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Engineering Achievements

Hybrid Rice

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1. Introduction

The cultivation of hybrid rice is one of the major achievements of modern agricultural science. In 1964, Longping Yuan became the first person to research male sterility in *indica* rice after observing a strain of natural hybrid rice displaying strong heterosis. In 1966, he was the first to publish a paper on the topic of "Male Infertility of Rice" and proposed the "three-line method" breeding approach to utilize rice heterosis, encompassing a male-sterile line, a maintainer line, and a restorer line [1]. This proposal acted as a prelude to research on hybrid rice in China. The three-line method and the subsequent two-line method of breeding hybrid rice were widely adopted and contributed significantly to food security in China. They also provided strong evidence for the heterosis of self-pollinating crops such as rice.

After more than 50 years of innovation, Chinese hybrid rice has become a staple of worldwide agricultural development. This article objectively, systematically, and comprehensively reviews and interprets the important events in the historical development of hybrid rice.

2. Overview of hybrid rice

Hybrid rice can be divided into three categories of strategic development: the three-line method, the two-line method, and the one-line method. As the application method becomes simpler, the efficiency increases. The level of heterosis is increasingly strong, which varies from species to subspecies and even includes distant heterosis [2].

The three-line method utilizes heterosis in the following three lines: the nucleo–cytoplasm interaction male sterility line (i.e., male-sterile line), the male sterility maintenance line (i.e., maintainer line), and the male sterility recovery line (i.e., restorer line). The male-sterile line provides a material basis for the production of a large number of hybrid seeds, the maintainer line is used to propagate the sterile line, and the restorer line is used to pollinate the sterile line to produce male-recovered hybrid rice seeds with heterosis (Fig. 1(a)) [2–4]. Chinese three-line hybrid rice was first used successfully in 1973, becoming a classic method of utilizing heterosis. The "three-line *indica* hybrid rice" won the China National Technical Invention Special Award in 1981.

The two-line method requires only sterile lines and restorer lines to utilize heterosis, while the most successful method is to utilize photo-thermo-sensitive genic male-sterile (PTGMS) lines, which display male sterility during long days and high temperatures, and male fertility during short days and low temperatures. Hybrid seeds are produced during the sterility period and sterile lines are produced by inbreeding during the fertility period, rendering the maintenance line unnecessary (Fig. 1(b)) [3,4]. Two-line hybrid rice was a significant scientific and technological achievement for China's agricultural community. First achieved in 1995, its annual planting area now accounts for more than 50% of hybrid rice varieties. The achievement "Research and Application of Two-line Hybrid Rice Technology" won the 2013 National Science and Technology Progress of China Special Prize. Third-generation hybrid rice, which can also be considered as a two-line method, in a sense, achieves heterosis through the self-breeding of common recessive nuclear male-sterile lines via genetic engineering technology. These varieties are currently being tested for production.

One-line hybrid rice breeds hybrids with fixed heterosis and no separation, and does not require annual hybrid seed production [2]. This technology is still being developed.

From an international perspective, Japanese scientists began research on *japonica* hybrid rice in the early 1950s. By the mid- to late-1960s, they had bred several *japonica* male-sterile lines, including Tengban 5. Of these, the Taichung 65 sterile line had a few homogenous restorer lines and the three-line method was used to produce *japonica* hybrid rice. However, no heterosis was identified due to the close relationship of the strains used and/or problems during seed production. Research about *japonica* hybrid rice in other countries beyond China is currently at a stagnation stage because no substantial breakthrough has been made and cannot be put into practice production [5]. Chinese scientists began researching the utilization of rice heterosis in 1961. They first succeeded in producing a three-line *indica* hybrid rice variety in 1973, after which heterosis was successfully demonstrated in the original two-line hybrid rice in 1995 [4]. As of 2019, China has bred more than 7000 hybrid rice varieties with a total planting area of about 6×10^8 hm^2 and an increased total grain output of

