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/m², 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
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; Mizuno 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 CO₂ 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 CO₂ 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 CO₂ concentration decrease. Nevertheless, they excluded the factors that lead to impaired photosynthesis when stomatal conductance declines with increased intercellular CO₂ 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
(2006) noted that the ribulose bisphosphate carboxylase (Rubisco) activity in chloroplasts declines dramatically under low light conditions. As an indispensable enzyme that regulates the biochemical process of photosynthesis, Rubisco plays an essential role in determining the photosynthetic rate of leaves (Okada and Katoh, 1998). Jiao and Li (2001) showed that light intensity alters the rates of non-photochemical quenching, electron transfer and quantum yield of PS II. Therefore, we believe that, to some extent, decreased Rubisco activity and changed electron transformation may be the reasons for the reduction of the net photosynthetic rate in rice leaves under low light conditions. The specific physiological mechanism involved here has not been convincingly explained and should be addressed more fully in future studies.

Responses of antioxidation of rice leaves to low light

The extent of the effects of low light on antioxidative and osmotic regulation characters of rice leaves depends on the genotype involved. In the variety that is tolerant to low light stress, enhanced superoxide dismutase and catalase activities, reduced malondialdehyde (MDA) content, and decreased peroxidase activity as well as soluble sugar and protein content are observed under low light conditions. In contrast, the variety that performs poorly shows the opposite characteristics. In general, superoxide dismutase, peroxidase and catalase are key enzymes used for scavenging reactive oxygen species, with soluble sugar as a vital osmotic regulation substance in plant cells (Zhang et al, 2007; Wang, 2011; Liu et al, 2012). MDA is the product of lipid peroxidation in cells, therefore, its content is consistently considered as symbolic of plant health and reflects the extent of cell membrane damage under stressful conditions, i.e. when MDA content is higher, more serious cell membrane damage occurs (Apel and Hirt, 2004; Volkov et al, 2006; Hu et al, 2008). Soluble protein, which includes many kinds of enzymes involved in metabolism, mainly regulates physiological metabolism and biosynthesis in plants (Zhang et al, 2007; Liu et al, 2012). Under low light conditions, the promotion of antioxidative enzyme activity and osmotic regulation for low light tolerant varieties can help maintain the scavenging of reactive oxygen species and the water potential in cells, and it can also minimize the adverse effects of low light on plant physiological metabolism. Nevertheless, the antioxidative and osmotic regulating systems tend to fail in varieties that are not tolerant to low light conditions, suggesting negative effects result in cell membrane damage. This has been proven by analyzing the related parameters reported in numerous studies (Kreiner et al, 2002; McDonald and Vanlerberghhe, 2005; Zhu et al, 2008; Liu et al, 2012).

Responses of accumulation, translocation and distribution of dry matter and nitrogen to low light in rice

Low light results in a reduction in the amount of dry matter produced in shoots and roots, as well as a lower overall dry matter weight for rice plants (Yamamoto et al, 1995). The rate of dry matter weight in shoots to the total (shoots + roots) in rice plants increases under low light conditions, suggesting that dry matter weight in roots decreases more than that of shoots. Similarly, an increased rate of dry matter weight in culm to the total shoot (culm + tillers) indicates a lower reduction in the dry matter weight of the culm when compared with that of tillers (Yamamoto et al, 1995). When low light intensity decreases, culm-sheath dry matter exports, and exportation and translocation rates all decrease, which leads to an increase in the rate of culm-sheath dry matter weight compared with the total dry matter weight of shoots as well as a reduction in the dry matter weight of panicles (Sun et al, 2012). Additionally, low light results in an increase in the rate of leaf and culm-sheath dry matter weight produced compared with the total dry matter weight of aboveground (leaves + culm + sheaths + panicles). Moreover, low light also decreases the dry matter weight in the panicles, showing that most of the dry matter produced is used to sustain the growth of leaves, culm and sheaths rather than being allocated to panicles (Ota et al, 1959; Wada, 1968; Ren et al, 2003a). Cao et al (2001) noted that the post-anthesis photosynthetic production of leaves and pre-anthesis dry matter stored in the culm and sheaths are the main sources of nutrients for developing rice panicles, accounting for about 60% and 40% of the total dry matter in the panicles, respectively. Consequently, the reduction of dry matter weight in panicles at maturity is believed to be the primarily cause of the decrease in photosynthetic assimilates and dry matter translocation under low light conditions (Ota et al, 1959; Tanaka and Matsushima, 1971; Zhu et al, 2008).
Low light also decreases the amount of nitrogen (N) transported from culm and sheaths to panicles, which triggers an increase in the percentage of N in leaves and culm-sheaths as well as a decrease in panicles compared with the total amount of N in aboveground (leaves + culm + sheaths + panicles). The results show that the amount of N allocated to panicles under low light conditions is less than that under natural light, and the amount of N used for the development of leaves and culm-sheath increases under low light conditions (Ren et al, 2003c).

