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Male Parent Plays More Important Role in Heat Tolerance in Three-Line Hybrid Rice

FU Guan-fu[1,#], ZHANG Cai-xia[1,#], YANG Yong-jie[1], XIONG Jie[2], YANG Xue-qin[1], ZHANG Xiu-fu[1], JIN Qian-yu[1], TAO Long-xing[1]

(*[1]National Key Laboratory of Rice Biology, China National Rice Research Institute, Hangzhou 310006, China; [2]Zhejiang Science & Technology University; [#]These authors contributed equally to this work*)

Abstract: Ten F_1 combinations with their male and female parents were employed to evaluate their heat tolerance during the flowering and early grain filling stages. The rice plants were subjected to heat stress (39 °C–43 °C) for 1–15 d during flowering. Based on the heat stress index, heat tolerance was only observed in the F_1 combinations H2 (K22A × R207), H3 (Bobai A × R207) and H4 (Bobai A × Minghui 63), whereas the others received above 0.5000 of heat stress index. Both parents of the tolerant combination (heat-tolerant × heat-tolerant) possessed heat tolerance, whereas the susceptible combinations were crossed by heat-tolerant (sterile lines) × heat-susceptible (restorer lines), heat-susceptible × heat-tolerant, or heat-susceptible × heat-susceptible parents. This result indicated that heat tolerance in rice was controlled by recessive genes. Thus, both parents should possess high temperature tolerance to develop heat-tolerant F_1 combinations. Furthermore, the heat stress index of F_1 combinations was significantly correlated with the heat stress index of restorer lines but not with the heat stress index of maintainer lines. This result suggested that male parents play a more important role in heat-tolerant combinations than female parents. Therefore, the heat susceptibility of the hybrid rice in China is mainly due to the wide application of low-heat-tolerant restorer lines with high yield in three-line hybrid rice breeding.

Key words: hybrid rice; genetic correlation analysis; heat stress; heat tolerance

The global climate is predicted to warm by an average of 2.5 °C–5.8 °C by the end of the 21st century (IPCC, 2014) because of increased emissions of CO_2 and other heat-trapping greenhouse gases, such as methane, nitrous oxide, ozone and water vapor (Maraseni et al, 2009; Smith and Olesen, 2010). Recent climatic conditions wherein extreme high temperatures with a daily average of above 38 °C and a daily maximum of 41 °C frequently last for over 15 d have exposed most crops worldwide to heat stress at some stages of their life cycles. Heat stress has become a primary abiotic factor that limits the productivity of plants, especially summer-sown crops such as rice (*Oryza sativa* L.), which is grown in subtropical and tropical regions.

Rice is an important cereal cultivated worldwide. Nearly half of the global population depends on rice, and a 0.6%–0.9% annual increase in rice production is needed until 2050 to support the demand of the growing population (Carriger and Vallee, 2007). Therefore, breeding high-yielding rice varieties remains a priority to ensure food security. In this case, hybrid rice breeding may be a great option because of its heterosis. Compared with conventional inbred rice, modern hybrid rice exhibit higher seedling vigor, tillering rate, growth rate, and yield potential (Ling et al, 1994; Xie et al, 1996). In 2012, the super hybrid rice Yongyou 12 grown in Zhejiang Province, China attained a record grain yield of 15.4 t/hm^2 (Pan et al,

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Corresponding author: TAO Long-xing (lxtao@mail.hz.zj.cn)

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2013). Given the higher spikelet number, hybrids possess a large yield advantage over conventional cultivars (IR64) at 29 °C and 35 °C, however, this advantage disappears at 38 °C (Madan et al, 2012). Temperature significantly influences seed-setting rate in all genotypes. In specific, the seed-setting rate of the hybrid decreases from 75%–80% at 29 °C to below 20% at 38 °C, whereas the conventional variety N22 can achieve 57% seed-setting rate at 38 °C (Madan et al, 2012). Over 80% of hybrid rice is heat-susceptible (Zhou et al, 2009; Hu et al, 2012).

