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Yield potential and radiation use efficiency of "super" hybrid rice grown under subtropical conditions

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ABSTRACT

China's "super" hybrid rice breeding project has developed many new varieties using a combination of the ideotype approach and intersubspecific heterosis. It is controversial whether these "super" hybrid varieties have increased the yield potential of irrigated rice. This study was conducted to compare grain yield and yield attributes among "super" hybrid, ordinary hybrid, and inbred varieties. Field experiments were done in Liuyang (moderate-yielding site) and Guidong (high-yielding site) counties, Hunan Province, China, in 2007 and 2008. Two varieties from each varietal group were grown in each field experiment under moderate and high N rates. Grain yield, yield components, aboveground total dry weight, harvest index, total N uptake, and crop radiation use efficiency (RUE) were measured for each variety. A significant difference in grain yield was observed among the varieties and varietal groups but not between the two N rates. "Super" hybrid varieties have increased rice yield potential by 12% compared with ordinary hybrid and inbred varieties. The higher grain yield of "super" hybrid varieties was attributed to improvement in both source and sink. "Super" hybrid varieties produced more biomass than ordinary hybrid and inbred varieties. Long growth duration and high accumulated incident radiation were partially responsible for high biomass production for the "super" hybrid varieties. "Super" hybrid varieties had significantly larger panicle size (spikelets per panicle) than ordinary hybrid and inbred varieties, which resulted in larger sink size (spikelets per m^2). Crop RUE did not explain the yield superiority of "super" hybrid rice. Our study suggests that "super" hybrid rice varieties do not necessarily require more N fertilizer to produce high grain yield.

1. Introduction

In the past 10 years, the growth of rice yield has dropped below 1% per year worldwide, but a rice yield increase of more than 1.2% per year will be required to meet the growing demand for food that will result from population growth and economic development in the next decade (Normile, 2008). To achieve this goal, great efforts should be made to breed new rice varieties with higher yield potential in order to enhance average farm yields (Peng et al., 2008).

The development of semi-dwarf varieties in the late 1950s in China (Huang, 2001) and early 1960s at the International Rice Research Institute (Chandler, 1982) dramatically increased the yield potential of irrigated rice. The yield potential of irrigated rice was further increased by the development of hybrid rice in 1976 in China (Yuan et al., 1994). Peng et al. (1999) reported that indica hybrid rice has increased yield potential by 9% over the best inbred cultivars in tropical irrigated lowlands.

In 1996, China established a nationwide mega-project on the development of "super" rice based on the ideotype concept (Cheng et al., 1998). In 1998, Prof. Longping Yuan proposed a strategy for developing "super" hybrid rice by combining an ideotype approach with the use of intersubspecific heterosis (Yuan, 2001; Wu, 2009). Up to 2001, 7 inbred and 44 hybrid varieties that met "super" rice criteria were released by provincial or national seed boards (Min et al., 2002). In 1998–2005, 34 commercially released "super" hybrid rice varieties were grown on a total area of 13.5 million ha and they produced an additional 6.7 million tonnes of rough rice in China (Cheng et al., 2007).

"Super" hybrid rice has the following morphological traits: moderate tillering capacity (270–300 panicles m^{-2}); heavy (5 g per panicle) and drooping panicles at maturity; panicle height of 60 cm (from soil surface to the top of panicles with panicles in natural position) at maturity; and long, erect, thick, narrow, and V-shaped top three leaves (Yuan, 2001). It was reported in several field studies that "super" hybrid rice varieties such as Liangyou-

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Table 1
Information about varieties used in the experiment.

Group	Variety	Type	Year of release	Female parent	Male parent
"Super" hybrid[a]	Liangyoupeijiu	Intermediate[b]	1999	Pei'ai64S	Yangdao 6
	Liangyou 293[c]	Intermediate	2006	P88S	0293
	Y-liangyou 1[c]	Indica	2006	Y58S	Yangdao 6
Ordinary hybrid[a]	Shanyou 63	Indica	1984	Zhenshan97A	Minghui 63
	II-you 838	Indica	1995	II-32A	Shuhui 838
Inbred	Yangdao 6	Indica	1997	Yangdao 4	Yan 3021
	Huanghuazhan	Indica	2005	Huangxinzhan	Fenghuazhan

[a] The "super" and ordinary hybrid varieties were developed using the two- and three-line method, respectively.
[b] The intermediate type between indica and japonica.
[c] Liangyou 293 and Y-liangyou 1 were used in 2007 and 2008, respectively.

peijiu and Xieyou 9308 produced 8–20% higher grain yield than ordinary hybrid check varieties such as Shanyou 63 and Xieyou 63 (Zong et al., 2000; Wang et al., 2002; Zhu et al., 2002). The high grain yield of "super" hybrid rice was attributed to more biomass production (Zong et al., 2000), high leaf area index (LAI) during the ripening phase (Lin et al., 2002), large leaf area duration (Katsura et al., 2007), and high productive tiller percentage (Wang et al., 2002). It was also reported that "super" hybrid rice had a high photosynthetic rate at the single-leaf level, slow leaf senescence, and tolerance of photoinhibition compared with ordinary hybrid rice (Chen et al., 2002; Wang et al., 2005, 2006).

