RESEARCH ARTICLE

SABRAO Journal of Breeding and Genetics
54 (5) 963-975, 2022
http://doi.org/10.54910/sabrao2022.54.5.1
http://sabraojournal.org/
pISSN 1029-7073; eISSN 2224-8978

DEVELOPMENT OF NEW RICE STRAIN WITH IMPROVED SINK SIZE AND SOURCE CAPACITY USING A MULTI-PARENT ADVANCED GENERATION INTERCROSS (MAGIC) APPROACH

M.F. ABBASI[1], A.U. DIN[1], and F.M. ABBASI[2*]

[1]Department of Biotechnology and Genetic Engineering, Hazara University, Mansehra, Pakistan
[2]Department of Agriculture, Hazara University, Mansehra, Pakistan
*Corresponding author's email: drfidaabbasi6@gmail.com
Email addresses of co-authors: abbasids91@gmail.com, geneticsaz@gmail.com

SUMMARY

A new rice strain that grows six feet tall with four times higher potential yield than the conventionally bred variety, JP5, was developed using the MAGIC approach. This new rice type underwent analysis on sink size and source capacity traits, including superior and inferior spikelets, vascular bundles of panicle neck and stem internode, tillering pattern, grain filling pattern, yield, and other morphological attributes. Results indicated that the new strain had more vascular bundles of the stem (42) and panicle neck (35), primary rachis branches of panicle (16.1), superior spikelets, and greater grain weight than the conventionally bred variety, JP5. The panicle measured 45 cm long, with fertile grains of 500 per panicle and a stem diameter of 1.2 cm. During the grain filling duration, the spikelets of this strain and superior spikelets of JP5 gained maximum weight earlier than the inferior spikelets of JP5. Six feet tall plants of this new strain with long and heavy panicles had greater stem wall thickness. There occurred a positive and significant correlation (0.97*) between yield and small vascular bundles of the panicle neck, lumen diameter (0.98*), leaf length (0.99**), leaf width (0.99**), flag leaf length (0.99**), flag leaf width (0.97*), panicle length (0.97*), fertile grains per panicle (0.98*), and plant height (0.97*). The study noted that improving sink size, source capacity, and transportation of assimilation contributed positively toward yield. This novel strategy for grain yield enhancement in rice proved beneficial for other cereals to get significant breakthroughs in their production for ensuring food security.

Keywords: Rice, sink size, source capacity, *Abbasi* strain, yield traits

Key findings: A new crop breeding methodology focusing on improved sink size, source capacity, and enhanced transportation of assimilate contributed toward the increased potential yield of newly developed rice strains. The strain could grow six feet tall with four-fold higher production than the conventionally bred variety, JP5.

Communicating Editor: Prof. Naqib Ullah Khan

Manuscript received: September 13, 2022; Accepted: November 14, 2022.

INTRODUCTION

The expected global demand for rice propels to increase by 1.5 times in 2050, with yield still stagnant for the last several years (Parida *et al*., 2022). A study identified and used a mutant *sd1* in a breeding program that resulted in a dwarf phenotype (Peng *et al*.,

To cite this manuscript: Abbasi MF, Din AU, Abbasi FM (2022). Development of new rice strain with improved sink size and source capacity using a multi-parent advanced generation intercross (MAGIC) approach. *SABRAO J. Breed. Genet.* 54(5): 963-975. http://doi.org/10.54910/sabrao2022.54.5.1.

2021). A quantum jump in rice production resulted in the 1960s using dwarfing gene and plant architecture that changed from tall to dwarf (Ao *et al*., 2008). It was first identified in the Chinese variety *Dee-geo-woo-gen* (DGWG), then crossed with Peta (tall) to develop IR8 (Khush *et al*., 2001). IR8 increased potential yield from 6 to 10 t/ha in irrigated areas of the world (Chandler, 1982). However, yield stagnation in *indica* rice began ever since the release of IR8 (Peng *et al*., 1999). This yield stagnation connects to plant type because it has many unproductive tillers, reduced sink size, and large leaf areas creating mutual shading and reduction in photosynthesis. Sustainable economic development and self-sufficiency in food with an ever-increasing population require a 1% increase annually in rice yield globally. This yield increase must be from the enhanced production from the same piece of land without sacrificing the ecosystem (Cassman, 1999; Tilman, 2002). The second jump in rice production of japonica-type rice occurred in 1976 in China through the development of hybrid rice (Yuan *et al*., 1994). The hybrid increased the potential yield by 15% to 25%.

In the mid-80s, rice yield started declining, 2.7% annual drop in 1980 and 1.1% in 1990 (Horie *et al*., 2005). Low sink capacity was the key factor of yield reduction (Kato and Takeda, 1996). Since then, efforts diverted to increasing sink size or increasing the number of spikelets per panicle, leading to the development of super rice in China (Cheng *et al.,* 2007) and the 'new plant type' (NPT) of the International Rice Research Institute (IRRI) (Peng *et al*., 2008), with heavy panicles and several spikelets per panicle. However, enhanced grain filling capacity, or sink capacity, remained the neglected area in cereal breeding research for getting noble breakthroughs in yield (Kato *et al*., 2007). Thus, the cultivars developed during this period had no significant increase in yield potential on account of poor grain-filling capacity (Yang *et al*., 2002), with a slow grain-filling rate (Ao *et al*., 2008) and a large number of unfilled grains. Grain-filling efficiency became crucial for yield and quality in rice (Zhao *et al*., 2022) and the rice breeding programs did not increase production because of poor grain filling (Parida *et al*., 2022). The position of the spikelets has a greater impact on the amount of translocated assimilates and grain-filling efficiency. The spikelets located on the apical branches have larger and heavier spikelets, while those on the lateral and secondary branches are smaller, with a large proportion remaining unfilled (Mohapatra *et al*., 1993; Yang *et al*., 2000; Yang *et al*., 2006).

Two sources of carbon are responsible for grain filling in cereals. The stored assimilates present in the culm and leaf sheaths are translocated toward the grains, and 30% of the cereals yield depends upon this source (Takai *et al*., 2005). The second carbon source for grain filling depends on the assimilated supply from flag leaf before or after anthesis (Samonte *et al*., 2001). Studies on poor grain filling of the inferior spikelets existed from different perspectives, including genetic control and expression of a gene involved in grain filling (You *et al.,* 2016), enzymatic activities during grain filling (Wang *et al*., 2015), assimilates supply for grain filling (You *et al*., 2017), hormones and their balance during grain filling, and sink-source relationship for grain filling (Okamura *et al*., 2018). The sink capacity measures the storage ability of plant photosynthetic products (Cui *et al*., 2015), and the high capability of rice plants for maximum storage results in higher potential yield (Yu *et al*., 2012; Zhai *et al*., 2020). To further increase the production of rice, scientists around the globe focus on recessive nuclear male sterile lines (NMS) for third-generation hybrid rice technology (Liao *et al*., 2021). Chen *et al*. (2022) reported that assimilate transport and nutrient uptake efficiency confirmed a crucial factor for high grain yield in rice.

