A hybrid sterile locus leads to the linkage drag of interspecific hybrid progenies

Mianmian Wang a, b, Jun Yang a, b, Jinping Wan a, c, Dayun Tao d, Jiawu Zhou d, Diqiu Yu a, c, *∗∗, Peng Xu a, c, *

* Key Laboratory of Tropical Plant Resources and Sustainable Use, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, 670223, Yunnan, China
** University of Chinese Academy of Sciences, Beijing, 100049, China
∗∗ Center of Economic Botany, Core Botanical Gardens, Chinese Academy of Sciences, Menglian, Mengla, 666303, Yunnan, China
∗∗∗ Yunnan Key Laboratory for Rice Genetic Improvement, Food Crops Research Institute, Yunnan Academy of Agricultural Sciences, Kunming, 650200, Yunnan, China

ARTICLE INFO

Article history:
Received 26 March 2020
Received in revised form 16 July 2020
Accepted 20 July 2020
Available online 25 July 2020

Keywords:
Interspecific hybridization
Linkage drag
Hybrid sterility
Segregation distortion

ABSTRACT

Interspecific hybridization plays an important role in rice breeding by broadening access to desirable traits such as disease resistance and improving yields. However, interspecific hybridization is often hindered by hybrid sterility, linkage drag, and distorted segregation. To mine for favorable genes from Oryza glaberrima, we cultivated a series of BC4 introgression lines (ILs) of O. glaberrima in the japonica rice variety background (Dianjingyou 1) in which the IL-2769 (BC4F10) showed longer sterile lemmas, wider grains and spreading panicles compared with its receptor parent, suggesting that linkage drag may have occurred. Based on the BC5F2 population, a hybrid sterility locus, S20, a long sterile lemma locus, G1-g, and a new grain width quantitative trait locus (QTL), qGW7, were mapped in the linkage region about 15 centimorgan (cM) from the end of the short arm of chromosome 7. The hybrid sterility locus S20 from O. glaberrima eliminated male gametes of Oryza sativa, and male gametes carrying the alleles of O. sativa in the heterozygotes were aborted completely. In addition, the homozygotes presented a genotype of O. glaberrima, and homozygous O. sativa were not produced. Surprisingly, the linked traits G1-g and qGW7 showed similar segregation distortion. These results indicate that S20 was responsible for the linkage drag. As a large number of detected hybrid sterility loci are widely distributed on rice chromosomes, we suggest that hybrid sterility loci are the critical factors for the linkage drag in interspecific and subspecific hybridization of rice.

Copyright © 2020 Kunming Institute of Botany, Chinese Academy of Sciences. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co., Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Rice (Oryza sativa L.) is a leading staple worldwide. Global food demands require the cultivation of high-quality, high-yield rice varieties that are resistant to multiple diseases. However, rice domestication resulted in a loss of genetic diversity, and rice yields have stagnated since the 1980s (Tanksley and Mccouch, 1997). Two major breakthroughs in rice yields have been facilitated by dwarf breeding and the generation of interspecific hybrids (Cheng et al., 2007; Peng et al., 2008). To increase genetic diversity of rice, breeders have focused on identifying genes responsible for desirable traits in relatives of cultivated rice varieties and transferring those genes to O. sativa (Xiao et al., 1998). However, reproductive barriers, such as hybrid sterility (Ouyang and Zhang, 2013), and linkage drag (Olsen et al., 2006; Palaisa et al., 2004) have prevented the transfer of desirable traits between cultivars and wild relatives.