Crop radiation use efficiency (RUE) is defined as the amount of biomass accumulated per unit solar radiation intercepted (Monteith, 1977). Both leaf photosynthetic rate and leaf N content affect crop RUE (Sinclair and Horie, 1989). Determining RUE is an important approach for understanding crop growth and yield (Sinclair and Muchow, 1999). Katsura et al. (2007, 2008) reported that RUE did not explain the yield superiority of Liangyoupeijiu compared with high-yielding Japanese rice varieties in Kyoto, Japan, or in Yunan, China.

Yield potential is defined as the yield of a variety when grown in environments to which it is adapted; with nutrients and water non-limiting; and with pests, diseases, weeds, lodging, and other stresses effectively controlled (Evans, 1993). Previous studies on yield and yield attributes of "super" hybrid rice were conducted mostly in one location, in a single season, at one N rate, or using only one "super" hybrid variety in comparison with a check variety. It is difficult to draw a concrete conclusion on the difference in yield potential between "super" hybrid rice and other varieties in these experiments. In our current study, we compared "super" hybrid rice varieties with ordinary hybrid and inbred varieties under moderate and high N rates at two locations and in 2 years. The objectives of this study were (1) to determine how much increase in rice yield potential was achieved by the development of "super" hybrid rice varieties, (2) to identify the key facts that contributed to the high grain yield of "super" hybrid rice, and (3) to compare radiation use efficiency among "super" hybrid, ordinary hybrid, and inbred varieties.

2. Materials and methods

Experiments were conducted in 2007 and 2008 in Liuyang (28°09′N, 113°37′E, 43 m asl) and Guidong (25°08′N, 113°02′E, 724 m asl) counties, Hunan Province, China. The soil of the Liuyang site was a clay with the following properties: pH 5.7, 7.6 g kg^{-1} organic matter, 157 mg kg^{-1} alkali-hydrolyzale N, 11.8 mg kg^{-1} available P, and 225 mg kg^{-1} available K. The soil of the Guidong site was a sandy loam with the following properties: pH 5.2, 12.3 g kg^{-1} organic matter, 237 mg kg^{-1} alkali-hydrolyzale N, 17.1 mg kg^{-1} available P, and 139 mg kg^{-1} available K. 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 varieties as subplots. The experiment was replicated four times and subplot size was 30 m^2. Two N treatments were moderate and high N rates. In the moderate N rate, 75, 30, 30, and 15 kg N ha^{-1} was applied at basal, midtillering, panicle initiation, and booting, respectively. In the high N rate, 125, 50, 50, and 25 kg N ha^{-1} was applied at basal, midtillering, panicle initiation, and booting, respectively. No N topdressing was done at booting in Liuyang in 2007. Total N rate was 135 and 225 kg ha^{-1} for the moderate and high N rates, respectively, in Liuyang in 2007. In the other three experiments, total N rate was 150 and 250 kg ha^{-1} for the moderate and high N rates, respectively.

Six varieties were used in each experiment. They belong to three groups: "super" hybrid rice (Liangyoupeijiu and Liangyou 293), ordinary hybrid rice (Shanyou 63 and II-you 838), and inbred varieties (Yangdao 6 and Huanghuazhan). In 2008, Y-liangyou 1 replaced Liangyou 293 because symptoms of blast disease appeared in some replications with this variety in Guidong in 2007. These varieties have been widely grown by rice farmers in China. Detailed information about them is given in Table 1.

Pre-germinated seeds were sown in a seedbed. Twenty- and 23-day-old seedlings were transplanted on 11 June 2007 and 15 June 2008 in Liuyang, respectively. Thirty-two- and 31-day-old seedlings were transplanted on 21 May 2007 and 23 May 2008 in Guidong, respectively. Transplanting was done at a hill spacing of 0.23 m × 0.23 m with two seedlings per hill. Phosphorus (50 kg P ha^{-1}) and zinc (5 kg Zn ha^{-1}) were applied and incorporated in all subplots 1 day before transplanting. Potassium (100 kg K ha^{-1}) was split equally at basal and panicle initiation. Crop management followed the standard cultural practices. The experimental field was kept flooded from transplanting until 10 days before maturity. Insects were intensively controlled by chemicals to avoid biomass and yield loss.

