



Erect panicle architecture contributes to increased rice production through the improvement of canopy structure

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Abstract The erect panicle architecture has contributed to the improvement of yield in *japonica* rice breeding, and recent molecular analysis has revealed the mechanisms involved in individual plant yield increases. However, the population structure is more important in rice production compared with individual plant yield. Our study compared the population canopy structure of a curved panicle variety Sasanishiki (WT) and an erect panicle mutant derived from CRISPR/Cas9 gene editing at the *DENSE AND ERECT PANICLE 1 (DEP1)* locus. The results showed that more light could reach to the leaves under the panicle in the *CRISPR-dep1* population compared with the WT. The canopy of the *CRISPR-dep1* population exhibited higher temperature and lower humidity compared with the WT after heading. A subsequent survey showed that the CO₂ concentration in the *CRISPR-dep1* population was significantly lower than that in the WT population from full heading to 15 days after heading. Moreover, the increase of biomass in the *CRISPR-dep1* population was greater than that in the WT. We noticed that the *CRISPR-dep1* mutant could achieve higher yield under low fertilization application compared with the WT under high

fertilizer application through increased transplant density. These traits could contribute to an agricultural sustainable development strategy. The quality investigation showed that the *dep1* allele increased the yield along with imposing a penalty on grain quality. Our study not only elucidated the mechanism of yield improvement in an erect panicle architecture variety from the perspective of population structure optimization but also provides a theoretical basis for supporting cultivation systems with the erect panicle architecture.

Keywords Rice · Canopy structure · Erect panicle · Yield · Grain quality

Introduction

Rice is one of mankind's major food staples. Given continuing population growth and increasing competition for arable land between food and energy crops, food security is becoming an ever more serious global problem. Improving crop productivity by selecting the components of grain yield and for optimal plant architecture has been the key focus of national and international rice breeding programs. The past century has witnessed two major breakthroughs in rice breeding. The first was the green revolution of the 1960s in which the development of semi-dwarf lines greatly enhanced the rice yield (Peng et al. 1999b). The second breakthrough was the application of heterosis in hybrid rice, which allowed a continuous increase in rice yield in the 1970s (Virmani et al. 1982; Yuan 1998b). Although these two

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breakthroughs dramatically improved the rice yield, the imminent food crisis that humanity will face in the next 50 years has forced breeders and scientists to search for the next breakthrough. To achieve this goal, national and international rice breeding programs have emphasized the improvement of crop productivity by selecting superior grain yield components and an ideal plant architecture (Huang et al. 2009; Khush 1999; Peng et al. 2008; Yuan 1998a). Since the 1980s, a number of high-yielding *japonica* rice strains whose architecture is characterized by dense and erect panicles have been released as commercial varieties.

Recent studies have revealed that the erect panicle architecture is conferred by a heterotrimeric G protein gene *DENSE AND ERECT PANICLE 1 (DEP1)* that significantly increases the grain yield per plant (Huang et al. 2009; Wang et al. 2009). *DEP1* has a modular arrangement with a conventional plant-specific G γ subunit protein domain at its N-terminus, followed cysteine-rich domain at the C-terminus (Huang et al. 2009). A self-inhibition model was constructed to explain the gain-of-function mechanism that the cysteine-rich domain at the C-terminus has an inhibitory effect on the G γ protein-like domain at N-terminus (Xu et al. 2016b). Clustered regularly interspaced short palindromic repeats (CRISPR)-associated (Cas) systems have been successfully used as an efficient genome editing tool in a numbers of species (Li et al. 2016; Ma et al. 2015; Shan et al. 2013). The CRISPR/Cas9 gene editing technology was used to verified the function of *DEP1* and other important yield-related genes, such as *GS3*, *IPA1*, and *Gn1a* (Li et al. 2016). However, for crops such as rice, maize, and sorghum, the high yield of individual plants does not guarantee a high yield per unit area. The population structure strongly influences the canopy temperature, the circulation of CO₂, the humidity, and the amount of sunlight penetration. The population structure of erect panicle varieties has a visual difference compared with normal varieties with curved panicles. The present study surveyed the canopy temperature, the circulation of CO₂ and moisture, and the sunlight penetration using the wild-type variety Sasanishiki (WT) and a mutant derived through CRISPR/Cas9 gene editing at the *DEP1* locus. These results not only revealed the mechanism of the yield improvement of erect panicle architecture through the perspective of population structure but they also provide a theoretical basis for supporting cultivation system of erect panicle architecture.

Materials and methods

Plant materials

The Japanese *japonica* variety Sasanishiki (WT) with curved panicles was used in this study as the wild type. Sasanishiki is a typical Japanese variety which was derived from an ancestor variety “Gimbozu,” and widely cultivated in Northeast of China before 1980s. Sasanishiki is a major backbone parent for rice breeding in China, and many currently utilized varieties in Northeast China share the genomic pedigree of Sasanishiki (Fig. S1). Our previous study had generated a *DEP1* mutant (CRISPR-*dep1*) under the genetic background of Sasanishiki using CRISPR/Cas9 gene editing technology (Li et al. 2018). We designed the sgRNA for CRISPR/Cas9 gene editing in the similar region of Shennong265 and Liaojing5 allele (Huang et al. 2009; Wang et al. 2009). Thus, the gene editing plant exhibited similar phenotype of Shenong265 and Liaojing5, as the *CRISPR-dep1* allele was also a gain-of-function mutant. We selected the mutant lines that showed erect panicle architecture without Cas9 protein insertion in the genome as mutant plant material (*CRISPR-dep1*).