Given the importance of source capacity and sink size for increased rice grain production, the study developed a new plant type (*Abbasi* rice strain) patented by the USA (Abbasi, 2016). The paper discusses the notable traits of this novel rice strain in comparison with a conventionally-bred and widely cultivated rice variety, namely JP5.

MATERIALS AND METHODS

Development of the *Abbasi* strain of rice

In a preliminary study**,** 200 landraces collected from different geographical regions of Pakistan underwent evaluation for yield and yield-attributing traits in 1999 and 2000. Based on this study, four landraces: 85-RGP-ARC (Acc335) and Mushkan (Acc367) from Punjab, Beyn (Acc3394) from Chitral, and Sugdasi (Acc3078) from Sindh gained selection (Iqbal *et al*., 2001) for onward use in a hybridization program. Similarly, based on the wider cultivation and adaptation in different agroecological zones of Pakistan, a selection of four rice varieties (IR6, KS282, JP5, and Basmati 385) took place for crossing with landraces. Thus, the breeding materials comprised eight parental genotypes (Table 1). The breeding methodology used in this study followed a report by Bandillo *et al*. (2013) for developing the MAGIC population (Figure 1). The selection of the desired plants started from generation four up to generation nine, resulting in a unique plant type that grows six feet tall (Figure 2).

Table 1. Rice germplasm used for the development of the *Abbasi* strain of rice.

No.	Varieties/lines	Accession number	Collection area
1	85-RGP-ARC	335	Punjab (Pakistan)
2	Mushkan	367	Punjab (Pakistan)
3	Beyn	3394	Chitral (Pakistan)
4	Sugdasi	3078	Sindh (Pakistan)
5	JP5	Cultivar	KPK (Pakistan)
6	IR6	Cultivar	Sindh (Pakistan)
7	Basmati385	Cultivar	Punjab (Pakistan)
8	KS282	Cultivar	Punjab (Pakistan)

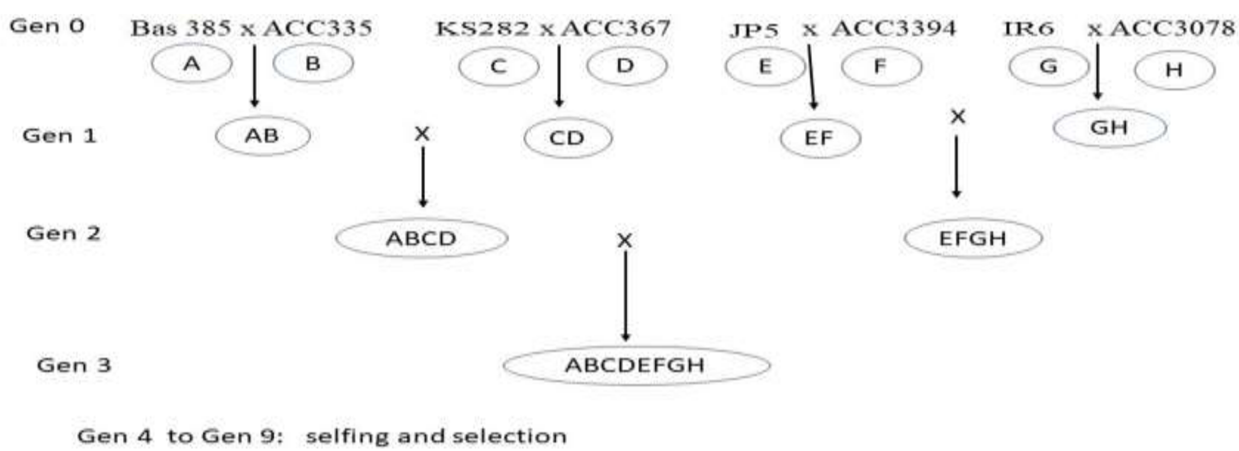

Figure 1. Breeding of *Abbasi* strain of rice using multi-parent advanced generation inter-cross populations (MAGIC) approach.

A B

Figure 2 (A-B). Six feet tall *Abbasi* strain of rice in the field (A) stiff stem, (B) plant at maturity with heavy panicle and resistant to lodging.

Field evaluation

The JP5 is a widely cultivated variety of Khyber Pakhtunkhwa, Pakistan. Its late-emerging tillers resulted in weaker stems, which adversely affected yield. For evaluation of the agronomic performance, the genotypes were transplanted at Hazara University, Mansehra, Pakistan, in 2017 and 2018. The raising of a first nursery ensued, followed by thirty-day-old seedlings transplanted with two seedlings per hill. The genotypes: JP5, *Abbasi* strain, and two sister lines (BR10, BR12) planted in a randomized complete block design involved three replications. The plot size measured 3 m × 5 m. Fertilizer application took place @ 120-60-0 NPK kg/ha. All the phosphorus and half of the nitrogen application occurred at the time of transplanting, and half of the remaining nitrogen was at the booting stage. Data recording on important agronomical and anatomical traits followed. Moreover, a thorough assessment of the tillers' contribution toward yield and rate of grain filling emerged.

Agronomic traits

The recorded data included days to flowering, plant height, leaf length, leaf width, flag leaf length, flag leaf width, panicle length, filled grains per panicle, 1000-grain weight, and yield per plant.

Assessment of the contribution of tillers to yield

The heterogeneous architecture caused the late-emerging tillers leading to inter-grain apical dominance. Initially, the selection occurred from the seedling at tillering stage. These selected seedlings initiated tillering from the single node with no further emergence or few tiller emergences from the other node(s). To assess the contribution of each tiller toward grain yield, acquired five plants randomly selected from each plot. Each tiller was thoroughly studied and compared with each plant's main tiller (apical dominance). The tillers of control variety (JP5) commenced division into three types: main stem (MS), early emerging tillers (EET), and late-emerging tillers (LET). The grains proceeded to harvest at maturity, then weighed and analyzed.

Determination of the rate of grain filling

The assessment of grain filling rate in superior and inferior spikelets employed a collection of 40 spikelets from the main tiller and 40 from lateral inferior branches of the panicle at 5, 10, 15, 20, 25, and 30 days after flowering. These spikelets were dried in an oven at 105°C for 30 min, then kept at 80°C to completely dry, then weighed. Calculating the grain filling rates of both the superior and inferior spikelets followed the methods Fujita *et al*. (1984) and Baillot *et al.* (2018) using the formula: R_{mean} = Y/D, where R_{mean} is the mean grain filling rate, Y is the final grain weight, and D is the time duration for grain filling.

Anatomical studies

For the analysis of lumen wall diameter, vascular bundles, stem wall thickness, and internode diameter, one-centimeter-long sections of internode of each genotype were sampled randomly from each replication. Preparing the internode sections used Formalin - Acetic Acid - Alcohol (FAA) 90:5:5 (v/v) and kept in paraffin. The slicing of sections at 20-25 µm in thickness used the microtome (Leica RM2125). After removing the paraffin, and staining the sections, used Safranin solution (1%), Ethanol (50%), Fast Green (0.1%), and Absolute Alcohol. The sections were dehydrated in isopropyl alcohol, mounted, and observed under a microscope for morphometric measurement of the cross-section for stem wall thickness (SWT), lumen diameter (LD), internode diameter (ID), and vascular bundles (VB).

