Experimental Agriculture (2024), vol. 60, e20, 1–12
doi:10.1017/S0014479724000140

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RESEARCH ARTICLE

Achieving super high yield in rice by simultaneously increasing panicle number and grain weight via improving pre-heading biomass production

Min Huang[1,2], Zhengwu Xiao[1,2], Shengliang Fang[3], Hengdong Zhang[4], Longsheng Liu[3], Fangbo Cao[1,2] and Jiana Chen[1,2]

[1]Rice and Product Ecophysiology, Key Laboratory of Ministry of Education for Crop Physiology and Molecular Biology, Hunan Agricultural University, Changsha 410128, China, [2]National Engineering Research Center of Rice, Hunan Agricultural University, Changsha 410128, China, [3]Hengyang Academy of Agricultural Sciences, Hengyang 421101, China and [4]Qianxinan Academy of Agricultural and Forest Sciences, Xingyi 562400, Guizhou
Corresponding author: Min Huang; Email: mhuang@hunau.edu.cn

(Received 13 March 2024; revised 02 May 2024; accepted 23 May 2024)

Abstract
Understanding the yield attributes of rice crops grown at super high-yielding sites is useful for identifying how to achieve super high yield in rice. In this study, field experiments were conducted in 2021 and 2022 to compare grain yield and yield attributes of ten high-yielding hybrid rice varieties between Xingyi (a super high-yielding site) and Hengyang (a site with typical yields). Results showed that Xingyi produced an average grain yield of 13.4 t ha^{-1} in 2021 and 14.0 t ha^{-1} in 2022, which were, respectively, 20% and 44% higher than those at Hengyang. Higher panicles per m^2 and higher grain weight were responsible for the higher grain yield at Xingyi compared to Hengyang. The higher values of panicles per m^2 and grain weight at Xingyi compared to Hengyang were due to greater source capacity resulting from improved pre-heading biomass production. This study suggests that simultaneously increasing panicle number and grain weight through improving pre-heading biomass production is a potential way to achieve super high yield in rice.

Keywords: biomass production; grain yield; rice

Introduction
Rice is the staple food for more than half of the global population, providing more than 20% of the calories consumed worldwide (Fukagawa and Ziska, 2019). China is the largest rice consumer globally, accounting for about 28% of global consumption (Yuan and Peng, 2022). To increase rice yield and ensure national food security, great efforts have been made in China to develop new rice varieties. Rice yield rose 30% due to the development of semi-dwarf varieties in the late 1950s to the early 1960s (Peng *et al.*, 2009). Through the development of hybrid varieties in the late 1970s, rice yield increased by an additional 10–20% (Peng *et al.*, 1999; Cheng *et al.*, 2007). By the 1990s to 2000s, the development of super hybrid varieties further increased rice yield by approximately 10% (Zhang *et al.*, 2009; Huang *et al.*, 2011a).

Rice yield is not only determined by the variety but also by the environment (Guo *et al.*, 2021). Super high rice yield (> 12 t ha^{-1}), including super hybrid rice varieties, is generally achieved at special eco-sites (i.e. super high-yielding sites) (Huang *et al.*, 2013a; Jiang *et al.*, 2016; Katsura *et al.*, 2008; Li *et al.*, 2009; Ying *et al.*, 1998). An understanding of yield attributes of rice crops grown at super high-yielding sites would provide useful information to identify feasible approaches for achieving super high yield in rice.

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Table 1. Soil chemical properties of the experimental fields before transplanting in 2021 and climatic conditions during the rice-growing season in 2021 and 2022 at two sites (Hengyang and Xingyi)

	Hengyang		Xingyi	
Parameter	2021	2022	2021	2022
Soil chemical property				
pH	5.85		7.46	
Organic matter (g kg^{-1})	33.0		47.5	
Total N (g kg^{-1})	1.06		1.72	
Total P (g kg^{-1})	0.60		1.21	
Total K (g kg^{-1})	8.17		8.18	
Available N (mg kg^{-1})	168		203	
Available P (mg kg^{-1})	20.8		32.1	
Available K (mg kg^{-1})	91		379	
Climatic factor				
Average daily mean temperature (°C)	28.9	29.1	23.7	22.9
Total incident solar radiation (MJ m^{-2})	1864	1761	2136	2477

Rice yield is determined by four components: panicles per m^2, spikelets per panicle, seed setting rate, and grain weight (Xiong *et al.*, 2022). However, there is no consistent conclusion about the key yield components for super high rice yield, and different studies have highlighted different components or combinations of components as being responsible. For example, Ying *et al.* (1998), Katsura *et al.* (2008), and Huang *et al.* (2013) reported that high panicles per m^2 and spikelets per panicle were responsible for the super high yield in rice. Li *et al.* (2009) reported that high panicles per m^2, seed setting rate, and grain weight were responsible for the super high yield in rice.