Field experiments

All of the materials were grown in the paddy rice field at the Experimental Farm of Shenyang Agricultural University (Shenyang, China; 34° 51' N, 135° 37' E) during the summer of 2017 and 2018. The WT and *CRISPR-dep1* plants were transplant into field with two levels of nitrogen amount applied and two transplant density treatments across 2 years, using a randomize complete block design with three replicates. Each plot was 40.32 m². The high-density cultivation was set as 30 cm × 10 cm intervals, and the low-density cultivation used 30 cm × 20 cm intervals. Fertilizers were applied with a basal dressing amount of 60 kg N per hectare, 90 kg P per hectare, and 90 kg K per hectare (low nitrogen fertilization), and 120 kg N per hectare, 90 kg P per hectare, and 90 kg K per hectare (high nitrogen fertilization). Seeds were sown in the seedling nursery on 24 April and transplanted with one seedling per hill on 23 May in both years. The light density, temperature, moisture, and CO₂ concentration of the high fertilizers and high-density transplanting treatment between WT and *CRISPR-dep1* plots were measured using an iMETOS system (Pessl Instruments GmbH, Werkesweg 107, 8160 Weiz, Austria) following the instruction manual.

Measurements of yield components and quality

To measure the growth rate of the plants, leaf emergence was periodically observed on the main shoot in three plants per plot. The number of tillers of three plants per plot was also counted weekly. At the full heading stage, when 90% of the stems of each plant had emerged from the panicle, the above-ground parts of eight plants were measured from each plot. These samples were then harvested and dried in an oven at 80 °C for 2 days to measure their dry weight. Next, at the mature stage (35 days after the full heading stage), the above-ground parts of 24 plants were harvested from each plot. After counting the panicle number of these plants, the panicles were hand-threshed and put into water. The filled grains, which sank in the water, were separated from unfilled grains, which did not sink in the water. The unfilled grains were further classified into empty (non-fertilized grains) and partially filled grains (poorly developed grains) with the naked eye. Seed sterility was determined by the ratio of non-fertilized grains to total grains. The filled and unfilled grains were then oven dried at 80 °C for 2 days to measure their dry weight. The number of grains per panicle and grain-filling percentage were calculated based on the above data. Three average-sized panicles were taken from each plot to observe the number of primary branches, number of secondary branches, and number of spikelets on each branch. Mature rice grains were milled after harvest, air dried, and stored at room temperature for 3 months. A total of 20 plants from the middle rows were harvested for each line. The brown rice ratio, milled rice ratio, and head rice ratio were calculated after the harvest. The grains were dehulled to produce brown rice using rubber roll sheller (THU testing hunsker, Satake, Hiroshima, Japan), and brown rice ratio was determined. Thereafter, the brown rice was milled with a rice-polishing machine (TM05 test mill, Satake). After milling, head rice and broken rice were separated; finally, the milled rice ratio and head rice ratio were expressed as percentages of the total weight of rough rice. Amylose content and gel consistency were assessed according to The National Standard of the People's Republic of China (GB/T17891–1999). Extraction and measurement of rice protein composition was performed as described by Tan et al. (1999). All of the samples were analyzed twice.

Statistical analysis

All data were analyzed using excel (2016) software (Microsoft, USA). Data were analyzed following analysis of variance (ANOVA) and means of materials and among treatments within a materials were compared based on the least significant difference (LSD) test at the 0.05 probability level.

Results

Generation of a *DEP1* mutant line with CRISPR/Cas9 gene editing technology

In order to compare the differences in population structure of erect panicle and curved panicle architectures caused by the *DEP1/dep1* allele, we used the *dep1* mutant generated by CRISPR/Cas9 gene editing technology under the genetic background of a famous Japanese *japonica* variety, Sasanishiki (WT) (Fig. 1). The mutant encoded a similar truncated *DEP1* protein as the *dep1* allele of SN265 (a widely released *japonica* commercial variety with erect panicles) (Li et al. 2018). The mutant exhibited erect panicle architecture, shorter panicles, and more grains per panicle compared with the WT. We crossed the mutant to the WT, and the panicle length of the F₂ population showed a 1:3 segregation, which confirmed the mutant in *dep1* locus corresponding to the erect phenotype (Fig. 1). We scanned the segregating groups and successfully identified a line (CRISPR-*dep1*) that had no Cas9 protein. We surveyed the plant architecture of the WT and CRISPR-*dep1* at full heading stage and full ripeness stage (Fig. 2). At the heading stage, no obvious difference in plant architecture between the WT and the CRISPR-*dep1* mutant was observed. Only the angle of third leaf in the WT was significantly larger than that of CRISPR-*dep1*. At the full ripeness stage, the angle of the panicle in the WT was dramatically increased, whereas the angle of the panicle in CRISPR-*dep1* was barely changed. The panicle neck angle of CRISPR-*dep1* was approximately 12.3°, whereas in the WT this was around 50°. The panicle length, plant height, culm height, and the length of flag leaf of the WT were significantly longer than those of CRISPR-*dep1*. There was no significant difference in the angle of the flag leaf between the WT and CRISPR-*dep1*.

