Agronomic performance of late-season rice in South China

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ABSTRACT
Improving rice yields is critical for global food security. China is a major rice-producing country having two rice cropping systems, i.e. single-season rice cropping system and a double-season system with both early- and late-season rice. There have been reports on the sink-source traits contributing to high grain yield for single- and early-season rice, but such information is limited for late-season rice. In this study, field experiments were conducted at the research farm of Guangxi University, Nanning, Guangxi Province, China in the late rice-growing season. Grain yield and sink-source traits were compared among five cultivars (Guiliangyou 2, Teyou 838, Y-liangyou 087, Teyou 582, and Yuxiangyouzhan) in 2012 and then three cultivars (Guiliangyou 2, Teyou 838, and Y-liangyou 087) in 2013. Y-liangyou 087 produced 6–26% higher grain yield than did the other cultivars. This higher grain yield was driven by improvements in sink-source capacity. Sink capacity was 8–31% higher in Y-liangyou 087 than in the other cultivars. Well-balanced relations between spikelets m⁻² and grain weight was responsible for the higher sink capacity in Y-liangyou 087. The result was that Y-liangyou 087 produced 11–17% greater biomass (source capacity) than did the other cultivars. The greater source capacity in Y-liangyou 087 was mainly attributed to higher radiation use efficiency (RUE). Our study suggests that enhancing sink capacity through balanced relations between number of spikelets per unit land area and grain size, while improving source capacity through increasing RUE is a feasible way to achieve higher grain yield of late-season rice in South China.

Introduction
Rice is the staple food for more than half of the world population (Yuan, 2014). Within a period of four decades from the 1960s to 1990s, rice production has more than doubled in most parts of the world and even tripled in certain countries (http://faostat.fao.org/). This was, primarily as the result of development of new cultivars such as semi-dwarf and hybrid cultivars and improvement in crop management practices such as fertilization and irrigation (Hongthong et al., 2012; Mae et al., 2006). Source capacity is usually expressed as the amount of biomass production, which is achieved through the plant’s photosynthesis capacities (Zhang et al., 2009). Biomass production is a product of the amount of radiation intercepted by the canopy and radiation use efficiency (RUE, i.e. biomass produced per unit of radiation intercepted). The former depends on incident radiation and intercepted percent (i.e. the fraction of incident radiation intercepted by the canopy) (Huang et al., 2016a). Incident radiation can be increased by prolonging the duration of growth, while an increase in intercepted percent can be achieved by improving morphological characteristics of the canopy such as leaf area index (De Costa et al., 2006; Ying et al., 1998; Zhang et al., 2009). In fact,
because the current durations coincide with suitable seasons that allow multiple cropping in a year, there is little interest in prolonging growth duration (Mitchell & Sheehy, 2006). Because most high-yielding cultivars are close to the optimum canopy architecture, it is difficult to improve canopy morphology (Peng, 2000; Phy o & Chung, 2013). Consequently, there have reports that modifications to RUE are likely to be more important for achieving a substantial increase in rice yield (Kajala et al., 2011; Mitchell & Sheehy, 2006). Source-to-sink translocation degree is often assessed by measuring harvest index (Sinclair, 1998), which is determined by the transient photosynthesis during grain formation and the remobilization of stored reserves into the growing grain (Blum, 1993). Although it is generally suggested that further improvement in rice is not driven by increasing harvest index (Huang et al., 2013a; Peng et al., 1999; Ying et al., 1998; Zhang et al., 2009a), a recent study showed that raising potential yield of short-duration rice cultivars is possible by increasing harvest index (Huang et al., 2015a).

