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Leaf photosynthetic performance related to higher radiation use efficiency and grain yield in hybrid rice

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ABSTRACT

Yield potential of hybrid rice has been increased by approximately 10% through breeding super hybrid rice. It is well documented that the yield superiority of super hybrid rice is related to higher radiation use efficiency (RUE). However, limited information is available on the factors that contribute to the higher RUE in super hybrid rice. In this study, field and pot experiments were conducted in 2012–2014 to compare yield attributes, RUE and leaf photosynthetic traits between a super hybrid rice cultivar Y-liangyou 087 and an ordinary hybrid rice cultivar Teyou 838. In the field experiments, Y-liangyou 087 produced 11% higher grain yield than Teyou 838. Total biomass was higher in Y-liangyou 087 than in Teyou 838, whereas the difference in harvest index was not significant. The difference in intercepted radiation was insignificant between Y-liangyou 087 and Teyou 838, while RUE was 14% higher in Y-liangyou 087 than in Teyou 838. Y-liangyou 087 had higher net photosynthetic rate than Teyou 838, especially at the late growth stages (heading and milking). In the pot experiment, higher net photosynthetic rate was also observed in Y-liangyou 087 than in Teyou 838. There were no significant differences in stomatal conductance and intercellular CO_2 concentration between Y-liangyou 087 and Teyou 838. Y-liangyou 087 had higher chlorophyll a content and equal chlorophyll *b* content than Teyou 838. Efficiency of excitation capture by open photosystem II (Fv/Fm) and quantum yield of photosystem II (ΦPSII) were higher in Y-liangyou 087 than in Teyou 838, while the difference in photochemical quenching coefficient was insignificant. Y-liangyou 087 had higher Rubisco content than Teyou 838. These results suggest that higher RUE and grain yield can be achieved by improving leaf photosynthetic traits including chlorophyll a content, Fv/Fm, ΦPSII and Rubisco content in hybrid rice.

1. Introduction

Global rice production must increase by approximately 1% annually to meet the growing demand for food that will result from population growth and economic development (Normile, 2008). To achieve this goal, great efforts should be made to breed new rice cultivars with higher yield potential to enhance average farm yield (Peng et al., 2008). Rice yield potential increased by about 30% due to the development of semi-dwarf cultivars in the 1950s and an additional 15–20% increase was achieved by the development of hybrid cultivars in the 1970s (Peng et al., 2009). To further increase the yield potential, several major national and international projects were initiated in the 1990s to develop super rice or super hybrid rice (Khush, 1996; Yuan, 2001). Over the past two decades, these projects have made significant progress. Typically, China's super hybrid rice breeding project has developed many new cultivars using a combination of the ideotype approach and intersubspecific heterosis (Cheng et al., 2007; Peng et al., 2008), and these cultivars have increased yield potential by approximately 10% over ordinary hybrid cultivars (Zhang et al., 2009; Huang et al., 2011).

Rice yield is determined by biomass production and harvest index. However, it is generally accepted that there is little scope to further increase harvest index (Evans and Fischer, 1999; Laza et al., 2003) and achieving greater rice yield mainly depends on increasing biomass production (Ying et al., 1998; Peng et al., 1999; Zhang et al., 2009; Huang et al., 2013). Biomass production is the product of intercepted solar radiation by the canopy and radiation use efficiency (RUE), and the former is determined by cumulative incident solar radiation and intercepted fraction (De Costa et al.,

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2006). It is well known that cumulative incident solar radiation is related to growth duration, while intercepted fraction is dependent on canopy morphological characteristics such as leaf area, angle and orientation (Ying et al., 1998; De Costa et al., 2006; Zhang et al., 2009). But in fact, there is little interest in prolonging growth duration because the current durations coincide with suitable seasons or allow multiple cropping in a year (Mitchell and Sheehy, 2006), and it is difficult to improve canopy morphology because most high-yielding cultivars are close to the optimum canopy architecture (Peng, 2000). Therefore, further increase biomass production in rice may be driven from the increased RUE rather than intercepted radiation (Mitchell and Sheehy, 2006). Consistently, Zhang et al. (2009) observed that higher biomass production in super hybrid rice was attributed to higher RUE than in ordinary hybrid rice. However, there is limited information available on the factors that contribute to the higher RUE in super hybrid rice compared with ordinary hybrid rice.

Crop RUE depends on gross photosynthesis, maintenance respiration and growth respiration (Charles-Edwards, 1982). However, reductions in respiration are unlikely to be achieved (Byrd et al., 1992) so achieving higher RUE depends on increasing photosynthesis (Mitchell and Sheehy, 2006). Leaf photosynthesis consists of several physiological processes, that is, light harvesting, photosystem II photochemistry and CO_2 assimilation (Kumagai et al., 2009). There have been many studies investigating the leaf photosynthetic characteristics of super hybrid rice (Wang et al., 2000; Zong et al., 2000; Li and Jiao, 2002; Zhai et al., 2002; Wang et al., 2006). The results showed that super hybrid rice cultivars generally had higher chlorophyll content, photochemical quenching coefficient (qP), quantum yield of photosystem II (ΦPSII), CO_2 assimilation capacity or efficiency, and net photosynthetic rate (Pn) than the ordinary hybrid check cultivars. It is tempting to speculate that an improved leaf photosynthetic performance may contribute to higher RUE in super hybrid rice than in ordinary hybrid rice. However, there is no direct evidence to confirm this.