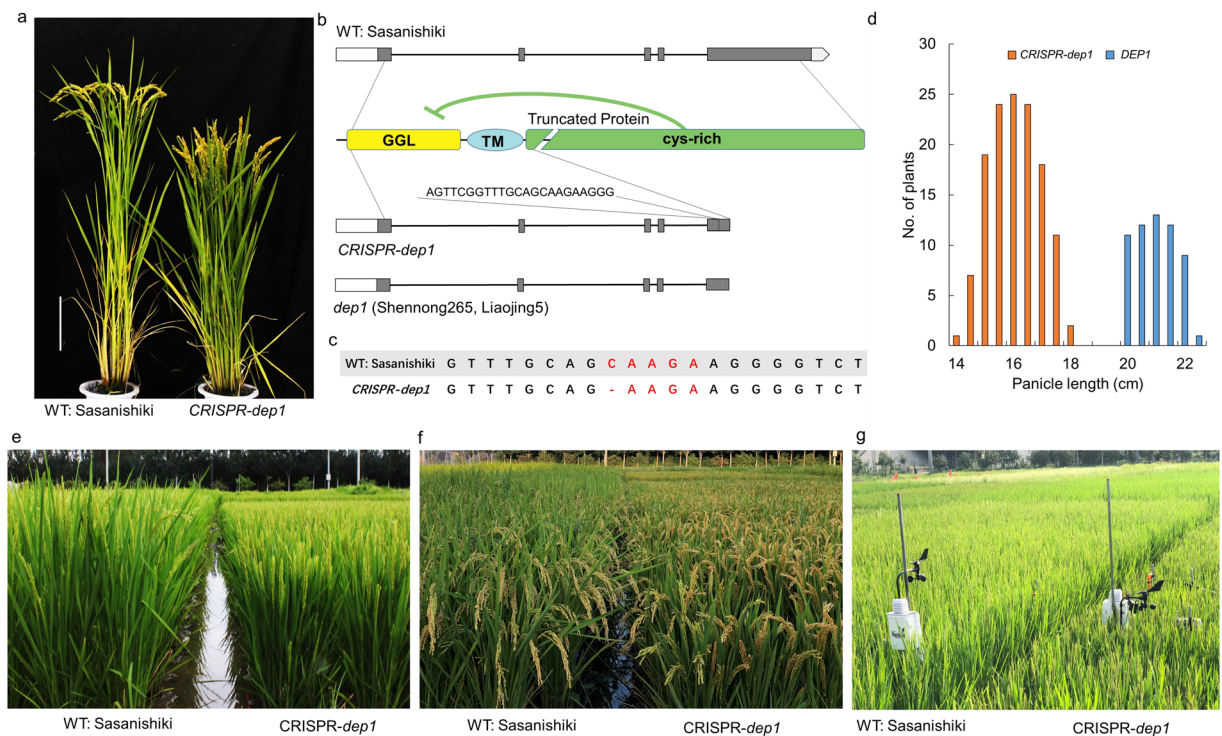


Fig. 1 The CRISPR/Cas9 genome edited plant of *DEPI*. **a** A CRISPR/Cas9 gene edited plant at the *DEPI* locus in pot. Scale bar, 20 cm. **b** Schematic diagram of the genomic region of *DEPI* (Sasanishiki), *CRISPR-dep1*, and *dep1* (Shennong265 and Liaojing5). A self-inhibition model was constructed to explain the gain-of-function mechanism. **c** Sequence alignment of the

sgRNA target region of the WT and *CRISPR-dep1* plants. **d** The panicle length of the F₂ population derived from the cross between *CRISPR-dep1* and the WT. **e** The WT and *CRISPR-dep1* in the field when the population reach heading. **f** The WT and *CRISPR-dep1* in the field when the population reach mature. **g** The iMETOS system in the field

The vertical distribution of light in different panicle architecture populations

The photosynthetic ability in the panicle is negligible, but the shadow of the panicle on lower

leaves may reduce photosynthetic products. In order to demonstrate the difference in light penetration between the two plant architectures, we surveyed the light density at different canopy heights at noon from full heading stage to full ripeness

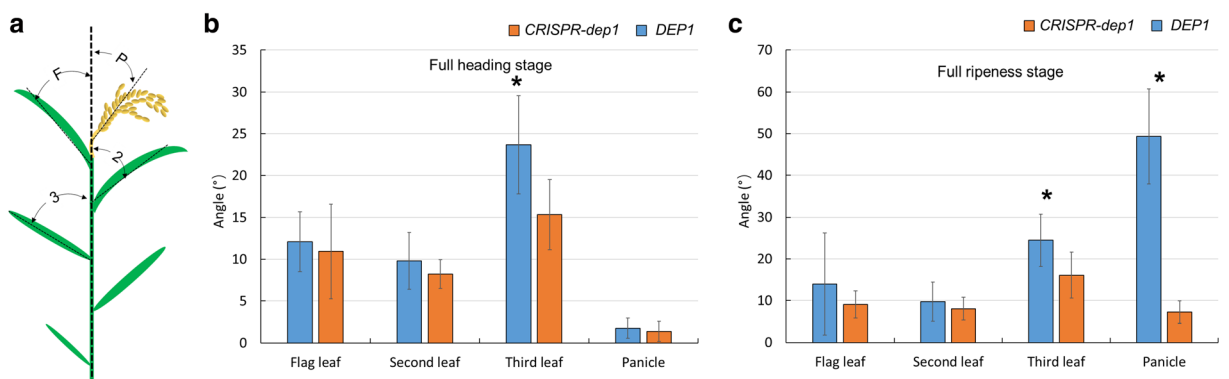


Fig. 2 The plant architecture of *DEPI* and *CRISPR-dep1* plants. **a** The model of angle measurement. P: the angle of the panicle; F: the angle of the flag leaf; 2: the angle of the second leaf; 3: the angle of the third leaf. **b** The angle measurement of *DEPI* and