Rice yield can also be expressed as a function of total biomass production and harvest index (Huang *et al.*, 2015). Although previous studies have documented that super high rice yield is attributable to high total biomass production rather than high harvest index (Huang *et al.*, 2013a; Katsura *et al.*, 2008; Li *et al.*, 2009; Ying *et al.*, 1998), the results of these studies concerning the characteristics of biomass production in super high-yielding rice crops are inconsistent. Ying *et al.* (1998) reported that super high-yielding rice crops had high biomass production capacity during the vegetative and grain-filling periods, whereas Katsura *et al.* (2008) reported that high biomass production capacity was observed during the grain-filling period but not during the vegetative period in super high-yielding rice crops.

In this study, we compared grain yield and yield attributes of ten high-yielding hybrid rice varieties between a super high-yielding site and a site with typical yields. The objectives of this study were to (1) clarify the key yield attributes responsible for the super high yield in rice and (2) potentially identify how to achieve super high yield in rice.

Materials and methods

Soils and climate

Field experiments were conducted at Xingyi (25°01′14′′ N, 104°55′45′′ E, 1165 m a.s.l.), Guizhou Province, and Hengyang (26°52′31′′ N, 112°30′07′′ E, 73 m a.s.l.), Hunan Province, China in 2021 and 2022. For rice production, Xingyi is a super high-yielding site, while Hengyang has typical yields. Soil chemical properties in the upper 20 cm layer of the experimental fields before transplanting in 2021 and climatic conditions (average daily mean temperature and total incident solar radiation) during the rice-growing season (from sowing to harvesting) in 2021 and 2022 are given in Table 1.

Experimental design and crop management

Ten high-yielding hybrid rice varieties (Guiliangyou 2, Jingliangyou 1468, Jingliangyou 534, Jingliangyouhuazhan, Longliangyouhuazhan, Xiangliangyou 900, Y-liangyou 1, Y-liangyou 2,

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Y-liangyou 900, and Yongyou 4949) were used in this study. Six of the ten varieties (Guiliangyou 2, Jingliangyouhuazhan, Longliangyouhuazhan, Y-liangyou 1, Y-liangyou 2, and Y-liangyou 900) are super hybrid rice varieties approved by the Ministry of Agriculture and Rural Affairs of China. The varieties were arranged in a randomised complete-block design with three replicates. The plot size was 15 m^2 at Xingyi and 20 m^2 at Hengyang.

Pre-germinated seeds were sown on a seedbed to raise seedlings. Two seedlings per hill were transplanted at a hill spacing of 20 cm × 20 cm. Basal fertiliser (90 kg N ha^{-1}, 90 kg P_2O_5 ha^{-1}, and 90 kg K_2O ha^{-1}) was applied 1 day before transplanting. The first top dressing (36 kg N ha^{-1}) was applied 7 days after transplanting. The second top dressing (54 kg N ha^{-1} and 90 kg K_2O ha^{-1}) was applied at the panicle initiation stage. Continuous flooding (5–10 cm water depth) was practised in all plots from transplanting until one week before maturity, when the plots were drained for harvesting. Plant diseases, insects, and weeds were intensively controlled by pesticides.

Sampling and measurements

Ten hills of rice plants were sampled from each plot at heading and maturity stages. The plants sampled at the heading stage were separated into stems, leaves, and panicles. Each organ was oven-dried at 70 °C to a constant weight to determine biomass. Plants sampled at maturity were hand threshed after counting panicle number. Filled and unfilled spikelets were separated by submerging them in tap water. Three subsamples of 30 g of filled spikelets and all unfilled spikelets were used to count spikelet numbers. The number of filled spikelets was counted with a digital automatic seed counter (SLY-C, Zhejiang Top Cloud-Agri Technology Co., Ltd., Hangzhou, China). The number of unfilled spikelets was counted manually. All plant organs were oven-dried at 70 °C to a constant weight to determine biomass. Yield components (panicles per m^2, spikelets per panicle, spikelets per m^2, seed setting rate, and grain weight), pre-heading biomass production (biomass production per m^2 at the heading stage), total biomass production (biomass production per m^2 at the maturity stage), post-heading biomass production (total biomass production – pre-heading biomass production), harvest index (filled grain biomass/total biomass production), source-sink ratio (total biomass production/spikelets per m^2), pre-heading crop growth rate (pre-heading biomass production/pre-heading growth duration), and post-heading crop growth rate (post-heading biomass production/post-heading growth duration) were calculated.

Rice plants were harvested from a 5 m^2 area in each plot to determine grain yield. Harvested grains were weighed after sun-drying. A subsample of 50 g of sun-dried grains was oven-dried at 70 °C to a constant weight to determine moisture content. Grain yield was calculated by adjusting to a moisture content of 14%.

Statistical analysis

All data were analysed separately for each year, using analysis of variance (Statistix 8.0, Analytical Software, Tallahassee, FL, USA). Linear regression analysis was employed to evaluate the relationships between grain yield and yield attributes (panicles per m^2, spikelets per panicle, spikelets per m^2, seed setting rate, grain weight, total biomass production, and harvest index) across ten hybrid rice varieties grown at two sites in 2 years.