RESULTS

The JP5 exhibited late tillering and had long apical dominance (Figure 3A). The newly developed line had reduced apical dominance at tillering stage (Figure 3B) and later at crop growth stages, resulting in a plant canopy with long and uniform panicles (Figure 3C). The pattern of grain filling in the spikelets of all the tillers of *Abbasi* strain (AS) showed to be similar to the superior spikelets of JP5. The AS spikelets attained the maximum grain weight (1.7mg day^{-1}) 15 days after flowering. However, the superior spikelets of JP5 gained maximum grain weight (1.6 mg day^{-1}) 20 days after flowering, with its inferior spikelets gaining a maximum weight (0.6 mg day^{-1}) 25 days after flowering (Figure 4). It indicates that the process of grain filling in AS and superior spikelets of JP5 was more rapid versus the inferior spikelets. The spikelets on the main stem and upper branches were considered the superior spikelets, while the spikelets on the lower secondary branches and from the late

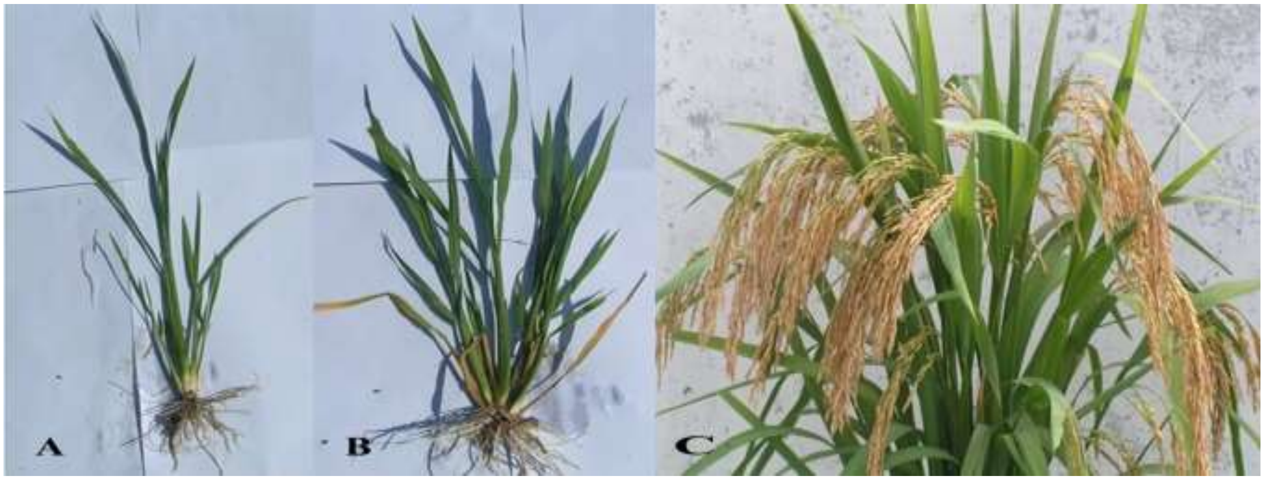

Figure 3 (A-C). Plant morphology of JP5 (control) and *Abbasi* strain of rice. (A) JP5 with long apical dominance and late emerging tillers, (B) *Abbasi* strain with reduced apical dominance, and (C) Uniform canopy of *Abbasi* strain

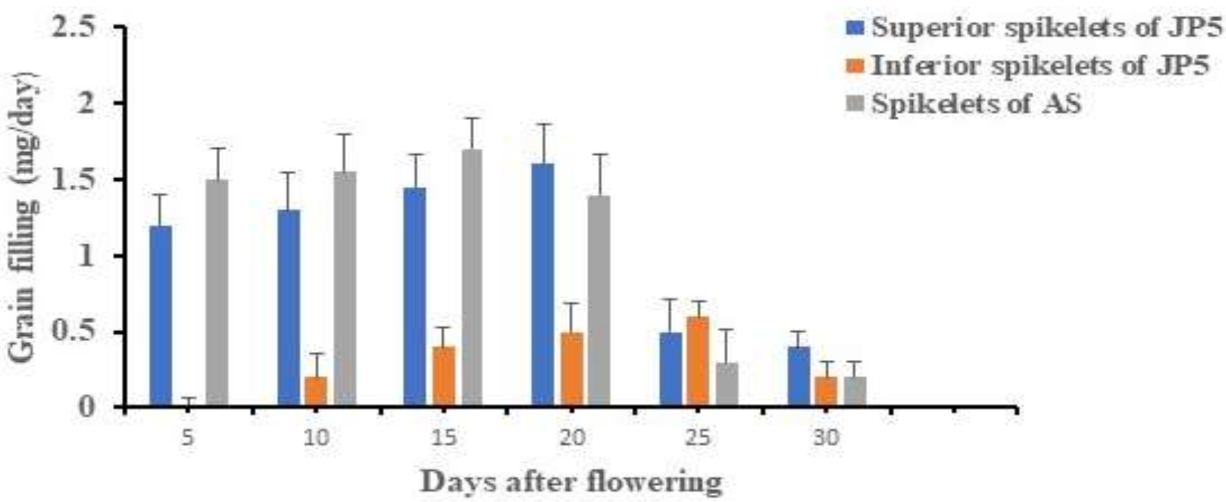

Figure 4. Grain filling per day after flowering of JP5 and *Abbasi* strain of rice.

emerging tillers as the inferior spikelets. The AS showed no main stem, and the canopy had a uniform height of panicles. The average grain weight (10 g) of all the tillers of AS was higher than the grain weight (8 g) of the MS of JP5, followed by EET (4 g) and 2g of LET (Figure 5).

The stem wall thickness, the number of small and large vascular bundles, and increased internode diameter added strength to the culm and are considered key components for lodging resistance. The stem diameter of JP5 displayed a size of 0.4 cm, while in AS, the value increased to 1.4 cm. A significant difference between the AS and the control line (JP5) appeared for internode diameter (ID), lumen diameter (LD), and stem wall thickness (SWT). The LD (8 mm), ID (14 mm), and SWT (3 mm) values recorded for AS showed higher than the corresponding values of LD (2 mm), ID (4 mm), and SWT (1 mm) for JP5 (Figure 6). Both the large and small vascular bundles of the panicle neck (26.2, 35) and the second internode (33.3, 42.1) of the stem of AS were higher than the corresponding values of panicle neck (14.1, 19.4) and the stem internode (14.2, 24.2) for JP5 (Figure 7).