CRISPR-dep1 plants at full heading stage. **c** The angle measurement of *DEPI* and *CRISPR-dep1* plants at full ripeness stage. An asterisk denotes significant at the 5% level

stage in 2017 and 2018. A similar degree of light penetration was observed between the WT and CRISPR-*dep1* at full heading stage in 2018. However, along with panicles beginning to curve in the WT, the light penetration of the WT was less than in CRISPR-*dep1* at 15 days after heading. The light density in the CRISPR-*dep1* population at 30 cm from the canopy was obviously greater than that of the WT. At full ripeness stage, the light penetration of CRISPR-*dep1* enlarged its advantage, and the leaves under the panicle received more light compared with the WT (Fig. 3). A similar trend was observed in 2017 (Fig. S2).

The daily changes in canopy conditions

We subsequently monitored the CO₂ concentration, temperature, and humidity of the canopy in two populations (Fig. 4). At full heading stage, the canopy temperatures of the WT and CRISPR-*dep1* were similar. From the 15 days after heading to the full ripeness stage, the temperature of CRISPR-*dep1* was higher than that of the WT, especially at noon. The canopy humidity of CRISPR-*dep1* was lower than that of the WT from heading to maturity. A similar trend was observed in 2017 (Fig. S3). Interestingly, we found that the CO₂ concentration of CRISPR-*dep1* was significantly lower

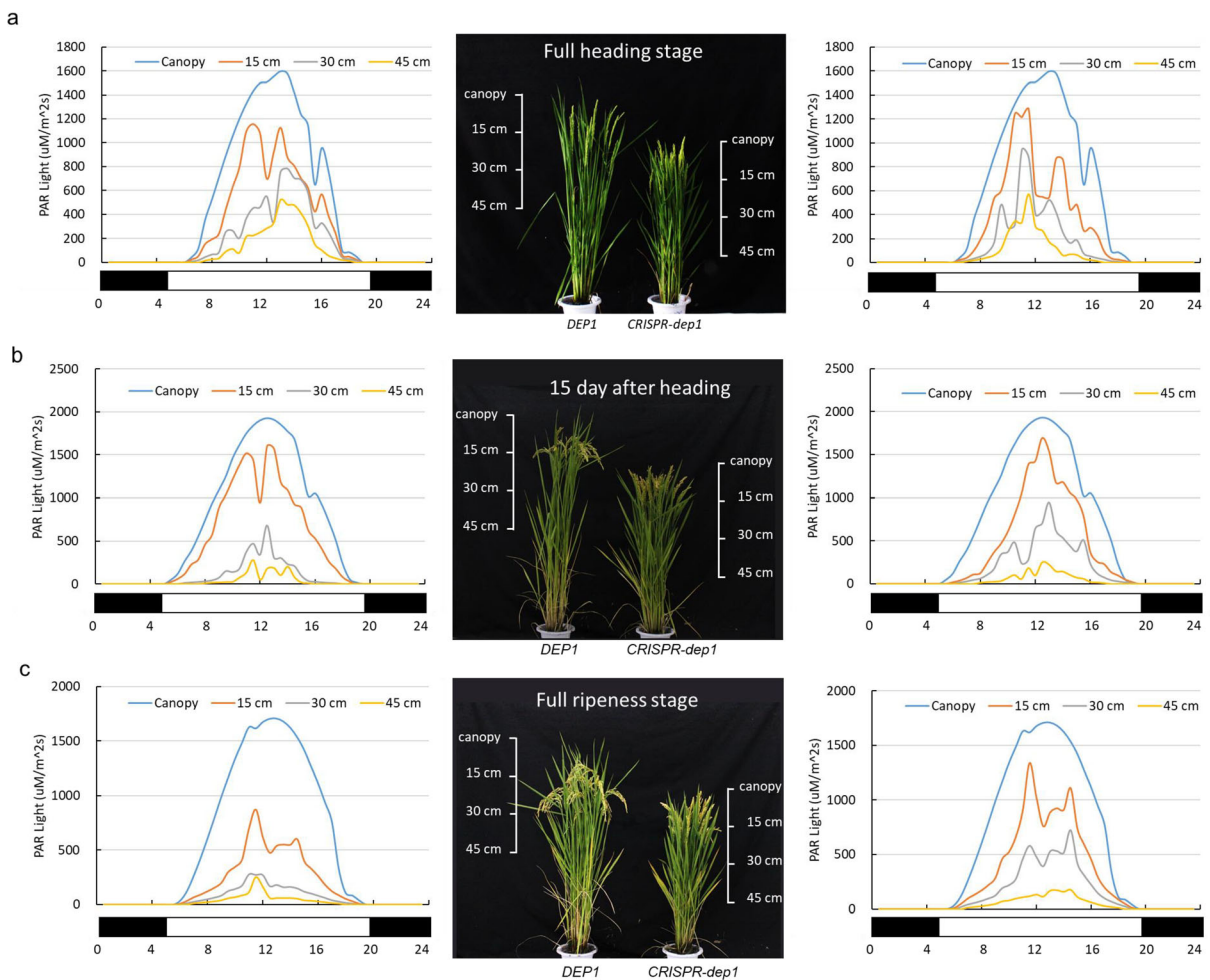


Fig. 3 The light penetration in canopy in 2018. **a** The light penetration from canopy to 45 cm from the canopy in *DEP1* population and *CRISPR-dep1* population at full heading stage. **b** The light penetration from canopy to 45 cm from the canopy in