Results

Because (1) the focus of this study was to compare grain yield and yield attributes between two sites and (2) the interactive effect of site and variety was either not significant or not consistent across 2 years for grain yield and most yield attributes (Tables 2–5), the following subsections primarily describe the main effects of site on grain yield and yield attributes.

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Table 2. Grain yield and yield components of ten hybrid rice varieties grown at two sites in 2021

Site	Variety	Grain yield (t ha^{-1})	Panicles m^{-2}	Spikelets panicle^{-1}	Spikelets m^{-2} ($\times 10^3$)	Seed setting rate (%)	Grain weight (mg)
Hengyang	Guiliangyou 2	10.7	268	209	56.0	81.0	24.8
	Jingliangyou 1468	11.8	313	187	58.5	86.1	23.4
	Jingliangyou 534	11.5	313	193	60.4	81.8	21.7
	Jingliangyouhuazhan	11.2	339	172	58.3	71.6	21.8
	Longliangyouhuazhan	11.7	291	216	62.9	73.9	23.2
	Xiangliangyou 900	10.5	244	254	62.0	63.5	26.3
	Y-liangyou 1	11.9	258	180	46.4	79.9	27.5
	Y-liangyou 2	10.4	298	203	60.5	68.4	24.9
	Y-liangyou 900	10.9	230	236	54.3	76.1	24.8
	Yongyou 4949	10.9	283	215	60.8	71.6	23.6
	Mean	**11.2**	**284**	**207**	**58.0**	**75.4**	**24.2**
	SD	0.6	34	25	4.9	6.9	1.8
Xingyi	Guiliangyou 2	11.9	350	184	64.4	79.0	26.6
	Jingliangyou 1468	13.8	321	205	65.8	79.2	26.3
	Jingliangyou 534	14.0	342	202	69.1	72.7	25.5
	Jingliangyouhuazhan	13.7	380	199	75.6	71.4	24.5
	Longliangyouhuazhan	13.7	348	186	64.7	80.6	28.1
	Xiangliangyou 900	14.1	239	270	64.5	72.2	30.1
	Y-liangyou 1	14.5	335	186	62.3	72.3	29.3
	Y-liangyou 2	13.5	319	203	64.8	73.2	26.0
	Y-liangyou 900	12.7	259	284	73.6	70.8	25.9
	Yongyou 4949	11.8	244	241	58.8	84.9	24.8
	Mean	**13.4**	**314**	**216**	**66.4**	**75.6**	**26.7**
	SD	0.9	49	36	5.1	4.9	1.9
Analysis of variance (*F*-value)							
Site		134.71**	19.18**	3.56^{NS}	30.06**	0.04^{NS}	576.20**
Variety		4.44**	12.21**	12.78**	2.01^{NS}	6.26**	107.69**
Site × variety		1.87^{NS}	2.91*	2.13^{NS}	2.12^{NS}	4.49**	16.40**

* and ** denote significance at $p < 0.05$ and $p < 0.01$, respectively. ^{NS} denotes non-significance at $p < 0.05$.

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Table 3. Grain yield and yield components of ten hybrid rice varieties grown at two sites in 2022

Site	Variety	Grain yield (t ha^{-1})	Panicles m^{-2}	Spikelets panicle^{-1}	Spikelets m^{-2} ($\times 10^3$)	Seed setting rate (%)	Grain weight (mg)
Hengyang	Guiliangyou 2	8.7	269	167	44.9	85.0	24.5
	Jingliangyou 1468	10.0	298	206	61.4	80.1	22.4
	Jingliangyou 534	10.2	283	213	60.3	84.8	20.9
	Jingliangyouhuazhan	10.1	300	187	56.1	72.9	20.7
	Longliangyouhuazhan	10.9	293	202	59.2	74.6	22.8
	Xiangliangyou 900	9.4	230	243	55.9	65.0	25.4
	Y-liangyou 1	9.3	253	189	47.8	75.4	26.5
	Y-liangyou 2	9.5	273	202	55.1	63.9	23.7
	Y-liangyou 900	8.3	233	238	55.5	71.4	23.4
	Yongyou 4949	10.3	243	242	58.8	76.7	23.5
	Mean	**9.7**	**268**	**209**	**55.5**	**75.0**	**23.4**
	SD	0.8	26	26	5.3	7.2	1.8
Xingyi	Guiliangyou 2	13.6	341	241	82.2	71.6	25.7
	Jingliangyou 1468	13.4	370	194	71.8	73.9	24.5
	Jingliangyou 534	13.9	356	201	71.6	71.0	26.0
	Jingliangyouhuazhan	12.9	388	201	78.0	63.9	24.6
	Longliangyouhuazhan	14.3	372	186	69.2	75.6	26.6
	Xiangliangyou 900	14.4	303	276	83.6	61.9	28.2
	Y-liangyou 1	15.5	343	197	67.6	77.0	30.5
	Y-liangyou 2	13.8	345	226	78.0	70.3	26.5
	Y-liangyou 900	13.4	296	277	82.0	61.0	25.9
	Yongyou 4949	14.9	276	257	70.9	77.5	24.7
	Mean	**14.0**	**339**	**226**	**75.5**	**70.4**	**26.3**
	SD	0.8	36	35	5.9	6.1	1.8
Analysis of variance (*F*-value)							
Site		756.79**	101.80**	10.78**	140.16**	9.19**	850.58**
Variety		5.37**	7.62**	11.86**	1.58^{NS}	5.64**	120.02**
Site × variety		4.23**	0.48^{NS}	2.99**	2.79*	2.12^{NS}	15.45**

* and ** denote significance at $p < 0.05$ and $p < 0.01$, respectively. ^{NS} denotes non-significance at $p < 0.05$.

