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Fertility behaviour of rice (*Oryza sativa)* lines with dominant male sterile gene and inheritance of sterility and fertility restoration

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Abstract

The genetic basis of male sterility and fertility restoration of the Pingxiang male-sterile rice (PMSR) was studied using progeny populations created between PMSR and 11 fertile lines. It was found that the male sterility was determined by two interacting (epistatic) dominant nuclear genes, one for sterility and one for fertility restoration. The dominant sterile gene expresses as male-sterility when existing solely, but as normally fertile when coexisting with the restoration gene. The individuals with only the restoration gene are normal and fertile.

A homozygous sterile line developed using PMSR by repeated selfing was characterised for its fertility behaviour under controlled and field conditions. Male fertility was affected by both temperature and photoperiod with temperature being more important. The critical temperature for inducing fertility was 27–28 °C. Blow this critical temperature, plants remained sterile, but become partially fertile at higher temperature. The panicle development stages that are sensitive to temperature were from differentiation of the secondary branch primordium (S3) to the meiotic division of the pollen mother cells (S6). Continuous high temperature (>30 °C) during these sensitive stages is necessary to maintain male fertility. Long photoperiod (15 h) induced partial fertility even under temperature, which could induce sterility. In practice, this line can be regarded as thermo-sensitive. In the sub-tropical zone, this line has complete sterile phase longer than 4 weeks and thus is suitable for hybrid production using the two-line system (a pair of pure sterile and fertile lines). Male sterile line required low temperature and short photoperiod to express male sterility, like the one derived from PMSR, has never been reported in any crop species. This line is also the first dominant nuclear male-sterile line that could be exploited for hybrid seed production using the two-line system.

Keywords: Fertility behaviour; Fertility restoration; Inheritance; Male sterility; Photoperiod; Rice; *Oryza sativa*; Thermosensitive; Two-line hybrid

1. Introduction

Rice (*Oryza sativa*) is the most important crop in the world, and used as staple food by more than half of the world population. Hybrid rice showed 15–20% higher yield than the best semi-dwarf inbred varieties (Virmani, 1996; Virmani et al., 2003). Hybrid breeding has played an important role in increasing rice yield in many rice producing countries, since its demonstrated success in 1970's in China. Hybrid rice technology is considered a viable option to further increase rice yields globally (Yuan, 1994; Virmani, 1994; He and Liu, 1998; Janaiah and Hossain, 2000). Two hybrid seed production systems have been successfully used in rice. The three-line system uses cytoplasmic male sterility (CMS), and the two-line system utilizes the environmentally induced male sterility (EGMS) (Yuan, 1998; Virmani et al., 2003). The two-line system simplifies the production of hybrid, since only a pair of pure fertile and sterile lines are required. It can also eliminate the potential negative effects associated with the CMS. Furthermore, the nuclear genes responsible for sterility are relatively easy to be transferred to diverse genetic background. However, owing to the limitation of the

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temperature and/or photoperiod requirement, an EGMS line can only be used in a relatively narrow zone, and suitable sterile lines must be developed for a target production environment.

The male sterility of all known genic male sterile lines used in hybrid rice production was conferred by recessive gene(s). Yan et al. (1989) identified a male sterile plant in the progenies of the crosses between the sterile F_2 plants of Pingai × Huaye and the fertile F_4 plants of the reciprocal cross Huaye × Pingai. A line was developed from this sterile plant, and named as Pingxiang male-sterile rice (PMSR) (Yan et al., 1989). PMSR is a mixture of sterile and fertile sister plants. The male sterility of this line is controlled by dominant gene(s), as indicated by the fact that the F_1 progenies of the crosses between sterile plants of PMSR and most of fertile cultivars consisted of both fertile and sterile plants (Yan et al., 1989; Cai and Liu, 1998). Therefore, PMSR is the first rice line with dominant nuclear male-sterile genes. Since then, several rice male sterile materials with dominant nuclear sterile genes have been reported by other authors. These include a photoperiod-sensitive line, 'CIS28-10S' (Huang, 1991), a thermo-sensitive line, '8987', (Li et al., 1987; Deng and Zhou, 1994) and two mutants selected from gamma-irradiated populations of southern US rice cultivars (Zhu and Rutger, 1999).