Plants were sampled from a 0.529-m^2 area (10 hills) at flowering to determine LAI with a leaf area meter (LI-3000A, LI-COR, Lincoln, NE, USA). At maturity, 10 hills were sampled diagonally from a 5-m^2 harvest area to determine aboveground total dry weight, harvest index, and yield components. Panicle number was counted in each hill to determine panicle number per m^2. Plants were separated into straw and panicles. Straw dry weight was determined after oven-drying at 70 °C to constant weight. Panicles were hand-threshed and the filled spikelets were separated from unfilled spikelets by submerging them in tap water. Three subsamples of 30 g of filled spikelets and 3 g of unfilled spikelets were taken to count the number of spikelets. Dry weights of rachis and filled and unfilled spikelets were determined after oven-drying at 70 °C to constant weight. Aboveground total dry weight was the total dry matter of straw, rachis, and filled and unfilled spikelets. Spikelets per panicle, grain-filling percentage (100 × filled spikelet number/total spikelet number), and harvest index (100 × filled spikelet weight/aboveground total dry weight) were calculated. Grain yield was determined from a 5-m^2 area in each plot and adjusted to the standard moisture content of 0.14 g H_2O g^{-1}. Nitrogen concentrations of straw, rachis, and filled and unfilled spikelets were determined by micro-Kjeldahl digestion, distillation, and titration (Bremner and Mulvaney, 1982) to calculate aboveground total N uptake.

Canopy light interception was measured between 1100 and 1300 h at midtillering, panicle initiation, booting, flowering, 15 days after flowering, and maturity using the SunScan Canopy Analysis System (Delta-T Devices Ltd., Burwell, Cambridge, UK). In each plot, 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 accumulated 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) × accumulated incoming radiation during the growth period]. Intercepted radiation during the entire growing season was the summation of intercepted radiation during each growth period. Radiation use efficiency (RUE) was calculated as the ratio of aboveground total dry weight to intercepted radiation during the entire growing season. Solar radiation and minimum and maximum temperatures were recorded daily using a Vantage Pro2 weather station (Davis Instruments Corp., Hayward, CA, USA).

Data were analyzed following analysis of variance (SAS Institute, 2003) and means of varieties were compared based on the least significant difference test (LSD) at the 0.05 probability level for each location and year.

3. Results

Average temperatures during the growing season in Liuyang were 2.8–4.1 °C higher than those in Guidong (Fig. 1). For maximum temperature, seasonal mean values of Liuyang vs. Guidong were 31.0 °C vs. 28.2 °C in 2007 and 32.3 °C vs. 28.3 °C in 2008. Seasonal average minimum temperatures were 23.5 and 20.0 °C in 2007 and 24.4 and 20.3 °C in 2008 for Liuyang and Guidong, respectively. Temperatures in Guidong were similar between 2007 and 2008, whereas 2008 was slightly hotter than 2007 in Liuyang. There was about a 10% difference in average daily solar radiation during the growing season between the two sites. Seasonal average daily radiation was 15.0 and 13.6 MJ m^{-2} day^{-1} for Liuyang and Guidong, respectively. The difference in seasonal average daily radiation between the 2 years was very small.

The varietal difference in grain yield was significant in all four experiments (Table 2). In Liuyang, Liangyoupeijiu produced the highest grain yield regardless of N rates in both years. Y-liangyou 1 produced a maximum grain yield of 11.49 t ha^{-1} in Guidong in 2008. In all four experiments, the lowest grain yield was observed in ordinary hybrid or inbred varieties. "Super" hybrid varieties as a group had higher grain yield than ordinary hybrid or inbred varieties consistently across location, year, and N rate. There was an insignificant difference in grain yield between ordinary hybrid and inbred varieties. In Guidong, average grain yield across two N rates and years was 11.15, 10.03, and 9.97 t ha^{-1} for "super" hybrid, ordinary hybrid, and inbred varieties, respectively.