DEP1 population and *CRISPR-dep1* population at 15 days after heading. **c** The light penetration from canopy to 45 cm from the canopy in *DEP1* population and *CRISPR-dep1* population at full ripeness stage

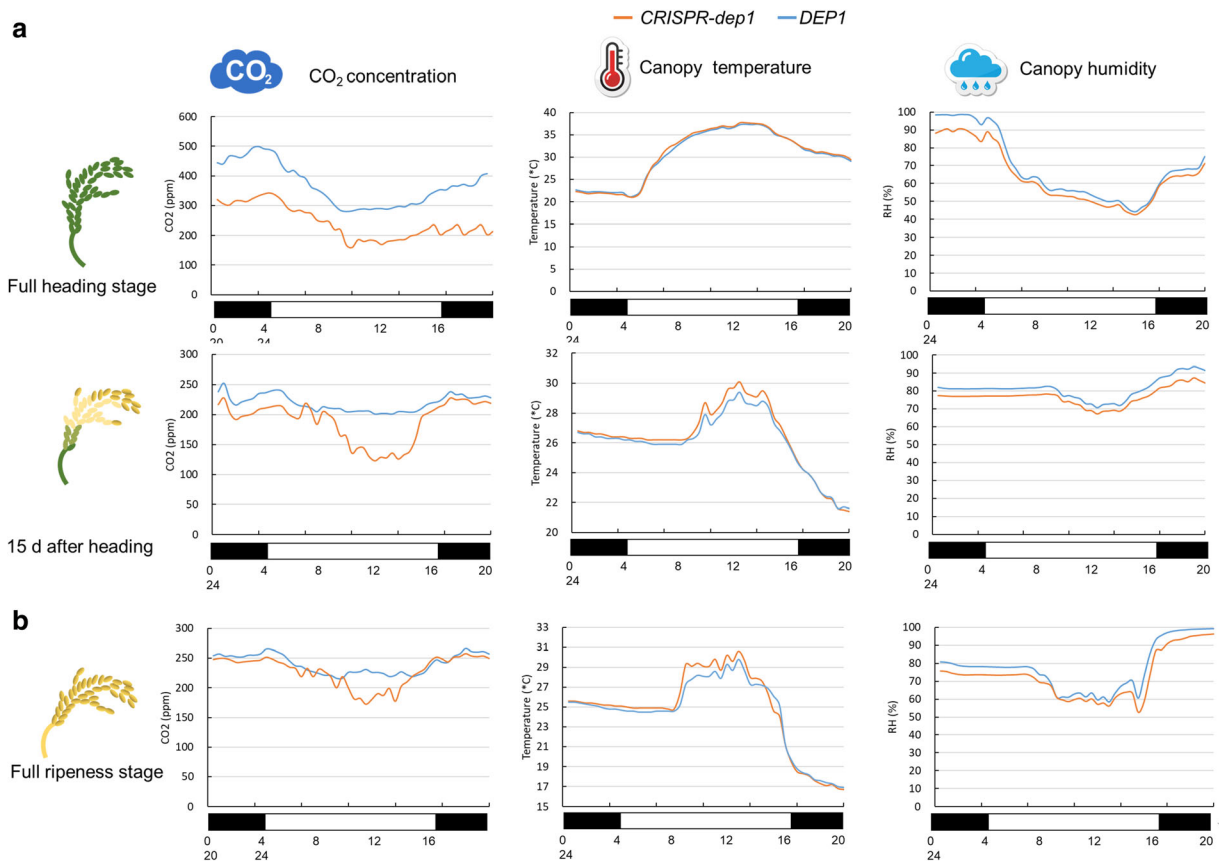


Fig. 4 The CO₂ concentration, canopy temperature, canopy humidity, and air circulation in the *DEP1* and *CRISPR-dep1* populations at full heading stage (a), 15 days after heading (b), and full ripeness stage (c) in 2018

than that of the WT at full heading stage, and the difference in CO₂ between WT and *CRISPR-dep1* became lesser from full heading stage to full ripeness stage. At 15 days after heading and ripeness stages, the *CRISPR-dep1* population only showed lower CO₂ concentration than WT population at midday-noon. These results indicated that the *CRISPR-dep1* population might have had a higher photosynthetic rate than that of the WT population at full heading stage. Taken together, the results suggest that the canopy in the *CRISPR-dep1* population exhibited lower CO₂ concentration, higher temperature, and lower humidity during the filling stage of rice.

The biomass and yield of different plant architecture populations

We subsequently investigated the biomass of the WT and *CRISPR-dep1* from heading to ripeness using a 14-day interval survey. The results were consistent with the

CO₂ concentration survey. The *CRISPR-dep1* population showed a higher increase rate than that of the WT population. These results implied that the higher photosynthetic rate in the *CRISPR-dep1* population from full heading stage to 15 days after heading produced more biomass than that of the WT population. Moreover, we found that the dry weight of panicles of the WT and *CRISPR-dep1* were similar at full heading stage. The panicle dry weight of *CRISPR-dep1* had a higher increase rate compared with that of the WT. These results indicated that a greater proportion of the biomass increase was accumulated into panicles in the *CRISPR-dep1* population compared with the WT. Based on our study and the report from other research team (X et al. 2019), the truncated *dep1* allele could significantly reduce the plant height and panicle length, but the effect on grain size was small. The length of grain in *CRISPR-dep1* was slightly shorter but wider than that of WT (Fig. 5). We then investigated the yield of the WT and *CRISPR-dep1* under different cultivation methods. Two