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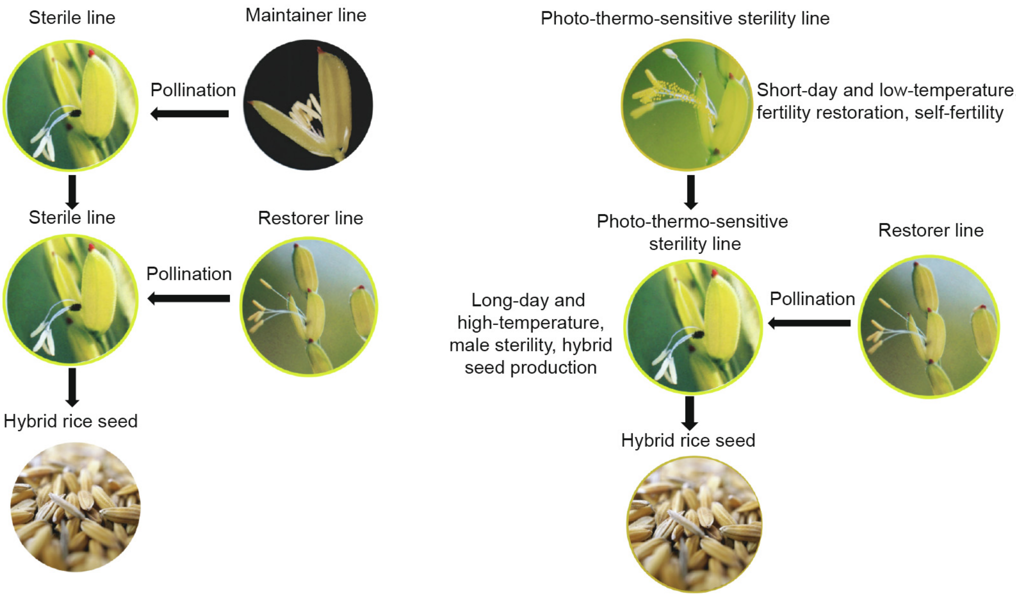

(a) (b)

Fig. 1. Schematic diagram of (a) three-line hybrid rice and (b) two-line hybrid rice.

nearly 9×10^8 t; these have fed an additional 2.3 billion people, thereby helping to ensure China's food security and strongly answering the question that was posed by Western scholars 25 years ago: "Who will feed the Chinese in the 21st century?"

In 1979, the United States introduced three *indica* hybrid rice varieties provided by the China National Seed Group Co., Ltd., which increased rice production by more than 165% compared with local improved varieties. This phenomenon became known as "Oriental Magic Rice" and attracted worldwide attention. Since 1980, when *indica* hybrid rice was introduced internationally, China has been a leading exporter of hybrid rice. Hybrid rice technology is listed by the Food and Agriculture Organization of the United Nations as the preferred method for increasing food production and solving the problem of food shortages in developing countries [4]. Many people have come to China to study and exchange information about hybrid rice technologies, including senior experts from the United States, Japan, and India, representatives from the International Rice Research Institute, the International Center for Tropical Agriculture, and other international organizations, and representatives from Bayer, DuPont Pioneer, Monsanto, the American RiceTec Inc., and other multinational seed companies. These organizations have utilized Chinese *indica* hybrid rice breeding technologies and introduced hybrid rice germplasm resources in order to perform localized hybrid rice research, making progress in these areas. However, the technical level of rice heterosis utilization of these organizations is still far behind that of China, due to a lack of talent, limited resources, and China's longer history of research. At present, Chinese hybrid rice has been successfully tested or developed in more than 60 countries including India, Bangladesh, Vietnam, the Philippines, Pakistan, the United States, Indonesia, Myanmar, Brazil, and Madagascar, with planting areas exceeding $6 \times 10^6\ \text{hm}^2\cdot\text{a}^{-1}$. In this way, China is providing a solution to global food-shortage problems [6].