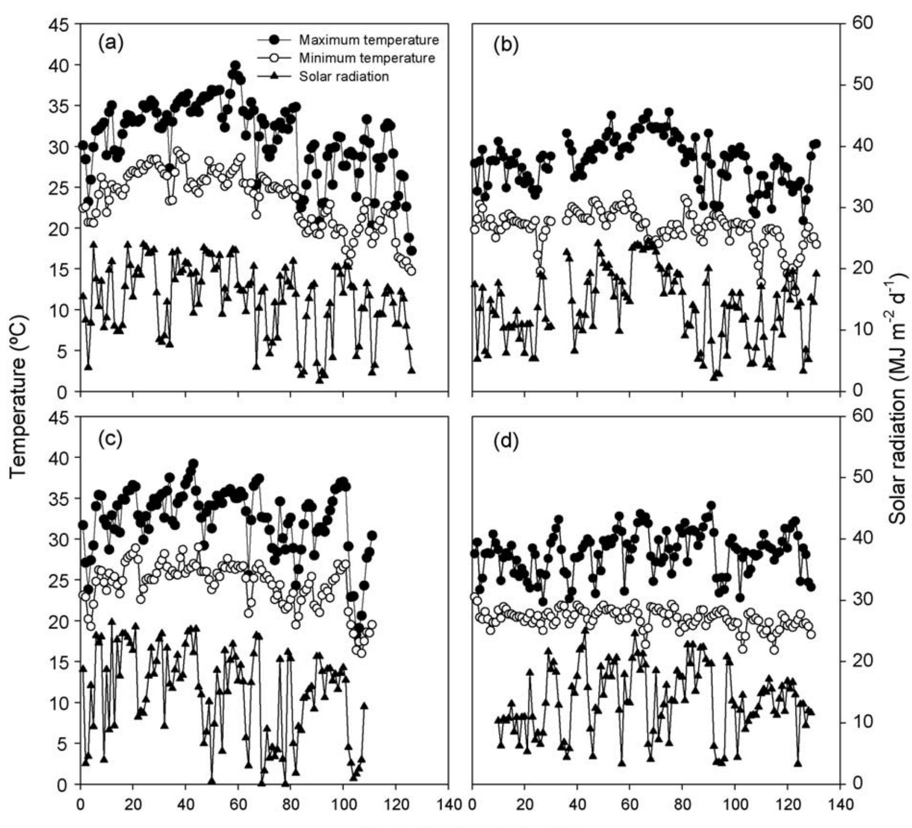

Fig. 1. Daily maximum and minimum temperatures and solar radiation during rice-growing season in Liuyang in 2007 (a), Guidong in 2007 (b), Liuyang in 2008 (c), and Guidong in 2008 (d). Liuyang and Guidong are two counties in Hunan Province, China.

Table 2
Grain yield (t ha^{-1}) of six rice varieties grown under two N rates in Liuyang and Guidong counties, Hunan Province, China, in 2007 and 2008.

Variety	Liuyang		Guidong	
	Moderate N[a]	High N	Moderate N	High N
2007				
Liangyoupeijiu	8.85 a	9.15 a	11.22 a	10.92 a
Liangyou 293	8.55 ab	9.01 ab	10.96 ab	10.96 a
Shanyou 63	8.29 b	7.84 de	9.89 b	10.17 ab
II-you 838	8.14 b	7.48 e	9.89 b	9.73 b
Yangdao 6	8.42 ab	8.34 cd	9.93 b	10.06 ab
Huanghuazhan	8.13 b	8.45 bc	10.16 ab	9.62 b
Mean	8.40	8.38	10.34	10.24
Analysis of variance				
N rate (A)	NS		NS	
Variety (B)	**		*	
A × B	*		NS	
2008				
Liangyoupeijiu	9.85 a	10.15 a	11.09 a	11.08 ab
Y-liangyou 1	9.78 a	9.86 a	11.48 a	11.49 a
Shanyou 63	8.17 b	8.00 c	10.24 b	9.88 c
II-you 838	8.52 b	8.00 c	10.45 b	10.01 c
Yangdao 6	8.64 b	8.82 b	9.59 c	9.77 c
Huanghuazhan	8.75 b	8.75 b	10.20 b	10.42 bc
Mean	8.95	8.93	10.51	10.44
Analysis of variance				
N rate (A)	NS		NS	
Variety (B)	**		**	
A × B	NS		NS	

Within a column for each year, means followed by the same letters are not significantly different according to LSD (0.05).
[a] Total N rate was 135 and 225 kg ha^{-1} for the moderate and high N rates, respectively, in Liuyang in 2007. In the other three experiments, total N rate was 150 and 250 kg ha^{-1} for the moderate and high N rates, respectively.
* Significance at the 0.05 level based on analysis of variance.
** Significance at the 0.01 level based on analysis of variance.
NS denotes non-significance based on analysis of variance.

Averaged across all four experiments and two N rates, "super" hybrid varieties produced 14% higher yield than ordinary hybrid varieties and 11% higher yield than inbred varieties. Grain yield was 23% and 17% higher in Guidong than in Liuyang in 2007 and 2008, respectively. The difference in grain yield between the 2 years was relatively small, especially in Guidong. Nitrogen rate had an insignificant effect on grain yield in all four experiments. The interactive effect between N and variety on grain yield was significant only in one out of the four experiments. Therefore, mean data across two N rates were presented in subsequent tables.

