Changsha, Hunan Province, China. He was born into an intellectual family in Beijing in September 1930. Due to Japanese aggression, he received his education at different primary and high schools around China from 1936 to 1949 and developed a keen interest in gardening and agronomy during this period. From August 1949 to August 1953, he selected and studied crops as his specialty at the Department of Agronomy of Southwest Agricultural College (now Southwest University).

From August 1953 to January 1971, he was a teacher at Anjiang Agricultural School in a remote area in Hunan Province. Prof. Yuan was a pioneer and leader in the field of hybrid rice research. As China in the 1960s encountered a serious famine, he noticed that many people starved to death because of the low rice yield and insufficient grain production, so he made up his mind to cultivate more high-yield rice for farmers. As early as July 1961, he found a "natural hybrid rice" plant that "stood out from the crowd". Through the experiment of artificial emasculation hybridization, it was confirmed that there was indeed significant heterosis in rice. In 1964, he decided to break through the forbidden zone of "rice and other self-pollinated crops have no heterosis" and take the lead in carrying out research on rice male sterility thereafter. He had his research results published in the article "male sterility of rice" in the Chinese Science Bulletin journal for the first time in 1966, which laid the theoretical foundation of hybrid rice technology ^[1]. Since then, his three-line hybrid rice research program has received national attention and support.

In 1970, Prof. Yuan's assistant identified a critical rice germplasm in wild rice (*Oryza rufipogon Griff*) for the three-line hybrid rice—wild abortive (WA) male sterile rice—in China's Hainan Province, providing a new opportunity for the successful exploitation of rice heterosis ^[2]. The WA male sterile line was then tested for crossing with inbred varieties. It was also found that good maintainer lines were early-season rice varieties with short-growth duration from China, and that good restore lines were long-growth duration rice varieties from Southeast Asia. From 1971, Yuan began to work at the Hunan Academy of Agricultural Sciences, where he developed the first three-line *indica* hybrid rice, Nan-You 2, which initially demonstrated strong hybrid heterosis in 1974. The hybrids showed a 20–30% potential yield increase over the inbreds in a large-scale testing ^[3], and thus the rice yield increased from 2 t ha⁻¹ to 6 t ha⁻¹ from the 1960s to 1980s. The extension area of hybrid rice increased from 375 ha to 8.4 million ha from 1975 to 1985 with strong government support. Since then, China's modern seed industry has been established and developed.

He set up the Hunan Hybrid Rice Research Center in 1984 and the China National Hybrid Rice Research and Development Center in 1995 in Changsha, Hunan Province. Under his research leadership, the production of hybrid rice seeds increased from 274.5 kg ha⁻¹ from 1975 to 2.25 t ha⁻¹ in 1990 through improved production techniques that included flowering synchronization, stage adjustment, and supplemental GA3 (gibberellic acid) application ^{[4][5]}.

In 1973, another Chinese researcher, Shi Mingsong, first discovered the nature mutation material, Nong-ken 58S, with the environment-conditioned genic male sterility (EGMS), in the field plants of a japonica rice cultivar, Nong-ken 58, in Hubei Province for the two-line system male sterile line, China [9]. Prof. Yuan's research team also found another new nature EGMS line, Annong-S, in 1987 ^[2], and proposed a strategy for the two-line system hybrid rice breeding using the EGMS materials including Nong-Ken 58S and Annong-S [8], which were later proven to be controlled by a noncoding 21nucleotide small RNA *PMS3* gene $^{[9][10]}$ and RNase Z^{S1} *TMS5* gene, respectively $^{[11]}$. His research team also developed the first commercial two-line hybrids with EGMS lines such as PeiAi 64S through crossing and backcrossing with Non-ken 58S, which showed remarkably strong heterosis. However, at the same time, the two-line hybrid rice under research encountered huge challenges. For instance, in 1989, it encountered a rarely low temperature (≤23.5 °C) in mid-summer, and the Photo-thermo-sensitive genic male sterile (PTGMS) rice used for hybrid rice seed production recovered its fertility under the low temperature, leading to the failure of the hybrid seed production. Many rice researchers were worried and disappointed about this failure, but Prof. Yuan thought calmly and put forward the technical strategy of cultivating a new Photo-thermo-sensitive genic male sterile (PTGMS) with the critical transition temperature of male sterility not exceeding 23.5 °C at the panicle development sensitive stage, so the research of the two-line hybrid rice came out of the difficulties later. P88S, Y58S, and other excellent two-line male sterile lines were also successfully developed by his research team and popularized in a large area [12][13].

