Rice Science, 2014, 21(5): 243−251

DOI: 10.1016/S1672-6308(13)60192-4

Available online at www.sciencedirect.com
ScienceDirect

Effects of Low Light on Agronomic and Physiological Characteristics of Rice Including Grain Yield and Quality

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Abstract: Light intensity is one of the most important environmental factors that determine the basic characteristics of rice development. However, continuously cloudy weather or rainfall, especially during the grain-filling stage, induces a significant loss in yield and results in poor grain quality. Stress caused by low light often creates severe meteorological disasters in some rice-growing regions worldwide. This review was based on our previous research and related research regarding the effects of low light on rice growth, yield and quality as well as the formation of grain, and mainly reviewed the physiological metabolism of rice plants, including characteristics of photosynthesis, activities of antioxidant enzymes in rice leaves and key enzymes involved in starch synthesis in grains, as well as the translocations of carbohydrate and nitrogen. These characteristics include various grain yield and rice quality components (milling and appearance as well as cooking, eating and nutritional qualities) under different rates of shading imposed at the vegetative or reproductive stages of rice plants. Furthermore, we discussed why grain yield and quality are reduced under the low light environment. Next, we summarized the need for future research that emphasizes methods can effectively improve rice grain yield and quality under low light stress. These research findings can provide a beneficial reference for rice cultivation management and breeding program in low light environments.
Key words: grain quality; grain yield; physiological characteristic; rice; low light; agronomic characteristic

Rice is the primary food source for about 65% of the world's population, which mainly grows as a rainy season crop in Southeast Asia and China, and is frequently exposed to poor light intensity at various stages of growth. Light intensity determines grain yield and quality (Seo and Chamura, 1980; Furuno et al, 1992; Wilson et al, 1992; Yao et al, 2000). Continuous cloudy days or rainfall during critical stages of growth, such as panicle differentiation or grain-filling stages, often induce great loss of grain yield and poor grain quality (Janardhan et al, 1980; Nayak and Minor, 1980; Praba et al, 2004). Low light stress has severely constrained rice yield in some rice-growing regions of the world, especially in Southeast Asia and China (Chaturvedi and Ingram, 1989; Ren et al, 2002). Sichuan, Yunnan and Guizhou provinces in Southwest China serve as staple rice cultivation regions but perennially suffer from low light stress because of their unique geographical positions. In these districts, cloudy or rainy days frequently occur with total solar radiations of 3 345–3 763 MJ/m^2, and sunshine hours are often less than 1 200 h per year (Huang, 1998). Rice, cultivated in the adjoining districts of the Yangtze Valley, also experiences low light stress because continuous rainfall often occurs during the grain filling stage (Li and Zhang, 1995). Therefore, the poor light environment often severely hampers normal plant development and adversely affects rice yield and quality in major rice-growing regions of China and other countries.

Because low light conditions can damage rice production dramatically, light intensity has received attention from researchers worldwide increasingly (Chaturvedi and Ingram, 1989; Thangaraj and Sivasubramanian, 1990; Nakano, 2000; Liu et al, 2007). Numerous simulations analyzing the effects of low light on rice development as well as grain yield and quality have been performed (Li L et al, 1997; Kobata et al, 2000; Liu et al, 2006b; Fu et al, 2009). A lack of adequate light strongly influences not only the duration of growth but also some agronomic traits of

Received: 25 March 2014; **Accepted:** 24 June 2014
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rice. For example, low light results in a prolonged period of growth and also increases plant height and leaf area (Ren et al, 2002; Liu et al, 2009). Before the heading stage, low light gives rise to a pronounced decrease in fertile panicles of rice plants. After the heading stage, shading causes impairment of the net photosynthetic rate as well as lower dry matter accumulation and sink capacity in rice plants, and this significantly reduces the number of filled grains and 1000-grain weight, thereby leading to decreased grain yield (Sato, 1956; Kato, 1986; Deng et al, 2009; Liu et al, 2009). Low light after the heading stage also results in poor appearances of rice grain and milling qualities, including a high percentage of chalky grains and also a reduced head yield. This may be primarily attributed to an insufficient supply of assimilates and decrease activity of a soluble starch branching enzyme involved in starch synthesis in grains (Tashiro and Ebata, 1975; Miizuno et al, 1992; Li T G et al, 1997; Ren et al, 2003b). In this review, based on previous reports, we mainly highlighted the negative effects of low light on the development of rice as well as on grain yield and quality in rice. We also discussed the physiological mechanisms related to variations in grain yield and quality observed under low light conditions. These results can help rice researchers better understand the relationship between light intensity and rice production, and facilitate further research related to effective cultivation practices and breeding strategies for the improvement of rice grain yield and quality in regions prone to low light conditions.

Morphological and photosynthetic responses of rice leaves to low light

Low light conditions result in significantly increased leaf length, leaf width, leaf area and growth duration, and the increases are enhanced with a reduction of light intensity (Ren et al, 2002; Ding et al, 2004). Leaf area only increases by 5.76% under 50% of natural light, however, it increases by 29.83% under 20% of natural light. Conversely, mesophyll thickness and the number of cells per square millimeter in leaves decrease by 14.61% and 15.86%, respectively, when rice plants are grown under 20% of natural light (Chonan, 1967).

Chlorophyll a and b are important pigments involved in the absorption and transmission of solar energy, with part of chlorophyll a involved in converting solar energy into electrochemical energy (Wang, 2011). Differences exist in the chlorophyll content produced in response to low light among varieties (Zhu et al, 2008; Liu et al, 2009). When subjected to low light for 15 d (when treatment had commenced at the initial heading stage), varieties that are tolerant to low light exhibit higher chlorophyll b and lower chlorophyll a/b content in their leaves when compared with those perform poorly in low light (Zhu et al, 2008). Similarly, leaf chlorophyll a and b content during the grain-filling stage is markedly enhanced in low light tolerant varieties after being treated by low light from the transplanting to the booting stages, whereas the opposite is found in varieties that perform poorly in low light (Liu et al, 2009). These results suggest that tolerant varieties capture as much solar energy as possible under low light conditions through increased leaf area and higher chlorophyll b content, demonstrating the morphological and physiological responses of rice plants when they experience low light stress (Ren et al, 2002). Low light negatively affects stomatal conductance (fewer stomata are produced per square millimeter) while it results in enhanced concentrations of intercellular CO_2 in rice leaves (Meng et al, 2002; Yang et al, 2011). Stomatal conductance decreases by 24.31% and 29.23% when light intensity decreases to 45% and 15% of natural light, respectively. A similar reduction is found in the number of stomata per square millimeter (10.29% and 12.52%), while the intercellular CO_2 concentration increases by 11.11% and 16.67%, respectively, under the same conditions. The net photosynthetic and respiration rates decline by 79.84% and 34.33% under low light, respectively, as compared to those under natural light. The respiration rate decreases more than the net photosynthetic rate, thus resulting in a higher ratio of respiration to net photosynthetic rates under low light than under natural light (Sato and Kim, 1980). Farquhar and Sharkey (1982) speculated that, under low light conditions, stomatal closure is the main constraint on photosynthesis if both stomatal conductance and intercellular CO_2 concentration decrease. Nevertheless, they excluded the factors that lead to impaired photosynthesis when stomatal conductance declines with increased intercellular CO_2 concentration. These results imply that a reduction of the net photosynthetic rate may not be strongly relevant to the promotion of stomatal closure and the decreased number of stomata produced under low light conditions. Photosynthesis is a complex physiological procedure in plants, including light absorption, energy conversion, electron transfer, adenosine triphosphate synthesis, key regulating enzyme activities, etc. Shi et al