Development of Wide-Compatible Indica Lines by Pyramiding Multiple Neutral Alleles of Indica–Japonica Hybrid Sterility Loci

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Since the development of indica hybrid rice in the 1970s, great success has been achieved in hybrid rice production in China and around the world. The utilization of intersubspecific indica–japonica hybrid rice has always been considered due to its stronger heterosis characteristics. However, indica–japonica hybrids face a serious problem of sterility, which hinders the exploitation of their heterosis. In the past decades, the genetic basis of indica–japonica hybrid sterility has been well studied. It was found that in sterile indica–japonica hybrids, female sterility was mainly controlled by the S5 locus and male sterility by the Sa, Sb, Sc, Sd, and Se loci. In this study, we developed wide-compatible indica lines (WCILs) by pyramiding multiple neutral (n) alleles of the hybrid sterility loci. First, we identified Sn alleles of the loci in single-segment substitution lines (SSSLs) in the genetic background of indica Huajingxian 74 (HJX74). Then, the Sn alleles of S5, Sb, Sc, Sd, and Se loci in SSSLs were pyramided in the HJX74 genetic background. The WCILs carrying Sn alleles at the S5, Sb, Sc, Sd, and Se loci showed wide compatibility with indica and japonica rice varieties. Therefore, the WCILs will be used to develop inter-subspecific indica–japonica hybrid rice with normal fertility.

Keywords: hybrid rice, heterosis, hybrid sterility, neutral allele, breeding by design

INTRODUCTION

Asian cultivated rice (Oryza sativa L.) is the staple food for more than half of the world’s population (Fukagawa and Ziska, 2019). The breeding of high-yielding varieties is essential for maintaining global food security (Peng et al., 2008; Khush, 2013). Since the 1970s, indica hybrid rice has been successfully developed in China and around the world (Yuan and Virmani, 1988; Cheng et al., 2007). However, the heterosis of intra-subspecific hybrid rice is limited, resulting in a yield plateau...
for production of hybrid rice (Peng et al., 2004; Cheng et al., 2007). There is great heterosis in inter-subspecific hybrids, and exploiting this heterosis has long been considered a promising approach to further increase the yield potential of rice (Khush, 2013; Zhang et al., 2021). However, the severe sterility associated with indica–japonica hybrid hinders the utilization of heterosis (Ikehashi and Araki, 1986; Ouyang and Zhang, 2018; Zhang, 2020, 2022).

The sterility of hybrids produced by crossing indica and japonica rice varieties can be attributed to female or embryo sac sterility and male or pollen sterility. The female sterility in hybrid is mainly controlled by the S5 locus, which was mapped on chromosome 6 (Ikehashi and Araki, 1986; Yanagihara et al., 1995; Ji et al., 2005; Qiu et al., 2005). The male sterility in hybrid is mainly controlled by Sa, Sb, Sc, Sd, and Se loci (Zhang and Lu, 1989, 1993; Zhang et al., 1993, 1994). Using molecular markers, Sa was found to be located on chromosome 1 (Zhuang et al., 1999; Su and Liu, 2003), Sb on chromosome 5 (Zhuang et al., 2002; Li et al., 2006), Sc on chromosome 3 (Zhang and Zhang, 2001; Yang et al., 2004), Sd on chromosome 1 (Li et al., 2008), and Se on chromosome 12 (Zhu et al., 2008). The S5, Sa, and Sc genes were then cloned and functionally analyzed (Chen et al., 2008; Long et al., 2008; Yang et al., 2012; Shen et al., 2017). The genetic model of hybrid sterility is the one locus spor-o gametophytic interaction model (Ikehashi and Araki, 1986; Zhang and Lu, 1993; Zhang, 2020). In this genetic model, it is assumed that indica varieties have S' allele, and japonica varieties have S' allele at the loci. At the S5 locus, the interaction between S' and S' causes the abortion of female gametes carrying S' allele (Ikehashi and Araki, 1986). At the Sa, Sb, Sc, Sd, and Se loci, the interaction between S' and S' causes the abortion of male gametes carrying S' allele (Zhang and Lu, 1993). At these loci, some varieties carry S'', a neutral allele, and the allelic interaction between S'/S'' and S'/S'' cannot cause the abortion of any gamete (Ikehashi and Araki, 1986; Zhang and Lu, 1993; Yang et al., 2012; Shen et al., 2017; Xie et al., 2017). The understanding of the genetic and molecular mechanisms of sterility in indica–japonica hybrids has laid the foundation for overcoming hybrid sterility.