Responses of rice grain yield and yield components to low light

Earlier studies revealed that rice plants grown under low light from the transplanting to the booting stages exhibit a 34.51% reduction in grain yield partly caused by a considerable decrease in the numbers of fertile panicles and grains per panicle produced (Liu et al, 2009). When exposed to low light for 10 d (starting from the heading stage), rice grain yield decreases by 14.99% because the seed-setting rate is significantly reduced (Table 1).

When grown under low light from the initial heading to maturity stages, rice grain yield decreases markedly (by 55.45%), which is directly ascribed to significant decreases in the seed-setting rate and 1000-grain weight (Table 1). Similar data was published by Matsushima et al (1953a, b), Janardhan et al (1980), Nayak and Minor (1980), and Voleti and Singh (1996). These results confirm that low light conditions during the panicle differentiation or grain-filling stages exert a greater adverse effect on rice grain yield than that during other growth stages, which better explains the greater loss in grain yield caused by low light during the reproductive stage (Matsushima et al, 1953b). Under low light, nutrient source organs (leaves + culm + sheaths) cannot provide adequate amounts of assimilates to meet the requirements of tiller emergence and grain growth because of the impaired photosynthetic rate (Janardhan and Murty, 1980). Previous studies have speculated about the possible physiological mechanisms causing this change (Janardhan and Murty, 1980; Mawaki et al, 1990). For example, under low light conditions, rice plants mainly receive diffused light including higher amounts of blue-purple light but lower amount of red light, and this may be associated with impaired photosynthesis and reduced photosynthetic production (Cooperative Group, 1995). Additionally, low light inhibits the translocation of assimilates from source organs to sink organs (grains) (Ota et al, 1959; Nayak and Minor, 1980). Other researchers found the responses of grain yield to low light differ for various varieties (Janardhan and Murty, 1980; Nayak and Minor, 1980; Voleti and Singh, 1996). In spite of detrimental effects on carbohydrate accumulation and transportation caused by low light, tolerant varieties maintain their carbohydrate production levels, due to higher chlorophyll content and efficiency in photosynthesis, and stronger antioxidant ability, which makes them more adaptable to low light conditions (Nayak et al, 1978; Nayak and Minor, 1980; Liu et al, 2012).

Responses of grain quality to low light

When rice is exposed to low light from the transplanting to the booting stages, head rice yield as well as amylose in grains increase while the percentage of chalky kernels and protein content decline (Table 2). Previous studies indicated that when low light is imposed during these stages, the source-sink ratio is markedly altered. That is, biomass of sink organs (the numbers of fertile panicles and grains per panicle, and grain size) is significantly reduced. Meanwhile, the photosynthetic capacity of source organs (leaves) recovers to a normal level when full light become available during the heading stage (Cai and Luo, 1999; Sun et al, 2012).

Table 1. Effects of low light on grain yield and yield components in rice (Cai and Luo, 1999; Liu et al, 2009; Sun et al, 2012).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No. of effective panicles per square millimeter</th>
<th>1000-grain weight (g)</th>
<th>No. of filled grains per panicle</th>
<th>Seed-setting rate (%)</th>
<th>Grain yield (g/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural light intensity (CK)</td>
<td>301.5</td>
<td>25.2</td>
<td>85.3</td>
<td>87.5</td>
<td>639.8</td>
</tr>
<tr>
<td>50% of natural light intensity</td>
<td>262.5</td>
<td>25.0</td>
<td>79.0</td>
<td>96.2</td>
<td>419.0</td>
</tr>
<tr>
<td>Natural light intensity (CK)</td>
<td>197.4</td>
<td>30.3</td>
<td>147.9</td>
<td>82.1</td>
<td>883.3</td>
</tr>
<tr>
<td>40% of natural light intensity</td>
<td>195.3</td>
<td>30.0</td>
<td>127.9</td>
<td>71.5</td>
<td>750.9</td>
</tr>
<tr>
<td>Natural light intensity (CK)</td>
<td>269.9</td>
<td>21.5</td>
<td>121.5</td>
<td>83.2</td>
<td>704.8</td>
</tr>
<tr>
<td>55% of natural light intensity</td>
<td>257.9</td>
<td>17.4</td>
<td>70.0</td>
<td>48.6</td>
<td>314.0</td>
</tr>
</tbody>
</table>