Since the 1980s, there has been an increased domestic and international focus on breeding super high-yield rice, which has encountered some difficulties. Researchers from Japan and the International Rice Research Institute failed to achieve their goals related to research on super-rice. China launched the "Super-Hybrid Rice Breeding Research Program" in 1998, and Chinese scientists have since adopted a high-yield rice breeding technology that involves a combination of morphological improvement and the utilization of heterosis [7]. These scientists have since met the breeding goals of the first phase of China's super-rice research program in 2000 (10.5 $\text{t}\cdot\text{hm}^{-2}$), the second phase in 2004 (12.0 $\text{t}\cdot\text{hm}^{-2}$) (Fig. 2), the third phase in 2012 (13.5 $\text{t}\cdot\text{hm}^{-2}$), and the fourth phase in 2014 (15.0 $\text{t}\cdot\text{hm}^{-2}$). In 2017, Chinese super-hybrid rice was tested in a 100 mu (6.67 hm^2) demonstration field in Handan City, Hebei Province, China, and the average yield reached 17.23 $\text{t}\cdot\text{hm}^{-2}$, generating the highest-yield rice grown in high-latitude areas around the world. In 2018, a 100 mu (6.67 hm^2) demonstration film in Gejiu City, Yunnan Province, China, increased the average yield per unit to 17.28 $\text{t}\cdot\text{hm}^{-2}$, thereby raising the world record for the highest-yield rice. This super-hybrid rice has met the breeding goals of China's four-stage super-rice research program, which was ranked in China's top ten scientific and technological programs by the Chinese Academy of Sciences and the Chinese Academy of Engineering in 2000, 2003, 2011, and 2014. Super-hybrid rice accounts for 75% of the 132 super-rice varieties that have been bred in China, while the quality of rice has also been significantly improved. The proportion of rice varieties at the third-class level or above increased from 32.0% in the 10th Five-Year Plan to 51.4% in the 13th Five-Year Plan. The extension area of super-hybrid rice currently accounts for over 30% of China's rice-growing land, making China the only country to successfully cultivate super-rice over large areas [8].

3. Three-line hybrid rice

There are over 60 kinds of Chinese three-line hybrid rice resources with cytoplasmic male sterility, including wild abortion (WA), Gang type, D type, Yinshui type, dwarf abortive (DA) type, Honglian (HL) type, K type, Maxie type, Baotai (BT) type, and Dian type. These varieties are typically classified into three types: WA, HL, and BT [2,4]. All varieties, regardless of type, must overcome three major barriers from the research stage to the application stage: the cultivation of male sterility maintainer lines, the selection of male sterility restorer lines, and the production of hybrid seeds (commonly known as "seed production").

Fig. 2. The second-phase super-hybrid rice variety "Y Liangyou No. 1," also known as "Waterfall Rice."

3.1. Breeding of male sterility maintainer lines

Naturally male-sterile plants exist in nature, and Chinese scientists were inspired to look for additional strains in 1961. By 1964, they identified *indica* varieties such as Dongting, Nantes, and Shengli, determining that only one in 50 000 natural male-sterile plants were pollen-free, anther degraded, or pollen aborted. Several rice breeding organizations across the country used a variety of methods, such as extensively measuring the maintainer line and artificially creating a maintainer line, to screen the male sterility maintainer lines by crossing and testing them with thousands of rice varieties. Unfortunately, none of these reached 100% maintenance sterility after six years of study. Subsequent studies demonstrated that these male sterility rice plants possess common nuclear male sterility, in which it is difficult to find maintainer lines. Even though they failed to identify a stable natural sterile line, Chinese scientists still believed that the original three-line plan would work (Fig. 3) and altered their strategies to identify male-sterile materials from wild rice or through distant hybridization. In the winter of 1970, a male-sterile plant was identified in the common wild rice population found in the wetlands of Nanhong Farm in Hainan Province. The anther of this sterility line was thin, yellow, and non-cracked, containing typical sterile pollen. It was named "wild abortion." Afterward, researchers from 19 provinces joined the program and conducted significant cross-testing on WA, finding that early *indica* germplasm in the Yangtze River Basin (e.g., Erjiunan 1 and Zhenshan 97) could maintain the male fertility of WA. They adopted a strategy known as "south-reproduction and north-selection" to accelerate the breeding process, performing back-to-back, multi-generation breeding for two years. This successfully bred a series of wild abortive male sterility lines such as Erjiunan 1A and Zhenshan 97A and their maintainer lines Erjiunan 1B and Zhenshan 97B, thus successfully cultivating a male sterility maintainer line. As such, the discovery of WA is considered to be a breakthrough in the study of hybrid rice in China [2].

In 1972, Chinese scientists discovered a male-sterile plant in the offspring of a hybrid variety resulting from Hainan Red awn wild rice and the Jiangxi local *indica* rice variety Liantangzao. This was a new variety, different from WA sporophyte sterility (with typically aborted pollen, when pollen abortion occurs in the late mononuclear stage) (Fig. 4(a)). Its male abortion type is gametophytic sterility (with spherical abortion pollen, where pollen abortion occurs in the second nuclear stage) (Fig. 4(b)). Successive crossing with Liantangzao successfully cultivated the HL cytoplasmic male-sterile line, HL A, and its maintainer line in 1974 [4].