With the development of molecular breeding technology, the concept of “breeding by design” was proposed (Peleman and van der Voort, 2003). To implement the strategy of rice breeding by design, a library of single-segment substitution lines (SSSLs) in rice was constructed by using 43 accessions from seven species of AA genome as donors of chromosome substitution segments in the genetic background of Huajingxian 74 (HXJ74), an elite indica variety from south China. A total of 2,360 HXJ74-SSSLs have been included in the library, which contains rich genetic resources for rice breeding techniques (Zhang et al., 2004; Xi et al., 2006; He et al., 2017; Zhao et al., 2019; Zhang, 2021). The HXJ74-SSSL library was used as a platform for designing new rice cultivars, and several cytoplasmic male sterility (CMS), maintainer, and restorer lines were developed (Dai et al., 2015, 2016; Luan et al., 2019). Therefore, target chromosome-segment substitution is a way to breeding by design in rice (Zhang, 2021).

With the understanding of the genetic and molecular mechanisms of indica–japonica hybrid sterility and the development of molecular breeding techniques, the breeding strategies for developing inter-subspecific indica–japonica hybrid rice were proposed (Zhang, 2020, 2022). One strategy for overcoming the hybrid sterility of indica–japonica rice is to develop indica-compatible japonica lines (ICJLs) (Zhang and Lu, 1999; Zhang, 2020). Recently, the ICJLs were developed by pyramiding S' allele at the Sb, Sc, Sd, and Se loci and S' allele at the S5 locus in japonica genetic background by marker-assisted selection (MAS). The ICJLs are compatible with indica but incompatible with japonica in pollen fertility and spikelet fertility (Guo et al., 2016). Another strategy for overcoming the hybrid sterility of indica–japonica rice is to develop wide-compatible indica lines (WCILs) (Zhang, 2020, 2022). Herein, we report the development of WCILs using the HJX74-SSSL library. By pyramiding S' allele at the S5, Sb, Sc, Sd, and Se loci in the HJX74 genetic background, the obtained WCILs were compatible with both indica and japonica rice in pollen fertility and spikelet fertility. The breeding of WCILs provides a technique to develop inter-subspecific indica–japonica hybrid rice.

**MATERIALS AND METHODS**

**Plant Materials and Field Trials**

Seven SSSLs carrying the Sc gene for hybrid male sterility in their chromosome substitution segments and seven SSSLs carrying the S5 gene for hybrid female sterility in their chromosome substitution segments were selected from the HXJ74-SSSL library (Supplementary Table 1). A set of indica and japonica varieties were used as testers to test the hybrid fertility. The genotypes of Sa, Sb, Sc, Sd, and Se loci for hybrid male sterility and S5 locus for hybrid female sterility have been identified in some of the testers. It was found that at these six loci, the indica variety Guang-lu-ai 4 (GLA4) carried the S' alleles, while the japonica variety Taichung 65 (T65) carried the S' alleles (Zhang et al., 1994; Guo et al., 2016). All the study samples were planted from 2008 to 2019 at the farm of South China Agricultural University, Guangzhou (23°07′N, 113°15′E). These plants were planted in two cropping seasons each year, with the first cropping season (FCS) running from late February to mid-July and the second cropping season (SCS) running from late July to mid-November. Seeds were sown in seedbeds, and seedlings were transplanted into the field. Field management, including irrigation, fertilization, and pest control, followed normal agricultural practices.

**Genotyping by Molecular Markers**

The SSR markers were selected on the rice microsatellite maps (McCouch et al., 2002; Zhang et al., 2007). The functional markers of the S5 gene were selected to identify the genotypes at the S5 loci (Sundaram et al., 2010; Du et al., 2011; Yang et al., 2012; Guo et al., 2016). Markers linked with the Sa, Sb, Sc, Sd, and Se loci were selected from the published studies (Yang et al., 2004, 2012; Li et al., 2006, 2008; Chen et al., 2008; Long et al., 2008; Zhu et al., 2008). New molecular markers were developed in this study (Supplementary Table 2). The PCR products were separated into 6% non-denaturing polyacrylamide gels (Panaud et al., 1996; Supple- mentary Table 2).
Phenotyping of Fertility and Agronomic Traits

To check pollen fertility, nine mature flowers were collected from the upper third of panicles during the flowering stage and fixed in FAA solution. Pollens were stained with the 1% I$_2$-KI solution containing 0.1% (w/v) iodine and 1% (w/v) potassium iodide. Pollens were divided into normal pollens and sterile pollens, which were further divided into stained abortive pollens (stained but small size) and empty abortive pollens (small size and empty) (Zhang and Lu, 1989). Three panicles per plant and 10–12 plants per line were used to examine the spikelet fertility, and 20–40 plants per line were used to investigate the agronomic traits.