China is one of the major rice-producing countries in the world. The annual total rice area in China is about 30 million ha or approximately 20% of the world rice area (Peng et al., 2009). There are two rice cropping systems in China: (1) single-season rice cropping system; and (2) double-season rice cropping system with early- and late-season rice (Huang et al., 2013b). Zhang et al. (2009) have reported that enhancing sink capacity through increasing the number of spikelets per unit land area and simultaneously improving source capacity through increased incident radiation by prolonging growth duration is responsible for the higher yield of single-season rice. Huang et al. (2016b) have stated that improving sink capacity while maintaining good translocation of pre-heading biomass into the grains is an effective way to achieve high yield for early-season rice. However, little is known regarding such information for late-season rice, which would be different from those for single- and late-season rice because climatic conditions vary in the different rice growing seasons. Typically, daily temperatures tend to increase during the early rice-growing season, whereas they tend to decrease during the late rice-growing season (Huang et al., 2017). In our present study, we compared grain yield and sink-source traits among several late-season rice cultivars in a subtropical environment of South China in two years. Our objective was to determine the sink-source traits that contribute to high grain yield of late-season rice.

Materials and methods

Field experiments were conducted at the research farm of Guangxi University, Nanning, Guangxi Province, China (22°51′ N, 108°17′ E, 78 m asl) in the late rice-growing seasons in 2012 and 2013. The site is located in a subtropical monsoon climate zone. The average daily mean temperature during the rice growing season was 26.5 °C in 2012 and 25.0 °C in 2013 (Figure 1). The soil of the experimental field was an Ultisol (USDA taxonomy) with the following chemical properties at the 0–20 cm layer: 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 NH₄OAc extractable K = 126 mg kg⁻¹.

Treatments were laid out in a split-plot design with N rates varied in the main plots and cultivars in the subplots. The experiment was replicated three times and subplot size was 30 m². Two N rates were evaluated: moderate (165 kg N ha⁻¹) and high (240 kg N ha⁻¹). Five cultivars, i.e. Guiliangyou 2, Teyou 838, Y-liangyou 087, Teyou 582, and Yuxiangyouzhan, were used in 2012, and three cultivars in 2013, i.e. Guiliangyou 2, Teyou 838, and Y-liangyou 087. These are cultivars widely grown by rice farmers in South China. Detailed information about them is given in Table 1.

Pre-germinated seeds were sown in a seedbed on 24 July. Twenty-day-old seedlings were transplanted with two seedlings per hill and a hill spacing of 20 cm × 20 cm. For

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Table 1. Information about rice cultivars used in the experiment.

| Cultivar           | Type               | Year of release | Female parent | Male parent |
|--------------------|--------------------|-----------------|---------------|-------------|
| Guiliangyou 2      | Two-line indica    | 2008            | Guik-2S       | Guihui 582  |
| Teyou 838          | Three-line indica  | 2000            | Longtepu A    | Fuhui 838  |
| Y-liangyou 087     | Two-line indica    | 2010            | Y58S          | R087        |
| Teyou 582          | Three-line indica  | 2009            | Longtepu A    | Gui 582     |
| Yuxiangyouzhan     | Indica inbred      | 2005            | TY36/IR100    | IR100       |

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Figure 1. Daily mean temperatures during the late rice-growing season in Nanning, Guangxi Province, China in 2012 and 2013.
both N rates, urea was used as the N fertilizer and applied in three splits: 50% as basal (1 day before transplanting), 30% at early-tillering (7 days after transplanting), and 20% at panicle initiation. Superphosphate was used as P fertilizer (54 kg P₂O₅ ha⁻¹) and applied as basal. Potassium chloride was used as the K fertilizer (180 kg K₂O ha⁻¹) and applied in three splits: 50% as basal, 30% at early-tillering, and 20% at panicle initiation. The experimental field was kept flooded with 5–10 cm depth of water from transplanting until 7 days before maturity. Insects, diseases, and weeds were intensively controlled by chemicals.

Plants were sampled from a 0.48 m² area (12 hills) in each subplot at heading. Leaf area was measured using a CI-203 leaf area meter (CID Inc., Vancouver, WA, USA), and leaf area index were calculated by dividing the total leaf area of the sample by the ground area sampled. At maturity, 12 hills were diagonally sampled from a 5 m² harvest area for each subplot. Panicle number of each hill was counted to determine panicles m⁻². Plants were hand threshed, and filled spikelets were separated from unfilled spikelets by submerging them in tap water. Dry weights of straw (including rachis) and filled and unfilled spikelets were determined after over-drying at 70 °C to constant weight. Three subsamples of 30 g of spikelets and all unfilled spikelets were taken to count the number of spikelets. Total biomass production was calculated as the total dry matter of straw and of filled and unfilled spikelets. Spikelets per panicle, spikelets m⁻² (panicles m⁻² × spikelets per panicle), spikelet filling percentage (100 × filled spikelet number/total spikelet number), grain weight, sink capacity (spikelets m⁻² × grain weight), and harvest index (filled spikelet weight/total biomass production) were calculated. Grain yield was determined from a 5 m² area in each subplot and adjusted to a standard moisture content of 0.14 g H₂O g⁻¹.

