**ABSTRACT**

Dense planting has been recommended as a promising practice for achieving greater grain yield. However, whether this practice is suitable for hybrid rice (*Oryza sativa* L.) is unknown. To evaluate the response of grain yield and canopy structure traits to planting density in hybrid cultivars, field experiments were conducted with inbred-indica (Huanghuazhan), inbred-japonica (Xiushui09), hybrid-indica (Tianyouhuazhan), and hybrid-japonica (Chunyou84 or Yongyou12) cultivars at five planting densities (40, 26.7, 20, 16.7, and 13.3 hills m\(^{-2}\), designated as D1, D2, D3, D4, and D5) in 2015 and 2016. Results showed that hybrid cultivars had 16.6 to 48.9% greater grain yield compared with inbred cultivars under the dense planting condition (D1 and D2), except for Tianyouhuazhan in 2015. The grain yield increased with increasing plant density in hybrid cultivars (except for Tianyouhuazhan in 2015), with the increase rates of 76.6, 108.0, and 138.6 kg \(\text{ha}^{-1}\) for hybrid-japonica-Chunyou84 (2015), hybrid-indica-Tianyouhuazhan (2016), and hybrid-japonica-Yongyou12 (2016), respectively. However, the yield performance was significantly affected by the climate condition under dense planting. The grain yield of hybrid cultivars in 2015 averaged 8.3 t ha\(^{-1}\), which was 36.3% lower than that in 2016 under dense planting (D1 and D2). We speculate that unfavorable climate would suppress the yield performance more under the dense planting conditions. Furthermore, results showed that greater plant density leads to an increase in plant radiation use efficiency, except for indica-hybrid-Tianyouhuazhan. This might be attributed to the upright top leaves when the planting density increased, which resulted in smaller leaf angles and extinction coefficient of the canopy.

**Core Ideas**

- Hybrid rice grain yield was evaluated under dense planting.
- Grain yield was greater in hybrid cultivars than in inbred cultivars under dense planting conditions.
- The yield performance under dense planting was significantly affected by the weather condition.

**Abbreviations:** DAT, days after transplanting; IRS, incident solar radiation; LAI, leaf area index; LI, light interception; PAR, RH, relative humidity; RUE, radiation use efficiency; SOM, soil organic matter.

**Rice** (*Oryza sativa* L.) is a staple food in Asia, accounting for approximately 47.8 and 38.5% of the productivity and planting areas for cereal crops in 2011, respectively (FAO, 2014). To meet the growing demand for food due to population growth over the past several decades, great efforts have been made to breed new hybrid rice cultivars with higher yield potential to improve average farm yields (Huang et al., 2017). However, the resultant yield rice cultivars have generally required more resources such as N and water (Huang et al., 2017; Wang and Peng, 2017) and wider growth space to realize the yield potential in practice (Ahmad et al., 2008; Wang et al., 2014; Wang and Peng, 2017).

Sparse planting methods help to alleviate the labor intensity of rice farmers who utilize traditional manual transplanting (Peng et al., 2009). However, with the growing number of farmers migrating from rural to urban areas for jobs (Levine et al., 2008), alternative rice planting methods that require less labor than traditional manual transplanting, such as direct-seeding and/or machine-transplanting, have been rapidly developed (Chen et al., 2017).

Recently, dense planting with mechanical assistance has been considered a promising choice and recommended as a practice for achieving greater grain yield with less resource inputs for rice (Huang et al., 2018; Lin et al., 2009; Zhu et al., 2016), wheat (*Triticum aestivum* L.) (Li et al., 2016; Liu et al., 2016), canola (*Brassica napus* L.) (Wang et al., 2015), and maize (*Zea mays* L.) (Chang et al., 2016; Shi et al., 2016). High planting density may be more practical for direct-seeded and machine-transplanted rice than for traditional manual transplanting in practice, as it can be achieved easily with less labor (Huang et al., 2018; Wang et al., 2014). However, whether hybrid rice could maintain its superior yield over inbred cultivars in dense planting conditions is still unknown. In addition, hybrid rice seed is far more expensive than inbred rice; therefore, there is also a need to evaluate the economic gain for hybrid rice before adopting dense planting.

A number of reports have been published on the effect of dense planting on crop grain yield and yield attributes. Liu et al. (2016) proposed that large-spike wheat would have greater productivity and planting areas for cereal crops in 2011, respectively (FAO, 2014). To meet the growing demand for food due to population growth over the past several decades, great efforts have been made to breed new hybrid rice cultivars with higher yield potential to improve average farm yields (Huang et al., 2017). However, the resultant yield rice cultivars have generally required more resources such as N and water (Huang et al., 2017; Wang and Peng, 2017) and wider growth space to realize the yield potential in practice (Ahmad et al., 2008; Wang et al., 2014; Wang and Peng, 2017).