Statistical Analysis

For statistical analysis, the percentage data were converted to the square root of the arcsine values. Student’s $t$-test was used to compare the data between the two groups. The Dunnett $t$-test was used to compare multiple groups with the control group. The least significance range (LSR) was used for the multiple range test among the multiple groups. The chi-square ($\chi^2$) test was used to detect the distorted segregation of three genotypes in F$_2$ populations according to the Mendelian ratio of 1:2:1. SPSS statistics 23.0 and Origin Pro 9.0 were used for data analysis and charting.

RESULTS

Genotypes of $S_a$, $S_b$, $S_c$, $S_d$, $S_e$, and $S_5$ Loci in Huajingxian 74

To identify the genotypes of $S_a$, $S_b$, $S_c$, $S_d$, $S_e$, and $S_5$ loci associated with hybrid sterility, HJX74 was test crossed with T65, a japonica variety with $S'$ alleles at these six loci, and GLA4, an indica variety with $S'$ alleles at these six loci (Zhang et al., 1994; Guo et al., 2016). The F$_1$ hybrids obtained from the cross of T65/GLA4 showed severe sterility, where the pollen fertility was only 20.51% and spikelet fertility was only 5.89%. In contrast, the F$_1$ hybrid of the HJX74/GLA4 cross showed normal pollen fertility and spikelet fertility of 92.39% and 93.39%, respectively. In the F$_1$ hybrids obtained from the cross of HJX74/T65, the pollen fertility was 72.89% and the spikelet fertility was 61.58%, which were significantly higher than those of T65/GLA4 and significantly lower than those of HJX74/GLA4 hybrids (Figure 1A). The results showed that the hybrid of HJX74/T65 exhibited partial pollen sterility and partial spikelet sterility.

The molecular markers linked to the $S_a$, $S_b$, $S_c$, $S_d$, $S_e$, and $S_5$ loci were used to investigate genotype segregation in the F$_2$ populations obtained from the crosses of HJX74/GLA4 and HJX74/T65. At the $S_b$, $S_d$, and $S_e$ loci, the genotype segregation of F$_2$ populations from both crosses fit the Mendelian ratio of 1:2:1. At the $S_a$, $S_c$, and $S_5$ loci, distorted segregation of the genotypes was detected in the F$_2$ population of HJX74/T65 but not in the genotypes of HJX74/GLA4. At the $S_t$ locus, the genotype ratios of $S_t^{HJX74}/S_t^{GLA4}$, $S_t^{HJX74}/S_t^{T65}$, and $S_t^{T65}/S_t^{T65}$ were 68:100:33, which significantly distorted from the Mendelian ratio of 1:2:1. At the $S_c$ locus, the genotype ratios of $S_c^{HJX74}/S_c^{GLA4}$, $S_c^{HJX74}/S_c^{T65}$, and $S_c^{T65}/S_c^{T65}$ were 69:70:3, which significantly...

FIGURE 1 | Genotypes of hybrid sterility loci $S_a$, $S_b$, $S_c$, $S_d$, $S_e$, and $S_5$ in HJX74. (A) Pollen and spikelet fertility of three parents and their F$_1$ hybrids. (B) Ratios of genotypes at $S_a$, $S_b$, $S_c$, $S_d$, $S_e$, and $S_5$ loci in the F$_2$ populations from the crosses between HJX74 and testers Taichung 65 (T65) and Guang-lu-ai 4 (GLA4). (C) Chromosome location and genotypes of the genes at the $S_a$, $S_b$, $S_c$, $S_d$, $S_e$, and $S_5$ loci in HJX74. Vertical bars represent rice chromosomes. P1P1, Genotypes of HJX74; P1P2, Heterozygous genotype; P2P2, Genotype of testers T65 ($S'/S'$) or GLA4 ($S'/S'$). Capital letters indicate statistical differences at the 0.01 probability level.