The AS displayed a higher number of primary rachis branches (16.1) per panicle than JP5 (12). The secondary rachis branches of AS have a value of 24.3 while those of JP5 at 20.4. Therefore, the higher number of primary and secondary branches per panicle

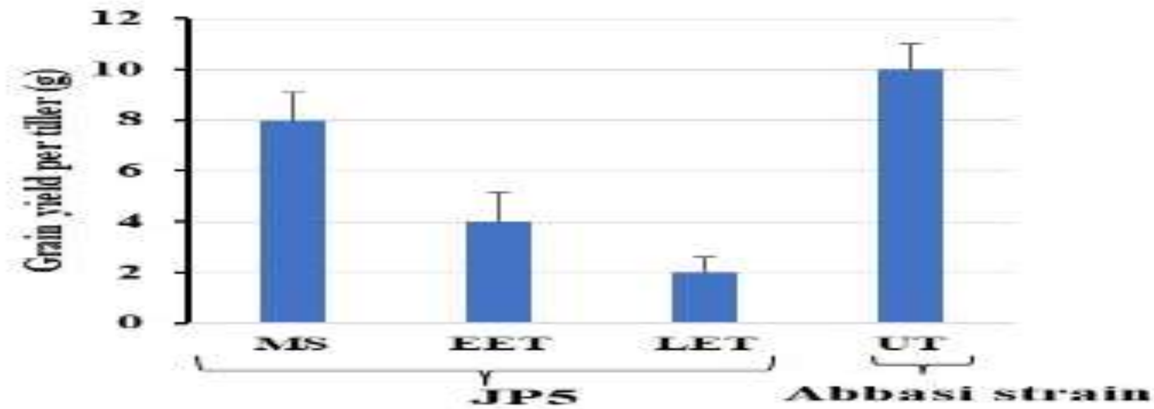

Figure 5. Variation in grain yield tiller^{-1} in JP5 and *Abbasi* strain of rice. MS (main stem), EET (early emerging tillers) LET (late-emerging tillers), and (UT) uniform tillering

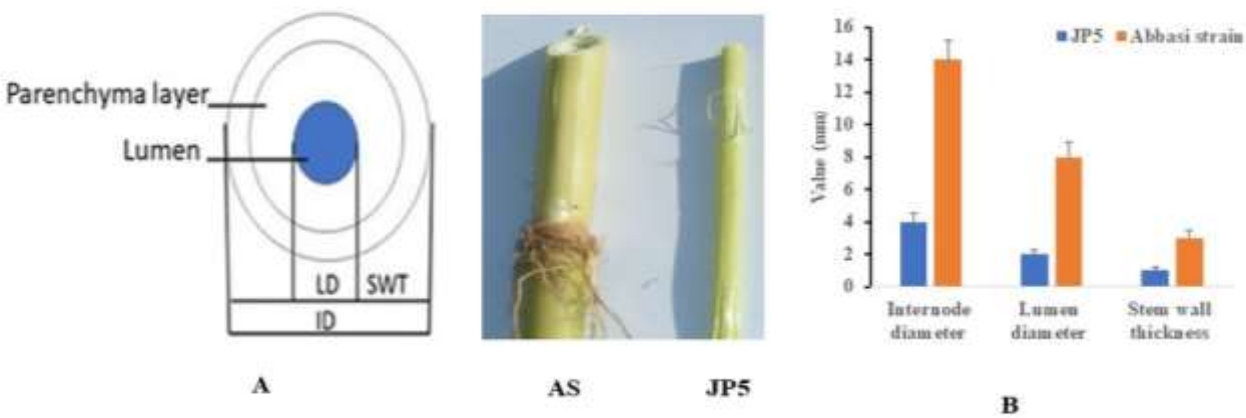

Figure 6 (A-B). The internal structure of the stem of JP5 and *Abbasi* strain of rice. A) Diagrammatic representation of the internal structure of stem and stem internode morphology B) Comparison of JP5 and *Abbasi* strain for internode diameter (ID), stem wall thickness (SWT), and lumen diameter (LD).

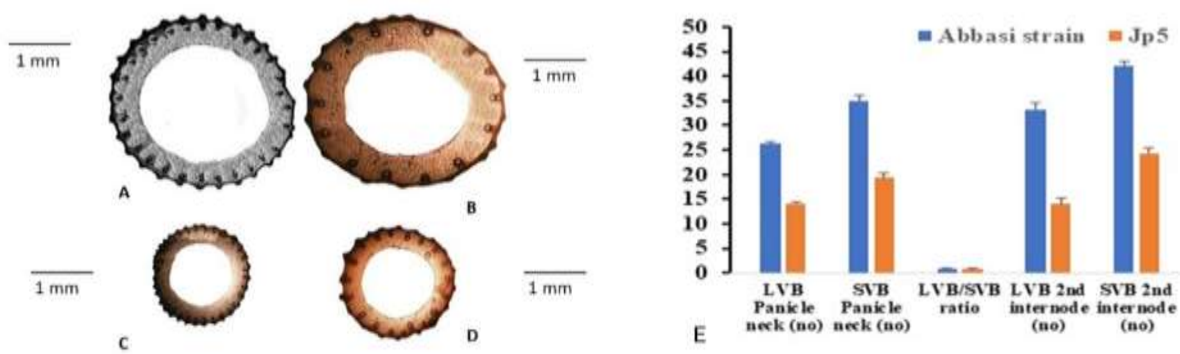

Figure 7 (A-E). Variation in assimilating capacity of *Abbasi* strain of rice and JP5. Vascular bundles of internode of Abbasi strain (A) JP5 (B) vascular bundles of panicle neck of *Abbasi* strain (C) JP5 (D), variation in small and large vascular bundles (E).

Figure 8. Variation in primary and secondary rachis branches of *Abbasi* strain of rice and JP5.

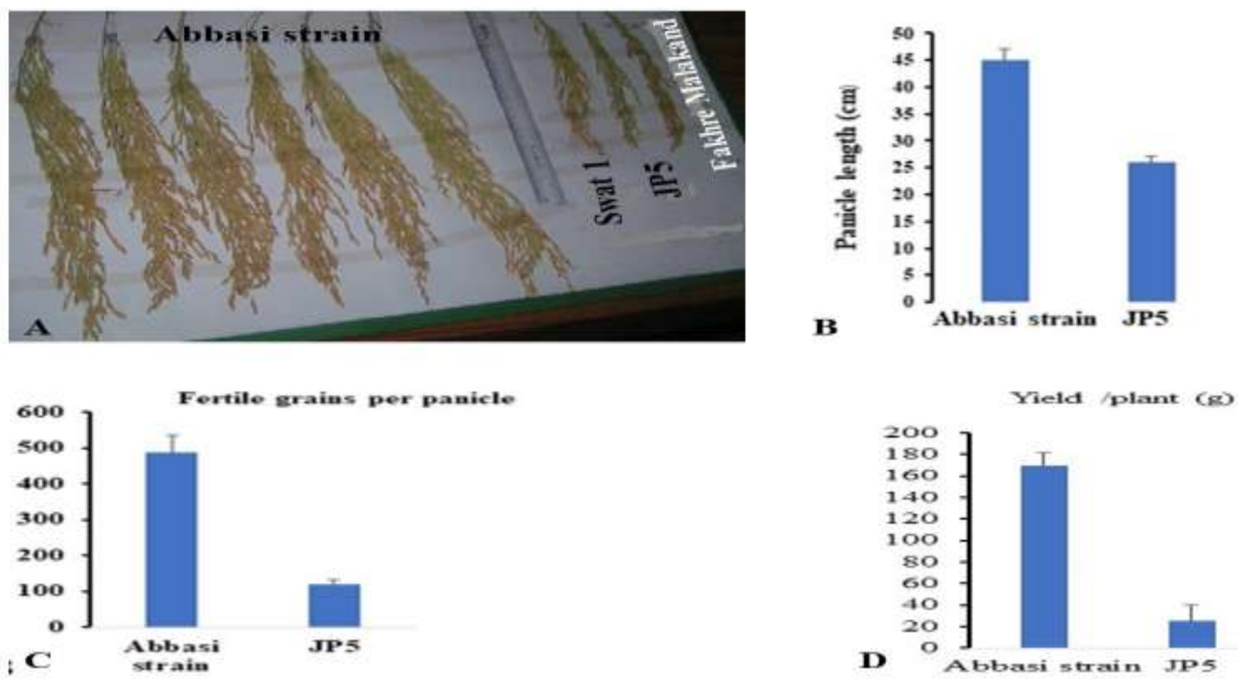

Figure 9 (A-D). Sink size of *Abbasi* strain of rice and JP5. (A) panicle morphology of *Abbasi* strain and cultivars of Khyber Pakhtunkhwa (B) panicle length (C) fertile grains per panicle (D) yield per plant.