Oryza glaberrima Steud. shares the same AA genome as O. sativa despite being derived from different ancestors (Pental and Barnes, 1999). Thus, interspecific hybridization plays an important role in rice breeding by broadening access to desirable traits such as disease resistance and improving yields. However, interspecific hybridization is often hindered by hybrid sterility, linkage drag, and distorted segregation. To mine for favorable genes from O. glaberrima, we cultivated a series of BC4 introgression lines (ILs) of O. glaberrima in the japonica rice variety background (Dianjingyou 1) in which the IL-2769 (BC4F10) showed longer sterile lemmas, wider grains and spreading panicles compared with its receptor parent, suggesting that linkage drag may have occurred. Based on the BC5F2 population, a hybrid sterility locus, S20, a long sterile lemma locus, G1-g, and a new grain width quantitative trait locus (QTL), qGW7, were mapped in the linkage region about 15 centimorgan (cM) from the end of the short arm of chromosome 7. The hybrid sterility locus S20 from O. glaberrima eliminated male gametes of O. sativa, and male gametes carrying the alleles of O. sativa in the heterozygotes were aborted completely. In addition, the homozygotes presented a genotype of O. glaberrima, and homozygous O. sativa were not produced. Surprisingly, the linked traits G1-g and qGW7 showed similar segregation distortion. These results indicate that S20 was responsible for the linkage drag. As a large number of detected hybrid sterility loci are widely distributed on rice chromosomes, we suggest that hybrid sterility loci are the critical factors for the linkage drag in interspecific and subspecific hybridization of rice.

Copyright © 2020 Kunming Institute of Botany, Chinese Academy of Sciences. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co., Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).
that regulate the sterility of interspecies compatibility of interspecies between these rice species is critical for overcoming the regulatory mechanisms that control reproductive isolation originally targeted are affected (Young and Tanksley, 1989). Linkage accompanied by linkage drag, in which traits other than those intersubspecies have yet to be elucidated.

In this study, we dissected an introgression segment in a high generation backcross introgression line (BC4F0) by using O. glaberrima as the donor in a japonica rice background. We mapped a hybrid sterility locus, S20, a long sterile lemma locus, G1-g, and a grain width QTL, qGW7, to a 15 cM-linkage region. S20 eliminated the male gametes of O. sativa, which led all hybrid progenies to have homozygous of O. glaberrima genotypes. The proportion of the differentiation genotypes of the fertility genes deviated from Mendelian segregation ratios. The same segregation distortion was observed for the linked traits G1-g and qGW7, implying an association with S20 that leads to linkage drag.

2. Materials and methods

2.1. Materials and growth

To raise a set of BC4 introgression lines (ILs), we used Dainjingyou 1 (DJY1), an elite japonica cultivar from Yunnan province (China), as the recurrent parent, and IRGC102555, an accession of O. glaberrima introduced from the International Rice Research Institute (IRRI), as the donor parent. To obtain BC4F1, IL–2769 (BC4F0) was backcrossed with DJY1 (Chen et al., 2018). The BC4F2 population was obtained from BC4F1 plants at the breeding base of Xishuangbanna Tropical Botanical Garden (XTBG), Mengla county, Yunnan province, China. DJY1, IL–2769, BC4F1, and BC4F2 populations were sown on seedbeds. When grown to quatrofoil stage, seedlings were transplanted to a field with 25 × 20 cm between plants. Field management was carried out in accordance with general rice production.

2.2. Morphological analysis

We measured the following agronomic traits of DJY1, IL–2769, BC4F1, and BC4F2 populations: plant height, panicle length, sterile lemma length, grain length, grain width, primary and secondary branch number, grain number per panicle, 1000-grain weight, pollen and spikelet fertility.

The BC4F1 and BC4F2 individuals were each used for genetic analysis. Pollen fertility was determined as described by Doi et al. (1998). Briefly, the panicles were sampled before anthesis and fixed in 70% ethanol, and then stained by I2–KI 1% solution. Pollen grains were classified as fertile or sterile. Sterile pollen was further classified as unstained withered sterile, unstained spherical sterile, and stained abortive (Li, 1980). At least three independent microscopic fields were viewed to calculate the ratio of fertile pollen grains.

2.3. DNA extraction and SSR analysis

DNA extraction was based on the cetyltrimethylammonium bromide (CTAB) method (Ling et al., 2018). A total of 450 simple sequence repeats (SSR), covering most of the rice genome, were used to screen polymorphisms between DJY1 and IL–2769. PCR amplifications were performed in a total reaction volume of 10 μL containing 10 ng DNA template, 1 × buffer, 0.5 μmol/L of each primer, 50 μmol/L of dNTPs and 0.5 U of Taq polymerase. PCR amplification was performed under the following conditions: pre-
denaturation at 94 °C for 3 min, 29 cycles of denaturation at 94 °C for 30 s, renaturation at 62 °C and extension at 72 °C for 25 s, followed by a final extension at 72 °C for 5 min. PCR products were visualized on 10% non-denatured polyacrylamide gel stained with silver nitrate (Bassam et al., 1991).