Prof. Yuan was a brave scholar who could discern the hopes and prospects from his research failures, and his determination grew stronger with each failure. In 1995, the two-line hybrid rice technology was successfully commercialized in China ^{[4][14]}. The two-line hybrid rice cultivars yielded 5–10% more than those of the three-line hybrid rice. Moreover, the grain quality, disease resistance, and seed costs have also been improved ^[5]. Therefore, two-line hybrid rice has made great contribution toward China's food security.

In 1989, the International Rice Research Institute (IRRI) launched the rice "new plant type breeding" program, which aimed at greatly improving the rice yield potential, with the goal of yielding 13~15 t h^{-1} by 2005, an increase of 20–30% production compared with the varieties popularized at that time. In 1994, the yield potential of the "new plant type rice" was reported by news media as "super rice", which expected to reach 12.5 t ha^{-1} in the tropical dry season plot experiment ^{[15][16]}. Corresponding to the IRRI (International Rice Research Institute)'s NPT (New Plant Type) breeding program, China also established a nationwide mega-project for the development of "super rice" in 1996 ^[17], and a "super hybrid rice" breeding program was thus started then by Prof. Yuan. Especially after the success of the two-line hybrid rice in 1995, he quickly engaged in targeting the super hybrid rice to further improve the utilization of rice heterosis to a higher level, which led to many super high-yielding hybrid rice varieties being developed from 1996 to 2015. The yield targets for this program have been achieved, increasing the average yield from 10.5 t ha^{-1} to 15 t ha^{-1} [18]. Currently, there have more than 100 super hybrid rice varieties recognized by the China Ministry of Agriculture (MOA), which have played an important role in rice production in China.

2. Story about Notable Contributions

The hybrid rice breeding strategy proposed by Prof. Yuan could be divided into three strategic development stages: the three-line method, two-line method, and one-line method, which is a strategy to change the breeding program from complex to simple and more efficient. Moreover, in regard to the level of rice heterosis utilization, it can also be divided into three strategic development stages: the utilization of heterosis among *indica* rice varieties and rice subspecies, and even distant heterosis toward an increasingly strong direction. According to his assumption, each stage of hybrid rice is a new breakthrough, which will increase the rice yield to a higher level.

He has always believed that cultivating apomixis lines to fix the F1 heterosis of rice is the best way to use rice heterosis in the future. Therefore, he deliberately arranged and carried out some exploration tests during the research. He organized the international symposium on rice apomixis in Changsha, China, in 1992. Due to the research on the genetics and embryology of rice materials with apomixis characteristics, especially the research on introducing apomixis genes from different genera into rice, being very difficult, these have remained in the exploratory stage. Prof. Yuan believed that we need to tackle the key problem of apomixis in rice resources through biotechnology, so he frequently encouraged young people to delve into this field for a long time.

Prof. Yuan was also greatly concerned about the rise in modern biotechnology. He was very sensitive to the full use of molecular biotechnology in order to improve hybrid rice breeding. This can be seen from his keen acceptance of carrying out rice genome sequencing research to focus on the basic research for hybrid rice. In 1999, under the background of 1% human genome sequencing in China, scholars from the Institute of Genetics and Developmental Biology of the Chinese Academy of Sciences prepared to implement the sequencing of the rice genome and consulted him about which rice cultivar should first be sequenced. Prof. Yuan also knew that the latest cutting-edge emerging biotechnology would have long-term special significance for the utilization of rice heterosis. He recommended the cultivar 9311 as a sequencing material because the hybrid rice LYP9 with the restore line 9311 showed good performance and high yield in the paddy fields at large-scale promotion at that time. The whole genome shotgun sequencing (WGS) method was then used for constructing the working framework map of the *Indica* rice 9311 genome, and thus the whole genome framework map of rice 9311 was released to the world. The relevant research was published as the cover paper in Science in April 2002 ^[19].