*Low light treatment conducted from the transplanting to booting stages for the rice variety Xingfeng; †Low light treatment conducted from the heading to 10 d after heading stages for the rice variety Chuanxiang 9838; ‡Low light treatment conducted from the initial heading to maturity stages for the rice variety Jingxian 39.
Table 2. Effects of low light on rice grain quality (Ren et al, 2003b; Liu et al, 2006b).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Brown rice yield (g/kg)</th>
<th>Milled rice yield (g/kg)</th>
<th>Head rice yield (g/kg)</th>
<th>Percentage of chalky kernel (%)</th>
<th>Amylose content (%)</th>
<th>Gel consistency (mm)</th>
<th>Protein content (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural light intensity (CK) a</td>
<td>793</td>
<td>643</td>
<td>529</td>
<td>12.5</td>
<td>13.5</td>
<td>-</td>
<td>10.37</td>
</tr>
<tr>
<td>50% of natural light intensity</td>
<td>789</td>
<td>621</td>
<td>554</td>
<td>0.0</td>
<td>16.1</td>
<td>-</td>
<td>9.83</td>
</tr>
<tr>
<td>Natural light intensity (CK) b</td>
<td>817</td>
<td>728</td>
<td>510</td>
<td>35.3</td>
<td>22.2</td>
<td>64.0</td>
<td>9.53</td>
</tr>
<tr>
<td>51% of natural light intensity</td>
<td>814</td>
<td>719</td>
<td>458</td>
<td>46.0</td>
<td>22.1</td>
<td>51.7</td>
<td>10.57</td>
</tr>
<tr>
<td>31% of natural light intensity</td>
<td>809</td>
<td>708</td>
<td>408</td>
<td>56.3</td>
<td>20.2</td>
<td>39.7</td>
<td>12.57</td>
</tr>
</tbody>
</table>

a Low light treatment conducted from the transplanting to booting stages for the rice variety Xingfeng; b Low light treatment conducted from the initial heading to 32 d after initial heading stages for the rice variety Gangyou 527.

Zhu et al, 2008; Goto and Kumagai, 2009; Liu et al, 2009). Therefore, we speculate that such changes in the light intensity may influence physicochemical metabolism within plants during the formation of grains and have an impact on quality. For example, a relatively adequate supply of assimilate to grains inevitably reduces the formation of chalky rice after plants are treated with low light before the heading stage, especially during the booting stage (Nagato and Chaudhry, 1970; Tashiro and Ebata, 1975; Yuan et al, 2005).

When rice is grown under low light for 32 d (starting from the initial heading stage), brown rice, milled rice and head rice yields, as well as grain amylose content and gel consistency decrease while the percentage of chalky kernels and grain protein content increase (Table 2). These findings verify that low light conditions during the grain-filling stage result in poor appearance and milling qualities of rice grains (Ren et al, 2003b). The values of peak viscosity and breakdown decrease while the amount of setback increases regardless of low light treatment during the vegetative (transplanting to initial jointing stages) or reproductive stage (from booting to heading stages), suggesting that low light has negative effects on the quality of rice grains (Table 3). Low light during the grain-filling stage results in a decreased supply of carbohydrates to grains as well as a decrease in starch synthase activity in grains, which directly inhibits grain filling and enhances the occurrence of chalky rice (Tashiro et al, 1980; Li et al, 2005, 2006). Li et al (2005) has demonstrated that increased activity of soluble starch branching enzyme impairs the accumulation of amylose in grains when grain amylose content is reduced under low light. Note that grain protein content increases under low light although the amount of N imported from culm and sheaths to grains declines (Ren et al, 2003b, c). According to these results, we infer that the decreased amount of starch is greater than that of protein in grains, thus leading to enhanced grain protein content under low light.

Relationship between sink and source under low light stress

When grown under low light conditions from the tillering to booting stages, soluble sugar and soluble protein contents in rice leaves as well as the number of fertile panicles decline significantly. However, soluble sugar and protein content recover to a normal level when the low light treatment is terminated, indicating that the ratio of source to sink capacity is enhanced after the shading treatment. When encountering low light from the heading to maturity stages, the photosynthetic ability of rice plants is inhibited, which is verified by the decreased chlorophyll content and impaired photosynthetic rate in leaves, additionally, the seed-setting rate and 1000-grain weight are also markedly reduced. Kobata et al (2000) reported that when rice is shaded during the early grain filling stage, shade does not affect the grain dry matter increment, nevertheless, if adequate assimilates are not available during the remainder of the grain filling stage, the final grain weight will be reduced significantly.