2.4. Linkage map

Linkage maps of qualitative traits and markers were developed using the MAPMAKER EXP 3.0 (Lander et al., 1987). The QTL Ici-Mapping V4.2 at logarithm of odds (LOD) scores > 2.5 was used for quantitative trait detection (Li et al., 2007). The Kosambi function was used to transform recombination frequencies of genetic distances. The genetic map was drawn using the Mapchart 2.32 (Voorrips, 2002).

2.5. Statistical analysis

The results are means ± standard deviation (SD). Statistical analysis was performed by IBM SPSS Statistics 20. Student’s t-tests were used for analysis the difference between the progeny and their parents.

3. Results

3.1. Phenotype comparison between the introgression line IL-2769 and the receptor parent DJY1

Phenotypic analysis of the IL-2769 and DJY1 showed significant or highly significant differences in several traits, including panicle length, secondary branch number, sterile lemma length, grain length, grain width, 1000-grain weight, grain number per panicle, plant height, spikelet fertility, and primary branch number, but not in pollen fertility (Table 1). Although the theoretical introgression ratio of the BC4 introgression line was 3.125%, there were still many significant differences between IL-2769 and the recurrent parent, implying that linkage drag might contribute to these differences.

3.2. Inheritance of traits in the IL-2769

To analyze the genetic basis of traits carried by the IL-2769, we crossed IL-2769 plants with DJY1. The hybrid (BC5F1) pollens were semi-sterile, showing stained abortive grains; however, spikelets were fertile. The BC5F1 hybrids showed phenotypes that were intermediate between or similar to their parents for the following traits: sterile lemma length, grain width, panicle length, primary branch number, secondary branch number, 1000-grain weight, grain number per panicle, and plant height. Among these traits, sterile lemma length, grain width, grain length and 1000-grain weight presented a similar continuous distribution. However, pollen fertility and sterile lemma presented a high frequency of 2.5 was used for quantitative trait detection (Li et al., 2007). The Kosambi function was used to transform recombination frequencies of genetic distances. The genetic map was drawn using the Mapchart 2.32 (Voorrips, 2002).

2.5. Statistical analysis

The results are means ± standard deviation (SD). Statistical analysis was performed by IBM SPSS Statistics 20. Student’s t-tests were used for analysis the difference between the progeny and their parents.

3. Results

3.1. Phenotype comparison between the introgression line IL-2769 and the receptor parent DJY1

Phenotypic analysis of the IL-2769 and DJY1 showed significant or highly significant differences in several traits, including panicle length, secondary branch number, sterile lemma length, grain length, grain width, 1000-grain weight, grain number per panicle, plant height, spikelet fertility, and primary branch number, but not in pollen fertility (Table 1). Although the theoretical introgression ratio of the BC4 introgression line was 3.125%, there were still many significant differences between IL-2769 and the recurrent parent, implying that linkage drag might contribute to these differences.

3.2. Inheritance of traits in the IL-2769

To analyze the genetic basis of traits carried by the IL-2769, we crossed IL-2769 plants with DJY1. The hybrid (BC5F1) pollens were semi-sterile, showing stained abortive grains; however, spikelets were fertile. The BC5F1 hybrids showed phenotypes that were intermediate between or similar to their parents for the following traits: sterile lemma length, grain width, panicle length, primary branch number, secondary branch number, 1000-grain weight, grain number per panicle, and plant height. Among these traits, sterile lemma length, grain width, grain length and 1000-grain weight presented a similar continuous distribution. However, pollen fertility and sterile lemma presented a high frequency of

| Traits                        | IL-2769          | DJY1          |
|-------------------------------|------------------|---------------|
| Grain number per panicle       | 73.20 ± 0.61**   | 68.30 ± 1.48**| 91.30 ± 1.52  |
| Plant height (cm)              | 98.4 ± 2.46**    | 101.8 ± 3.87**| 94.57 ± 3.52  |

* and ** indicate significant differences from control at p < 0.05 and p < 0.01, respectively; the BC4F1 and IL-2769 columns are marked in comparison with DJY1.