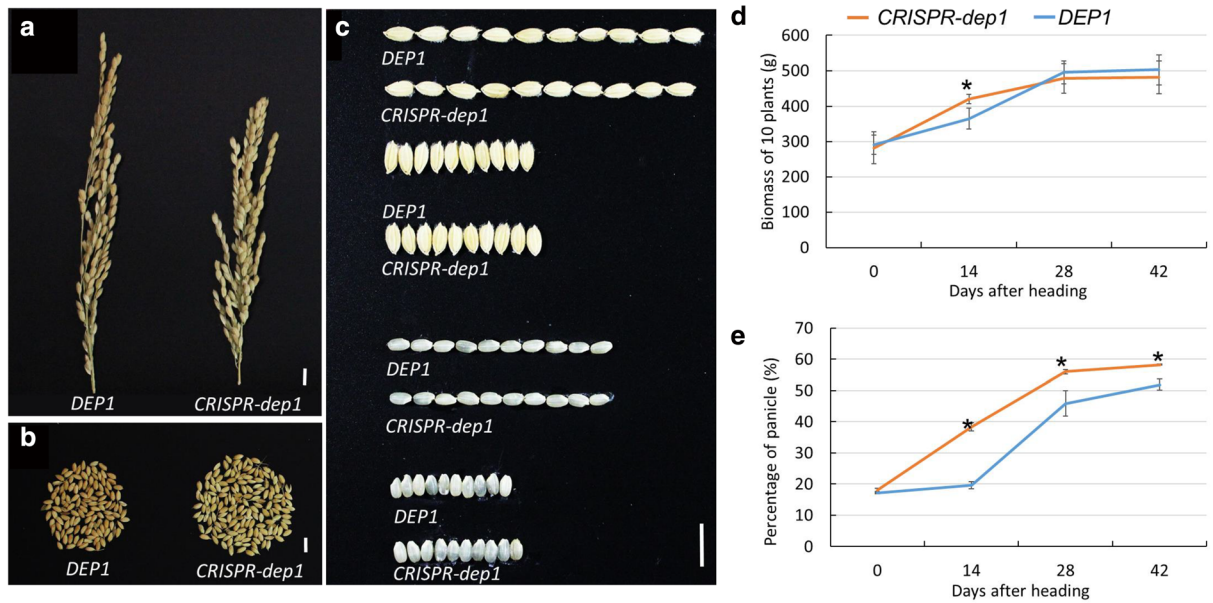


Fig. 5 The biomass and yield performance of WT and *CRISPR-dep1* plants. **a** The panicles of the WT and *CRISPR-dep1* plants. **b** The grain numbers per panicle of the WT and *CRISPR-dep1* plants. **c** The grain size of the WT and *CRISPR-dep1* plants. **d** The biomass of the WT and *CRISPR-dep1* plants from heading to

full ripeness during a 14-day interval survey. **e** The percentage of panicle to the whole biomass of the WT and *CRISPR-dep1* plants from heading to full ripeness during a 14-day interval survey. An asterisk denotes significant at 5% level. Bar = 1 cm

levels of fertilization and two transplanting densities were used in this experiment. The results showed that the high level of fertilization significantly increased the yield per unit of the WT, whereas the high transplant density negatively affected yield of the WT. However, the high level of fertilization also significantly increased the yield per unit of *CRISPR-dep1*, but the high transplant density positively affected grain yield. The *CRISPR-dep1* harvested more grains per unit under the cultivation method of low fertilization and high transplant density than the WT under the cultivation method of high fertilization. The yield components in 2017 also observed similar trend (Table 1). Thus, we could increase the grain yield of *CRISPR-dep1* through increasing the transplant density without increasing the amount of fertilizer.

The quality of different plant architecture populations

As the erect panicle varieties were considered to be only of mediocre eating quality, we conducted a quality investigation to elucidate whether *dep1* imposed a penalty in regard to quality in rice production (Fig. 6). The results confirmed that the *dep1* allele imposed such a penalty in grain quality. The *dep1* allele decreased the

grain shape (the ratio of grain length to grain width), which subsequently increased the head rice ratio. The *dep1* allele also strongly affected chalkiness and related traits. The chalkiness ratio and the chalkiness level were significantly higher in *CRISPR-dep1*. The *CRISPR-dep1* had higher amylose content and protein content compared with those of the WT. We compared the texture properties of cooked rice between the WT and *CRISPR-dep1*. The results showed that the *CRISPR-dep1* had a higher hardness score but a lower stickiness score compared with the WT. *CRISPR-dep1* also had a lower taste score than the WT.