Among all varieties, Huanghuazhan had the highest panicles per m^2 (Tables 3 and 4). There was no consistent difference in panicles per m^2 among the three varietal groups. The "super" hybrid varieties had a moderate number of panicles compared with other varieties. Guidong produced about 10% more panicles than Liuyang. "Super" hybrid varieties had an average of 195 spikelets per panicle, which was 21% and 16% higher than ordinary hybrid and inbred varieties, respectively. An insignificant difference in panicle size (spikelets panicle^{-1}) was observed between the two sites. The "super" hybrid varieties and Huanghuazhan produced significantly more spikelets per m^2 than the other three varieties. Sink size (spikelets m^{-2}) was 8–13% higher in Guidong than in Liuyang. In general, grain-filling percentage was the lowest in Shanyou 63 and highest in Huanghuazhan. There was no consistent difference in grain-filling percentage among the three varietal groups. The average grain-filling percentage was slightly higher in Guidong than in Liuyang. A consistent varietal difference was observed in grain weight. Yangdao 6 had the highest grain weight, followed by the two ordinary hybrid varieties, two "super" hybrid varieties, and Huanghuazhan.

"Super" hybrid varieties had longer growth duration than the other varieties (Tables 5 and 6). Huanghuazhan had the shortest growth duration. Consistently longer growth duration was observed in Guidong than in Liuyang. Ordinary hybrid varieties generally had the highest LAI at flowering. A higher LAI in Guidong than in Liuyang occurred only in 2007. The varietal difference in harvest index and aboveground total N uptake was small and inconsistent across experiments. There was an inconsistent difference in harvest index and N uptake among the varietal groups. Guidong had about 30% higher total N uptake than Liuyang.

"Super" hybrids had slightly higher accumulated incident radiation than the other varieties due to their long growth duration (Tables 7 and 8). However, intercepted radiation was not necessarily higher in "super" hybrid varieties because their canopy light interception was lower than that of ordinary hybrid varieties. The higher canopy light interception of ordinary hybrid varieties was due to their higher LAI. There was an inconsistent difference in accumulated incident and intercepted radiation between the two sites. Guidong generally had higher canopy light interception than Liuyang. On average, "super" hybrid varieties produced 8% higher aboveground total dry weight than ordinary hybrid and inbred varieties. There was no difference in total dry weight between ordinary hybrid and inbred varieties. Total dry weight was 17–20% higher in Guidong than in Liuyang. Ordinary hybrid varieties had 10–12% lower RUE than the other two varietal groups. The

Table 3
Yield components of six rice varieties grown in Liuyang and Guidong counties, Hunan Province, China, in 2007. Data are the means across two N rates.

Variety	Panicles m^{-2}	Spikelets panicle^{-1}	Spikelets m^{-2} ($\times 10^3$)	Grain filling (%)	Grain weight (mg)
Liuyang					
Liangyoupeijiu	260.0 b	192.2 a	49.9 a	72.0 bc	23.0 c
Liangyou 293	251.9 bc	190.0 a	47.8 a	72.7 b	22.7 c
Shanyou 63	237.8 c	158.1 c	37.5 b	69.4 c	26.5 a
II-you 838	207.9 d	172.6 b	35.7 b	74.5 b	25.8 b
Yangdao 6	209.8 d	168.8 bc	35.4 b	80.2 a	26.3 a
Huanghuazhan	301.4 a	166.8 bc	49.8 a	78.7 a	18.8 d
Mean	244.8	174.7	42.7	74.6	23.9
Guidong					
Liangyoupeijiu	264.8 b	195.3 a	51.5 a	76.8 bc	24.2 d
Liangyou 293	262.5 b	194.3 a	51.0 a	77.5 bc	24.5 d
Shanyou 63	292.9 a	149.3 e	43.6 bc	75.6 c	26.5 b
II-you 838	253.0 b	167.6 cd	42.3 c	80.3 b	25.4 c
Yangdao 6	224.3 c	179.1 bc	40.2 c	80.5 b	28.4 a
Huanghuazhan	305.3 a	156.8 de	47.7 ab	84.5 a	20.9 e
Mean	267.1	173.7	46.1	79.2	25.0

Within a column for each site, means followed by the same letters are not significantly different according to LSD (0.05).

Table 4
Yield components of six rice varieties grown in Liuyang and Guidong counties, Hunan Province, China, in 2008. Data are the means across two N rates.

Variety	Panicles m^{-2}	Spikelets $panicle^{-1}$	Spikelets m^{-2} ($\times 10^3$)	Grain filling (%)	Grain weight (mg)
Liuyang					
Liangyoupeijiu	225.6 c	221.0 a	49.8 a	74.5 d	23.4 e
Y-liangyou 1	244.5 b	181.6 b	44.2 b	84.4 b	24.1 d
Shanyou 63	228.4 c	158.8 c	36.3 c	74.3 d	27.5 b
II-you 838	215.5 cd	158.8 c	34.1 d	81.7 c	26.6 c
Yangdao 6	203.1 d	175.6 b	35.5 cd	81.3 c	27.9 a
Huanghuazhan	301.0 a	143.7 d	42.5 b	89.4 a	20.0 f
Mean	236.4	173.3	40.4	80.9	24.9
Guidong					
Liangyoupeijiu	260.9 b	192.7 a	50.0 a	86.1 ab	24.2 e
Y-liangyou 1	266.4 b	191.4 a	50.9 a	82.8 c	25.2 d
Shanyou 63	270.5 b	156.6 d	42.2 b	77.8 d	27.4 b
II-you 838	253.7 b	168.4 cd	42.3 b	85.7 abc	27.0 c
Yangdao 6	207.2 c	181.9 ab	37.5 c	83.8 bc	28.0 a
Huanghuazhan	296.3 a	173.8 bc	51.1 a	88.6 a	21.5 f
Mean	259.2	177.5	45.7	84.1	25.5

Within a column for each site, means followed by the same letters are not significantly different according to LSD (0.05).