3.3. Correlation analysis of traits in BC5F2 population

Correlation analysis of traits showed that pollen fertility, sterile lemma length, grain width, grain length and 1000-grain weight were significantly correlated with each other; and panicle length, primary branch number, secondary branch number were also significantly correlated with each other. The primary branch number and secondary branch number were significantly correlated with grain width, grain length, and 1000-grain weight (Table 2). These results suggest that the related traits might be clustered on the same chromosomes.

3.4. QTL mapping and analysis

A total of 450 SSR markers with polymorphisms between the two parents, DJY1 and IRGC102555, were used to survey the introgression segments in IL-2769. We found a 15-cM introgression segment on the short arm of chromosome 7 and used 13 SSR markers to screen the introgression region for genotypes of 178 BC5F2 individuals. Based on the phenotypes and genotypes of BC5F2 individuals, two loci and a QTL from O. glaberrima were mapped to the introgression region (Fig. 3). A hybrid sterility locus was restricted to a 1.7-cM region flanked by RM20866 and RM20896, and co-segregated with SSR marker RM20894. This mapping region was similar to the region of S20 identified in a cross between O. sativa and O. glaberrima (Doi et al., 1999) and named S20. The long sterile lemma locus was located at a 1.2-cM region flanked by RM20943 and RM5752, which was adjacent to long sterile lemma (G1) (Yoshida et al., 2009; Liu et al., 2016), and was designated G1-g as it came from O. glaberrima. In addition, we mapped a new grain width QTL (gGW7) flanked by RM20866 and RM20933, which may explain 39.3% of phenotype variation (Table 3).

3.5. Genotypic distribution of the corresponding molecular markers of linked traits

We further analyzed genotypic segregation ratios by SSR markers closely linked to mapping traits. RM20894 co-segregated with S20 and their offspring’s genotypes were homozygotes of O. glaberrima (GG) and heterozygotes (GS), but not homozygotes of O. sativa (SS). The pollen grains of GG homozygotes showed normal pollen fertility, and heterozygotes exhibited semi-sterility. These results indicate that the interaction between S20-g and S20-s led to the complete ablation of the male gametes carrying the allele of
Fig. 1. Phenotypes of BC$_3$F$_1$, DJY1 and IL-2769. (a–c) Pollen fertility of DJY1, BC$_3$F$_1$ hybrid and IL-2769, respectively; (d) Grain comparison of DJY1 and IL-2769 (n = 15); (e) Panicle type of DJY1, BC$_3$F$_1$ hybrid and IL-2769; (f) Plant architecture of two parents.

Fig. 2. Distribution of traits in BC$_3$F$_2$ population.
S20-s in the heterozygotes, which resulted in segregation distortion in BC5F2 population. Similarly, G1-g and qGW7, which were tightly linked to marker RM5752 and RM20866, respectively, also showed segregation distortion (Table 4). Likewise, the O. sativa homozygous genotypes of linked G1-g and qGW7 were seldom produced in BC5F2 progenies, and the homozygous GG and heterozygous produced an approximately 1:1 segregation ratio in BC5F2 progenies. The homozygous GG genotypes showed genetic stability, and potentially reduced the frequency of chromosome exchange in progenies. These results indicate that S20 led to linkage drag of traits in the introgression segment from O. glaberrima.

4. Discussion

More than 50 hybrid sterility loci from Oryza have been identified. These interspecific and indica-japonica intersubspecific hybrid sterility loci are distributed on most rice chromosomes (Ouyang et al., 2009). Most of them follow the one-locus allelic interaction model (Kitamura, 1962). The genetic basis for hybrid sterility in rice has been divided into two types: pollen killers and gamete eliminators (Sano, 1990). A single pollen killer locus produces segregation ratios of 1:1, consisting of heterozygotes and homozygotes of only one parent; in contrast, a gamete eliminator locus produces only individuals homozygous for one parent (Rick, 1966). In this study, we detected linkage drag caused by a hybrid sterility locus, which we call S20 because it is located in a region similar to that of the S20 previously identified in a cross between O. sativa and O. glaberrima (Doi et al., 1999). Widely distributed hybrid sterility loci have the same effect on the linkage traits as S20. Therefore, we speculate that these loci are the critical factors for the formation of linkage drag.