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distorted from the Mendelian ratio. Distorted segregation was also detected at the S5 locus, where the genotype ratios of S5HJX74/S5HJX74, S5HJX74/S5T65, and S5T65/S5T65 were found to be 72:65:43 (Figure 1B). In addition, HJX74 was tested using a group of indica and japonica testers. The results showed that distorted segregation was detected only at the Sa, Sc, and S5 loci in the crosses of HJX74/japonica testers (Supplementary Table 3).

These results indicated that HJX74 carried S′/S′ at the Sa, Sc, and S5 loci and S′/S′ at the Sb, Sd, and Se loci (Figure 1C). At the Sa and Sc loci, the allele interaction between S′ of HJX74 and S′ of japonica testers caused the abortion of male gametes carrying S′ in hybrids, resulting in the significant reduction of plants with S′/S′ in the F2 populations. At the S5 locus, the allele interaction between S5′ of HJX74 and S5′ of japonica testers caused the abortion of female gametes carrying S5′ in hybrids, resulting in the significant reduction of plants with S5′/SS′ in the F2 populations. At the Sb, Sd, and Se loci, allele interaction between S′ of HJX74 and S′ of japonica testers or S′ of indica testers could not cause the abortion of any gamete in hybrids, and genotype segregation in the F2 populations fit the Mendelian ratio of 1:2:1 (Supplementary Table 3). In addition, compared with the Sc locus, the Sa locus showed weak distorted segregation, where $\chi^2(1:2:1) = 34.00–62.27$ in the five segregation populations of the Sc locus, while $\chi^2(1:2:1) = 9.36–12.19$ in the three segregation populations of the Sa locus (Supplementary Table 3). The results showed that the hybrid male sterility caused by the interaction between S′ and S′ at the Sa locus was weaker than that at the Sc locus.

Genotypes of the S5 Locus in the Substitution Segments of Single-Segment Substitution Lines

To screen the Sc gene, seven SSSLs carrying the Sc locus on the substitution segments obtained from different donors were selected from the HJX74-SSSL library (Supplementary Table 1). The pollen fertility of F1 hybrids from the crosses between the SSSLs and HJX74 was over 90% (Figure 2A). The SSSLs were then tested with three indica testers and three japonica testers. Four SSSLs (01-03, 05-03, 06-03, and 14-03) and HJX74 showed significantly higher pollen fertility in their F1 hybrids with indica testers than those obtained with japonica testers. In contrast, the other three SSSLs (11-03, 22-03, and 27-03) did not show a significant difference in the pollen fertility of F1 hybrids between the crosses with indica and japonica testers (Figure 2B). Two SSSLs (06-03 and 27-03) were then selected to detect the segregation of Sc genotypes in F2 populations obtained from the crosses with T65. In the F2 population of the T65/27-03 cross, the Sc genotypes of T65/T65, T65/27-03, and 27-03/27-03 segregated in the ratios of 40:83:53, which fit the Mendelian ratio of 1:2:1. In contrast, the F2 population of the T65/06-03 cross, the genotype ratios of T65/T65, T65/06-03, and 06-03/06-03 were 23:64:69, which significantly distorted from the Mendelian ratio (Figure 2C). These results indicated that at the Sc locus, SSSLs 11-03, 22-03, and 27-03 carried the S′ allele, while 01-03, 05-03, 06-03, and 14-03 carried the S′ allele.

Genotypes of the S5 Locus in the Substitution Segments of Single-Segment Substitution Lines

To screen the S5 gene, seven SSSLs carrying the S5 locus in the substitution segments obtained from different donors were selected from the HJX74-SSSL library (Supplementary Table 1). The genotypes of the S5 locus in the SSSLs were detected by functional markers. The results showed that in the substitution segments, three SSSLs (04-06, 13-06, and 14-06) carried S5′, one SSSL (10-06) carried S5′, and the other three SSSLs (21-06, 23-06, and 27-06) carried S5″ (Supplementary Table 4).

Five genotypes of the S5 locus were obtained from the F1 hybrids crossed by seven SSSLs (Supplementary Table 5). The pollen fertility of hybrids was normal in all crosses, ranging from...
93.04 to 94.42%. The spikelet fertility of S5/S5, S5/S5, S5/S5, and S5/S5 genotypes was normal (from 89.84% to 91.28%), but that of S5/S5 genotype from the crosses between 10-06 carrying S5/S5 and SSSLs carrying S5/S5 was only 68.34%, which was significantly lower than the spikelet fertility of the other four genotypes (Figure 3A and Supplementary Table 5).