In addition, Prof. Yuan always tried to achieve a perfect combination of application and foundation research. In the practice of hybrid rice breeding, he once summed up his experience with deep thinking, "there are two effective ways to improve rice yield through breeding: one is morphological modification and improvement, and the other is the utilization of heterosis". Morphological improvement itself has limited potential. However, if heterosis is not combined with morphological improvement, there cannot be a satisfactory result, either. Other breeding approaches and advanced technologies including genetic engineering should eventually be implemented into good morphology and strong heterosis, otherwise they will not contribute to improving the yield. On the other hand, the further development of breeding to a higher level must rely on the progress of biotechnology. These insights of his play an important role in guiding young researchers to achieve accurate comprehension in their breeding practice.

Prof. Yuan was good at the traditional breeding of hybrid rice, but he thought that the potential of traditional breeding technology had its limitations. He proposed that the combination of traditional breeding with biotechnology was the right path for rice breeding in the future, which was also a good approach in selecting super hybrid rice with great potential. Molecular breeding technology and related basic research have played an important role in improving the yield of hybrid rice breeding. In 2001, Dr. Xiao Jinhua at Cornell University, who had been a master's student of Prof. Yuan, published a research paper in Nature—Genes from Wild Rice Improve Yield ^[20]. He was acutely aware of the power of boosting hybrid rice breeding, and organized a research team to make use of the favorable genes in wild rice with marker assisted selection. Two yield increasing QTL loci from wild rice (*O. rufipogon*) were identified. Through molecular marker assisted selection and field phenotype selection, an excellent restorer line, Q611, with one of the above wide rice QTL loci was thus bred. The yield of its hybrid rice was significantly higher than that of the check variety in the experimental demonstration of late-season rice ^[21].

In August 2009, the Chinese state councilor Yandong Liu visited Prof. Yuan and inspected the Hunan Hybrid Rice Research Center. Prof. Yuan proposed establishing a state laboratory to carry out basic and applied research related to hybrid rice and to cultivate a group of talents in hybrid rice research. In October 2011, the State Key Laboratory of Hybrid Rice was officially approved by the Ministry of Science and Technology of China, relying on the Hunan Hybrid Rice Research Center in Changsha, Hunan and Wuhan University in Wuhan, Hubei. Its research directions have focused on the rice heterosis mechanism, rice development and fertility mechanism, hybrid rice germplasm innovation and gene discovery, super hybrid rice breeding, hybrid rice breeding and seed science, super high yield physiology, and the ecology of hybrid rice according to the development needs of the hybrid rice discipline. These six directions are mutually supportive and cross integrated to jointly serve the theme of the sustainable development of hybrid rice.

Next, a heterosis research group was established in the state lab, and Prof. Lihuang Zhu was honored to serve as the principle investigator in the research direction of the rice heterosis mechanism. The research team mainly included Dr. Yeyun Xin, Dr. Zhiyuan Huang, and Dr. Qiming Lv, with the targeted research around Prof. Yuan's proposal on exploring and revealing the mechanism of rice heterosis. A high-density SNP marker linkage map of the LYP9-derived RIL population was constructed for the detection of yield-related. A total of 27 and 25 QTL for all traits were mapped independently on the rice chromosomes by the RIL (a recombinant inbred line) and RILBC1 (RIL population backcrossed with maternal parent) populations, respectively. The heterosis gene *RH8* in rice was identified by using RIL s and RILBC1. *RH8* was also the known rice gene *Ghd8*, which affected the number of grains per panicle, plant height, and heading date ^[22]. The yield of different types of hybrid rice increased 10–15% than that of male parent or inbred varieties. The yield advantage of hybrid rice was obvious, but not all yield trait components showed advantages. It was confirmed that the grain number per panicle (GNP) was the major yield advantage trait of the hybrid rice cultivars of China, were selected for genome sequencing. A difference in the hybrid rice crossing patterns between the three- and two-line superior hybrid lines was found. The loci linked to heterosis, which included 98 in superior three-line hybrids and 36 in superior two-line