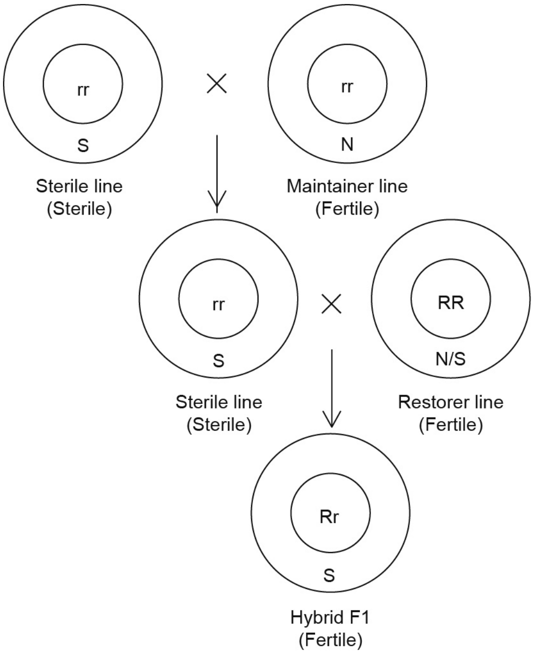

Fig. 3. Principle diagram of three-line breeding. S: Cytoplasmic male sterility factor; N: cytoplasmic male fertility factor; R: male fertility restoration dominant gene; r: male fertility restoration recessive gene.

In 1966, Japanese researchers crossed the female Indian *indica* rice variety Chinsula Baoluo II with the Taiwan Province *japonica* rice variety Taichung 5 to breed the BT-type male-sterile line, which possesses gametophytic sterility (with staining abortion pollen, where pollen abortion occurs in the trinucleate stage) (Fig. 4(c)) [9]. In 1972, Chinese scientists introduced this male sterility variety, which is the most widely used cytoplasmic male sterility variety, into China's three-line hybrid *japonica* rice. Using test crosses, the majority of *japonica* rice varieties were found to maintain their sterility. The first *japonica* rice BT cytoplasmic male sterility line, Liming A, was successfully bred in 1975 [4].

3.2. Breeding of male-sterile restorer line

Of the three lines, the male-sterile lines and the maintainer lines were successfully bred after overcoming several difficulties. Finding a restorer line was also difficult. Generally speaking, the breeding of restorer lines and sterile lines began at the same time; however, some researchers thought that the seeds of the hybrids would not bear fruit after the nuclear replacement between WA and cultivated rice, meaning that no restoration could be found and that hybrids held no advantage. This was a critical question, and "hybrid rice research" was proposed as a key research project to stimulate national collaboration in China. Beginning in the winter of 1972, the three-line selection method now focused on the selection of restoration lines. Researchers from over ten provinces used a variety of rice seeds to test many restorer lines and found that the recovery genes of WA cytoplasmic male sterility were primarily distributed in closely related low-latitude tropical rice varieties. Use of the IR varieties of the International Rice Research Institute, Taiyin1, IR24, IR661, Gu154, and other germplasm could well recover the fertility of WA male sterility. The three-line system containing the WA male-sterile line, maintainer line, and restorer line was successfully developed in 1973 [2]. The first batch of WA hybrid rice combinations—such as Nanyou 2 and Shanyou 2—was then bred. In 1976, China began to use hybrid rice on a

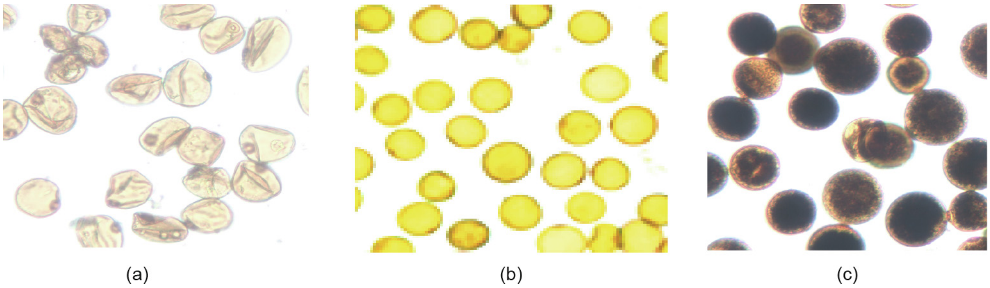

Fig. 4. Three types of cytoplasmic male-sterile abortion pollens. (a) WA type abortion pollen (sporophyte sterility); (b) HL type abortion pollen (gametophyte sterility); (c) BT type abortion pollen (gametophyte sterility). Reproduced from Ref. [9] with permission of Science China Press, © 2012.

large scale, becoming the first country in the world to successfully utilize heterosis in rice production.