Sparse planting methods help to alleviate the labor intensity of rice farmers who utilize traditional manual transplanting (Peng et al., 2009). However, with the growing number of farmers migrating from rural to urban areas for jobs (Levine et al., 2008), alternative rice planting methods that require less labor than traditional manual transplanting, such as direct-seeding and/or machine-transplanting, have been rapidly developed (Chen et al., 2017).

Recently, dense planting with mechanical assistance has been considered a promising choice and recommended as a practice for achieving greater grain yield with less resource inputs for rice (Huang et al., 2018; Lin et al., 2009; Zhu et al., 2016), wheat (*Triticum aestivum* L.) (Li et al., 2016; Liu et al., 2016), canola (*Brassica napus* L.) (Wang et al., 2015), and maize (*Zea mays* L.) (Chang et al., 2016; Shi et al., 2016). High planting density may be more practical for direct-seeded and machine-transplanted rice than for traditional manual transplanting in practice, as it can be achieved easily with less labor (Huang et al., 2018; Wang et al., 2014). However, whether hybrid rice could maintain its superior yield over inbred cultivars in dense planting conditions is still unknown. In addition, hybrid rice seed is far more expensive than inbred rice; therefore, there is also a need to evaluate the economic gain for hybrid rice before adopting dense planting.

A number of reports have been published on the effect of dense planting on crop grain yield and yield attributes. Liu et al. (2016) proposed that large-spike wheat would have greater

**Effect of Dense Planting of Hybrid Rice on Grain Yield and Solar Radiation Use in Southeastern China**

Song Chen, Min Yin, Xi Zheng, Shaowen Liu, Guang Chu, Chunmei Xu, Dangying Wang, and Xiufu Zhang*

*Corresponding author (Zhangxiufu@caas.cn).

Co-first authors. Received 4 July 2018. Accepted 29 Oct. 2018.

Sciences, Zhejiang Univ., Hangzhou, 310029 China. S. Chen and X. Zheng, The Faculty of Agriculture, Life and Environmental Sciences, Hangzhou 310006, Zhejiang, China; and China National Rice Research Inst., Chinese Academy of Agricultural Sciences, Hangzhou 310006, Zhejiang, China; and X. Zheng, The Faculty of Agriculture, Life and Environmental Sciences, Zhejiang Univ., Hangzhou, 310029 China. S. Chen and M. Yin contributed equally to this work and should be considered co-first authors. Received 4 July 2018. Accepted 29 Oct. 2018.

**Abbreviations:** DAT, days after transplanting; IRS, incident solar radiation; LAI, leaf area index; LI, light interception; PAR, RH, relative humidity; RUE, radiation use efficiency; SOM, soil organic matter.

Published in Agron. J. 111:1229–1238 (2019)
doi:10.2134/agronj2018.07.0430

Supplemental material available online
Available freely online through the author-supported open access option

Copyright © 2019 by the American Society of Agronomy
5585 Guilford Road, Madison, WI 53711 USA
This is an open access article distributed under the CC BY license (https://creativecommons.org/licenses/by/4.0/)
potential than small-spike to increase yield for better single-hill productivity by increasing plant density. Li et al. (2010) reported that the increased grain yield from dense planting might be a result of the increase in the number of spikelets. Nakano et al. (2012) found that the grain yield, percentage of filled spikelets, and 1000-grain weight increased under dense planting conditions in forage rice. Huang et al. (2018) investigated machine-transplanted double cropping rice and found that increasing hill density can compensate for yield loss from reduced N input. An increase in crop yield under dense planting was reported as a consequence of the rise in biomass (Katsura et al., 2010; San-Oh et al., 2008), which might be attributed to the greater potential capacity of the crop canopy to capture solar radiation, water, and nutrients in the deep soil layer (Dingkuhn et al., 2015; Du et al., 2015). For example, increased leaf area index (LAI) and an effective blade spatial arrangement ensure that plant photosynthesis meets the needs of high yield (Yoshida, 1981). In addition, crop solar radiation use efficiency (RUE), which could be affected by both leaf photosynthetic rate and N content (Clair and Horie, 1989), might also be sensitive to density changes. Meanwhile, growth duration and accumulated incident radiation were also affected by dense planting (Zhang et al., 2015). Chen et al. (2014) proposed that designing crop canopies to make the maximum use of solar radiation and periods with favorable temperatures is critical to achieve yield with less input. In this regard, increasing the planting density is a possible way to manipulate the structure of the population and canopy in agronomic practice.

High grain yield of hybrid rice has been obtained when this rice was bred under sparse planting conditions to achieve greater biomass production (Huang et al., 2016; Katsura et al., 2007; Laza et al., 2001), longer leaf area duration (Jiang et al., 2015), large LAI (Lin et al., 2009), and high productive tiller percentage (Wang et al., 2014). However, few studies have reported the effect of dense planting on RUE, especially for hybrid rice cultivars. Therefore, the objectives of the present study are (i) to examine the difference in the response of grain yield to dense planting cultivation between inbred and hybrid cultivars; and (ii) to evaluate canopy light interception and RUE of hybrid cultivars under a series of planting densities in comparison to the inbred cultivars.