Crosses of PMSR and some fertile varieties yield completely fertile F_1s (He et al., 1997; Cai and Liu, 1998). Studies showed that the fertility of PMSR could be partially restored under high temperature (>30 °C), and selfed seed could be produced (Yan et al., 1989; He et al., 1997, 1999; Cai and Liu, 1998). Therefore, PMSR may be used to develop male sterile lines for hybrid seed production using the two-line system. Several lines homozygous for the sterile gene have been developed by repeated selfing (He et al., 1997). However, the genetic mechanism of the observed male sterility and fertility restoration of PMSR has not been well characterised (Cai and Liu, 1998; He et al., 1999).

The objectives of this study were to establish the genetic mechanism of male sterility and fertility restoration of PMSR, and to characterise promising homozygous sterile lines under controlled and natural conditions for its fertility behaviour in order to evaluate its usefulness for hybrid production using the two-line system.

2. Materials and methods

2.1. Inheritance of sterility

Eleven crosses were made using PMSR as female parent and 11 fertile cultivars including Erliuzhaizao, Italy B, Gui 99, IR24, Miyang 23, Erjiuai, Zigui, Penglaidao, Maiyingdao, Pingai 58 and IR 30 as male parents. Based on the male fertility of the F_1 plants were tested for male fertility under normal field conditions in Nanchang, China. Based on the male fertility of the F_1 plants, these 11 fertile cultivars were classified into restorer (all F_1 plants are fertile) and non-restorer (some of the F_1 plants are fertile) groups. Crosses were also made between these two groups. F_2 families were obtained by selfing the fertile F_1 plants. For the cross combinations involving the restorers, sterile F_2 individuals were crossed to non-restorer fertile cultivars. PMSR was also grown under high temperature in a glasshouse (>30 °C) to induce fertility and obtain selfed seed.

2.2. Fertility behaviour characterisation

2.2.1. Controlled conditions

One sterile and one fertile line developed from the original PMSR line were sown separately on May 30th, 2000 in 4 l plastic pots. Plants of the fertile line were used as control. Five seedlings per pot were kept when the seedlings were about 20-day old. When plants reached the first bract primordium differentiation stage (about 25–26 days before heading), pots were transferred to growth cabinets. Temperature treatments were applied until heading. Plants were then transferred to a field under ambient condition in Wuhan, China (temperature was 30/28 °C and photoperiod was 11.5 h). Treatments included six combined maximum and minimum temperatures, designated using their mid-point value, 25 °C (28/22 °C), 27 °C (29/25 °C), 28 °C (30/26 °C), 30 °C (32/28 °C), 32 °C (34/30 °C) and 34 °C (36/32 °C), and one constant temperature (26 °C).

To determine the panicle development stages that are sensitive to high temperature, sterile plants at different panicle development stages were subjected to high temperature (33/27 °C) treatment. Following Rangaswamy (1993), the panicle development was divided into eight stages (Table 1). The development stages of plants were

Table 1
Panicle development stages and their durations in rice (*Oryza sativa*)[a]

Stage no.	Stages	Duration (day)	Days before heading
S1	Differentiation of first bract primordium	2	25–26
S2	Differentiation of primary branch primordium	3	22–24
S3	Differentiation of secondary branch primordium	3	19–21
S4	Differentiation of stamen and pistil primordium	4	15–18
S5	Pollen mother cell formation	3	12–14
S6	Meiotic division of pollen mother cell	3	9–11
S7	Pollen filling	6	3–8
S8	Pollen ripening	2	1–2

[a] Taken from Rangaswamy (1993).