The segregation of S5 genotypes in F2 populations obtained from three heterozygous genotypes, S5/S5, S5/S5, and S5/S5, was detected by using the functional markers of the S5 gene. Distorted segregation was detected in the S5/S5 segregation population produced from the crosses between 10-06 carrying S5/S5 and SSSLs carrying S5/S5, but was not detected in the segregation populations of S5/S5 from 21-06/10-06 and of S5/S5 from 21-06/13-06 (Figure 3B).

The three SSSLs with S5, 21-06, 23-06, and 27-06, were tested for their wide compatibility by crossing with indica and japonica testers. The F1 hybrids from all crosses showed high spikelet fertility, from 80.28% to 95.05%. As a control, the spikelet fertility when tested with indica and japonica varieties (Table 11). The results showed that WCILs carried the Sa gene in the HJX74 genetic background, and the interaction between Sa from WCILs and Sa from japonica testers caused some male gametes with Sa to become abortive in F1 hybrids obtained from the crosses of WCILs with japonica testers.

Three indica lines, GLA4 carrying the genotype of Sa, Sb, Sb, Sc, Sd, Sd, Se, and S5, HJX74 carrying the genotype of Sa, Sb, Sc, Sd, Sd, Se, and S5, and WCIL 2223 carrying the genotype of Sa, Sb, Sc, Sd, Se, and S5, were selected to test their compatibility with eight japonica varieties of different ecotypes. In the F1 hybrids of GLA4 with eight japonica varieties, pollen fertility was 13.24–90.68% with an average of 46.94%, and spikelet fertility was 5.89–92.95% with an average of 44.40%. In the F1 hybrids of HJX74 with eight japonica varieties, pollen fertility was 75.19–95.74% with an average of 85.37%, and spikelet fertility was 58.34–93.90% with an average of 74.69%. On comparison of data, pollen fertility was 82.35–95.79% with an average of 88.82%, and spikelet fertility was 89.19–94.29% with an average of 91.73% in the F1 hybrids of WCIL 2223 with the eight japonica varieties (Supplementary Table 13). The results showed that WCIL 2223 had higher and wider compatibility with japonica varieties than GLA4 and HJX74. The pollen fertility and spikelet fertility in F1 hybrids of WCIL with various japonica varieties were normal or near normal.

**DISCUSSION**

**Sterility or Compatibility of Hybrids Between indica and japonica Subspecies Is a Complex Trait**

In the past decades, the genetic basis of indica–japonica hybrid sterility has been understood. In indica–japonica hybrid sterility, the S5 locus was found to be responsible for female sterility, and the Sa, Sb, Sc, Sd, and Sc loci were responsible for male sterility. Following the tri-allele pattern and the one-locus sporogametophytic interaction model, the allele interaction between S' and S' leads to the abortion of male or female gametes carrying S', whereas the allele interaction between S'' and S' or S' does not lead to the abortion of any gamete (Zhang, 2020, 2022). Thus, the sterility or compatibility of hybrids between indica
and japonica subspecies is a complex trait that is controlled by multiple genes. Due to the diversity of indica and japonica rice varieties, the genotypes of hybrid sterility vary greatly among different varieties, particularly modern varieties, resulting in different crossing combinations with different degrees of hybrid sterility. In addition, the effects of alleles obtained from different donors are quantitatively different, resulting in the continuous variation of fertility at a single locus (Zhang et al., 1993, 1994). The molecular basis of allele diversity has been revealed by the cloned genes of S5 (Chen et al., 2008; Yang et al., 2012), Su (Long et al., 2008; Xie et al., 2017), and Sc (Shen et al., 2017). In this study, we found that HJX74, the recipient of SSSLs, carried the S\(^n\) allele at the Sb, Sd, and S\(e\) loci but the S\(i\) allele at the S5, Sa, and Sc loci (Figure 1). In addition, the effect of S\(a\) was weaker than that of S\(c\) in HJX74 (Supplementary Table 3). The identification of genotypes that lead to hybrid sterility provided a prerequisite for improving the compatibility of HJX74.