Daily incident radiation was recorded using a Vantage Pro2 automatic weather station (Davis Instruments Corp., Hayward, CA, USA). Intercepted radiation was determined according to Huang et al. (2016c) with a SunScan canopy analysis system (Delta-T Devices Ltd, Burwell, Cambridge, UK). Intercepted percent (100 × intercepted radiation/incident radiation) and RUE (total biomass production/intercepted radiation) were calculated.

Data were analyzed by analysis of variance with the use of Statistix 8.0 software (Tallahassee, FL, USA). The least significant difference test (LSD) was employed to compare means of cultivars at the 0.05 probability level.

**Results and discussion**

The cultivar difference in grain yield was significant in both years (Table 2). In 2012, Y-liangyou 087 produced the highest grain yield, followed by Guiliangyou 2, Teyou 838, Teyou 582, and Yuxiangyouzhan. Average grain yield across the two N rates for Y-liangyou 087 was 13–26% higher than that for the other four cultivars. In 2013, the highest grain yield was again recorded from Y-liangyou 087. Averaged across two N rates, grain yield was 6% (not significant) and 10% higher from Y-liangyou 087 than from Guiliangyou 2 and Teyou 838, respectively. These demonstrate that Y-liangyou 087 is a desirable late-season rice cultivar for achieving high grain yield. Because of this, the following analysis and discussion on sink-source traits in late-season rice mainly focuses on this cultivar. N rate had no significant effect on grain yield in either 2012 or 2013 (Table 2). This finding is consistent with that reported in single-season rice by Zhang et al. (2009). It suggests that late-season rice does not necessarily require more N fertilizer to produce high grain yield. The interaction effect between cultivar and N rate on grain yield was not significant in either year (Table 2). Thus, mean data across the two N rates are presented in the subsequent tables, making interpretation easier.

Sink capacity in Y-liangyou 087 was 13–31% higher than that for the other four cultivars in 2012 (Table 3). In 2013, Y-liangyou 087 had higher sink capacity by 8% (not significant) and 14% compared with Guiliangyou 2 and Teyou 838, respectively. Total biomass production was 12–17% higher

### Table 2. Grain yield (t ha⁻¹) of rice cultivars grown under two N rates in Nanning, Guangxi Province, China, in late season in 2012 and 2013.

| Cultivar          | 2012       | 2013       | Mean       | 2012       | 2013       | Mean       |
|-------------------|------------|------------|------------|------------|------------|------------|
|                   | Moderate N⁺ | High N     | Mean       | Moderate N⁺ | High N     | Mean       |
| Guiliangyou 2     | 8.21       | 8.29       | 8.25b      | 8.19       | 8.23       | 8.21ab     |
| Teyou 838         | 8.17       | 8.32       | 8.25b      | 8.02       | 7.83       | 7.93b      |
| Y-liangyou 087    | 9.04       | 9.64       | 9.34a      | 8.42       | 8.96       | 8.69a      |
| Teyou 582         | 8.02       | 8.15       | 8.09b      | –          | –          | –          |
| Yuxiangyouzhan    | 7.45       | 7.33       | 7.39c      | –          | –          | –          |

Analysis of variance

Cultivar (C) **
N rate (N) NS
C × N NS

Note: Means of cultivars with the same letters in each year are not significantly different according to LSD (0.05).