Since 1978, the cultivation of WA restorer lines has progressed from screening foreign germplasm to domestic production. Restorer lines created by combining restorer line × restorer line, restorer line × excellent line germplasm, reincarnation selection, and molecular marker-assisted selection reduce the risk of genetic uniformity from the extroverted restorer line and promote the renewal of WA hybrid rice varieties. As a typical example, Minghui 63 was bred by restorer line × restorer line technology in 1981. This restorer line has high-combination ability and displays wide adaptability and a strong resistance to disease; it has 34 breeding combinations and a promotion area exceeding 8×10^7 hm^2 [4].

The relationship between the HL restorer line and the maintainer line is different from that of the WA type. Most WA-type restorer lines can maintain the sterility or recover half the sterility of HL type, while few conventional *indica* rice varieties in the Yangtze River Basin (e.g., Yangdao 6, Teqing, and E32) are highly recoverable. It was not until the late 1990s that the three lines of HL hybrid *indica* rice were successfully realized.

Chinese scientists discovered that *indica* rice from the Yangtze River Basin in China contains a restorer gene that can restore the cytoplasmic male sterility of the BT variety. In 1975, the *indica* restorer gene was transferred to *japonica* rice through an artificial restoration technology known as "*indica*–*japonica* bridging," which created restorer gene resources for the BT male-sterile lines. Due to the lack of genetic resources for the recovery of BT male sterility lines, C57 was China's best chance for the three-line breeding system of BT *japonica* rice. In 1990, the first BT three-line hybrid *japonica* combination, Liyou 57, was finally developed and is now widely used [4].

3.3. Seed production

After the three-line hybrid rice system was successfully implemented, scientists still needed to solve the issue of seed production in order to make the hybrid rice available on a large scale. Since heterosis only appears in the first generation of hybrids, it is necessary to produce seeds each year to obtain the first generation of hybrid seeds. There are three stages in the research of this seed production technology, from exploration to maturity [2].

At the beginning of research on seed production, it was thought that the insufficient amount of pollen in the restoration line was the primary reason for the low seed yields. As such, additional male parents were planted and the females were planted closer to the males to increase pollen density, such that the female received more pollen, increasing seed production. Subsequent research indicated that these measures can disperse approximately 450 grains of pollen per unit area (i.e. 1 cm^2), which exceeded the threshold necessary for cross-pollination. However, increasing the pollen density did not increase the yields as expected. The small-area seed production output was less than $0.09\ t{\cdot}hm^{-2}$ in 1973.

As scientists continued to research seed production, they determined that yield was not affected by the amount of pollen, but by the overlapping flowering stage. This ensured that the pollen was scattered evenly on the stigma of the female. Based on this new understanding, a new method of seed production technology was implemented, with the small-area seed production output subsequently reaching $0.45\ t{\cdot}hm^{-2}$ by 1975.

Due to the continuous expansion of the planting area and the significantly increasing yield of hybrid rice, domestic demand for hybrid rice seeds increased sharply to 60 000 mu (4000 hm^2) in 1976. At that time, scientists had only produced seeds for a few square hectometers, and meeting the demand of 4000 hm^2 was a significant undertaking. They ensured that the male and female parents were properly flowered and explored new strategies, including selection of the seed production area, parental seedling transplanting, parental population construction, parental flowering period prediction, flowering time regulation, gibberellin spraying, assisted pollination (Fig. 5), isolation, and impurity removal. By the mid-to-late 1980s, a complete, mature, and efficient method for seed production using the three-line hybrid method was implemented, and the output of large-scale seed production exceeded $3\ t{\cdot}hm^{-2}$. This provided adequate technical support for the rapid and stable development of hybrid rice in China.

4. Two-line hybrid rice

The fertility of two-line hybrid rice is controlled only by the nucleus and can be categorized as either photo-sensitive or thermo-sensitive, based on the primary and secondary effects of light and temperature on the fertility of the genic male-sterile line. Since there is no limit from the restorer line or the maintainer line, the high rate of resource utilization makes it easier to breed high-yielding, high-quality, multi-resistance hybrid rice. This is a more advanced method than the three-line method.