Table 5
Growth duration, leaf area index (LAI) at flowering, harvest index, and aboveground total N uptake of six rice varieties grown in Liuyang and Guidong counties, Hunan Province, China, in 2007. Data are the means across two N rates.

Variety	Growth duration (days)	LAI at flowering	Harvest index (%)	Total N uptake (kg ha^{-1})
Liuyang				
Liangyoupeijiu	123	6.09 b	45.1 cd	182.5 a
Liangyou 293	123	5.68 b	46.4 bc	176.3 ab
Shanyou 63	115	6.95 a	44.5 d	169.1 ab
II-you 838	115	7.14 a	46.3 bc	168.4 b
Yangdao 6	115	5.48 bc	47.3 b	169.8 ab
Huanghuazhan	107	4.99 c	49.3 a	170.7 ab
Mean	116	6.06	46.5	172.8
Guidong				
Liangyoupeijiu	128	7.21 b	48.7 a	225.6 ab
Liangyou 293	130	7.23 b	49.3 a	213.4 b
Shanyou 63	126	8.55 a	45.7 b	212.7 b
II-you 838	126	8.51 a	45.2 b	229.2 ab
Yangdao 6	126	7.21 b	45.6 b	245.4 a
Huanghuazhan	120	7.17 b	47.5 ab	218.5 b
Mean	126	7.65	47.0	224.1

Within a column for each site, means followed by the same letters are not significantly different according to LSD (0.05).

Table 6
Growth duration, leaf area index (LAI) at flowering, harvest index, and aboveground total N uptake of six rice varieties grown in Liuyang and Guidong counties, Hunan Province, China, in 2008. Data are the means across two N rates.

Variety	Growth duration (days)	LAI at flowering	Harvest index (%)	Total N uptake (kg ha^{-1})
Liuyang				
Liangyoupeijiu	110	6.99 a	48.8 b	182.9 ab
Y-liangyou 1	110	5.34 c	51.0 a	192.9 a
Shanyou 63	101	6.99 a	44.6 d	166.6 c
II-you 838	101	6.80 a	46.3 c	184.7 ab
Yangdao 6	106	5.70 b	46.9 c	171.1 bc
Huanghuazhan	97	5.21 c	48.3 b	165.8 c
Mean	104	6.17	47.7	177.3
Guidong				
Liangyoupeijiu	128	5.86 b	50.8 a	227.4 ab
Y-liangyou 1	128	5.32 c	52.2 a	217.1 b
Shanyou 63	123	6.72 a	47.4 c	227.1 ab
II-you 838	123	6.92 a	50.4 ab	246.3 a
Yangdao 6	128	5.73 bc	46.6 c	228.5 ab
Huanghuazhan	118	5.92 b	48.5 bc	227.0 ab
Mean	125	6.08	49.3	228.9

Within a column for each site, means followed by the same letters are not significantly different according to LSD (0.05).

Table 7
Radiation use efficiency and its related parameters of six rice varieties grown in Liuyang and Guidong counties, Hunan Province, China, in 2007. Data are the means across two N rates.

Variety	Incident radiation (MJ m^{-2})	Intercepted radiation (MJ m^{-2})	Intercepted percent (%)	Total dry weight (g m^{-2})	Radiation use efficiency (g MJ^{-1})
Liuyang					
Liangyoupeijiu	1864	1402 a	75.2 b	1830 a	1.31 a
Liangyou 293	1864	1381 b	74.1 c	1701 b	1.23 b
Shanyou 63	1754	1381 b	78.7 a	1547 cd	1.12 c
II-you 838	1754	1370 b	78.1 a	1483 d	1.08 c
Yangdao 6	1754	1266 c	72.2 d	1579 c	1.25 ab
Huanghuazhan	1663	1176 d	70.8 e	1499 cd	1.27 ab
Mean	1776	1330	74.8	1606	1.21
Guidong					
Liangyoupeijiu	1708	1414 a	82.8 b	1972 a	1.39 abc
Liangyou 293	1618	1328 b	82.1 bc	1986 a	1.50 a
Shanyou 63	1666	1421 a	85.3 a	1878 ab	1.33 c
II-you 838	1666	1417 a	85.1 a	1909 ab	1.35 bc
Yangdao 6	1666	1346 b	80.8 c	2008 a	1.49 a
Huanghuazhan	1583	1227 c	77.5 d	1776 b	1.45 ab
Mean	1651	1359	82.3	1922	1.42

Within a column for each site, means followed by the same letters are not significantly different according to LSD (0.05).