Table 4. Biomass production and harvest index of ten hybrid rice varieties grown at two sites in 2021

Site	Variety	Biomass production (g m^{-2})			Harvest index
		Pre-heading	Post-heading	Total	
Hengyang	Guiliangyou 2	947	690	1637	0.58
	Jingliangyou 1468	1318	738	2056	0.52
	Jingliangyou 534	1418	381	1799	0.52
	Jingliangyouhuazhan	1352	483	1835	0.49
	Longliangyouhuazhan	1400	470	1870	0.50
	Xiangliangyou 900	1290	545	1835	0.48
	Y-liangyou 1	1247	464	1711	0.52
	Y-liangyou 2	1240	620	1860	0.48
	Y-liangyou 900	1241	508	1749	0.50
	Yongyou 4949	995	538	1533	0.58
	Mean	**1245**	**544**	**1789**	**0.52**
	SD	158	110	143	0.04
Xingyi	Guiliangyou 2	1365	687	2052	0.57
	Jingliangyou 1468	1831	490	2321	0.51
	Jingliangyou 534	1721	487	2208	0.50
	Jingliangyouhuazhan	1807	498	2305	0.49
	Longliangyouhuazhan	1642	707	2349	0.54
	Xiangliangyou 900	1515	700	2215	0.55
	Y-liangyou 1	1737	464	2201	0.52
	Y-liangyou 2	1653	515	2168	0.49
	Y-liangyou 900	1695	606	2301	0.51
	Yongyou 4949	1202	794	1996	0.54
	Mean	**1617**	**595**	**2212**	**0.52**
	SD	200	119	116	0.03
Analysis of variance (*F*-value)					
Site		141.28**	1.12^{NS}	105.15**	0.99^{NS}
Variety		11.92**	1.23^{NS}	3.54**	18.97**
Site × variety		1.39^{NS}	1.02^{NS}	0.44^{NS}	5.93**

** and ^{NS} denote significance at $p < 0.01$ and non-significance at $p < 0.05$, respectively.

Grain yield and yield components

Grain yield significantly differed with site in both 2021 and 2022 (Tables 2 and 3). Grain yield at Xingyi ranged from 11.8 to 14.5 t ha^{-1} in 2021 and from 12.9 to 15.5 t ha^{-1} in 2022, showing respective averages of 13.4 and 14.0 t ha^{-1}. The average grain yield was 20% and 44% higher at Xingyi than at Hengyang in 2021 and 2022, respectively.

Panicles per m^2, spikelets per m^2, and grain weight were significantly different between sites in both 2021 and 2022, while the differences in spikelets per panicle and seed setting rate between sites were not significant in either 2021 or 2022 (Tables 2 and 3). Average panicles per m^2, spikelets per m^2, and grain weight were, respectively, higher at Xingyi than at Hengyang by 11%, 14%, and 10% in 2021 and by 26%, 36%, and 12% in 2022. Linear regression analysis showed that grain yield was significantly positively related to panicles per m^2, spikelets per m^2, and grain weight (Figure 1A, C, and E) but was not significantly related to spikelets per panicle and seed setting rate (Figure 1B and 1D).

Biomass production and harvest index

Pre-heading biomass production and total biomass production were significantly different between sites in both 2021 and 2022, whereas the difference in post-heading biomass production was only significant in 2022 (Tables 4 and 5). Xingyi had higher average pre-heading biomass production and total biomass production than Hengyang by 30% and 24% in 2021 and by 40% and 45% in 2022, respectively. There was no significant difference in harvest index between sites in either 2021 or 2022. Linear regression analysis showed that grain yield was significantly positively

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Table 5. Biomass production and harvest index of ten hybrid rice varieties grown at two sites in 2022