4.1. Discovery and application of photo-sensitive and thermo-sensitive genic male sterility resources

In 1973, Chinese scientists discovered three natural male-sterile plants in the first-season late *japonica* variety Nongken 58. After over ten years of research, they developed the photo-sensitive sterile line Nongken 58S and established a system for using heterosis and a photosensitized two-line method for hybrid seed production under long-day, high-temperature conditions and self-propagation sterile lines under short-day, low-temperature conditions [2]. The genetic behavior of Nongken 58S sterility is complex, and the photo-sensitive nucleus sterility genes that control its male fertility are *pms1*, *pms2*, and *pms3*. *pms3* is a single-base mutation of a non-coding RNA gene on chromosome 12 that decreases the

Fig. 5. Artificially assisted pollination for hybrid rice seed production.

transcription of LDMAR under long-day conditions, resulting in the early death of anthers in Nongken 58S and leading to male sterility. It is the most important source of sterility genes for photo-sensitive *japonica*-type genic sterile lines (Fig. 6(a)) [10]. In 1991, the Nongken 58S photo-sensitive nucleus sterility gene was transferred to *indica* rice and the first *indica*-type PTGMS line, Peiai 64S, was produced. In 1994, the first two-line hybrid *indica* combination was bred and the first-generation backbone parent of two-line hybridization, Peiai 64S, won China's National Science and Technology Progress Award in 2001.

In 1987, Chinese scientists identified a natural male-sterile plant in *indica* rice that displayed male sterility under high-temperature conditions and male fertility under low-temperature conditions. From it, they bred an *indica*-type temperature-sensitive sterile line, Annong S-1. Based on its thermo-sensitive characteristics, they established a thermo-sensitive two-line method using heterosis to produce hybrid seeds under high-temperature conditions and inbreeding sterile lines under low-temperature conditions [11]. The temperature-sensitive nucleus sterility of Annong S-1 is regulated by the recessive single gene *tms5* on chromosome 2 (Fig. 6(b)). *tms5* encodes an RNase Z^{S1}, and its 71st C→A mutation leads to high-temperature nucleus male sterility [12]. *tms5* has a simple genetic behavior and is currently the most widely used genetic resource in China's two-line hybrid rice, accounting for more than 80% of two-line hybrid rice.

4.2. Theoretical innovation

Following the discovery of photo-sensitive and thermo-sensitive genic male sterility resources, two-line hybrid rice research was listed as a special item in the National High-tech R&D Program (863 Program) in 1987, with 16 research groups designated for that purpose. The depth and breadth of two-line hybrid rice research was insufficient due to a limit on research materials and experimental conditions in the early research stages. In particular, the understanding of the laws of fertility conversion of PTGMS lines was incomplete. It was assumed that fertility was controlled by the length of day and that fertility conversion was unrelated to temperature. Due to a lack of basic theoretical research, most dual-use genic sterile lines bred during these early stages have no practical use. For example, in the middle and lower reaches of the Yangtze River during the summer of 1989, three consecutive days below 23.5 °C restored the fertility of all PTGMS lines, leading to serious setbacks in the study of two-line hybrid rice. This caused scientists to consider the response of fertility to temperature. The key was to reveal the basic laws of the relationship between fertility in PTGMS lines and light and temperature.

In the early 1990s, Chinese scientists conducted in-depth research on the fertility conversion of Nongken 58S and Annong S-1, identifying the roles of light and temperature in fertility conversion. By experimenting with different light lengths and temperature conditions, they systematically studied the fertility conversion of PTGMS lines, established the fertility conversion pattern of photo-sensitive and thermo-sensitive rice, and elucidated the relationship between fertility conversion and changes in light and temperature. This research provided the theoretical groundwork for breeding practical PTGMS lines (Fig. 7) [2,3].