Table 8
Radiation use efficiency and its related parameters of six rice varieties grown in Liuyang and Guidong counties, Hunan Province, China, in 2008. Data are the means across two N rates.

Variety	Incident radiation (MJ m^{-2})	Intercepted radiation (MJ m^{-2})	Intercepted percent (%)	Total dry weight (g m^{-2})	Radiation use efficiency (g MJ^{-1})
Liuyang					
Liangyoupeijiu	1635	1283 a	78.5 b	1776 a	1.38 ab
Y-liangyou 1	1641	1227 b	74.8 c	1758 ab	1.43 a
Shanyou 63	1579	1266 a	80.2 a	1666 bc	1.32 bc
II-you 838	1579	1270 a	80.4 a	1600 c	1.26 c
Yangdao 6	1607	1186 c	73.8 cd	1714 ab	1.45 a
Huanghuazhan	1531	1110 d	72.5 d	1576 c	1.42 a
Mean	1595	1224	76.7	1682	1.38
Guidong					
Liangyoupeijiu	1704	1354 b	79.4 b	2056 a	1.52 b
Y-liangyou 1	1704	1315 c	77.1 cd	2035 a	1.55 b
Shanyou 63	1654	1376 ab	83.2 a	1899 c	1.38 c
II-you 838	1670	1388 a	83.1 a	1939 bc	1.40 c
Yangdao 6	1704	1327 c	77.9 bc	1885 c	1.42 c
Huanghuazhan	1579	1204 d	76.3 d	2002 ab	1.66 a
Mean	1669	1327	79.5	1969	1.49

Within a column for each site, means followed by the same letters are not significantly different according to LSD (0.05).

difference in RUE between "super" hybrid and inbred varieties was insignificant. Higher RUE was observed in Guidong than in Liuyang.

4. Discussion

"Super" hybrid rice varieties outyielded ordinary hybrid and inbred varieties across two locations and two N rates in both 2007 and 2008. Higher grain yield of "super" hybrid rice was also reported in previous studies (Zong et al., 2000; Wang et al., 2002; Zhu et al., 2002; Katsura et al., 2007, 2008). However, these studies were usually conducted at one location, in a single season, at one N rate, or using only one "super" hybrid variety in comparison with a check variety. Therefore, it is difficult to conclude whether "super" hybrid rice has increased rice yield potential based on the results of these experiments. In our current study, we compared "super" hybrid rice varieties with several ordinary hybrid and inbred varieties under moderate and high N rates at two locations and in 2 years. Because of intensive crop management practices, major abiotic and biotic stresses that caused yield reductions were not observed in all four field experiments and a high average grain yield of more than 8 and 10 t ha^{-1} was achieved in Liuyang and Guidong, respectively. According to the definition of yield potential (Evans, 1993), varieties in this study had expressed their potential in grain production under the climatic conditions of our field experiments. Averaged across two N rates and 2 years, "super" hybrid varieties produced 13% and 11% higher grain yield than ordinary hybrid and inbred varieties in Liuyang and Guidong, respectively. We conclude that "super" hybrid varieties have increased rice yield potential by 12% under the field conditions of our experiments.

The higher grain yield of "super" hybrid varieties was attributed to improvement in both source and sink. For the source, "super" hybrid varieties produced higher aboveground total dry weight than ordinary hybrid and inbred varieties except for Guidong in 2007. Long growth duration and high accumulated incident radiation were partially responsible for the high biomass production for "super" hybrid varieties. Although "super" hybrid varieties had lower intercepted radiation than ordinary hybrid varieties, their higher RUE was responsible for higher biomass production compared with ordinary hybrids. During ripening phase, "super" hybrid varieties had 25% and 8% more biomass accumulation than ordinary hybrid and inbred varieties, respectively (data not shown). For the sink, "super" hybrid varieties had 21% and 16% more spikelets per panicle than ordinary hybrid and inbred varieties, which resulted in more spikelets per m^2 for "super" hybrid varieties than for ordinary hybrid and inbred varieties except for Huanghuazhan. Although "super" hybrid varieties did not show superiority in harvest index (except for Guidong in 2007), grain-filling percentage, grain weight, and panicle number, their values were relatively high so that the advantage of high biomass production and a large number of spikelets was not offset by other components or attributes of grain yield. Katsura et al. (2007, 2008) also reported that high yield of "super" hybrid rice was associated with high leaf area duration and more biomass production. Zhu et al. (2002) attributed the high yield of "super" hybrid variety Xieyou 9308 to its large panicle size. More importantly, the large panicles of Xieyou 9308 were achieved not at the expense of panicle number and grain-filling percentage. Zhu et al. (2002) reported that Xieyou 9308 had 52% more spikelets per panicle than an ordinary hybrid check variety, Xieyou 63, but panicle number per m^2 of Xieyou 9308 was less than 5% lower than that of Xieyou 63 and grain-filling percentage was similar between the two varieties.