hybrids, were identified ^[23]. Prof. Yuan was very pleased with these research achievements. He affirmed their efforts to explain the mechanism of rice heterosis and provide an important theoretical basis for the application of breeding. He also put forward the viewpoint of increasing rice yield by increasing the biomass with plant height increase. His guidance has led the direction for the team's further research.

3. Implications for Sciences, Humanities

As Prof. Yuan mentioned, the development of science and technology is endless. In 2019, he once again put forward a development strategy for hybrid rice. He took the three-line hybrid rice with the cytoplasmic male sterile line as the first-generation of hybrid rice, and the two-line hybrid rice with the Photo-thermo-sensitive genic male sterile (PTGMS) line as the second-generation of hybrid rice; the genetically engineered male sterile lines as the third-generation hybrid rice, the hybrid rice with the genetically modified C4 gene as the fourth-generation hybrid rice, and finally, the hybrid rice with a fixed heterosis of apomixis as the fifth-generation hybrid rice. The genetically engineered male sterile lines had the advantage of the stable infertility found in the three-line male sterile lines and the capacity for free mating as shown in the two-line male sterile lines, and also overcame the combination limitations of the three-line male sterile lines and the risk failure of seed production found in the two-line hybrid rice $^{[24]}$. Prof. Yuan gave strong support to the third-generation hybrid rice, which had already achieved important progress $^{[25]}$. Just two years before his death, he was satisfied with the progress and further launched the latest third-generation hybrid rice varieties for demonstration. This is the "1500 kilogram project" proposed by him, that is, the project of applying the new achievements of the third-generation hybrid rice to make the annual yield of double-cropping rice reaching 22.5 t ha⁻¹. At the same time, in order to meet the needs of the food security of the country, he organized researchers to carry out the breeding of salt and cadmium tolerant hybrids, which have also made important progress.

Prof. Yuan once said he had the two dreams, one is "enjoy the cool under the rice plants taller than men", and another is "hybrid rice could be grown all over the world to help solve global food scarcity". He also hoped that the development of hybrid rice could benefit people worldwide. His greatest wish is to develop hybrid rice for the benefit of the people all over the world. He published more than 60 research papers in hybrid rice. Since 1980, Prof. Yuan has trained more than 30 doctors and masters in China and 14,000 researchers and technicians from over 80 rice growing and less-developed countries, and served as a chief consultant to the FAO since 1990. Those trained researchers and technicians have become an important force in the development of hybrid rice in their home countries.

4. Honors

He was elected as an honorary member of the Chinese Academy of Engineering in 1995 and the U.S. Academy of Sciences class in 2006. For his outstanding contributions, he was awarded numerous honors and prizes including the first China National Special Invention Prize in 1981, the UNESCO Science Prize in 1987, the National Supreme Science and Technology Top Awards in 2000, the World Food Prize in 2004, the Wolf Prize in Agriculture in 2004, the Special Prize of National Science and Technology Progress Award in 2014, LUI Che Woo Prize in 2016, China's Medal of the Republic in 2019, and so on. Up to now, he accepted more than 20 awards totally. Many hardships in scientific research and innovation accompanied Prof. Yuan throughout his life as well as brilliant achievements. In addition to his research, Prof. Yuan also had a great passion for his family, life, nature, music, sports, and reading, and enjoyed chatting with all kinds of people. Although he has left us, his diligent pursuit of the bright prospect of hybrid rice is still shining like his thoughts, and continue to illuminate the way to the future.

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