		Biomass production (g m^{-2})			
Site	Variety	Pre-heading	Post-heading	Total	Harvest index
Hengyang	Guiliangyou 2	846	692	1538	0.55
	Jingliangyou 1468	1360	597	1957	0.48
	Jingliangyou 534	1165	625	1790	0.52
	Jingliangyouhuazhan	1183	399	1582	0.46
	Longliangyouhuazhan	1342	485	1827	0.47
	Xiangliangyou 900	1169	487	1656	0.48
	Y-liangyou 1	1355	399	1754	0.47
	Y-liangyou 2	1196	485	1681	0.43
	Y-liangyou 900	1287	530	1817	0.44
	Yongyou 4949	1003	705	1708	0.54
	Mean	**1191**	**540**	**1731**	**0.48**
	SD	164	110	125	0.04
Xingyi	Guiliangyou 2	1455	890	2345	0.55
	Jingliangyou 1468	1911	607	2518	0.44
	Jingliangyou 534	1751	881	2632	0.43
	Jingliangyouhuazhan	1774	661	2435	0.43
	Longliangyouhuazhan	1716	776	2492	0.48
	Xiangliangyou 900	1751	889	2640	0.48
	Y-liangyou 1	1664	1037	2701	0.51
	Y-liangyou 2	1399	1152	2551	0.49
	Y-liangyou 900	1768	855	2623	0.43
	Yongyou 4949	1489	750	2239	0.52
	Mean	**1668**	**850**	**2518**	**0.48**
	SD	165	163	145	0.04
Analysis of variance (*F*-value)					
Site		141.75**	20.15**	206.44**	1.44^{NS}
Variety		5.57**	0.65^{NS}	1.65^{NS}	12.76**
Site × variety		1.19^{NS}	0.99^{NS}	0.78^{NS}	4.19**

** and ^{NS} denote significance at $p < 0.01$ and non-significance at $p < 0.05$, respectively.

related to total biomass production (Figure 2A) but was not significantly related to harvest index (Figure 2B).

Source-sink ratio, crop growth duration, and crop growth rate

The difference in source-sink ratio between sites was significant in both 2021 and 2022 (Figure 3). The average source-sink ratio was 7% higher at Xingyi than at Hengyang in both 2021 and 2022. Pre-heading and post-heading growth durations were significantly different between sites in both 2021 and 2022 (Figure 4A and 4B). Average pre-heading growth duration was longer at Xingyi compared to Hengyang by 18 days in 2021 and by 17 days in 2022. The average post-heading growth duration was 3 days shorter and 12 days longer at Xingyi than at Hengyang in 2021 and 2022, respectively. Pre-heading crop growth rate significantly differed between sites in both 2021 and 2022, whereas the difference in post-heading crop growth rate between sites was only significant in 2022 (Figure 4C and 4D). The average pre-heading crop growth rate was higher at Xingyi compared to Hengyang by 9% in 2021 and by 20% in 2022.

Discussion

In this study, rice crops produced an average grain yield of nearly 14.0 t ha^{-1} at Xingyi. This yield level is comparable to that reported at this site by Jiang *et al.* (2016), who showed that two super hybrid rice varieties produced an average grain yield of 13.5 t ha^{-1} across 2 years at Xingyi under fertilised conditions. The highest grain yield at Xingyi in this study was 15.5 t ha^{-1}, which is

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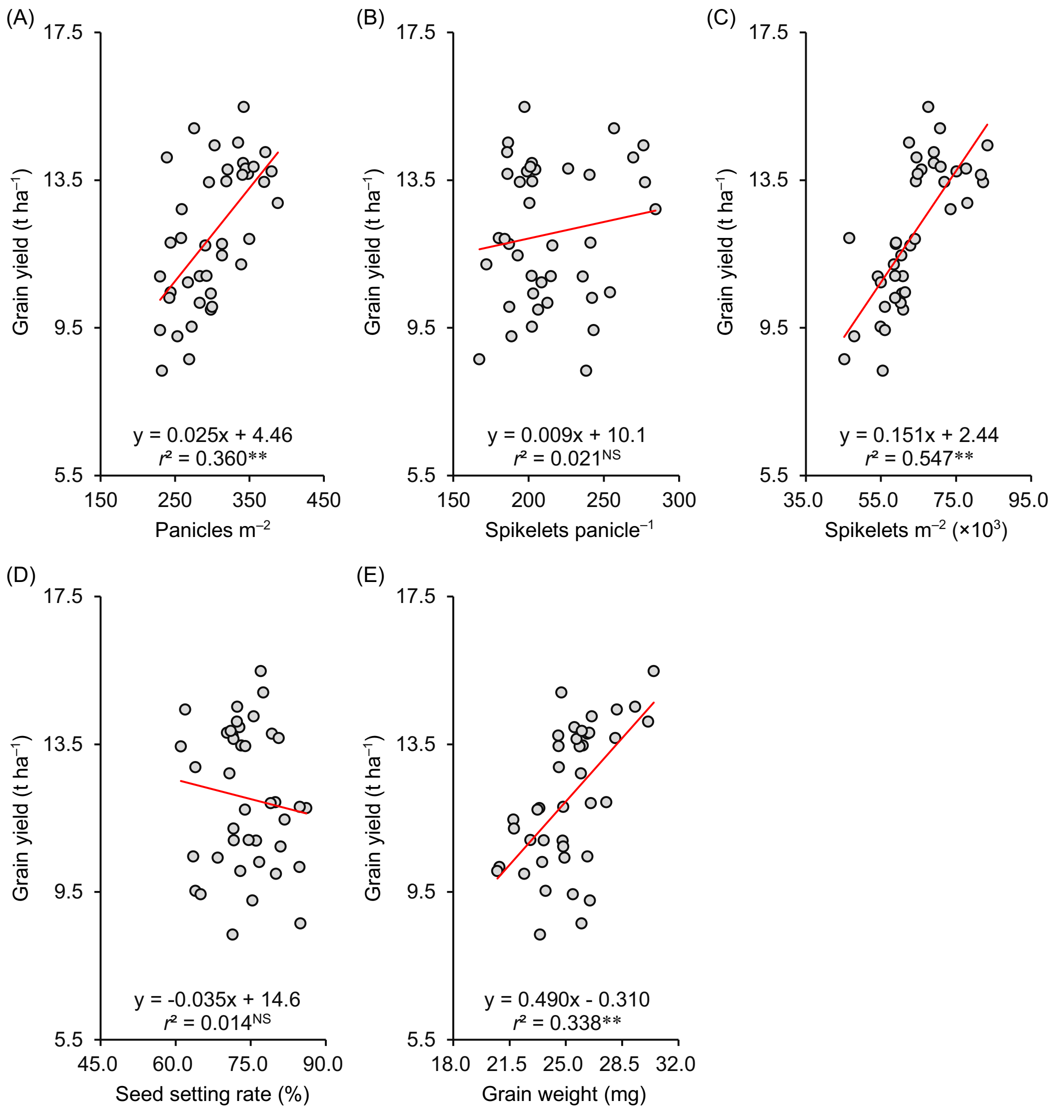

