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Shading stress increases chalkiness by postponing caryopsis development and disturbing starch characteristics of rice grains

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ABSTRACT

Chalkiness, one of the key factors in determining the market price and quality of rice grains, is markedly influenced by the environment. This study aimed to investigate the effectiveness of shading on rice chalkiness by conducting a field experiment in Wenjiang, Sichuan, China, in 2013 and 2015. Rice cultivars IIyou 498 and Yixiangyou 2115 were selected and shaded during the grain filling period; this resulted in a 53% shading environment. The results showed that chalkiness, caryopsis and amyloplast development, amylose content, and amylopectin chain-length distribution of rice grains, were markedly affected by shading. Shading significantly increased chalky rice rate and chalkiness degree of rice grains at the bottom of the panicle, which contributed to the increase in chalkiness of the entire panicle. Shading had a greater influence on grains at the bottom spikelet positions than on those at the top and middle positions. More loosely packed amyloplasts with greater airspace and reduction in amylose content of grains at the bottom spikelet positions were possibly due to the significant delay in the development of caryopsis. Furthermore, except for the bottom spikelet positions of Yixiangyou 2115, a reduction in short-length chains coupled to an increase in long-length chains of amylopectin was noted under shading. Shading increased rice chalkiness primarily by postponing caryopsis development at the bottom spikelet positions and disturbing the starch characteristics of rice grains. Therefore, more attention needs to be focused on the grains positioned at the bottom of panicle.

1. Introduction

Consumed by more than half the population around the world, rice (*Oryza sativa* L.) is one of the most important cereal crops for humans. Therefore, improvement of grain yield is an essential requirement in rice production. However, with economic development and improvement in living standards, consumers are increasingly paying attention to high quality in products (Zhou et al., 2015).

Grain quality is a combination of physical and chemical properties providing specific attributes to rice for use by customers (Zhou et al., 2015). Chalkiness, one of the major concerns in rice production, detracts from the appearance, milling, cooking, eating, and nutritional quality of rice and is widely considered as one of the key factors in determining the value of rice grains globally (Peng et al., 2014; Yoshioka et al., 2007; Yu et al., 2017). Therefore, breeders and producers place considerable emphasis on reducing chalkiness.

Chalkiness is associated with the development of numerous air spaces between loosely packed amyloplasts, which is controlled by starch synthesis and starch granule structure and arrangement (Myers et al., 2000; Tashiro and Wardlaw, 1991; Yu et al., 2017). Depending on the position of the chalky part in the endosperm, chalkiness is conventionally classified into five categories: white-cored, milky white, white-back, white-based, and white-belly types (Ishimaru et al., 2009; Tashiro and Wardlaw, 1991). In general, white-cored, milky white, and white-belly are the three most frequent chalky types of indica hybrid rice. Chalkiness is influenced by rice variety and environmental factors (Gong et al., 2017; Zhao and Fitzgerald, 2013; Zhou et al., 2015). Environmental factors, such as nitrogen application, as well as temperature, have significant effects on chalkiness (Lo et al., 2016; Zhou et al., 2015). Thus, a significant positive correlation was found between

Abbreviations: DP, degree of polymerization; SH-20, 20 days after shading at the heading stage; SH-30, 30 days after shading at the heading stage; R-10, 10 days after return to control light level

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chalkiness and temperature (Chen et al., 2013); further, high temperature reduced the production of starch synthesis enzymes, while it increased that of starch hydrolyzing enzymes, such as α-amylase, thereby increasing grain chalkiness (Hakata et al., 2012; Suriyasak et al., 2017). Furthermore, Zhao and Fitzgerald (2013) suggested that chalkiness decreased with increasing vapor pressure deficit, but increased with higher relative humidity.

Shading stress caused by industrial development and environmental changes has become a limitation to rice production in China, especially in the southwest (Pan et al., 2016; Wang et al., 2015). Shading produces a series of changes in the morphological and physiological characteristics of rice, such as reduction in total root length, leaf photosynthesis, stem mechanical strength, total nutrient accumulation, spikelet fertility, and grain weight, as well as variations in dry matter accumulation and redistribution, which finally results in a marked decrease in grain yield (Pan et al., 2016; Wang et al., 2015; Wu et al., 2017; Zhang et al., 2017). However, the effect of shading on rice production is noted on not only yield but also on grain quality. Thus, Mo et al. (2015) reported that shading significantly increased protein content of rice grains. Our own previous studies showed that shading disrupted starch components and increased grain chalkiness; thus, remarkably damaging the appearance, milling, cooking, and eating qualities of rice (Ren et al., 2003; Wang et al., 2013). However, the mechanism by which shading increases rice grain chalkiness is not fully understood.

Therefore, in this study, field experiments were conducted using two light treatments and two rice varieties with different chalkiness characteristics. The specific objectives of the study were to (a) investigate the effects of shading on chalkiness, amyloplast structure, caryopsis development, amylose content, and amylopectin chain-length distribution of rice grains; and (b) assess the relationship of chalkiness with caryopsis development and starch characteristics. In addition, we aimed to provide useful information for the breeding of high-quality rice varieties under abiotic stress.