### MATERIALS AND METHODS

#### Site Description

Field experiments were performed in 2015 and 2016 at the experimental farm of the China Rice Research Institute (120.2°E, 30.3°N, with an altitude of 11 m above sea level). The site is located on the Yangtze River plain in southeastern China. The area is characterized by a subtropical monsoon climate with annual mean temperatures of 13 to 20°C, ranging from 2°C in January to 35°C in July, and mean annual precipitation of 1200 to 1600 mm, with approximately 80% falling between April and September. The soil is a ferric-accumulic stagnic anthrosol.

Statistics related to climate conditions during the growth period and the soil fertility traits of the experimental site can be found in Fig. 1 and Table 1. Soil sampling and properties were determined according to the Laboratory Manual for Agriculture and Soil Analysis (Pao, 2005). Briefly, soil samples were collected from the 0- to 20-cm soil layer before the rice season. The replicate was a composite sample that consisted of 20 to 25 sampling points (each 2.5 cm in diameter) that were sampled in an “S” type distribution in a plot. The soil samples were sieved through a 2-mm sieve after removing the stones, crop straw, and root material, and then the samples were air-dried. The dried soil samples were divided into two parts, ground with wooden blocks, and sieved by 0.25- and 0.15-mm sieves. Total N and total P was determined by the Kjeldahl method, available N (Alkali N) was measured using the alkali decomposition diffusion method, available P was extracted with 0.5 mol L⁻¹ NaHCO₃ and determined by the molybdenum antimony colorimetric method, available K was extracted by 1 mol L⁻¹ ammonium acetate extraction and determined by flame photometry, soil pH was determined (1:5 water suspension) with a pH meter, cation exchange capacity was determined by the ammonium acetate extraction method, electrical conductivity was measured using a digital conductivity meter, and soil organic matter (SOM) was determined by a dichromate gravimetrically (105°C for 48 h). The soil properties were based on the dry weight of the soil. Meteorological data were observed using a self-recording titype meteorological station (R800, Technosolutions Ltd., Beijing, China).

#### Experimental Design and Plant Cultivation

Five rice varieties were used in the experiment in the single season. They belonged to four rice groups: inbred-indica (Huanghuazhan), hybrid-indica (Tianyouhuazhan), inbred-japonica (Xiushui09), and hybrid-japonica (Chunyou84 in 2015 or Yongyou12 in 2016). These cultivars have been widely grown by local farmers. In 2016, hybrid-japonica Yongyou12 replaced hybrid-japonica Chunyou84 because the symptoms of false smut (Ustilaginoidea virens (Cooke) Takah) appeared in 2015.

In terms of our results, the impact of false smut on the RUE is limited because it happened at the grain-filling period and infects the spikelet, so the biomass production and leaf development are seldom affected. Therefore, the data for RUE are valid. The grain yield loss due to the false smut might be less than 5% (Ju Luo, personal communication, 2018). Furthermore, we found the grain yield was still greater in hybrid-japonica Chunyou84 than in the other cultivars even under the stress of false smut. Therefore, the stress of false smut might not be a major factor in yield difference for the 2015 data.

The field experiment utilized a split-plot with block design with three replications. The main plot treatments were planting densities: D1 (10 × 25 cm, 40 hills m⁻²), D2 (15 × 25 cm, 26.7 hills m⁻²), D3 (20 × 25 cm, 20 hills m⁻²), D4 (25 × 25 cm, 16.7 hills m⁻²), and D5 (30 × 25 cm, 13.3 hills m⁻²). The subplot treatment was rice cultivars. The D1 was added in 2016, because the optimal density was not occurred before D2 in 2015.

Seeds were sown on the nursery bed in mid-May, and rice seedlings with three fully expanded leaves were transplanted into the paddy field with one plant per hill (about 25–30 d after sowing). For fertilizer management, total amounts of 142.5 N, 135 K, and 101.3 kg ha⁻¹ P were applied in all of the plots. Approximately 50% of the N fertilizer in the form of compound fertilizer (15–15–15, N–P₂O₅–K₂O) was incorporated as basal fertilizer 1 d before transplanting. The remaining N fertilizer was broadcast as urea at the tillering and booting stages of the rice, comprising 30% and 20% of the total N, respectively. Potassium fertilizer was applied to each plot, with 50% and
50% as basal dressing and topdressing at panicle initiation, respectively. Phosphorous fertilizer was applied to each plot, with 100% as basal dressing in the form of compound fertilizer (15–15–15, N–P₂O₅–K₂O) and superphosphate. Crop management followed the local high-yield practices. Weeds, insects, and diseases were controlled as required to avoid yield loss.