appeared a one of the vital factors for an enhanced yield of AS than that of JP5 (Figure 8). Similarly, the panicle length of AS exhibited considerably higher (45 cm) versus JP5 (25 cm) (Figure 9). A similar trend followed for the increased number of filled grains per panicle for AS (500) than JP5 (95). Overall, the increase in filled grains per panicle of AS compared with JP5 relates to higher values for primary rachis and secondary rachis branches per panicle, vascular bundles of panicle, and stem internode. It also implied there occurred an active assimilates transport from source to sink during grain filling duration in AS.

Yield and yield attributing traits of AS and two sister lines gained compared with JP5. Results indicated that the yield of AS (170 g $plant^{-1}$) and sister lines, BR10 (159 g $plant^{-1}$) and BR12 (170 g $plant^{-1}$), indicated substantially higher than JP5 (35 g $plant^{-1}$). A similar trend followed for the increased leaf length (118 cm), leaf width (2.0 cm), flag leaf length (102 cm), flag leaf width (2.3 cm), panicle length (45 cm), 1000-grain weight (40.0 g), and plant height (190 cm) of AS compared with JP5. However, the JP5 displayed a short-duration variety compared with AS (Tables 2 and 3).

Table 2. Mean square for yield and yield attributing traits of rice genotypes at Hazara University Mansehra during the 2018 rice growing season.

Traits	Replications df = 2	Genotypes df = 3	Error df = 6
Days to flowering	1.75	5.00	12.08
Plant height	1.75	1958.7**	9.75
Leaf length	1.00	3262.7**	8.33
Leaf width	0.0675	0.807*	0.16
Flag leaf length	15.75	3810.0**	7.42
Flag leaf width	0.17896	1.03*	0.11
Panicle length	6.25	225.0*	31.2
Filled grain panicle^{-1}	558.3	93952.1**	708.3
1000-grain weight	42.33	130.6**	13.3
Yield plant^{-1}	5.20	13017.0**	28.6

**, * = Significant at 1% and 5 % probability levels, respectively.

Table 3. Yield and yield attributing traits of *Abbasi* rice strain, its sister lines compared with JP5.

Name of advanced lines	LL (cm)	LW (cm)	FLL (cm)	FLW (cm)	PL (cm)	FGPP (no)	TGW (g)	PLH (cm)	DF (no)	Yield plant^{-1} (g)
Abbasi strain	118	2.0	102	2.3	45	500	40.0	190	118	170
BR10	111	2.0	99	2.2	40	410	30.0	173	117	159
BR12	112	2.1	110	2.6	40	403	31.33	177	116	170
JP5 (control)	48	1.0	33	1.25	25	95	24.0	131	115	35
Grand Mean	97.25	1.77	86	2.1	37.5	352.08	31.33	167.75	116.5	133.5
LSD $_{0.05}$	5.76	0.80	5.44	0.69	11.17	53.17	7.29	6.24	2.88	10.68

LL = Leaf length, LW = Leaf width, FLL = Flag leaf length, FLW = Flag leaf width, PL = Panicle length, FGPP = Filled grain per panicle, TGW = 1000-grain weight, PLH = Plant height, DF = Days to flowering.

Correlation coefficient

The correlation coefficient of yield and yield attributing anatomical traits appear in Table 4. There expressed a significantly positive correlation of yield with small vascular bundles of the panicle neck (0.97*), LD (0.98*), primary rachis branches (0.99**), leaf length (0.99**), leaf width (0.99**), flag leaf length (0.99**), flag leaf width (0.97*), panicle length (0.97*), fertile grain per panicle (0.98*), and plant height (0.97*). All these traits are part of the source capacity, except panicle length and fertile grain per panicle, which are considered the traits of sink capacity. Both large and small vascular bundles of the second internode and panicle neck notably and positively correlated with primary rachis branches. The primary rachis branches have more superior grains per panicle, leading to higher grain yield. Plant height revealed positively and significantly correlated with lumen diameter (0.99**), internode diameter (0.99**), leaf length (0.95*), flag leaf length (0.95*), panicle length (0.99**), and fertile grains per panicle (0.99**). Plant height is a stem trait, and from these results, plant height contributed positively to the photosynthesis process. The synthesized assimilates, in turn, enhanced the yield of active translocation from the stem toward the grains.

DISCUSSION

Improvement in source capacity, sink capacity, and translocation capacity of assimilates from source to sink enhanced the potential yield of *Abbasi* rice strain four times the conventionally bred variety, JP5. The yield of this strain proved higher on account of larger panicles, a higher number of filled spikelets per panicle, and more grain weight. The panicle architecture of rice constitutes the number of grains per panicle, determined by vascular bundles of the internode and panicle neck (Chen *et al.,* 2020). The number of spikelets and filled grains determine the grain yield, as reported by Kato and Takeda (1996). Moreover, a significant positive correlation between sink size and yield appeared. These results agree with the conclusions of several studies (Song *et al*., 1990; Saitoh *et al*., 1991; Shi *et al*., 1996). *Abbasi* strain has a sizable number of food and water-carrying organs (vascular bundles) compared with JP5, which

Table 4. Correlation coefficient between the attributes of sink size and source capacity in JP5 and *Abbasi* rice strain.