Transferring favorable alleles into O. sativa from its wild relatives will be beneficial for crop breeding. Hybrid sterility is the main reproductive barrier. Most hybrid sterility loci that have been detected are derived from wild relatives and can eliminate the gametes of O. sativa. Linkage drag may be caused by sterility loci that hinder the production of recombinant progenies with desirable traits and increase obstacles during breeding. Some loci

Table 2
Correlative coefficient among different traits (n = 178).

| Traits | PF | SF | PL | PBN | SN | SLL | GL | GW | TGW |
|--------|----|----|----|-----|----|-----|----|----|-----|
| PF     | 1  |   |    |     |  1 |    |    |    |     |
| SF     | 0.789** | 1  |  1 |     |  1 |    |    |    |     |
| PL     | 0.070 |  1 |  1 |     |  1 |    |    |    |     |
| PBN    | 0.114 |  1 |  1 |     |  1 |    |    |    |     |
| SN     | 0.007 |  1 |  1 |     |  1 |    |    |    |     |
| SLL    | 0.567** | 1  |  1 |     |  1 |    |    |    |     |
| GL     | 0.567** | 1  |  1 |     |  1 |    |    |    |     |
| GW     | 0.679** | 1  |  1 |     |  1 |    |    |    |     |
| TGW    | 0.679** | 1  |  1 |     |  1 |    |    |    |     |

S20-s in the heterozygotes, which resulted in segregation distortion in BC5F2 population. Similarly, G1-g and qGW7, which were tightly linked to marker RM5752 and RM20866, respectively, also showed segregation distortion (Table 4). Likewise, the O. sativa homozygous genotypes of linked G1-g and qGW7 were seldom produced in BC5F2 progenies, and the homozygous GG and heterozygous produced an approximately 1:1 segregation ratio in BC5F2 progenies. The homozygous GG genotypes showed genetic stability, and potentially reduced the frequency of chromosome exchange in progenies. These results indicate that S20 led to linkage drag of traits in the introgression segment from O. glaberrima.

Fig. 3. The positions of linkage traits in the introgression region at the end of the short arm of chromosome 7.

Table 3
Identification of grain width QTL in BC5F2 population.

| QTL | Marker Interval | LOD | A  | D   | R² (%) |
|-----|----------------|-----|----|-----|--------|
| qGW7| RM20866-RM20933| 56.58| 0.32| 0.18| 39.33  |

A: Additive effect, D: Dominant effect, allele from O. glaberrima; R²: Proportion of the phenotypic variance explained by the QTL.

Table 4
Genotypic distribution of the corresponding molecular markers of linked traits.

| Loci  | Linkage markers | No. of genotype | χ² (1:2:1) | P     |
|-------|-----------------|-----------------|-----------|-------|
| S20   | RM20894         | SS 81 SG 81 GG  | 75.16     | 4.78E09E-17 |
| G1-g  | RM5752          | SS 87 SG 87 GG  | 75.75     | 3.55E01E-17 |
| GW7   | RM20866         | SS 82 SG 82 GG  | 74.53     | 6.55E02E-17 |

SS, SG and GG indicate DJY1-homozygous, heterozygous and O. glaberrima-homozygous genotypes, respectively.
associated with yield, resistance and other favorable traits are linked with hybrid sterility loci. A number of hybrid sterility loci have been extensively studied, including S10 with Grain Size 6 (GS6) (Sun et al., 2013), S27 with PLANT ARCHITECTURE AND YIELD 1 (PAP1) (Zhao et al., 2015), S31 with small and round seed 3 (SRS3) and grain size 5 (GS5) (Kitagawa et al., 2010; Li et al., 2011). In our study, we also observed segregation distortion (likely influenced by S20) for G1–g, which is located within a 1.2-cM region flanked by RM20943 and RM5752, and is adjacent to long sterile lemma (G1) (Yoshida et al., 2009; Liu et al., 2016). Another linked trait, qGW7, produces similar segregation distortion. These results imply that linkage drag occurred during interspecific hybridization.

Hence, it is increasingly urgent to find strategies that break interspecific hybrid sterility and linkage drag. Recent studies have shown that exploring or constructing neutral wide-compatibility loci in natural variation, or using near isogenic lines of hybrid ste- rility genes could bridge the gaps between parents and offspring and further break hybrid sterility (Koide et al., 2018; Li et al., 2018), which could provide new insights into breaking the linkage drag efficiently.