**Sampling and Measurement**

In both years, 12 hills were sampled from each plot at early tillering (15–20 d after transplanting [DAT]), mid-tillering (35–45 DAT), heading, mid-grain filling (15 d after heading), and physiological maturity. The heading stage was defined as the date when 95% of the panicles had emerged, and the plant reached physiological maturity when 95% of spikelets had turned yellow. The growth period was defined as the days from seed sowing to plant physiological maturity.

Samples were separated into plant tissues (green leaf blades, dead leaf blades, culms plus leaf sheaths, and panicle) and oven-dried for 2 h at 105°C to deactivate the enzymes. At 75°C, the constant weight was measured to determine the dry weight of the constituent organs. The LAI was determined with a leaf area meter (LI-3000A, LI-COR, Lincoln, NE). Panicle samples from maturity were hand-threshed to measure the number of filled and unfilled spikelets. The filled spikelets were separated by submerging the hand-threshed spikelets in a NaCl solution with a specific gravity of 1.06 g m⁻³. The filled spikelets were then hulled and oven-dried at 105°C to a constant weight to determine the dry weight of the grain.

**Table 1. Soil properties of the experimental rice paddy field.**

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>P</th>
<th>Available N</th>
<th>Available P</th>
<th>Available K</th>
<th>pH</th>
<th>SOM †</th>
<th>CEC †</th>
</tr>
</thead>
<tbody>
<tr>
<td>2015</td>
<td>0.20</td>
<td>0.05</td>
<td>118.51</td>
<td>9.03</td>
<td>71.46</td>
<td>6.49</td>
<td>3.39</td>
<td>17.58</td>
</tr>
<tr>
<td>2016</td>
<td>0.25</td>
<td>0.05</td>
<td>130.50</td>
<td>8.93</td>
<td>70.65</td>
<td>5.68</td>
<td>3.89</td>
<td>16.42</td>
</tr>
</tbody>
</table>

† SOM, soil organic matter; CEC, cation exchange capacity.
Hills collected from the center part of each 5m² plot were used to determine the grain yield. Unhulled (rough) rice grain was obtained after reaping, threshing, and wind selection. The weight of the rice grain was adjusted to a moisture content of 14%.

Canopy light interception was measured between 1100 and 1300 h at intervals of 7–10 d and 15–20 d before and after heading, respectively, using the AccuPAR LP-80 (LP-80, Decagon Devices Ltd., Pullman, WA). In each plot, the light bar was placed above the canopy and 10–20 cm above the water surface in succession to measure the light intensity above and inside the canopy, respectively. Three measurements were taken within rows and another three between rows. Light interception (LI) was calculated as the percentage of incoming light intensity that was intercepted by the canopy. Intercepted radiation was calculated according to the integration method (Zhang et al., 2009). The RUE through the whole growth period was calculated based on the linear regression method (Monteith and Moss, 1977).

Data Analysis

All of the data were subjected to analysis of variance (ANOVA) using SAS 8.0 statistical software (2003; SAS Institute Inc., Cary, NC). Two-way ANOVA was used to compare the effect of the rice cultivar and planting density on grain yield and RUE for each year. Means of values were subjected to Tukey’s HSD test at the 0.05 probability level. The yield increment to the increasing plant density of each cultivar was evaluated by calculating the slope between the grain yield and planting density, and Pearson correlation analysis was conducted to evaluate the r and p-values for the slope.

RESULTS

Weather Condition

The daily average temperature and solar radiation during the course of study in 2015 and 2016 are shown in Fig. 1. The average daily temperature, average relative humidity (RH), total incident solar radiation (IRS), and total rainfall during the crop season (May to November) were 22.3 and 24.1°C, 77.9 and 77.6%, 2128.4 and 2340.8 MJ m⁻², and 14469.9 and 15283.3 mm in 2015 and 2016, respectively. Compared to 2015, 2016 had greater (10.0%) total IRS, but lower (−15.0%) total rainfall. The difference was even larger during the reproductive stage (August to September). The average daily temperature, average RH, total IRS, and total rainfall during the reproductive stage were 27.3 and 30.2°C, 76.5 and 68.9%, 383.8 and 542.8.2 MJ m⁻², and 268.2.8 and 155.4 mm in 2015 and 2016, respectively. The total IRS during the reproductive stage and the average RH were 41.4% higher and 10.6% lower, respectively, in 2016 than in 2015. Furthermore, the rainfall was 72.6% higher during the reproductive stage in 2015 compared to 2016. Generally, greater RH and rainfall would increase the risk of disease and insects, which has been confirmed in current study in 2015 based on field observation. In summary, the comprehensive weather conditions in 2016 were better than in 2015 for rice growth and yield production.