Discussion

Breeding to improve plant architecture has tremendously contributed to the increase in rice production. The semi-dwarf varieties greatly enhanced rice yield in the 1960s (Peng et al. 1999a). The ideal plant architecture was based on the foundation of semi-dwarf breeding. Erect panicle architecture has been extensively used in *japonica* rice breeding (Qian et al. 2016). The northeast area and downstream region of the Yangtze River represent over 70% of the entire *japonica* rice cultivated area in China. At present,

Table 1 The yield performance under different cultivation methods

Allele	Density	Fertilization	Biomass per plant (g)	Yield per plant (g)	Harvest index	Yield (g/m ²)
The yield performance under different cultivation methods in 2018						
<i>DEPI</i>	High	High	49.67 ± 1.80c	21.53 ± 2.47ef	0.43 ± 0.03bc	689.09 ± 78.88abc
	Low	High	98.22 ± 5.46a	43.6 ± 2.28ab	0.44 ± 0.00bc	697.61 ± 36.5abc
	High	Low	40.11 ± 1.37c	17.05 ± 0.37f	0.43 ± 0.01c	545.54 ± 11.87c
	Low	Low	85.88 ± 12.44a	37.13 ± 5.29bc	0.43 ± 0.00bc	594.09 ± 84.6bc
<i>CRISPR-dep1</i>	High	High	57.05 ± 7.49bc	28.76 ± 3.5cde	0.50 ± 0.00ab	920.42 ± 111.94a
	Low	High	99.96 ± 9.85a	50.15 ± 1.63a	0.50 ± 0.03ab	802.34 ± 26.02ab
	High	Low	48.55 ± 4.73bc	25.41 ± 2.67	def0.52 ± 0.00a	813.18 ± 85.54ab
	Low	Low	80.18 ± 6.96ab	34.16 ± 0.08 cd	0.43 ± 0.04bc	546.52 ± 1.35c
The yield performance under different cultivation methods in 2017						
<i>DEPI</i>	High	High	48.82 ± 0.86d	19.23 ± 0.89d	0.39 ± 0.01abc	615.31 ± 28.37bc
	Low	High	91.69 ± 3.77a	38.98 ± 0.42a	0.43 ± 0.02abc	623.74 ± 6.69bc
	High	Low	55.98 ± 1.45d	18.28 ± 0.75d	0.33 ± 0.02c	584.91 ± 24.14bc
	Low	Low	78.86 ± 0.41b	30.60 ± 0.94bc	0.39 ± 0.01bc	489.57 ± 14.98c
<i>CRISPR-dep1</i>	High	High	67.93 ± 0.39c	30.33 ± 1.00abc	0.45 ± 0.01ab	970.43 ± 32.06a
	Low	High	88.51 ± 1.80ab	39.75 ± 4.61a	0.45 ± 0.04ab	635.96 ± 73.78b
	High	Low	58.22 ± 2.50d2	7.71 ± 0.79c	0.48 ± 0.03a	886.86 ± 25.17a
	Low	Low	78.93 ± 6.46b	37.51 ± 3.76ab	0.47 ± 0.01a	600.16 ± 60.18bc

Letter difference means significant at 5% probability levels by Duncan's new multiple range method in each year

more than 50% of the *dep1*-carrying cultivars are propagated in the northeast of China. At the downstream region of the Yangtze River, nearly all of the *japonica* varieties have the erect panicle architecture. Moreover, the cultivation area for erect panicle varieties has annually increased in the *japonica* zone (Xu et al. 2016a). Although recent molecular studies have demonstrated that the *DEPI* locus corresponded to erect panicles and the molecular mechanism of yield increase for individual plants became clear, the contribution of erect panicle architecture to population canopy improvement was unexplored. Since the application of semi-dwarf breeding, the leaf area index (LAI) has significantly increased. However, modern rice breeding is no longer simply the pursuit of high LAI, but rather the enhancement of the population photosynthesis and material production capacity through the improvement of population structure and canopy light reception. As most leaves are below the panicle, the curved panicle at the filling stage may influence population-level photosynthesis. Many lines of evidence indicate that solar radiation has a positive impact on rice growth and development, and solar radiation required by rice crops at different phenological stages differs (Peng et al. 2004; Islam and Morison 1992; Yoshida and Parao 1976). Our study has shown that

more light could reach the leaves under the panicle, especially at 15 days after heading in *CRISPR-dep1* compared with the WT. Compared with the canopy of the WT, the canopy of *CRISPR-dep1* had higher temperatures and lower relative humidity. The higher temperature of the canopy during the last phase of the filling stage might mitigate the effect of low temperature northeast of China, thereby aiding the accumulation of photosynthate. The high humidity of the canopy might lead to increased incidence of diseases and insect pests. The lower humidity of the canopy in *CRISPR-dep1* might enhance the resistance to diseases and insect pests. The subsequent survey showed that the CO₂ concentration in the *CRISPR-dep1* population was significantly lower than that in the WT population from full heading to 15 days after heading. Moreover, the increase in biomass in the *CRISPR-dep1* population was higher than in the WT during this period. A higher proportion of biomass was accumulated into panicles in the *CRISPR-dep1* population compared with the WT population.

The WT and *CRISPR-dep1* populations showed diversity in yield performance under different cultivation methods. As expected, both WT and *CRISPR-dep1* exhibited the highest individual plant yield under high fertilizer