Crop RUE did not explain the yield superiority of "super" hybrid varieties, which is in agreement with findings of Katsura et al. (2007, 2008). There are many methods for estimating RUE (Sinclair and Muchow, 1999). One method is to calculate RUE using canopy light extinction coefficient (K), LAI, and crop growth rate (Monteith, 1977; Katsura et al., 2008). The second method is to fit a linear relationship between cumulative biomass accumulation and cumulative radiation interception, with RUE calculated as the slope of the linear relationship (Sinclair and Muchow, 1999). In our study, we calculated RUE as the ratio of aboveground total dry weight at maturity to accumulative intercepted radiation during the entire growing season. The average RUE across all treatments in our study was 1.38 g MJ^{-1} using our method and 1.36 g MJ^{-1} using the method of Sinclair and Muchow (1999). The correlation coefficient (r) was 0.87 between the two methods. Katsura et al. (2008) estimated the RUE of rice varieties grown in Kyoto and Yunnan using the method of Monteith (1977) and reported a slightly higher average RUE of 1.47 g MJ^{-1}. Calculated values based on leaf N content and photosynthetic rate combined with experimental observation indicate that RUE in non-stressed rice crops was approximately 1.4 g MJ^{-1} (Sinclair and Horie, 1989), which is very close to the values of crop RUE determined in our study.

There was no significant difference in grain yield between ordinary hybrid and inbred varieties. Ordinary hybrid varieties had 10–12% lower RUE than "super" hybrid and inbred varieties. Low RUE might have limited the grain yield of ordinary hybrid varieties. Low RUE also suggests that ordinary hybrid varieties had low rates of single-leaf photosynthesis compared with the other two varietal groups (Sinclair and Horie, 1989). Therefore, hybrid vigor was not associated with high single-leaf photosynthetic rates. Between the two inbred varieties, low tillering and few panicles resulted in small sink size for Yangdao 6, whereas low grain weight was responsible for the low grain yield of Huanghuazhan.

Increasing N rates from 135 to 225 kg ha^{-1} in Liuyang in 2007 and from 150 to 250 kg ha^{-1} in the other three experiments did not result in significantly higher grain yield for any varieties. There was no consistent difference in total biomass production and harvest index between the two N treatments (data not shown). Huang et al. (2008) determined the N response of Liangyoupeijiu and Shanyou 63 over a wide range of N rates (60–410 kg ha^{-1}) in Hubei Province, China. They reported that both varieties required a minimum total N rate of 120–150 kg ha^{-1} to produce maximum grain yield. This suggests that "super" hybrid rice varieties do not necessarily require more N fertilizer to produce high grain yield.

About a 20% difference in grain yield existed between Liuyang and Guidong. The high grain yield of Guidong was attributed to high biomass production and N uptake, more panicles and large sink size, high grain-filling percentage, and high RUE. Solar radiation did not explain the yield difference between the two sites because (1) seasonal average daily radiation was 10% higher in Liuyang than in Guidong, (2) there was no clear difference in the seasonal pattern of radiation between the two sites (Fig. 1), and (3) accumulative intercepted radiation during the entire growing season was only 2–8% higher in Guidong than in Liuyang. Therefore, lower maximum and minimum temperatures probably explained the high yield in Guidong. Liuyang had 2.8–4.1 °C higher seasonal average temperature than Guidong. The higher temperature resulted in shorter growth duration in Liuyang. High maximum temperature during flowering reduced spikelet fertility and grain-filling percentage (Yoshida et al., 1981). High minimum temperature increased maintenance respiration and reduced dry matter accumulation (Peng et al., 2004). Guidong had 17–20% higher biomass production and 29–30% higher N uptake than Liuyang. Leaf N concentration was higher in Guidong than in Liuyang. Both higher leaf N concentration and lower maintenance respiration were associated with higher RUE in Guidong than in Liuyang.

5. Conclusions

"Super" hybrid varieties produced more biomass than ordinary hybrid and inbred varieties. Long growth duration and high accumulated incident radiation were partially responsible for high biomass production for the "super" hybrid varieties. "Super" hybrid varieties had significantly larger panicle size than ordinary hybrid and inbred varieties, which resulted in large sink size. Crop RUE of "super" hybrid varieties was similar to that of inbred varieties, but was higher than that of ordinary hybrid varieties. We conclude that "super" hybrid varieties have increased rice yield potential by 12% compared with ordinary hybrid and inbred varieties under the field conditions of our experiments.

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