Grain Yield and Its Components

Both cultivar and planting density affected the grain yield in the 2 yr of the study (Fig. 2). For inbred cultivars, the maximum yields occurred when the planting density increased to D3 (20 hill m⁻²) and D2 (26.7 hill m⁻²) in 2015 and 2016, respectively. For 2015, the highest yields were 7.10 and 7.75 t ha⁻¹ for inbred-indica Huanghuazhan and inbred-japonica Xiushui09, respectively; for 2016, they were 11.10 and 9.20 t ha⁻¹ for inbred-indica Huanghuazhan and inbred-japonica Xiushui09, respectively. The grain yields did not differ significantly along with planting densities, except for inbred-indica Huanghuazhan in 2016, of which the grain yield was significantly greater in D2 than in D5. For hybrid cultivars, the grain yield generally increased along with the tested planting density, while the magnitude varied by year (Fig. 2 and Table 2). On average, the grain yield increased with increasing plant density in hybrid cultivars, except for hybrid-indica Tianyouhuazhan in 2015. The grain yield increased at the rate of 76.6, 108.0, and 138.6 kg Hill⁻¹ ha⁻¹ in hybrid-japonica Chunyou84 (2015), hybrid-indica Tianyouhuazhan (2016), and hybrid-japonica Yongyou12 (2016), respectively, with increasing plant density. For both years, the hybrid cultivars had higher grain yield than the inbred cultivars under dense planting. Grain yields from D2 (26.7 hills m⁻²) were 12.7 to 25.3 and 16.6 to 28.5% greater in hybrid rice than in inbred rice in 2015 and 2016, respectively, while the grain yield from D1 (40 hills m⁻²) was 23.3 to 46.9% greater in 2016. Notably, significant yearly difference in grain yield was observed between 2015 and 2016, being 35.89% greater in 2016 than in 2015.

Compared to 2016, the yield loss in 2015 might be attributed to (i) the lower total amount of incident radiation during the growth season (−10%) and reproductive stage (−41.4%); (ii) the increased RH (+10.6%) and total rainfall (+72.6%); and (iii) the greater damage from disease and insects induced by the increased RH and the amount of rainfall. The results indicated
that the unfavorable climate would suppress the yield more in the dense planting condition.

The interaction effect of plant density and cultivar on panicle m\(^{-2}\), grain filling rate, and grain weight was not significant (Table 3). The panicle m\(^{-2}\) was generally improved along with increasing planting density in both years. For 2015, the panicle number reached the highest value (243.7 panicle m\(^{-2}\)) in D3, while the highest value (312.5 panicle m\(^{-2}\)) occurred in D1 for 2016. In addition, the number of panicles m\(^{-2}\) was greater in the inbred cultivars than in the hybrid ones. However, the difference in panicle m\(^{-2}\) varied with cultivar types, about 3.7 to 6.2 and 21.8 to 45.7% higher for indica and japonica cultivars, respectively. The grain setting decreased with the increasing planting density in 2015, but no significant difference in planting density was found in 2016. Furthermore, the difference between inbred and hybrid was significant, being 7.2 and 20.2% greater in inbred cultivars than in hybrid ones in 2015 and 2016, respectively.

The grains panicle\(^{-1}\) was affected by both planting density and rice cultivar. For inbred cultivars, it was unchanged regardless of the increasing planting density in both years (Fig. 3). However, increasing planting density generally reduced the grains panicle\(^{-1}\) by 8.5 to 22.5% in hybrid cultivars, except for hybrid-indica Tianyouhuazhan in 2015, in which no significant difference was found (Fig. 3). In addition, hybrid cultivars had more grains panicle\(^{-1}\) in contrast to inbred cultivars in both years, being 11.6 to 47.8% in indica cultivars and 46.7 to 232.0% in japonica cultivars across the planting densities.

In summary, the average grain yield was 8.3 to 22.4% greater in the hybrid groups than in the inbred ones for both years (Fig. 2). The hybrid cultivars were characterized as having fewer panicles m\(^{-2}\) and inferior grain setting rate, but they compensated with higher grain number per panicle (18.9 to 187.1%) in contrast to the inbred cultivars across planting densities. However, an interaction effect of cultivar and planting density was observed in the grains panicle\(^{-1}\), which decreased in the hybrid cultivars (except for hybrid-indica Tianyouhuazhan in 2015) and remained consistent in the inbred groups along with the increasing planting density (Fig. 3).

**Radiation Use Efficiency and Its Related Parameters**

In general, both planting density and cultivar affected the RUE (Table 4). The RUE increased with increasing planting density in both years, except for hybrid-indica Tianyouhuazhan, which had a constant RUE across planting densities.