**Hybrid Sterility in indica–japonica Rice Can Be Overcome by Developing ICJLs and Wide-Compatible indica Lines**

Based on the tri-allele pattern and the one-locus sporogametophytic interaction model, the indica–japonica hybrid sterility can be overcome by developing ICJLs and WCILs (Zhang and Lu, 1999; Zhang, 2020, 2022). ICJLs can be developed by transferring the S\(i\) allele from indica to japonica rice. In hybrids between indica varieties having S\(i\) allele and ICJLs having S\(i\) allele in japonica genetic background, the S\(i\)/S\(i\) genotype cannot cause the abortion of any gamete. In a previous study, we transferred the S\(i\) allele from indica donors to the japonica T65 variety to develop ICJLs, which carry the S\(i\) allele at hybrid sterility loci in the japonica genetic background. The result was that ICJLs were compatible with indica but incompatible with japonica rice (Guo et al., 2016). In another method, WCILs can be developed by transferring the S\(n\) allele from donors to indica rice. In hybrids between WCILs having S\(n\) allele in indica genetic background and japonica varieties having S\(i\) allele, the S\(n\)/S\(i\) genotype cannot cause the abortion of any gamete. In this study, we pyramided the S\(n\) allele of SSSLs to develop WCILs, which carry S\(n\) allele in indica HJX74 genetic background. The result was that WCILs showed wide compatibility, which was compatible with both indica and japonica rice varieties (Figures 4, 5). These results showed that the breeding of ICJLs and WCILs is practicable and that the indica–japonica hybrid sterility could be overcome by using ICJLs and WCILs.

**The Single-Segment Substitution Line Library Is a Powerful Platform for Developing Wide-Compatible indica Lines**

The development of WCILs requires pyramiding S\(n\) alleles of multiple hybrid sterility loci to improve compatibility. The breeding of WCILs is a challenging task because it is a time-consuming and laborious technique. First, the S\(n\) alleles of the S5,
Sa, Sb, Sc, Sd, and Se loci need to be identified and selected from a wide range of genetic resources. Second, Scn alleles of multiple loci need to be pyramid in an indica genetic background by MAS. In addition, WCILs need to have improved traits to be used as parents of indica–japonica hybrid rice. Over the past two decades, we have constructed a HJX74-SSSL library, which is used as a platform for rice design (Zhang, 2021). Using this platform, a series of CMS, maintainer, and restorer lines were developed (Dai et al., 2015, 2016; Luan et al., 2019). In this study, we identified Scn alleles at the S5, Sb, Sc, Sd, and Se loci from the HJX74-SSSL library. Since HJX74, the recipient of SSSLs, carried the Scn alleles at Sb, Sd, and Se loci, but the Si alleles at S5, Sa, and Sc loci, the SSSLs carrying Scn or Scn alleles were selected from the HJX74-SSSL library (Figures 2, 3). The Scn and Scn of the SSSLs were then pyramid in the HJX74 genetic background. Nine WCILs carrying Scn alleles at the S5, Sb, Sc, Sd, and Se loci in the HJX74 genetic background were developed (Figures 4, 5). The results show that the HJX74-SSSL library is a powerful platform for developing WCILs possessing the complex trait of wide compatibility.

**Wide-Compatible indica Lines Will Be Used to Develop indica–japonica Hybrid Rice**

It is believed that inter-subspecific hybrids have stronger heterosis than intra-subspecific hybrids (Fu et al., 2014; Birchler, 2015). Therefore, the exploitation of inter-subspecific heterosis for the production of improved rice varieties has long been considered (Cheng et al., 2007; Zhang, 2020). The main obstacle in utilizing inter-subspecific heterosis in rice is the indica–japonica hybrid sterility. In this study, WCILs were developed using the HJX74-SSSL platform. The WCILs had compatibility with a wide range of japonica varieties (Figure 5 and Supplementary Table 13). Therefore, the development of WCILs is an effective approach to overcoming the problem...
of indica–japonica hybrid sterility in breeding practice. By further improving their fertility restoration ability, WCILs can be improved to produce wide-compatible indica restorer lines (WCIRLs). Using the HJX74-SSSL platform, a series of WCIRLs is being developed and will be used to develop indica–japonica hybrid rice by crossing with japonica male sterile lines. Therefore, it is expected that indica–japonica hybrid rice will be the rice of next generation (Zhang, 2022).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

GZ designed and supervised the work, analyzed the data and wrote the manuscript. JG, YL, and LX performed most of the experiments and compiled the experimental data. TY, JZ, ZD, GT, KS, XL, WY, and QT conducted a part of the experiments. HZ, RZ, and SW prepared the experimental materials and supervised some experiments. All authors read and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2022.890568/full#supplementary-material
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