Author contributions
Conceptualization, PX. and D.Y.; methodology, D.T. and P.X.; validation, M.W. and J.Z.; formal analysis, J.Z. and J.W.; investigation, M.W. and J.Y.; resources, D.T. and P.X.; data curation, M.W.; writing–original draft preparation, M.W.; writing–review and editing, PX. and J.W.; supervision, PX. and D.Y.; funding acquisition, P.X. and D.Y. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest
The authors declare that they have no conflict of interest.

Acknowledgments
The authors thank the Public Technology Service Center, Kish- uangbanna Tropical Botanical Garden, Chinese Academy of Sciences for technical support. This work was supported by “One-Three-Five” Strategic Planning of Chinese Academy of Sciences (2017XTBG-T02) and Strategic Leading Science and Technology Program (XDA24030301 and XDA24040308).

References
Attere, A.F., 1983. Reaction of Oryza glaberrima accessions to yellow rice mottle virus. Plant Dis. 67, 420–421.
Bassam, B.J., Caetano-Anollés, G., Gresshoff, P.M., 1991. Fast and sensitive silver staining of DNA in polyacrylamide gels. Anal. Biochem. 196, 80–83.
Brown, A.H.D., Lawrence, G.J., Jenkins, M., et al., 1989. Linkage drag in backcross breeding in barley. J. Hered. 80, 234–239.
Chen, X.Q., Xu, P., Zhou, J.W., et al., 2018. Mapping and breeding value evaluation of a semi-dominant semi-dwarf gene in upland rice. Plant Divers. 40, 238–244.
Cheng, S.H., Zhang, J.Y., Fan, Y.Y., et al., 2007. Progress in research and development on hybrid rice: a super-domesticate in China. Ann. Bot. 100, 959–966.
Doi, K., Yoshimura, A., Iwata, N., 1998. RFLP mapping and QTL analysis of heading date and pollen sterility using backcross populations between Oryza sativa L. and Oryza glaberrima Steud. Breed Sci. 48, 295–300.
Doi, K., Taguchi, K., Yoshimura, A., 1999. RFLP mapping of S20 and S21 for F1 pollen semi-sterility found in backcross progeny of Oryza sativa and O. glaberrima. Rice Genet. Newsl. 16, 65–68.
Ghesquière, A., Séquier, J., Second, G., et al., 1997. First steps towards a rational use of African rice. Oryza glaberrima, in rice breeding through a ‘contig line’ concept. Euphytica 96, 31–39.
Kitagawa, K., Kuriniemi, S., Oki, K., et al., 2010. A novel kinesin 13 protein regulating rice seed length. Plant Cell Physiol. 51, 1315–1325.
Kitamura, E., 1962. Studies on cytoplastic sterility of hybrids in distantly related varieties of rice. (Oryza sativa L.). Jap. J. Breed. 2, 81–84.
Koide, Y., Ogin, A., Yoshikawa, T., et al., 2018. Lineage-specific gene acquisition or loss is involved in interspecific hybrid sterility in rice. Proc. Natl. Acad. Sci. U.S.A. 115, E1955–E1962.
Lander, E.S., Green, P., Abrahamson, J., et al., 1987. MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experi-mental and natural populations. Genomics 93, 398.
Li, H., Ye, C., Wang, J., 2007. A modified algorithm for the improvement of composite interval mapping. Genetics 173, 361–374.
Li, J., Zhou, J.W., Xu, P., et al., 2018. Neutral alleles at hybrid sterility loci of Oryza glaberrima from AA genome relatives in genus Oryza. Breed Sci. 68, 343–351.
Li, Y.B., Fan, C.C., Xing, Y.Z., et al., 2011. Natural variation in GS3 plays an important role in regulating grain size and yield in rice. Nat. Genet. 43, 1266–1269.
Li, Z.R., 1980. A preliminary discussion about the classification of male sterile lines of rice in China. Acta Agron. Sin. 6, 17–26.
Ling, F., Wu, H., Lin, Y.J., et al., 2018. A rapid method for rice DNA extraction. Bio-101, e1010101.