<table>
<thead>
<tr>
<th>Year</th>
<th>Rice type</th>
<th>Cultivar</th>
<th>Slope</th>
<th>(r)</th>
<th>(p)-value</th>
<th>Slope</th>
<th>(r)</th>
<th>(p)-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Grain yield</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>kg m(^{-2})</td>
<td></td>
<td></td>
<td>m(^{-2})</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2015</td>
<td>Hybrid</td>
<td>Tianyouhuazhan</td>
<td>24.3</td>
<td>0.272</td>
<td>0.393</td>
<td>3.1</td>
<td>0.367</td>
<td>0.240</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chunyou84</td>
<td>76.6</td>
<td>0.675</td>
<td>0.016</td>
<td>14.6</td>
<td>0.905</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2016</td>
<td>Inbred</td>
<td>Xiushui09</td>
<td>29.4</td>
<td>0.463</td>
<td>0.129</td>
<td>18.1</td>
<td>0.812</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Hybrid</td>
<td>Tianyouhuazhan</td>
<td>108.0</td>
<td>0.859</td>
<td>&lt;0.0001</td>
<td>1.1</td>
<td>0.085</td>
<td>0.765</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chunyou84</td>
<td>138.6</td>
<td>0.920</td>
<td>&lt;0.0001</td>
<td>8.1</td>
<td>0.755</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Inbred</td>
<td>Xiushui09</td>
<td>57.5</td>
<td>0.526</td>
<td>0.044</td>
<td>10.5</td>
<td>0.870</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

### Table 2. Grain yield and RUE related to plant density with different cultivars in 2015 and 2016.†

<table>
<thead>
<tr>
<th>Variety (V)</th>
<th>**</th>
<th>**</th>
<th>**</th>
<th>**</th>
<th>**</th>
<th>**</th>
<th>**</th>
<th>**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Planting density (D)</td>
<td>**</td>
<td>**</td>
<td>*</td>
<td>ns§</td>
<td>**</td>
<td>*</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

**Significant at the 0.05 level.**

**Significant at the 0.01 level.**

† D1–D5 refer to planting densities of 40, 26.7, 20, 16.7, and 13.3 hills m\(^{-2}\), respectively.

‡ Within a column, means followed by the same letters are not significantly different according to Tukey’s HSD test (\(p < 0.05\)).

§ ns, not significant.
for which no significant difference in RUE was found among planting densities (Fig. 4). The effect of the cultivar on RUE varied with planting density and year. For japonica rice, the average RUE was consistently higher in the hybrid (Chunyou84 or Yongyou12) than in the inbred cultivars (Xiushui09), being 8.1 to 14.5 and 4.0 to 11.5% higher in 2015 and 2016, respectively. For indica rice, the difference in RUE between hybrid and inbred cultivar varied within years. Compared to the hybrid-indica Tianyouhuazhan, higher RUE was found in inbred-indica Huanghuazhan (inbred) in 2015, while there was minimal varietal difference among cultivars in 2016 in the dense planting condition (D1 and/or D2).

Owing to the longer growth duration (about 40 d) of japonica cultivars compared to indica ones, the result in incident radiation was similar to that in RUE. The incident radiation measurements were also 20.7 and 11.5% higher in 2016 than in 2015 for indica and japonica cultivars, respectively (Table 4). The total aboveground dry weight improved with increasing planting density, except for hybrid-indica Tianyouhuazhan, whose total aboveground dry weight did not differ significantly among the planting densities in both years. In 2015, hybrid-japonica Chunyou84 had the highest total dry weight, followed by inbred-japonica Xiushui09, hybrid-indica Tianyouhuazhan, and inbred-indica Huanghuazhan. In 2016, the hybrid cultivars had more dry weight than the inbred cultivars: 24.2 and 14.5% higher in the japonica and indica groups, respectively. The intercepted radiation across the cultivars increased at the rates of 5.0 and 3.9 MJ Δhill−1 m−2 in 2015 and 2016, respectively, with the increasing planting density. The intercepted radiations were, on average, 6.3 and 11.5% greater in hybrid cultivars than in inbred ones in the indica and japonica groups, respectively. Similar results were also found for the light intercepted percentage, except for the hybrid-indica Tianyouhuazhan in 2015.

**DISCUSSION**

**Effect of Planting Density on Hybrid Rice**

Numerous studies have reported the effect of planting density on the high yield of elite rice cultivars. Most of these studies focused on quantifying the optimal density for a specific cultivar in certain practices and environments. High plant density might increase interplant competition for resources, and it has been reported to result in less grain yield per plant (Nakano et al., 2012; Rossini et al., 2011; Shi et al., 2016; Wang et al., 2015). However, there is a great difference in the optimal density in the reported literatures. Lin et al. (2009) investigated the hybrid rice cultivars Guodao-6 and Eryou 7954 and found that both had the optimal yield output at a density of 15 plants m−2. Li et al. (2015) found that the grain yield of early season rice (Luliangyou 996) increased with planting density, but the late season grain yield (cultivar Ganxin 688) was higher with medium planting density (15–20 hills m−2). Wang et al. (2014) also found that a higher yield was obtained at the planting space of 25 × 17 cm (about 23 hills m−2) with Guodao-6 in direct seeding rice. However, recent studies have reported that the highest yield was achieved at the maximum tested planting density. Teng et al. (2016) evaluated four planting densities.
from 13.3 to 26.7 hills m\(^{-2}\)) in machine-transplanted hybrid rice and found that the grain yield was highest in the densest treatment. Similarly, Jiang et al. (2017) tested three planting densities (12.0, 16.5, and 22.5 hills m\(^{-2}\)), and observed the highest grain yield (10.87–11.72 t ha\(^{-1}\)) from high-density planting. These reports are partly in agreement with our results that hybrid rice might be more suitable for the dense planting.