Figure 1. Relationships between grain yield and yield components in ten hybrid rice varieties grown at two sites (Hengyang and Xingyi) in 2 years (2021 and 2022). ** denotes a significant relationship at $p < 0.01$. ^{NS} denotes a non-significant relationship at $p > 0.05$.

slightly higher than the lower boundary of the previously reported highest grain yields (15.2–18.5 t ha^{-1}) in Taoyuan, Yunnan Province, China (Katsura *et al.*, 2008; Li *et al.*, 2009; Ying *et al.*, 1998), a well-known site where the highest rice yield in the world has been recorded (Zhong *et al.*, 2020). These findings support that Xingyi is a typical super high-yielding site for rice production.

Xingyi produced more than 30% higher average grain yield of rice than Hengyang. From the point of view of ecological characteristics, both higher soil fertility and better climatic conditions during the rice-growing season (lower daily mean temperature and higher total incident solar radiation) were responsible for the higher grain yield of rice at Xingyi than at Hengyang (Table 1). From the point of view of yield components, the yield advantage at Xingyi compared to Hengyang was related to both higher panicles per m^2 and higher grain weight. This finding is not in

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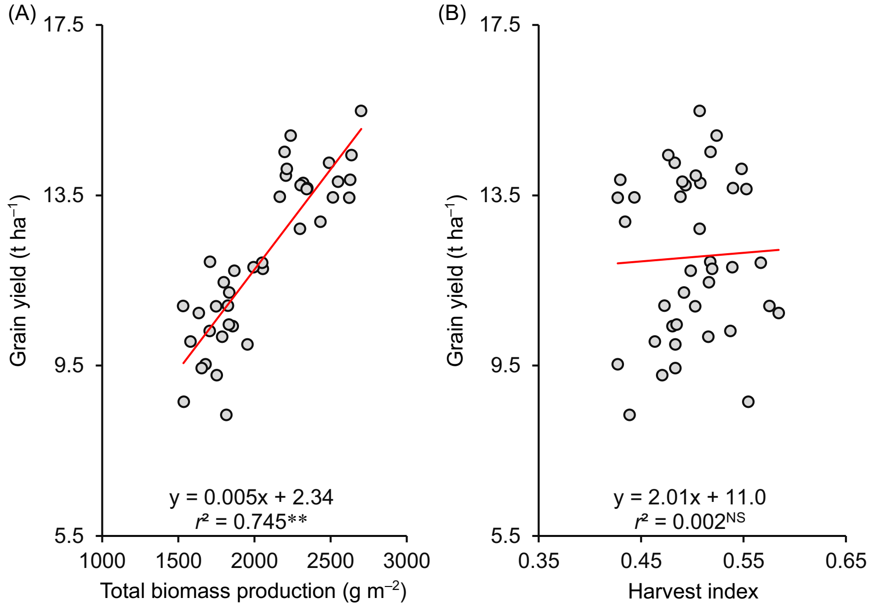

Figure 2. Relationships of grain yield to total biomass production (A) and harvest index (B) in ten hybrid rice varieties grown at two sites (Hengyang and Xingyi) in 2 years (2021 and 2022). ** denotes a significant relationship at $p < 0.01$. NS denotes a non-significant relationship at $p > 0.05$.