Liu, M.J., Li, H.F., Su, Y.L., et al., 2016. G1/E1E functions in the development of rice lemma in addition to determining identities of empty glumes. Front. Plant Sci. 7, 1006.
Liu, W.Q., Fan, Y.Y., Chen, J., et al., 2009. Avoidance of linkage drag between blast resistance gene and the QTL conditioning spikelet fertility based on genotype selection against heading date in rice. Rice Sci. 16, 21–26.
Olsen, K.M., Caiicedo, A.L., Polato, N., et al., 2006. Selected cultures under domestication: evidence for a sweep in the rice waxy genomic region. Genetics 173, 975–983.
Ouyang, Y.D., Chen, J.J., Ding, J.H., et al., 2009. Advances in the understanding of inter-subspecific hybrid sterility and wide-compatibility in rice. Chin. Sci. Bull. 54, 2332–2341.
Ouyang, Y.D., Zhang, Q.F., 2013. Understanding reproductive isolation based on the rice model. Annu. Rev. Plant Biol. 67, 111–135.
Palaia, K., Morgante, M., Tingey, S., et al., 2004. Long-range patterns of diversity and linkage disequilibrium surrounding the maize Y1 gene are indicative of an asymmetric selective sweep. Proc. Natl. Acad. Sci. U.S.A. 101, 9885–9890.
Peng, S., Khush, G.S., Virk, P., et al., 2008. Progress in ideotype breeding to increase rice yield potential. Field Crop. Res. 108, 32–38.
Pental, D., Barnes, S.R., 1985. Interrelationship of cultivated rice Oryza sativa and O. glaberrima with wild O. perennis complex. Theor. Appl. Genet. 70, 185–191.
Rick, C.M., 1966. Abortion of male and female gametes in the tomato determined by allelic interaction. Genetics 53, 85–96.
Sano, Y., 1990. The genic nature of gamete eliminator in rice. Genetics 125, 183–191.
Sun, L.J., Li, X.J., Fu, Y.C., et al., 2013. GSR, a member of the GRAS gene family, negatively regulates grain size in rice. J. Integr. Plant Biol. 55, 938–949.
Tankersley, S.D., 1993. Mapping polygenes. Annu. Rev. Genet. 27, 205–233.
Tankersley, S.D., McCouch, S.R., 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. Science 277, 1063–1066.
Voorrips, R.E., 2002. MapChart: software for the graphical presentation of linkage maps and QTLs. J. Hered. 93, 77–78.
Xiao, J., Li, J., Grandillo, S., et al., 1998. Identification of trait-improving quantitative trait loci alleles from a wild rice relative. Oryza sativa. Genetica 100, 899–909.
Xie, Y.Y., Shen, R.X., Chen, L.T., et al., 2019. Molecular mechanisms of hybrid sterility in rice. Sci. China Life Sci. 62, 737–743.
Xie, P., Tao, D.Y., Hu, F.Y., et al., 2005. Interspecific hybridization of cultivated rice for breeding japonica rice in Yunnan province. Chin. J. Rice Sci. 19, 41–46.
Yokoo, M., Fujimaki, H., 1971. Tight linkage of blast-resistance with late maturity observed in different indica varieties of rice. Jpn. J. Breed. 21, 35–39.
Yoshida, A., Suzuki, T., Tanaka, W., et al., 2009. The homeotic gene long sterile lemma (G1) specifies sterile lemma identity in the rice spikelet. Proc. Natl. Acad. Sci. U.S.A. 106, 20103–20108.
Young, N.D., Tankersley, S.D., 1989. RFLP analysis of the size of chromosomal segments retained around the Tm-2 locus of tomato during backcross breeding. Theor. Appl. Genet. 77, 353–359.
Zhao, L., Tan, L.B., Zhu, Z.F., et al., 2015. PAV1 improves plant architecture and en-hances grain yield in rice. Plant J. 83, 528–536.
Zhu, G., Wang, S., Huang, Z., et al., 2018. Rewiring of the fruit metabolome in tomato breeding. Cell 172, 249–261 e12.
Zhuang, J.X., Wu, J.L., Fan, Y.Y., et al., 2001. Genetic drag between a blast resistance gene and QTL conditioning yield trait detected in a recombinant inbred line population in rice. Rice Genet. Newsl. 18, 69–70.