However, we found that the grain yield increase of hybrid rice under dense planting was largely dependent on the climate (Fig. 2). In 2016, the growth of hybrid rice under high planting density (26.7–40 hills m\(^{-2}\)) resulted in a remarkable yield superior to that under low planting density (13.3 hills m\(^{-2}\)). However, the grain yield of hybrid rice stagnated with increasing density in 2015. This might be attributed to the poor climate in 2015, which included low solar radiation and high RH and rainfall during the reproductive stage. Dense planting might also have raised the risk of yield loss, such as by disease and insects (Peng et al., 2009; Wang and Peng, 2017) and partly resulted in the yield loss at harvest. We speculate that the unfavorable climate not only limited the yield potential but also increased the risk of damage from diseases and insects and therefore suppressed the yield performance more in the dense planting condition.

Canopy Light Interception and Radiation Use Efficiency

Although various factors, including planting method, soil nutrient supply, water irrigation, and pest and insect control are expected to influence rice grain yield, light is considered to be the most important environmental factor that influences the growth and grain yield performance in a rice paddy field (Farque et al., 2001; Peng, 2000; San-Oh et al., 2006; Zhang et al., 2015). Biomass is the product of intercepted solar radiation by the canopy and RUE, and the former is determined by incident solar radiation and light interception rate (De Costa et al., 2006). The light interception of a crop canopy is very important for canopy photosynthetic assimilation (San-Oh et al., 2008). Our study found that both cultivar and planting density affected the canopy light interception (Table 4).

Table 4. Radiation use efficiency and its related parameters for rice varieties grown under increasing planting density.

<table>
<thead>
<tr>
<th>Density/cultivar</th>
<th>2015</th>
<th>2016</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total dry wt.</td>
<td>Incident radiation</td>
</tr>
<tr>
<td></td>
<td>g m(^{-2})</td>
<td>MJ m(^{-2})</td>
</tr>
<tr>
<td>D1†</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>D2</td>
<td>1684a</td>
<td>1639</td>
</tr>
<tr>
<td>D3</td>
<td>1622b</td>
<td>1639</td>
</tr>
<tr>
<td>D4</td>
<td>1459c</td>
<td>1639</td>
</tr>
<tr>
<td>D5</td>
<td>1426c</td>
<td>1639</td>
</tr>
<tr>
<td>Chunyou84</td>
<td>1880a</td>
<td>1818</td>
</tr>
<tr>
<td>Yongyou12</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Tianyouhuazhan</td>
<td>1349c</td>
<td>1461</td>
</tr>
<tr>
<td>Huanghuazhan</td>
<td>1338c</td>
<td>1461</td>
</tr>
<tr>
<td>Xiushui09</td>
<td>1619b</td>
<td>1818</td>
</tr>
</tbody>
</table>

ANOVA

<table>
<thead>
<tr>
<th>Variety (V)</th>
<th>**</th>
<th>**</th>
<th>**</th>
<th>**</th>
<th>**</th>
<th>*</th>
<th>**</th>
<th>**</th>
<th>**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Planting density (D)</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>ns§</td>
<td>ns§</td>
<td>ns§</td>
<td></td>
</tr>
</tbody>
</table>

* Significant at the 0.05 level.  
** Significant at the 0.01 level.  
† D1–D5 refer to planting densities of 40, 26.7, 20, 16.7, and 13.3 hills m\(^{-2}\), respectively.  
‡ Within a column, means followed by the same letters are not significantly different according to Tukey’s HSD test (\(p < 0.05\)).  
§ ns, not significant.

From the data, it is evident that the yield gain was significant for planting density under high planting density (26.7–40 hills m\(^{-2}\)) and the yield gain was higher at high planting density (26.7–40 hills m\(^{-2}\)). However, the yield gain was not significant for planting density under high planting density (13.3 hills m\(^{-2}\)).
The average light intercepted rate and intercepted radiation were 1.7 to 8.2 and 3.7 to 12.9% higher in hybrid cultivars than in inbred ones, respectively. Meanwhile, the average light interception and intercepted radiation increased along with the planting density at the rate of 0.24–0.32% Δhilf−1 and 3.9–5.0 MJ m−2 Δhilf−1, respectively (Table 4). These results were in agreement with those of previous studies (Chen et al., 2003; Gu et al., 2017; San-Oh et al., 2006).