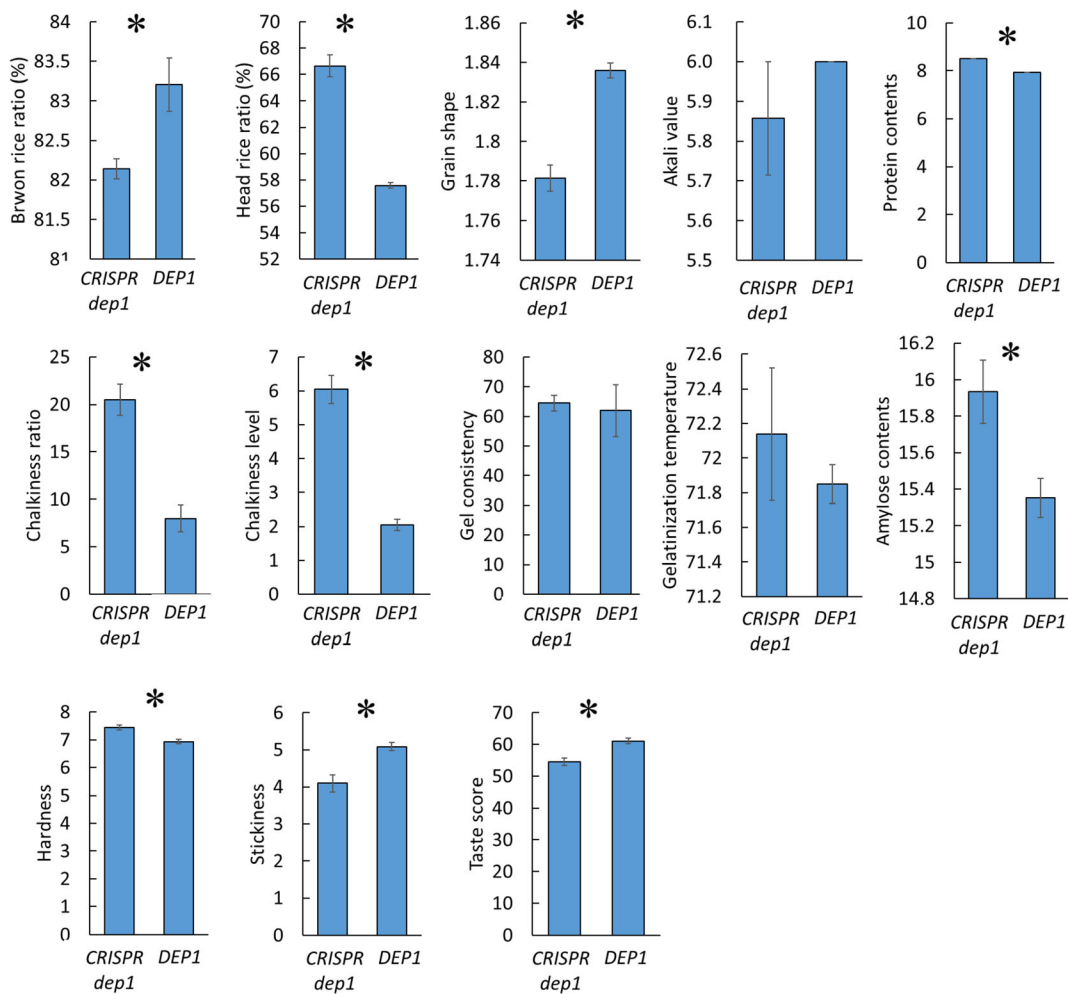


Fig. 6 The quality trait and texture properties of cooked rice derived from *CRISPR-dep1* and *DEP1* plants. An asterisk denotes significant at the 5% level

application and low transplant density cultivation. When we investigated the yield per unit area, we found that the highest yield per unit area for the WT was under high fertilizer application and low transplant density cultivation, whereas the highest yield per unit area for *CRISPR-dep1* was achieved under high fertilizer application and high transplant density cultivation. These results indicated that the dense plant architecture of erect panicles improved the population canopy structure, and eventually increased the yield per unit area through increasing the number of plants per unit area. We noticed that the *CRISPR-dep1* could achieve higher yield per unit area under low fertilizer application cultivation than the WT under high fertilizer application cultivation through increasing the transplant density. These traits could contribute to a sustainable development strategy. Thus, the erect panicle architecture is

another important heritable morphological trait after semi-dwarf breeding and is the ideal plant architecture needed to meet the requirements of super high-yield rice breeding.

CRISPR-associated (Cas) systems have become an efficient genome editing tool in gene function research. As *DEP1* plays a crucial role in rice production, the function of *DEP1* was verified by several research team using CRISPR/Cas9 technology (Li et al. 2016; Shen et al. 2017; Wang et al. 2017; Li et al. 2019; Sun et al. 2018). The CRISPR/Cas9 gene editing plants could be divided into two types: type I, the sgRNA was designed in a similar region of Shennong265, and Liaogeng5 in exon 5, which only eliminated the Cys-rich region (Li et al. 2016; Li et al. 2019); type II, the sgRNA was designed in the first exon of *DEP1* which eliminated both G γ protein region and Cys-rich region (Sun et al.

2018; Shen et al. 2017). The type I CRISPR/Cas9 gene editing plant showed an erect panicle architecture, an increase in grain number per panicle, and a reduction in plant height, panicle length, and grain length. The type II plants also exhibited an erect panicle architecture, but a reduction in grain number per panicle and setting rate. The phenotype of transgenic plant in present study was similar to type I gene editing plant. Moreover, both type I and type II transgenic plants showed a reduction in grain length which caused a decrease of 1000 grain weight. Our study showed that truncated *dep1* (25.43 ± 0.37 g) had a similar 1000 grain weight compare with that of *DEP1* (25.58 ± 0.25 g), as the truncated *dep1* allele could increase the width of grain (Fig. 5). The present study has demonstrated that an imposed penalty for grain quality was a pleiotropic effect of the *dep1* allele. The *dep1* allele might increase the amylose and protein contents, leading to higher scores for hardness and lower scores for of stickiness, and eventually cause decreases in the taste score. This result was consistent with erect panicle varieties being of only mediocre eating quality. Thus, high-yield and high-quality erect panicle varieties might be generated through the combination of the *dep1* allele and other premium grain quality alleles through rationally designed breeding.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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