Table 3. Effects of low light on rapid viscosity analysis (RVA) characteristics profile in rice (Wang et al, 2013).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Peak viscosity</th>
<th>Trough viscosity</th>
<th>Final viscosity</th>
<th>Breakdown</th>
<th>Setback</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural light intensity (CK) a</td>
<td>373.61</td>
<td>209.49</td>
<td>407.33</td>
<td>164.13</td>
<td>33.72</td>
</tr>
<tr>
<td>47% of natural light intensity</td>
<td>380.64</td>
<td>203.87</td>
<td>397.23</td>
<td>176.77</td>
<td>17.19</td>
</tr>
<tr>
<td>Natural light intensity (CK) b</td>
<td>351.54</td>
<td>208.00</td>
<td>375.85</td>
<td>143.54</td>
<td>24.31</td>
</tr>
<tr>
<td>47% of natural light intensity</td>
<td>308.14</td>
<td>181.91</td>
<td>349.03</td>
<td>126.24</td>
<td>40.89</td>
</tr>
</tbody>
</table>

a Low light treatment conducted from the tillering to elongation stages for the rice variety Gangyou 527; b Low light treatment conducted from the booting to heading stages for the rice variety Gangyou 188.
Therefore, we speculate that under low light conditions, the ratio of source to sink in rice may decrease from the heading to maturity stages.

**Perspective**

Numerous experimental data and related reports have confirmed that low light markedly affects agronomic and physiological traits of rice plants, hampering the underlying physiological metabolisms, including photosynthesis, respiration, antioxidant characteristic as well as the conversion and distribution of carbon and nitrogen (Sato, 1956; Li L et al, 1997; Ren et al, 2002; Zhu et al, 2008). Such changes eventually result in decreased rice grain yield and quality with a poor production of tillers, impaired capacity for panicles to differentiate, an abnormal grain-filling process, and sophisticated variability of activities of enzymes controlling starch grain synthesis (Nakano, 2000; Wang et al, 2001; Ren et al, 2003b; Li et al, 2005). Furthermore, responses of rice yield components and quality to low light differed substantially depending on diverse growth stage. That is, low light at the vegetative stage mainly decreases the number of productive panicles per unit area and eating quality, and that at the productive stage primarily results in the decreased number of grains per panicle, grain size and appearance, milling and eating qualities (Ren et al, 2003b; Liu et al, 2006a; Goto and Kumagai, 2009). The results suggest that when plants receive only low light during the reproductive stage, it generates a strong influence on rice grain yield and quality than those receive low light during the vegetative stage. Previous reports also indicate that when plants are grown under low light, they exhibit different effects on rice yield depending on the varieties used (Völeti and Singh, 1996; Liu et al, 2012). Low light tolerant varieties can maintain a more efficient photosynthetic rate and effective antioxidant capacity under low light, because they can maintain higher chlorophyll content and antioxidant enzyme activity level, thereby minimizing grain yield loss (Nayak et al, 1978; Liu et al, 2012). However, susceptible varieties suffer from a lack of the ability to adapt to low light conditions because of a significant difference in variety (Nayak et al, 1978; Völeti and Singh, 1996).

Currently, scientists have basically determined that the detrimental effects of low light are in relation to rice morphological and physiological characteristics and grain yield and quality. Few reports describe how to alleviate the negative influence of low light, so additional related research is needed in the future (Okamoto, 1970; Agarie et al, 1992). Based on previous reports and our research, we believe two important channels exist for improving rice grain yield and quality under low light conditions. First, varieties with high tolerance to low light should be planted and observed in regions with poor light conditions. Additional research is needed to determine whether some of the physiological traits mentioned above, such as chlorophyll content, can be used as indicators of tolerance to low light conditions for breeding work. Thilmony et al (2009) confirmed that the promoter of LP2 gene in rice is highly responsive to light. Hence, improving the inherent resistance of rice to low light by a molecular method is of great importance for breeding a tolerable cultivar that can thrive under low light stress. Second, related studies need to draft optimum agronomic measurements to cope with low light stress. Okamoto (1970) and Tamaki et al (1999) noted that the application of both silica and/or organic fertilizer can mitigate the damage caused by low light conditions during rice development. Hence, in the future, new research should focus on strengthening the resistance of rice plants to low light conditions by adopting suitable cultivation practices, including improving the supply and translocation efficiency of assimilate and analyzing the appropriate application of new fertilizers and commercial plant growth regulators to rice plants and fields.

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