The average canopy light interception, defined as the ratio of accumulated intercepted to incident solar radiation during the growth period, could be significantly affected by the accumulated intercepted solar radiation pre- and post-canopy closure. When the LAI is smaller than the critical value or significant mutual shading does not occur (San-Oh et al., 2006), so-called pre-canopy closure, the rate of canopy LI is significantly affected by the LAI, and the cumulated intercepted solar radiation is the product of the averaged LI and the length of this period. Also, after canopy closure, the LI rate depends on the penetration of solar radiation into the canopy (Peng, 2000), which is affected by the amount and distribution of leaf area and leaf angles in a crop canopy (Stewart et al., 2003). The former might be the dominant factor in the greater average LI in dense planting. Compared to sparse planting, the rice plant growth under dense planting had greater LAI (Supplemental Table S2) and shorter tillering duration (Supplemental Table S3), which minimized the waste of incident solar radiation pre-canopy closure and increased the cumulated intercepted solar radiation for a similar growth period.

However, the source of varietal difference of LI might be varied between japonica and indica cultivars. For japonica cultivars (hybrid-japonica Chunyou84, hybrid-japonica Yongyou12, and inbred-japonica Xishui09), a greater LI in both pre- and post-canopy closure (Supplemental Table S3) and a shorter tillering duration (Supplemental Table S3) result in a greater LI in hybrid cultivars than in inbred ones (Table 4 and Fig. 4). However, for indica cultivars, the LAIs were higher in hybrid cultivars than in inbred ones at the early and middle tillering stage, but unchanged at the flowering stage (Supplemental Table S2). These results suggest a smaller canopy variation between hybrid and inbred cultivars in indica rice than in japonica rice. However, only one cultivar was used in the current research, and further study is needed to confirm this conclusion. In addition, the upright leaves in hybrid-japonica Chunyou84 and hybrid-japonica Yongyou12 permit sunlight to be transmitted through the crop canopy and yield a small extinction coefficient at post-canopy closure (Gu et al., 2017). The smaller extinction coefficient indicates a more uniform light distribution in the canopy (Gu et al., 2017; San-Oh et al., 2006) and leads to a smaller leaf angle and deeper light penetration (Gu et al., 2017).

In the current research, both dense planting and hybrid cultivars (indica or japonica group) are correlated with an increase in RUE, except for hybrid-japonica Tianyouhuazhan in 2015 (Fig. 4). The top leaves of the plant were tended to be upright when the planting density increased, which resulted in smaller leaf angles and extinction coefficient of the canopy (Gu et al., 2017). The uniform canopy structure minimizes the saturation of upper leaves and light starvation of the lower leaves (Peng et al., 2008) and leads to higher quantum efficiency (Ph/photosynthetically active radiation [PAR]) and PAR-saturation of canopy photosynthesis at higher PAR (San-Oh et al., 2008). However, the lack of response of RUE to the planting density in hybrid-indica Tianyouhuazhan might be related to the leaf characteristic traits or tillering capacity, and further research is needed to locate the source of the insensitivity. Higher RUE was generally achieved by either enhancing the leaf photosynthesis with similar light interception or decreasing the maintained respiration to reduce biomass loss (Huang et al., 2016; Stewart et al., 2003). Hybrid cultivars are known to have great biomass production, generally attributed to the rapid tillering production rate and erect leaves that improve the LAI, make the light distribution uniform, and increase light use efficiency in the canopy (Huang et al., 2017; Li et al., 2016; Md et al., 2013). However, our results suggested that superior light interception of indica or japonica hybrid cultivars might result from the enhanced leaf morphology rather than tillering capacity, especially under dense planting. For example, reducing the self-shading among leaves (erect leaves) would allow more radiation to penetrate into the lower parts of the canopy (Liu et al., 2016; Wang and Peng, 2017). Therefore, the current results indicate that breeding cultivars suitable for dense planting should focus on leaf morphology rather than tillering capacity to improve light use efficiency.

CONCLUSIONS

Both cultivar and planting density affect grain yield and RUE. Our study showed that the grain yield increased with increasing planting density in hybrid rice. However, the yield performance was significantly affected by the weather conditions. We speculate that unfavorable climate not only limited the yield potential but also increased the risk of diseases and insects and therefore suppressed yield performance more in the dense planting condition. Greater plant density leads to an increase in RUE, perhaps because the top leaves of the plant were tended to be upright when the planting density increased, which resulted in smaller leaf angles and extinction coefficient of the canopy. The current research suggests that it is possible to close the yield gap for a certain area by using hybrid cultivars under dense planting, but there was a greater risk of yield loss caused by weather conditions.

ACKNOWLEDGMENTS

This research was supported in part by grants from the National Key Research and Development Program of China (2016YFD0300208-02, 2016YFD0300108), the National Natural Science Foundation of China (31671638), the National Rice Industry Technology System (CARS-01-04A), and the MOA Special Fund for Agro-scientific Research in the Public Interest of China (201203096).

SUPPLEMENTAL MATERIAL

Table S1. Economic profit of cultivars under dense planting conditions.
Table S2. Specific leaf area and leaf area index of rice cultivars grown under increasing planting density.
Table S3. Tillering traits of rice cultivars grown under increasing planting density.

REFERENCES