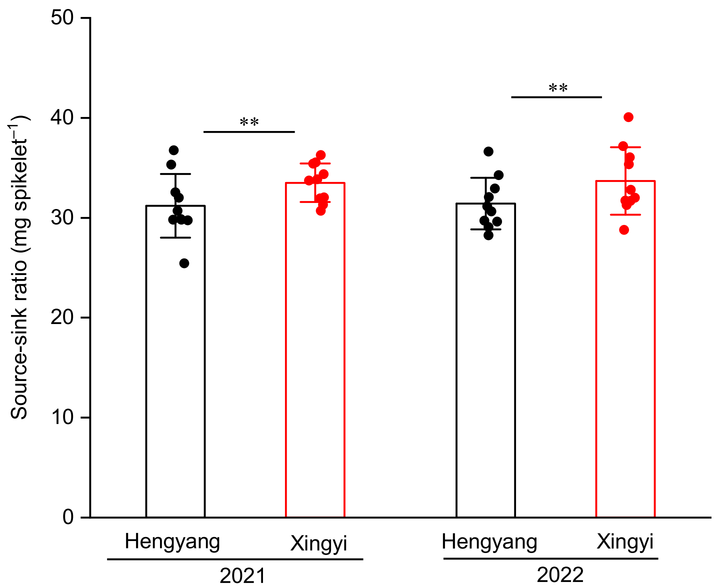

Figure 3. Source-sink ratios of ten hybrid rice varieties grown at two sites (Hengyang and Xingyi) in 2 years (2021 and 2022). Columns and error bars are mean ± SD of ten varieties. Each circle represents the mean of three replicates of a variety. ** denotes a significant difference between the two sites at $p < 0.01$.

agreement with that reported in previous studies (Huang *et al.*, 2013a; Katsura *et al.*, 2008; Li *et al.*, 2009; Ying *et al.*, 1998), which showed that the difference in grain yield between super high-yielding sites and those with typical yields was attributable to the differences in panicles per m^2

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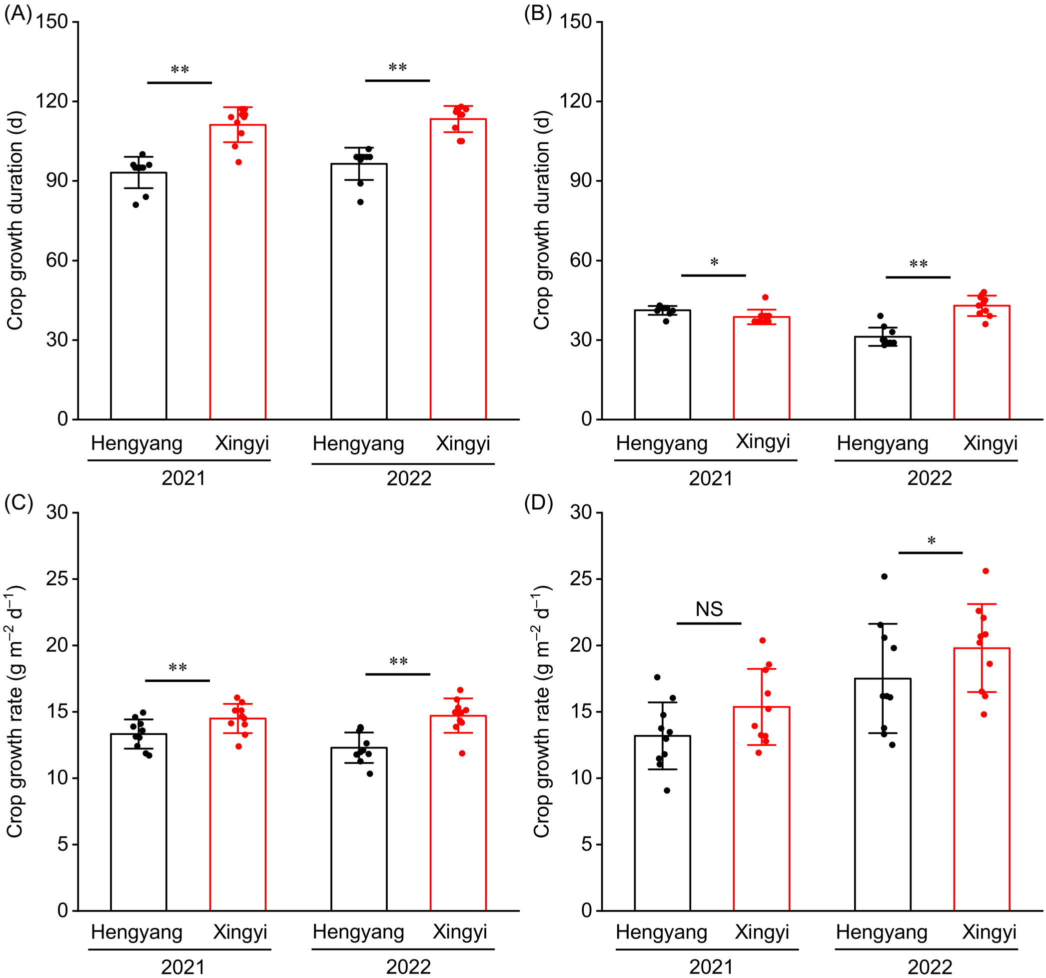

Figure 4. Crop growth durations (A and B) and crop growth rates (C and D) during the pre-heading period (A and C) and the post-heading period (B and D) of ten hybrid rice varieties grown at two sites (Hengyang and Xingyi) in 2 years (2021 and 2022). Columns and error bars are mean ± SD of ten varieties. Each circle represents the mean of three replicates of a variety. * and ** denote significant differences between sites at $p < 0.05$ and $p < 0.01$, respectively. ^{NS} denotes a non-significant difference between sites at $p < 0.05$.

and spikelets per panicle or the differences in panicles per m^2, seed setting rate, and grain weight. These results demonstrate that there are multiple approaches to achieving super high rice yield, and this study suggests a new one, that is, simultaneously increasing panicles per m^2 and grain weight.