Several years were spent researching the fertility conversion characteristics of sterile lines under different ecological conditions and artificial light and temperature conditions in Nongken 58S and Annong S-1. In both the photo-sensitive and thermo-sensitive lines, temperature was found to largely affect fertility conversion. Scientists discovered the fertility change law of PTGMS genes in different genetic backgrounds. By combining the meteorological data from different ecological regions, they determined that the

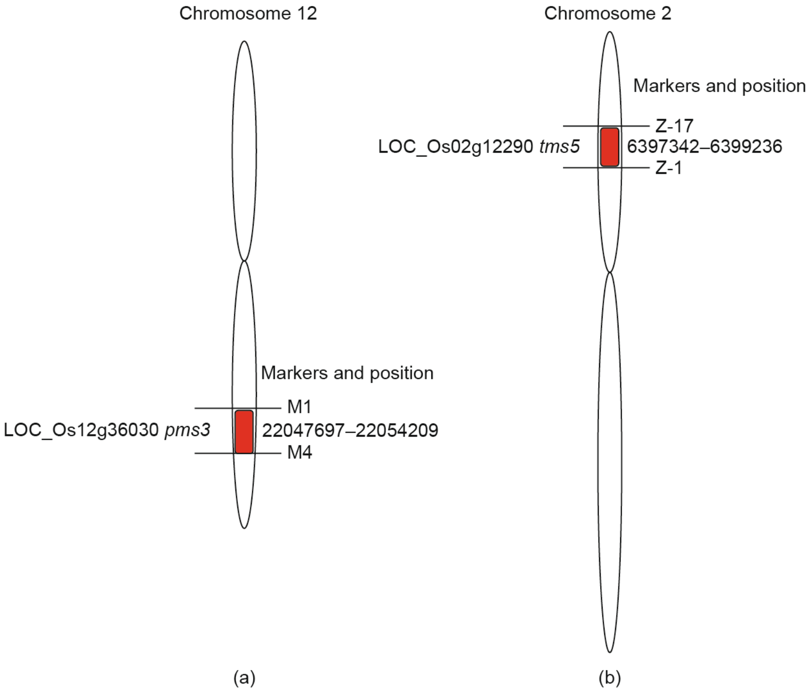

Fig. 6. Genes controlling (a) photo-sensitive and (b) thermo-sensitive nuclear sterility.

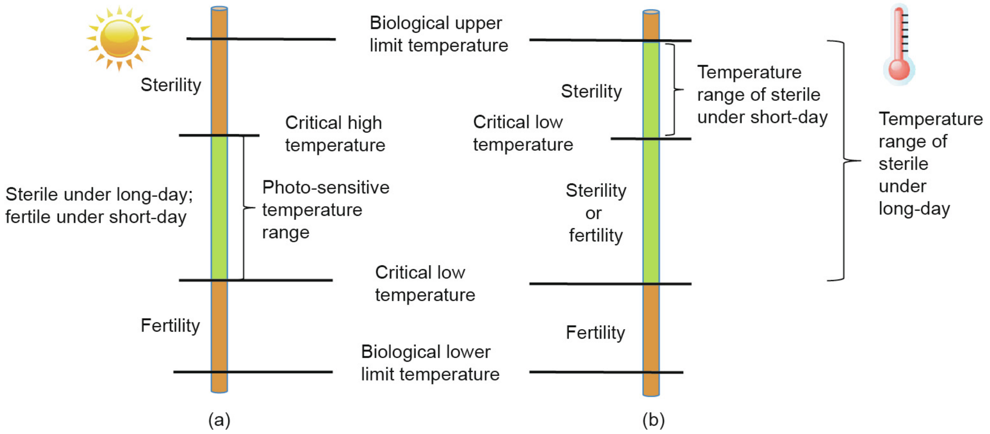

Fig. 7. The photo-thermal model of fertility conversion of (a) photo-sensitive and (b) thermo-sensitive sterile rice.

key to selecting a practical PTGMS line was a low threshold temperature. For example, the temperature in the middle reaches of the Yangtze River is below 23.5 °C, which is the upper limit for sterile varieties. This temperature value is based on an analysis of 50 years of meteorological data in the middle and lower reaches of the Yangtze River, and has subsequently been proven through years of trial and error. This temperature is key to successfully breeding two-line hybrid rice.