Attributes	PRB	SRB	LVB panicle	SVB panicle	LVB 2nd internode	SVB 2nd internode	LD	ID	SWT	LL	LW	FLL	FLW	PL	FGPP	TGW	PLH	DF	YPP
PRB		0.80	0.96*	0.99**	0.97*	0.96*	0.99**	0.97*	0.86	0.97*	0.97*	0.97*	0.93	0.99**	0.99**	0.86	0.99	0.86	0.99**
SRB			0.92	0.74	0.88	0.86	0.88	0.77	0.53	0.87	0.87	0.89	0.95*	0.77	0.77	0.63	0.80	0.41	0.86
LVB panicle				0.93	0.99**	0.99**	0.97*	0.90	0.70	0.99**	0.99**	0.99**	0.99**	0.93	0.94	0.73	0.94	0.67	0.99**
SVB panicle					0.95*	0.94	0.97*	0.97*	0.87	0.96*	0.95*	0.95*	0.89	0.99**	0.99**	0.86	0.99**	0.90	0.97*
LVB 2^{n} internode						0.99**	0.97*	0.91	0.72	0.99**	0.99**	0.99**	0.98*	0.95*	0.95*	0.74	0.95*	0.72	0.99
SVB 2^{nd}internode							0.95*	0.88	0.68	0.99**	0.99**	0.99**	0.97*	0.93	0.94	0.69	0.93	0.70	0.99
LD								0.98*	0.85	0.96*	0.96*	0.97*	0.95*	0.98*	0.98*	0.88	0.99**	0.8	0.98*
ID									0.94	0.90	0.90	0.91	0.87	0.99*	0.98*	0.95**	0.99**	0.89	0.93
SWT										0.72	0.71	0.72	0.65	0.90	0.89	0.98	0.90	0.96*	0.77
LL											0.99**	0.99**	0.98*	0.95*	0.96*	0.73	0.95*	0.72	0.99**
LW												0.99**	0.98*	0.95*	0.95*	0.73	0.95*	0.72	0.99**
FLL													0.99	0.95*	0.95*	0.74	0.95*	0.71	0.99**
FLW														0.90*	0.90	0.70	0.91	0.61	0.97*
PL															0.99**	0.90	0.99**	0.89	0.97*
FGPP																0.89	0.99**	0.89	0.98*
TGW																	0.91	0.90	0.78
PLH																		0.87	0.97*
DF																			0.77

PRB = Primary rachis branches, SRB = Secondary rachis branches, LVB = Large vascular bundles, SVB = Small vascular bundles, LD = lumen diameter, ID = internode diameter, SWT = Stem wall thickness, LL = Leaf length, LW = Leaf width, FLL = Flag leaf length, FLW = Flag leaf width, PL = Panicle length, FGPP= Filled grain per panicle, TGW = 1000-grain weight, PLH = Plant height, YPP = Yield per plant

enhanced its yield. Earlier reports indicated that sink strength and source capacity determined the potential yield of rice (Zhai *et al*., 2020). The sink is the organ that either stores or uses assimilate (Chen *et al*., 2020), including new tissues, reproductive organs, panicles, and grains (Pan *et al*., 2018). Large sink size promotes the production of abscisic acid and carbon and nitrogen metabolism. The sink capacity is the internal driving force for high grain yield in rice (Counce and Wells, 1990). Increasing sink size without improvement of source capacity does not significantly increase the potential rice yield. The classic example is the new plant type (NPT) of IRRI (Cheng *et al*., 2007; Peng *et al*., 2008) with heavier panicles and higher spikelets per panicle (Peng *et al*., 1999). However, lower grain filling capacity (Yang *et al*., 2002), accompanied by a slow grain filling rate (Ao *et al*., 2008), with a higher number of unfilled grains, were limiting factors resulting in a lower potential yield (Kato *et al*., 2007). These limitations for getting enhanced yield in IRRI NPTs gained resolution in the latest study through increasing sink size and source capacity, leading to increase grain filling efficiency and high yield.

The newly developed *Abbasi* rice strain stands six feet tall and demonstrated resistance to lodging at maturity compared with JP5, which has a weak stem. The AS has higher small and large vascular bundles of stem internodes, more stem wall thickness, and greater stem diameter versus JP5. Improving grain yield and lodging resistance requires increasing stem thickness (Zhang *et al*., 2013). To gain plant strength in cereals results from the morphology and internal structure of the stem (Zhang *et al*., 2016). Lodging resistance in rice comes from higher culm wall thickness, more thickness of mechanical tissue, and a higher number of small and large vascular bundles (Duan *et al*., 2004). Overcoming the lodging problem gave rise to dwarfing gene (Khush, 1999), which limits canopy photosynthesis (Kuroda *et al*., 1989) and reduces culm thickness (Okuno *et al*., 2014). Plants, therefore, would not experience the risk of lodging with thick stems (Islam *et al*., 2007). A higher number of vascular bundles, recorded in AS, enhanced assimilates transport to the developing grains, which increased grain filling efficiency. Vascular bundles provide mechanical support to plants with a pivotal role in stem strength and determining the panicle structure (Qi *et al*., 2011).

Abbasi rice strain exhibited all productive tillers compared with JP5, which had late emerging tillers and inter-grain apical dominance that ultimately led to the production of inferior spikelets. It could be the reason for the lower potential yield of JP5. Tillering is an essential yield component for rice grain production (Cheng *et al.,* 2022). However, it is worth mentioning that most do not contribute to grain production, especially the late emerging tillers (Yang and Zhang, 2010). Earlier studies indicated that plants with apical dominance failed to exploit the available nutrient with reduced yield (Haris, 1974)**.** The reduction in the apical dominance yielded a higher number of superior spikelets in AS. Several studies concluded that the reduced assimilates supply in the early stages of the grain filling could be a limiting factor for the low grain weight of inferior spikelets (Zhu *et al*., 1988). An increase in the number of spikelets per panicle without improving the translocation ability of photosynthate may not increase the yield because of poor grain fertility (Yang *et al*., 2000). The AS has a large panicle size and more filled grain per panicle versus JP5. Large panicle size provides more photosynthetic area and, thus, contributes more to grain filling (Chang *et al*., 2020), and it can directly influence the grain yield (Zhao *et al.,* 2020). It could be one of the main reasons for a higher filled grains panicle $^{-1}$ that ultimately lead to the higher potential yield of AS.

A significantly positive correlation of grain yield with source capacity and other translocation traits was also one of the major contributing factors to the high yield of AS. Similar results have been reported by Hayashi (1976) explaining that large vascular bundles of internode positively correlated with primary and secondary branches of panicles. It might be due to their role in the synthesis and supply of photosynthate to the developing grains. Zhang *et al*. (2002) reported a connection of vascular bundles with the leaf, stem, and panicle for facilitating the transport of assimilation. It indicated that the synthesis and supply of the food assimilated to the developing grains could be limiting factors for the yield of conventional rice. Rice yield is influenced by the number and size of the vascular bundles responsible for providing food and water to the grains. In the latest study, the role of the larger vascular bundles was quite evident for the high yield of AS.

CONCLUSIONS

Improvement of source capacity, sink size, and photosynthate mobilization during grain filling in AS enhanced its potential yield. Increasing the number of vascular bundles of both neck and internodes facilitated efficient transporting and unloading of assimilates in spikelets. An increased number of primary rachis branches of panicles enhanced the grain filling efficiency and increased grain weight. The superior spikelets had greater weight, which lead to greater potential yield. The plant with reduced apical dominance allowed the growth of a uniform tillering pattern, which reduced the inferior spikelets. Taller stems of AS and greater flag leaf length and width increased the photosynthetic area and contributed toward the accumulation of assimilates, later translocated efficiently toward grains. Similarly, greater stem wall thickness reduced the lodging of AS at maturity. Additionally, AS is highly suitable for growing in flash flood-prone areas of the world, containing three to four feet of water standing in the field after the flood.