Panicle number is closely associated with the number of tillers, which is regulated by carbohydrate supply (Huang *et al.*, 2011b). In this study, the higher panicles per m^2 at Xingyi compared to Hengyang could be partially explained by higher pre-heading biomass production. In addition, previous studies have shown strong compensation between panicles per m^2 and spikelets per panicle in rice crops (Ying *et al.*, 1998; Huang *et al.*, 2013a). However, in this study, the higher panicles per m^2 at Xingyi did not lead to lower spikelets per panicle than at Hengyang, indicating reduced compensation between the two components at Xingyi. In general, decoupling the compensatory relationship between panicles per m^2 and spikelets per panicle can be accomplished by increasing biomass production during panicle formation (Huang *et al.*, 2013a). This might be

https://doi.org/10.1017/S0014479724000140 Published online by Cambridge University Press

also responsible for the reduced compensation between the two components at Xingyi in this study, where pre-heading biomass production was higher at Xingyi than at Hengyang.

Grain weight is determined by source capacity (biomass production) and the allocation of biomass to grains (Ntanos and Koutroubas, 2002). In this study, because there was no significant difference in harvest index between Xingyi and Hengyang, the higher grain weight at Xingyi should be attributable to greater source capacity compared to Hengyang. This was supported by a higher source-sink ratio at Xingyi than at Hengyang. The source-sink ratio is the ratio of total biomass production to spikelets per m^2, and a higher source-sink ratio can be achieved by increasing total biomass production or/and decreasing spikelets per m^2. In this study, the higher source-sink ratio at Xingyi was attributable to higher total biomass production because Xingyi had higher spikelets per m^2 than Hengyang.

Total biomass production can be increased by increasing pre-heading and/or post-heading biomass production. In this study, the higher total biomass production at Xingyi compared to Hengyang was mainly attributable to higher pre-heading biomass production because there was no consistent difference in post-heading biomass production between the two sites across 2 years. This finding is not in agreement with that reported in previous studies (Katsura *et al.*, 2008; Ying *et al.*, 1998), which showed that super high-yielding sites had higher post-heading production than sites with typical yields.

Biomass production is a function of growth duration and crop growth rate (Zheng *et al.*, 2022). In this study, both longer pre-heading growth duration and higher pre-heading crop growth rate were responsible for the higher pre-heading biomass production at Xingyi compared to Hengyang. Crop growth duration is closely associated with temperature, with a lower temperature leading to a longer duration (Huang *et al.*, 2013b). This is also why pre-heading growth duration was longer at Xingyi than at Hengyang in this study. A high crop growth rate can be achieved by increasing photosynthetic capacity and/or decreasing respiration rate (Yamori, 2020). In this study, the leaf biomass at heading was 6% and 31% higher at Xingyi than at Hengyang in 2021 and 2022, respectively (data not shown), indicating that rice plants grown at Xingyi might have higher leaf area index and hence higher photosynthetic capacity than those grown at Hengyang. In addition, rice plants at Xingyi might have a lower respiration rate than those at Hengyang because a lower temperature leads to a lower respiration rate (Li *et al.*, 2021). These results highlight the need for further investigations to determine the characteristics of photosynthesis and respiration in rice crops grown at super high-yielding sites.

Conclusions

Ten high-yielding hybrid rice varieties produced an average grain yield of nearly 14.0 t ha^{-1} at Xingyi (a super high-yielding site), which was more than 30% higher than that at Hengyang (a site with typical yields). The higher grain yield at Xingyi than at Hengyang was attributable to higher panicles per m^2 and higher grain weight. Greater source capacity resulting from improved pre-heading biomass production was responsible for the higher panicles per m^2 and the higher grain weight at Xingyi than at Hengyang. This study suggests a potential strategy for achieving super high yield in rice – namely, that super high yield in rice can be achieved in rice by simultaneously increasing panicle number and grain weight via improving pre-heading biomass production.

Acknowledgements. The authors thank other members of the Rice and Product Ecophysiology for their help with this study.

Funding statement. This work was supported by the Earmarked Fund for China Agriculture Research System (CARS-01).

Competing interests. The authors declare none.

https://doi.org/10.1017/S0014479724000140 Published online by Cambridge University Press

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Cite this article: Huang M, Xiao Z, Fang S, Zhang H, Liu L, Cao F, and Chen J. Achieving super high yield in rice by simultaneously increasing panicle number and grain weight via improving pre-heading biomass production. *Experimental Agriculture*. https://doi.org/10.1017/S0014479724000140

https://doi.org/10.1017/S0014479724000140 Published online by Cambridge University Press