*Total N rate was 165 kg ha⁻¹ for moderate N and 240 kg ha⁻¹ for high N.
*Significance at the 0.05 probability level; **Significance at the 0.01 probability level; NS denotes non-significance.
in Y-liangyou 087 than in the other four cultivars in 2012. In 2013, Y-liangyou 087 produced 12% and 11% higher total biomass than did Guiliangyou 2 and Teyou 838, respectively. Harvest index in Y-liangyou 087 was equal to that in Teyou 838, 4–6% lower than that in Guiliangyou 2 and Teyou 582, and 11% higher than that in Yuxiangyouzhan in 2012. In 2013, harvest index in Y-liangyou 087 was equal to that of Teyou 838 and lower than that of Guiliangyou 2. These results indicate that the higher grain yield in Y-liangyou 087 was driven by the increased sink-source capacity rather than by degree of sink-to-source translocation. This is in agreement with most of the previous studies (Huang et al., 2013a; Peng et al., 1999; Ying et al., 1998; Zhang et al., 2009), but not with a recent study of Huang et al. (2015a). Because the present study involves more cultivars than did the study of Huang et al. (2015a), the results generated in the present study should be more conclusive. Huang et al. (2015a) observed that Guiliangyou 2 had equal biomass production but a higher harvest index and grain yield than did Yuxiangyouzhan. A similar result could be obtained by comparing these two cultivars in the present study (Tables 2 and 3). Further, Huang et al. (2015a) found that the high harvest index in Guiliangyou 2 was attributable to higher remobilization of stored reserves. Although the importance of rapid translocation of stored reserves on high grain filling and grain yield has been reported (Yoshinaga et al., 2013), high remobilization of stored reserves may also result in earlier plant senescence (Yang & Zhang, 2010) and consequently it may reduce biomass production during grain-filling period and grain yield (Hirel et al., 2007). Therefore, a higher harvest index is not always better. It is generally accepted that the harvest index of modern high-yielding rice cultivars is around 0.5 (Khush, 1995). Consistently, in this study, Y-liangyou 087 produced the highest grain yield and had a harvest index of 0.50 to 0.51. These facts suggest that increasing biomass production is more effective than enhancing harvest index to further improve the grain yield of late-season rice.

Y-liangyou 087 had 14–31% more panicles m⁻² than did the other four cultivars in 2012 (Table 4). Again in 2013, panicles m⁻² were higher in Y-liangyou 087 than in Guiliangyou 2 and Teyou 838 by 16% and 17%, respectively. Spikelets panicle⁻¹ in Y-liangyou 087 were not significantly different from the number with Teyou 838 and Yuxiangyouzhan and were 16–19% lower than that in Guiliangyou 2 and Teyou 582 in 2012. In 2013, Y-liangyou 087 had 24% lower and 15% higher spikelets panicle⁻¹ than did Guiliangyou 2 and Teyou 838, respectively. Spikelets m⁻² in Y-liangyou 087 was comparable to that in Guiliangyou 2 and Teyou 582 and 11–30% more than that in Teyou 838 and Yuxiangyouzhan in 2012. In 2013, Y-liangyou 087 had 12% lower and 34% higher spikelets m⁻² than did Guiliangyou 2 and Teyou 838, respectively. The difference in spikelet filling percentage was relatively small among cultivars in both years. Grain weight in Y-liangyou 087 was 7–18% larger than that in Guiliangyou 2, Teyou 582, and Yuxiangyouzhan in 2012, and 12% smaller than that in Teyou 838. In 2013, Y-liangyou 087 had 23% higher and 16% lower grain weight than did Guiliangyou 2 and Teyou 838, respectively. These results reveal that the higher sink capacity in Y-liangyou 087 was attributed to a well-balanced relation between spikelets m⁻² and grain weight. In cereal crops, the compensations among yield components are always arising, either from the physiological competition or developmental allometry (Huang et al., 2011; Ying et al., 1998). It is generally accepted that increasing spikelets panicle⁻¹ is a better

Table 3. Sink capacity, total biomass production, and harvest index of rice cultivars grown in Nanning, Guangxi Province, China, in late season in 2012 and 2013.