ACKNOWLEDGMENTS

The authors would like to thank the Pakistan Agriculture Research Council and the Ministry of Food Security for supporting the research through the Agriculture Linkage Program Grant vide No. F.2-203/2016 (ALP)-PARC (P) from 2016-18.

REFERENCES

Abbasi FM (2016). *Abbasi* strain of rice. Patent available at https://patft.uspto.gov/netacgi/nph-: Parser?Sect1=PTO1&Sect2=HITOFF&d=PALL&p=1&u=%2Fnetahtml%2FPTO%2Fsrchnum.htm&r=1&f=G&l=50&s1=9313977.PN.&OS=PN/9313977&RS=PN/9313977.

Ao H, Wang S, Zou Y, Peng S, Tang Q, Fang Y, Chen Y, Xiong C, Xiao A (2008). Study on yield stability and dry matter characteristics of super hybrid rice. *Sci. Agric. Sin*. 41: 1927-1936.

Baillot N, Girousse C, Allard V, Pissalou AP, Gouis LJ (2018). Different grain-filling rates explain grain weight differences along the wheat ear. *PLoS ONE* 13(12): https://doi.org/10.1371/journal.pone.0209597.

Bandillo N, Raghavan C, Muyco PA, Sevilla MAL, Lobina IT, Dilla-Ermita CJ, Chih-Wei T, McCouch S, Thomson M, Mauleon R, Singh KR, Gregorio G, Redoña E, Leung H (2013). Multi-parent advanced generation inter-cross (magic) populations in rice: Progress and potential for genetics research and breeding. *Rice* 6: 11. http://www.thericejournal.com/content/6/1/11.

Cassman KG (1999). Ecological intensification of cereal production systems: Yield potential, soil quality, and precision agriculture. *Proc. Nat. Acad. Sci. USA.* 96: 5952-5959.

Chandler JR (1982). An adventure in applied science. In: A history of the International Rice Research Institute. IRRI, Los Banos, Philippines.

Chang TG, Song QF, Zhao HL, Chang S, Xin C, Qu M, Zhu XG (2020). An *in situ* approach to characterizing photosynthetic gas exchange of rice panicle. *Plant Methods* 16:92. https://doi.org/10.1186/s13007-020-00633-1.

Chen C, Yu X, Gao Y, Xu J, Shu X, Tang D, Huang J, Wang Y, Yao Y, Dong G (2020). Differential nitrogen uptake and utilization in rice genetic populations with contrasting sink capacity. *Southwest China J. Agric. Sci.* 33: 2707–2713.

Chen T, Yang X, Fu W, Li G, Feng B, Fu G, Tao L (2022). Strengthened assimilate transport improves the yield and quality of super rice. *Agronomy* 12:753. https://doi.org/10.3390/agronomy12040753.

Chen Y, Zhang YJ, Zhang HL, Zhu A, Huang J, Zhang H, Gu JF, Liu LJ, Yang JC (2020). Effects of plant spacing on grain yield and population quality in mechanically-transplanted rice with good tasting quality. *Chinese J. Rice Sci*. 34(6): 550-560.

Cheng F, Bin S, Iqbal A, He L, Wei S, Zheng H, Yuan P, Liang H, Ali I, Xie D, Yang X, Xu A, Ullah S, Jiang L (2022). High sink capacity improves rice grain yield by promoting nitrogen and dry matter accumulation. *Agronomy* 12: 1688. https://doi.org/10.3390/agronomy12071688.

Cheng S, Zhuang J, Fan Y, Du J, Cao L (2007). Progress in research and development on hybrid rice: A super-rice domesticated in China. *Ann. Bot*. 100: 959-966.

Counce PA, Wells BR (1990). Rice plant population density effect on early-season nitrogen requirement. *J. Prod. Agric*. 3: 390-393.

Cui J, Xu K, Shi J, Wu Z, Chen Z, Zhang Z, Wu C (2015). Changes in sink-source variation characteristics of different rice varieties. *Chinese J. Bot*. 50: 699-705.

Duan CR, Wang BH, Wang PQ, Wang DH, Cai SX (2004). Relationship between the minute structure and the lodging resistance of rice stems. *Colloids Surf B. Bioint*. 35: 155-158.

Fujita K, Coronel VP, Yoshida S (1984). Grain-filling characteristics of rice varieties (*Oryza sativa* L.) differing in grain size under controlled environmental conditions. *Soil Sci. Plant Nutr.* 30 (3): 445-454.

Haris P (1974). A possible explanation for plant yield increases following insect damage. *Agro-Ecosystems* 1: 219-225.

Hayashi H (1976). Studies on large vascular bundles in paddy rice plant and panicle formation: Relationships between the number of large vascular bundles in the culm and the plant types. *Proc. Crop Sci. Soc*. *Japan*.45: 322 - 327.

Horie T, Shiraiwa T, Homma K, Katsura K, Maeda Y, Yoshida H (2005). Can yields of lowland rice resume the increases that showed in the 1980s. *Plant Prod. Sci*. 8: 259-274.

Iqbal M, Abbasi FM, Salim M, Ahmed HM, Sagar MA (2001). Selection of breeding parents from different landraces of rice. *Pak. J. Biol. Sci.* 4(4): 357-358.

Islam MS, Peng S, Visperas RM, Ereful N, Bhuiya M, Julfiquar A (2007). Lodging related morphological traits of hybrid rice in a tropical irrigated ecosystem. *Field Crops Res*. 101: 240-248.

Kato T, Shinmura D, Taniguchi A (2007). Activities of enzymes for sucrose–starch conversion in developing endosperm of rice and their association with grain-filling in extra-heavy panicle types. *Plant Prod. Sci*. 10: 442-450.

Kato T, Takeda K (1996). Associations among characters related to yield sink capacity in space-planted rice. *Crop Sci.* 36: 1135-1139.

Khush GS (1999). Green revolution: Preparing for the 21st century. *Genome* 42: 646-655.

Khush GS, Coffman WR, Beachell HM (2001). The history of rice breeding: IRRI's contribution. In: WG Rockwood (ed.); Rice Research and Production in the 21st Century. Symposium Honoring Robert F. Chandler, Jr., International Rice Research Institute, Los Banos, Philippines. 117-135.

Kuroda E, Ookawa T, Ishihara K (1989). Analysis of the difference in dry matter production between rice cultivars with different plant heights in relation to gas diffusion inside stands. *Jpn. J. Crop Sci*. 58: 374-382.

Liao C, Yan W, Chen Z, Xie G, Deng XW, Tang X (2021). Innovation and development of the third-generation hybrid rice technology. *Crop J*. 9: 693-701.

Mohapatra PK, Pate Rl, Sahu SK (1993). The time of flowering affects grain quality and spikelet partitioning within the rice panicle. *Aust. J. Plant Physiol*. 20: 231-242.

Okamura M, Arai-Sanoha Y, Yoshida H, Mukouyama T, Adachia S, Yabe S, Nakagawa H, Tsutsumi K, Taniguchi Y, Kobayashia N, Kondoa M (2018). Characterization of high-yielding rice cultivars with different grain-filling properties to clarify limiting factors for improving grain yield. *Field Crops Res*. 219: 139-147.