Previous studies indicated that heat stress occurred at the flowering stage can significantly increase the spikelet sterility of rice due to the inhibition of anther dehiscence (Matsui et al, 2000, 2005), pollen germination (Song et al, 2001; Wassmann and Dobermann, 2007), and pollen tube elongation (Tang et al, 2008), especially for the heat-susceptible varieties. Heat tolerance in rice is quantitatively controlled by multiple genes and/or major genes, and several quantitative trait loci (QTLs) controlling heat tolerance have been detected in rice (Zhang et al, 2009; Jagadish et al, 2010; Cheng et al, 2012; Ye et al, 2012). In addition, heat shock proteins reportedly impart thermo-tolerance in rice (Yamanouchi et al, 2002; Wang et al, 2004; Hu et al, 2009; Shah et al, 2011). However, the heat susceptibility widely found in three-line hybrid rice combinations remains unexplained to date. Heat tolerance in three-line hybrid rice significantly correlates with their parents (Gong et al, 2008). Kuang et al (2002) reported that the three-line hybrid rice IIyou 7 exhibits a higher heat tolerance than Shanyou 63 because the male parent of the former displays higher heat tolerance than that of the latter. Similar results were observed by Li et al (2004), who suggested that heat tolerance in three-line hybrid rice mainly depends on the male parent. The female parent is also considered to influence the heat tolerance of three-line hybrid rice (Gong et al, 2008). However, the relationship in heat tolerance between the hybrid rice and their parents remains unclear, and none of the hybrid rice widely planted in China has been reported to have high and stable grain yield under heat stress during the flowering stage. Thus, in this study, four sterile lines and four restorer lines differing in heat tolerance (Fu et al, 2012) were selected to cross each other to clarify the relationships in heat tolerance between the hybrid rice and their parents, and to explain the heat susceptibility generally found in hybrid rice in China.

MATERIALS AND METHODS

Rice materials

Four pairs of maintainer lines and their corresponding sterile lines K22B/K22A (heat-tolerant), Bobai B/Bobai A (heat-tolerant), Neixiang 85B/Neixiang 85A (heat-susceptible), and Zhong 9B/Zhong 9A (heat-susceptible), and four restorer lines Minghui 63 (heat-tolerant), R207 (heat-tolerant), Chuannong 527 (heat-susceptible), and Milyang 46 (heat-susceptible) were selected. The rice maintainer lines were used to evaluate their heat tolerance, whereas their sterile lines were used to cross with the rice restorer lines to generate F_1 combinations. The following 10 F_1 combinations were obtained: H1 (Zhong 9A × Minghui 63), H2 (Bobai A × Minghui 63), H3 (K22A × R207), H4 (Bobai A × R207), H5 (K22A × Chuannong 527), H6 (Neixiang 85A × Chuannong 527), H7 (Zhong 9A × Chuannong 527), H8 (K22A × Milyang 46), H9 (Zhong 9A × Milyang 46), and H10 (Bobai A × Milyang 46).

Plant cultivation and treatments

This study was conducted at the experimental fields of China National Rice Research Institute, Hangzhou, during 2009–2011. In 2009, four sterile lines and four restorer lines were crossed to generate F_1 seeds. These seeds were divided into two groups: one was planted in 2010, and the other was planted in 2011. The seeds were incubated in 0.01% methylene dithiocyanate at 30 °C for 2 d, germinated in an incubator at 37 °C for 1 d, and then directly sown in pots (30 cm × 30 cm) each filled with 15 kg (dry weight) paddy soil. Each pot was fertilized with 15 g rapeseed cake. Rice plants were grown until the main stem flowering under natural condition in the net house. Then, the plants were subjected to heat stress for 15 d in the greenhouse with an automatic temperature control system to regulate the temperature at 39 °C–43 °C from 9:00 AM to 15:00 PM. After the respective temperature treatments, the plants were returned to the net house (natural condition) with daily mean temperatures of 28.8 °C and 30.4 °C, relative humidities of 70.5% and 66.7%, and illumination intensities of 5.51 and 6.12 klux as measured with a meteorological automatic recorder (ZDR-34, Hangzhou, China) until maturity in 2010 and 2011, respectively. The plants were sampled to determine the number of panicle per plant, number of grains per panicle, 1000-grain weight, and