| Cultivar        | Sink capacity (g m⁻²) | Total biomass production (g m⁻²) | Harvest index |
|-----------------|-----------------------|----------------------------------|---------------|
| 2012            |                       |                                  |               |
| Guiliangyou 2   | 1046b                 | 1412b                            | 0.54a         |
| Teyou 838       | 1040b                 | 1464b                            | 0.51b         |
| Y-liangyou 087  | 1194a                 | 1640a                            | 0.51b         |
| Teyou 582       | 1060b                 | 1405b                            | 0.53a         |
| Yuxiangyouzhan  | 908c                  | 1403b                            | 0.46c         |
| 2013            |                       |                                  |               |
| Guiliangyou 2   | 1116ab                | 1415b                            | 0.55a         |
| Teyou 838       | 1064b                 | 1429b                            | 0.50b         |
| Y-liangyou 087  | 1210a                 | 1588a                            | 0.50b         |

Notes: Data are the means across two N rates (165 and 240 kg ha⁻¹). Within a column for each year, data followed by the same letters are not significantly different according to LSD (0.05).

Table 4. Yield components of rice cultivars grown in Nanning, Guangxi Province, China, in late season in 2012 and 2013.

| Cultivar        | Panicles m⁻² | Spikelets panicle⁻¹ | Spikelets m⁻² (× 10⁴) | Spikelet filling (%) | Grain weight (mg) |
|-----------------|--------------|---------------------|------------------------|----------------------|-------------------|
| 2012            |              |                     |                        |                      |                   |
| Guiliangyou 2   | 212c         | 192a                | 40.7ab                 | 84.8a                | 25.8c             |
| Teyou 838       | 219bc        | 152c                | 33.3c                  | 83.6ab               | 31.3a             |
| Y-liangyou 087  | 269a         | 161bc               | 43.3a                  | 81.1b                | 27.7b             |
| Teyou 582       | 206c         | 198a                | 40.8ab                 | 81.4b                | 26.0c             |
| Yuxiangyouzhan  | 233b         | 166b                | 39.0b                  | 82.0ab               | 23.4d             |
| 2013            |              |                     |                        |                      |                   |
| Guiliangyou 2   | 231b         | 203a                | 46.9a                  | 80.1a                | 23.8c             |
| Teyou 838       | 228b         | 135c                | 30.8c                  | 77.8a                | 34.8a             |
| Y-liangyou 087  | 267a         | 155b                | 41.4b                  | 75.9a                | 29.3b             |

Notes: Data are the means across two N rates (165 and 240 kg ha⁻¹). Within a column for each year, data followed by the same letters are not significantly different according to LSD (0.05).
RUE that was 6% (not significant) and 14% higher than in Guiliangyou 2 and Teyou 838, respectively. These results demonstrate that the higher source capacity in Y-liangyou 087 was mainly due to improvement in RUE. Crop RUE is determined by gross photosynthesis, maintenance respiration, and growth respiration. However, reductions in respiration are unlikely to be achieved, so reaching higher RUE will depend on increasing photosynthesis (Mitchell & Sheehy, 2006). Consistently, Huang et al. (2016c) observed that Y-liangyou 087 had higher chlorophyll a content, greater efficiency of excitation capture by open photosystem II, a higher quantum yield of photosystem II, more Rubisco content, and consequently, a higher net photosynthetic rate than Teyou 838. Moreover, Y-liangyou 087 is a late-stage vigor cultivar (Huang et al., 2015b). Huang et al. (2016c) have observed that the photosynthetic advantage in Y-liangyou 087 relative to Teyou 838 was larger at the ripening stage than at the stage of early growth. This indicates that Y-liangyou 087 was more adaptable to low temperatures during the late stage of the late rice-growing season (Figure 1). This might also be a reason for the higher RUE in Y-liangyou 087. It suggests that selecting late-stage vigor cultivars would be helpful to achieve higher grain yield of late-season rice.

**Conclusion**

It is concluded that higher grain yield of late-season rice can be achieved by enhancing sink capacity through balanced relations between number of spikelets per unit land area and grain size and meanwhile improving source capacity through increasing RUE in South China.

**Author contributions**

Conceived and designed the experiments: MH, LJ, & YZ. Performed the experiments: MH, SS, XZ, JC, & FC. Analyzed the data: MH. Wrote the paper: MH.
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