Okuno A, Hirano K, Asano K, Takase W, Masuda R, Morinaka Y, Ueguchi-Tanaka M, Kitano H, Matsuoka M (2014). A new approach to increasing rice lodging resistance and biomass yield through the use of high gibberellins-producing varieties. *Plos ONE* 9: 1-12.

Pan L, Chang T, Chang S, Ouyang X, Qu M, Song Q, Xiao L, Xia S, Deng Q, Zhu X (2018). Systems model-guided rice yield improvements based on genes controlling the source, sink, and flow. *J. Integr. Plant Biol*. 60: 1154-1180.

Parida AK, Sekhar S, Panda BB, Sahu G, Shaw PB (2022). Effect of panicle morphology on grain filling and rice yield: Genetic control and molecular regulation. *Front. Genet*. 13:876198. https://doi: 10.3389/fgene.2022.876198.

Peng S, Cassman KG, Virmani SS, Sheehy J, Khush GS (1999). Yield potential trends of tropical since the release of IR8 and its challenge of increasing rice yield potential. *Crop Sci*. 39: 1552-1559.

Peng S, Khush GS, Virk P, Tang Q, Zou Y (2008). Progress in ideotype breeding to increase rice yield potential. *Field Crops Res.* 108: 32-38.

Peng Y, Hu Y, Qian Q, Ren D (2021). Progress and prospect of breeding utilization of green revolution gene *sd1* in rice. *Agriculture*.11: 611. https://doi.org/10.3390/agriculture11070611.

Qi W, Sun F, Wang Q, Chen M, Huang Y, Feng YQ (2011). Rice ethylene-response ap2/erf factor OsEATB restricts internode elongation by down-regulating a gibberellin biosynthetic gene. *Plant Physiol*. 157: 216-228.

Saitoh K, Kasiwagi S, Kinoshita T, Ishihara K (1991). Characterization of dry matter production process in high yielding rice varieties: IV dry matter accumulation in the panicle. *Jpn. J. Crop Sci*. 60: 255-263.

Samonte SOBP, Wilson LT, McClung AM, Tarpley L (2001). Seasonal dynamics of non-structural carbohydrate partitioning in 15 diverse rice genotypes. *Crop Sci*. 41: 902-909.

Shi CJ, Qin DL, Tsuda M, Matsumoto Y (1996). High yielding performance of paddy rice activated in Yunnan province China: II spikelets production of japonica F1 hybrid rice Yu Za 29. *Jpn. J. Crop Sci*. 65: 22-28.

Song XF, Agata W, Kawamitsu Y (1990). Studies in dry matter and grain production in F1 hybrid rice in China: II characteristics in grain production. *Jpn. J. Crop Sc*i. 59: 29-33.

Takai T, Fukuta Y, Shirawa T, Horie T (2005). Time-related mapping of quantitative trait loci controlling grain-filling in rice. *J. Exp. Bot*. 56: 2107-2118.

Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S (2002). Agricultural sustainability and intensive production practices. *Nature* 418: 671-677.

Wang ZQ, Xu YJ, Chen TT, Zhang H, Yang JC, Zhang JH (2015). Abscisic acid and the key enzymes and genes in sucrose-to-starch conversion in rice spikelets in response to soil drying during grain filling. *Planta* 241: 1091-1107. https://doi: 10.1007/s00425-015-2245-0.

Yang J, Peng S, Visperas RM, Sanico AL, Zhu Q, Gu S (2000). Grain-filling pattern and cytokinin content in the grains and roots of rice plants. *Plant Growth Regul*. 30: 261-270.

Yang J, Zhang J, Wang Z, Liu K, Wang P (2006). Post-anthesis development of inferior and superior spikelets in rice in relation to abscisic acid and ethylene. *J. Exp. Bot*. 57:149-160.

Yang JC, Zhang JH (2010). Grain filling problem in "super" rice. *J. Exp. Bot.* 61: 1-5. doi: 10.1093/jxb/erp348.

Yang Y, Peng S, Zhang Z, Wang Z, Visperas RM, Zhu Q (2002). Grain and dry matter yields and partitioning of assimilates in japonica/indica hybrids. *Crop Sci*. 42: 766-772.

You CC, Chen L, He HB, Wu LQ, Wang SH, Ding YF (2017). Itarq-based proteome profile analysis of superior and inferior spikelets at early grain filling stage in japonica rice. *BMC Plant Biol*. 17:100. https://doi: 10.1186/s12870-017-1050-2.

You CC, Zhu HL, Xu BB, Huang WX, Wang SH, Ding YF (2016). Effect of removing superior spikelets on grain filling of inferior spikelets in rice. *Front. Plant Sci*. 7: 1161. https://doi: 10.3389/fpls.2016.01161.

Yu X, Wang Y, Yuan Q, Zhong J, Chen C, Yang B, Hu D, Wang Y, Dong G, Huang J (2012). Study on the characteristics of the source and sink in conventional *japonica* rice cultivars with high nitrogen uptake efficiency. *J. Yangzhou Univ*. 33: 54-60.

Yuan L, Yang Z, Yang J (1994). Hybrid rice in China. In: SS Virmani, (ed.), Hybrid rice technology: New developments and future prospects. International Rice Research Institute, Los Banos, Philippines, 143-147.

Zhai L, Wang F, Yan A, Liang C, Wang S, Wang Y, Xu J (2020). Pleiotropic effect of gnp1 underlying grain number per panicle on the sink, source, and flow in rice. *Front. Plant Sci.* 11: 933 https:// doi: 10.3389/fpls.2020.00933.

Zhang J, Li GH, Song YP, Zhang WJ, Yang CD, Wang SH, Ding YF (2013). Lodging resistance of super-hybrid rice Y Liangyou 2 in two ecological regions. *Acta Agron. Sin*. 39: 682-692.

Zhang W, Wu L, Wu X, Ding Y, Li G, Li J, Weng F, Liu Z, Tang S, Ding C, Wang S (2016). Lodging resistance of japonica rice (*Oryza sativa* L.): Morphological and anatomical traits due to top-dressing nitrogen application rates. *Rice* 9: 31. https:// doi 10.1186/s12284-016-0103-8.

Zhang ZH, Li P, Wang JX, Tan CJ, Hu ZL, Zhu YG, Zhu LH (2002). Identification of quantitative trait loci (QTLs) for the characters of vascular bundles in peduncle related to *indica*-*japonica* differentiation in rice (*Oryza sativa* L.). *Euphytica* 128: 279-284.

Zhao C, Liu G, Chen Y, Yan JY, Shi Y, Zhao L, Liao P, Wang W, Xu K, Dai Q, Huo Z (2022). Excessive nitrogen application leads to lower rice yield and grain quality by inhibiting the grain filling of inferior grains. *Agriculture*. *12*(7): 962. https://doi.org/10.3390/ agriculture12070962.

Zhao Q, Hao X, Ali I, Iqbal A, Jiang L (2020). Characterization and grouping of all primary branches at various positions on a rice panicle based on grain growth dynamics. *Agron. J.* 10: 223.

Zhu Q, Cao X, Luo Y (1988). Growth analysis in the process of grain filling in rice. *Acta Agron. Sin*. 14: 182-193.