The purposes of this study were to (1) compare the yield attributes, RUE and leaf photosynthetic traits between a representative super hybrid rice cultivar and an ordinary hybrid rice cultivar and (2) identify the photosynthetic traits that contribute to higher RUE and grain yield in hybrid rice.

2. Materials and methods

2.1. Plant materials

Two rice cultivars, Y-liangyou 087 and Teyou 838, were used in this study. Y-liangyou 087 is a super hybrid cultivar released in 2010 with Y58S as the female parent and R087 as the male parent. Y58S, developed by crossing AnnongS-1, Changfei22B, Lemont and Pei'ai64S (Deng, 2005), is one of the top-performing male sterile lines in China (Xia et al., 2011). Pei'ai64S belongs to the intermediate type with *indica*, temperate, and tropical *japonica* ancestries and has good plant type and high combining ability (Deng, 2005; Cheng et al., 2007). In addition to Y-liangyou 087, there are several super hybrid rice cultivars, such as Y-liangyou 1 and Y-liangyou 2, that were developed by using this male sterile line. These cultivars are characterized by long, erect, thick, narrow, and V-shaped top three leaves and are among the best representatives of super hybrid rice in China. Teyou 838 is an ordinary hybrid cultivar (Longtepu-A × Fuhui 838) released in 2000. This cultivar is often used as a check cultivar because of its high grain yield and yield stability (Wei, 2009; Huang et al., 2015). Another important reason for choosing Y-liangyou 087 and Teyou 833 in this study was that these two cultivars have been widely grown by rice farmers in the study region.

2.2. Field experiment

Field experiments were conducted at the Experimental Farm of Guangxi University (22°51′ N, 108°17′ E, 78 m asl), Guangxi Province, China in late-rice growing season in 2012 and 2013. The soil of the experimental field was an Ultisol (USDA taxonomy) with pH = 6.75, organic matter = 32.3 g kg^{-1}, NaOH hydrolysable N = 120 mg kg^{-1}, Olsen P = 31.6 mg kg^{-1}, and NH_4OAc extractable K = 126 mg kg^{-1}. The soil test was based on samples taken from the upper 20 cm of the soil.

Treatments were arranged in a split-plot design with N rates as main plots and cultivars as subplots. The experiment was replicated three times and subplot size was 30 m^2. Two N rates were 165 (moderate N) and 240 kg N ha^{-1} (high N). For both the moderate and high N rates, urea was used as N fertilizer and was split-applied with 50% as basal (1 day before transplanting), 30% at early-tillering (7 days after transplanting) and 20% at booting.

Pre-germinated seeds were sown in a seedbed on 24 July. Twenty-day-old seedlings were transplanted at a hill spacing of 20 cm × 20 cm with two seedlings per hill. Superphosphate was used as P fertilizer with a rate of 54 kg P_2O_5 ha^{-1} and was applied as basal. Potassium chloride was used as K fertilizer with a rate of 180 kg K_2O ha^{-1} and was split-applied with 50% as basal, 30% at early-tillering and 20% at booting. The experimental field was kept flooded from transplanting until 7 days before maturity. Insects were intensively controlled by chemicals to avoid yield loss.

Canopy light interception was measured between 11:00 and 13: 00 at mid-tillering, booting (30 days before heading), heading, milking (15 days after heading), and maturity using a canopy analysis system (SunScan, Delta-T Devices Ltd., Burwell, Cambridge, UK). In each subplot, light intensity inside the canopy was measured by placing the light bar in the middle of two rows and slightly above the water surface. Three readings were taken within rows and another three between rows. Incoming light intensity was recorded simultaneously when canopy light intensity was measured. Canopy light interception was calculated as the percentage of incoming light intensity that was intercepted by the canopy [100 × (incoming light intensity – light intensity inside canopy)/incoming light intensity]. Intercepted radiation during each growth period was calculated using the average canopy light interception and cumulative incoming solar radiation during this growth period [1/2 × (canopy light interception at the beginning of the growth period + canopy light interception at the end of the growth period) cumulative incident radiation during the growth period]. Intercepted radiation during the entire growing season was the summation of intercepted radiation during each growth period. RUE was calculated as the ratio of total biomass to intercepted radiation during the period from transplanting to maturity. Solar radiation was recorded daily using an on-site automatic weather station (Vantage Pro2, Davis Instruments Corp., Hayward, CA, USA). Pn was measured on eight uppermost fully expanded leaves for each subplot at booting, heading and milking using a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE, USA). The measurement was made between 9:00 and 11: 00 when photosynthetic active radiation above the canopy was 1000–1200 μmol m^{-2} s^{-1}. Plants were sampled from a 0.48-m^2 (12 hills) in each subplot at maturity. Plant samples were separated into straw (including rachis), filled and unfilled spikelets and oven-dried at 70 °C to constant weight. Total biomass production was the summation of straw, and filled and unfilled spikelets dry matter. Daily biomass production was calculated by dividing total biomass production by growth duration from transplanting to maturity. Harvest index was calculated (100 × filled spikelet weight/total biomass). Grain yield was determined from a 5-m^2 area in each subplot and adjusted to the standard moisture content of 0.14 g H_2O g^{-1}. Daily grain yield

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