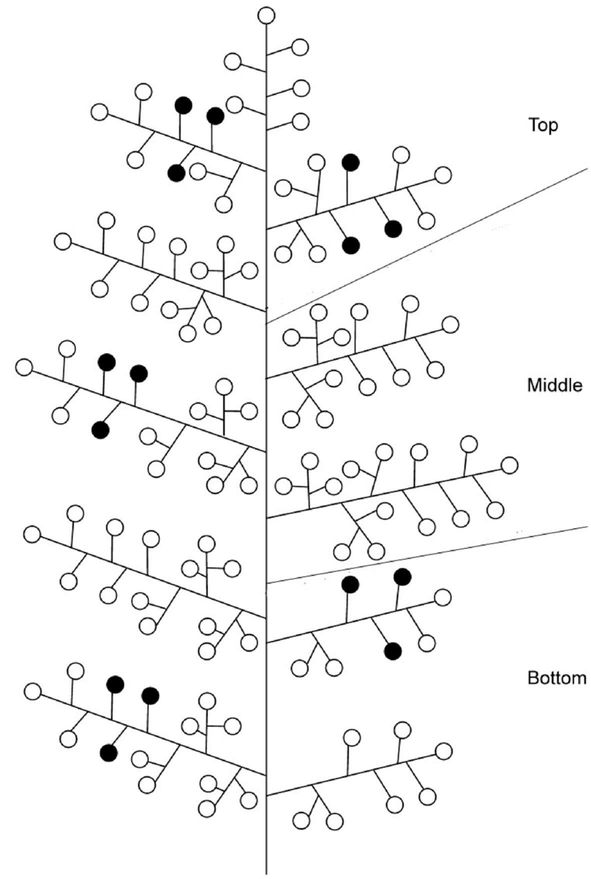

Fig. 1. Diagram of spikelets on a rice panicle. Black circles represent the location of the spikelets as grouped in this study.

2. Materials and methods

2.1. Study site and materials

Field experiments were conducted at the Huihe farm of the Sichuan Agricultural University in Wenjiang (30°43′N and 103°52′E), Sichuan Province, China, in 2013 and 2015. Wenjiang experienced a subtropical humid monsoon climate, with average air temperature and precipitation of 24.9 °C and 1222.0 mm from May to September in 2013, and 23.7 °C and 593.1 mm in 2015, respectively. The soil was a medium loam which, in 2013, showed 28. 7 g kg^{-1} organic matter, 1.7 g kg^{-1} total nitrogen (N), 0.69 g kg^{-1} total phosphorus (P), 17.3 g kg^{-1} total potassium (K), 143.0 mg kg^{-1} alkali hydrolysable N, 17.1 mg kg^{-1} Olsen-P, and 63.5 mg kg^{-1} exchangeable K. Two years later, in 2015, the same soil showed 28.2 g kg^{-1} organic matter, 2.1 g kg^{-1} total N, 0.62 g kg^{-1} total P, 15.1 g kg^{-1} total K, 138.0 mg kg^{-1} alkali hydrolysable N, 11.0 mg kg^{-1} Olsen-P, and 119.0 mg kg^{-1} exchangeable K. Two mid-late indica hybrid rice varieties bred by Sichuan Agricultural University were used in the study: IIyou 498, a high-yield, high-chalkiness variety, and Yixiangyou 2115, a high-quality, low-chalkiness variety.

2.2. Experimental design and management

A two-factor, randomized block experiment with three replications was conducted to investigate the effect of rice variety (IIyou 498 and Yixiangyou 2115) and shading stress (no shading control (CK) and 53% shading) in 2013 and 2015. For the shading treatment, rice plants were covered with a single layer of white cotton yarn screen from heading (August 6, 2013 and August 9, 2015) until 30 d after heading (September 4, 2013 and September 7, 2015). The screens were 2 m high and sufficiently large to maintain good ventilation and prevent lateral sunlight penetration, while reducing radiation by about 53% (Wang et al., 2013, 2015).

The dimensions of each plot were 3.0 m × 10.0 m in both years. On May 19, 2013 and on May 31, 2015, about six-week-old seedlings were transplanted at a spacing of 33.3 cm × 20.0 cm with two plants per hill. Fertilization in all treatments consisted in 180 kg hm^{-2} of N as urea, 90 kg hm^{-2} of P_2O_5 as single superphosphate, and 180 kg hm^{-2} of K_2O as potassium chloride (Wang et al., 2013). The high-efficiency irrigation technique described by Wang et al. (2015) was used for water management. Pesticides were used to manage diseases, insects, and weeds.

2.3. Sampling and measurements

2.3.1. Labeling of the panicles and spikelets

At the heading stage, 300 similar-sized panicles per plot were labeled with small plastic tags in 2015. Spikelets were classified into top, middle, and bottom groups based on the number of primary branches (Fig. 1). For example, if the primary branch number was 11, spikelets on the fourth branch or higher counting from the panicle top, the fourth branch or lower counting from the panicle base and the rest of the branches, were classified into the top, bottom, and middle groups, respectively. Additionally, 200 primary spikelets from each spikelet position directly attached to each primary branch were labeled with a black marker.

2.3.2. Dry weight dynamics and morphologic observation of caryopsis

In 2015, 15 labeled panicles were sampled and divided into top, middle, and bottom positions at 20 and 30 days after heading, at 10 days after return to control light level, and at harvest. Spikelets were