The threshold temperature increased significantly after breeding several generations of the PTGMS line, which made the seeds of the sterility line unsuitable for seed production. For example, the critical temperature for the fertility conversion of the sterile line Peiai 64S, which was the most widely used PTGMS line in the production of two-line hybrid rice in China, was 23.3 °C when it passed the provincial appraisal in 1991. After selecting and retaining seeds per conventional breeding procedures and methods, the fertility conversion temperature of the sterile line increased from generation to generation, reaching 24.2 °C in 1993 and as high as 26 °C in some regions in 1994. This phenomenon became known as the "genetic drift" of the threshold temperature [4]. Research on the stability and variability of the fertility inheritance of PTGMS lines became known as the genetic drift law of PTGMS lines. As the number of breeding generations increased and the threshold temperature of population sterility gradually increased, the mechanism of genetic drift of the PTGMS threshold point became better understood. The mechanism behind fertility conversion characteristics is a qualitative trait and the threshold temperature of infertility is a quantitative trait, providing theoretical support for the production of sterile line stocks. These findings demonstrated that the sensitive part during temperature-based fertility conversion is the young panicle and the sensitive period is from the pollen mother cell formation to meiosis. The part that is sensitive to light is the leaf, and the sensitive period is from the second branch to the meiosis period. These results provided a theoretical basis for the production of hybrid rice seeds via the two-line method [3].

4.3. Technological innovation

Early PTGMS lines were difficult to use due to the high-temperature threshold for sterility. As such, research on the fertility conversion characteristics of sterile lines under different ecological conditions and artificial light and temperature conditions was performed for several years. The practical technology for the identification and breeding of PTGMS lines was thus established, laying the foundation for the application of two-line hybrid rice. Meteorological analyses and a decision-making system for the production of two-line hybrid rice seeds were established based on the fertility conversion characteristics of sterile lines and 50 years of climate data from different ecological regions in China. This system is based on the core technical indicators of the three safety periods (female parent fertility safety period, heading and flowering safety period, and mature safety period) and provides technical support for the large-scale application of two-line hybrid rice. In addition, reproductive technologies were established—such as winter breeding in the low-latitude Hainan Province, two-season breeding in summer and autumn, irrigating with normal and cold water, and summer breeding in high altitudes with naturally low temperatures—thus laying the groundwork for large-scale seed production.

A set of procedures for the production of core seeds and stocks of the PTGMS lines were carefully designed to stabilize the sterility conversion temperature and address the inconsistent critical temperature of group sterility in PTGMS lines (Fig. 8). During these procedures, it is important to use the temperature threshold of 23.5 °C as a condition for identifying the PTGMS lines and to subsequently obtain its core seed. The core seed is used

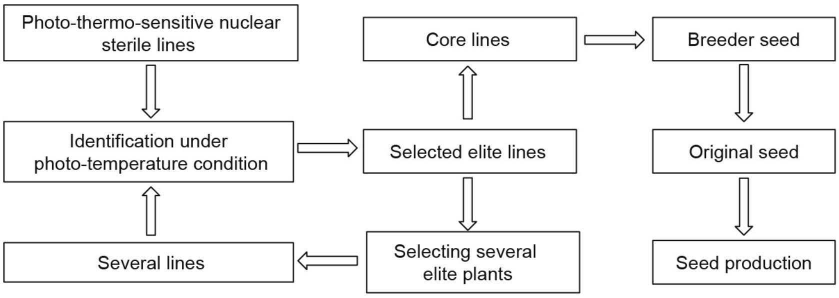

Fig. 8. Production procedures of core seeds and original seeds of the photo-thermo-sensitive sterile line.

to produce the breeder seed, which in turn is used to produce the original seed. The cycle then repeats itself in order to effectively guarantee the relative stability of the sterile threshold temperature and prevent the fertility threshold temperature of the sterile line from drifting, thus ensuring safe production of two-line hybrid rice [2,3].

5. Conclusion

The story of the success of Chinese hybrid rice demonstrates the innovative spirit of Chinese scientists at all stages of hybrid rice research. It also demonstrates the collaborative spirit of organized national research during a critical period; an example is the establishment of the National Hybrid Collaboration Group after WA was discovered and the establishment of the national two-line method hybrid rice "863" special collaborative research group following the discovery of Nongken 58S and Annong S-1.

The large-scale cultivation of hybrid rice is a significant international breakthrough in agricultural science and technology and has contributed to a better understanding of crop heterosis theory and seed breeding. It has also promoted the development of crop genetics and breeding disciplines. Hybrid rice not only provides new methods for utilizing heterosis in other crops, but also contributes to food security in China and the rest of the world. Further research on hybrid rice is aided by advances in our understanding of germplasm resources and innovations in breeding technologies, and focuses on the fixing of heterosis, research on super-high-yield varieties, and the creation of simple, efficient, and wide-adaptation varieties.

Acknowledgements

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