



Article

Comparison of the Source–Sink Characteristics between Main Season and Ratooning in Rice (*Oryza sativa* L.)

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Abstract: **Objectives:** In order to find out the differences in source–sink characteristics of ratooning rice and main season rice and find approaches to increase the grain yield of ratooning rice, a sowing-by-stage method was adopted to synchronize main season rice with ratooning rice and induce their key growth stages under similar environmental conditions. The source–sink characteristics of four varieties under similar ecological conditions of main and ratooning rice were examined in 2019 and 2020. **Results:** The main results were: (1) The leaf area index (LAI) of the ratooning rice ranged from 0.54 to 1.44, while that of the LAI of main season rice was 4.67–7.71. The LAI of ratooning rice was much smaller than that of the main season rice; the former was only approximately 1/7–1/5 of the latter. (2) The photosynthesis (Pn) and net assimilation rate (NAR) of the ratooning rice were significantly higher than those of the main season rice before the milking–maturing stages. Still, at the late maturing stage, no definite tendency existed. (3) Ratooning rice transported ¹⁴C-assimilate from the flag leaf to the panicle at an estimated 81.43%, while main season rice transported 63.95%. The main stem's top first and second internodes have been observed to be a major location for the ¹⁴C-assimilate in main season rice. (4) The grain yield of main season rice was 6029–7929 kg ha^{−1} while the grain yield of ratooning rice ranged from 2363–3297 kg ha^{−1}. The sink capacity of the main season rice was approximately 2.4–3.6 times that of ratooning rice. The catalase activity of the rachis branches of the ratooning rice was higher than that of the main season rice. (5) The grain/leaf area (sink/source) ratio in the ratoon season rice was 1.69–2.46 times higher than that of the main season rice. **Conclusions:** The grain yields of ratooning rice were determined by the interaction of source and sink capacity while those of main season rice were mainly increased by enhancing sink capacity. Choosing varieties with heavier 1000 grain weight, exerting the advantages of higher photosynthetic rate and net assimilation rate of ratooning rice, promoting leaf area, and improving the transportation capacity of carbohydrate are the main approaches to increase the grain yield of ratooning rice.

Keywords: rice; ratooning rice; source–sink characters; sowing by stages



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1. Introduction

Rice feeds over 2 billion of the world's population [1]; however, with urbanization and industrialization, the available land for rice cultivation is decreasing [2]. This poses a threat to food security around the world. Ratooning rice is a kind of rice cropping system which makes dormant axillary buds in the stubble of main crop rice sprouts and heads, and another crop can be harvested after regenerating tillers from the last cropping [3]. It has the advantages of saving time, labor, and fertilizer, as well as environmental protection, high efficiency, and simplification. It is considered the main rice planting method to increase

the rice multiple cropping index in areas where the photothermal effect is enough for one cropping. Still, it is insufficient for two croppings within one year [4]. In China, there are 15 provinces suitable for ratooning rice, with an area of approximately 0.7 million hectares, while the potential area is about 13.28 million hectares [5]. In the province of Fujian, the highest yield of ratooning rice reached 9.7 t ha^{-1} [6]; in the province of Hubei, the highest yield of ratooning rice was recorded at 9.8 t ha^{-1} [7]; and in the city of Chongqing, the yield record of ratooning rice was 8.5 t ha^{-1} [8]. However, the average yield of ratooning rice is 3.64 t ha^{-1} in China [9].

Rice ratooning has been exploited and practiced in China for over 1700 years [10]. However, the theoretical studies on ratooning rice began in the 1930s, when the main attention was on the effects of dormancy buds in different nodes of the main stems [11], axillary buds [12], and cultivation techniques on the grain yield for ratooning rice [13,14]. Limited research has been conducted on the effects of different source–sink characteristics of ratooning rice on grain yield [15], in which some research results have agreed that ratooning rice had a smaller source size, lower sink capacity, a higher sink–source ratio, and higher productivity per unit of leaf area [16]. The spikelet number per panicle of ratooning rice is usually much lower than that of the main season rice because there are fewer and smaller leaves per stem in ratooning rice.

However, such results were usually obtained under different ecological conditions for the main season rice and ratooning rice [17], for which the disturbance from environmental factors was not eliminated. In this study, it was determined that main season rice and ratooning rice under the same ecological conditions had the same heading stage and key growth stages through the use of a method of sowing by stage; ratooning rice and main season rice were compared based on their source–sink characteristics.

2. Materials and Methods

2.1. Trial Design

2.1.1. Trial Materials and Locations

The experiments were conducted from 2019 to 2020 in the city of Liuyang, province of Hunan, a typical double-cropping rice area. The four rice varieties used were Longliangyou 072 (two-line hybrid, abv. LLY072), Shenyong 9576 (three-line hybrid, abv. SY9576), Xiangwanxian 10 (inbred, abv. XWX10), and Minghui 63 (inbred, abv. MH63).

2.1.2. Experimental Design

During 2019 and 2020, these experiments were conducted. A sowing-by-stages was implemented to realize simultaneous heading between the main season rice and the ratooning rice, and the early season included sowing dates of March 30, April 4, and April 9, while the late season included sowing dates of June 15, June 20, and June 25. Among the 4 varieties, for LLY072 and SY9576, ratooning rice from the treatment of sowing on March 30 and main season rice sowed on June 15 had the same heading stage, while for other varieties, ratooning rice from the treatment of sowing on March 30 and main season rice sowed on June 20 had the same heading stage. Then, all the samples were gathered from the plants of the main season rice and ratooning rice with the same heading stage.

The seedlings were raised in a plastic pan, with 2–3 seeds per hole (2.5 cm in diameter) for hybrid rice and 4–5 seeds per hole for inbred rice. The transplanting date was April 30 for early-season rice and July 20 for late-season rice, with 16.7 cm to 20 cm spaces. Each treatment set had 3 replicates, and 20 m^2 was set up for each plot. The basal fertilizer was 750 kg ha^{-1} of compound fertilizer (NPK: 15–15–15) and 750 kg ha^{-1} of rapeseed cake (NPK: 4.60–2.48–1.40); 150 kg ha^{-1} of urea (NPK: 46–0–0) and potassium chloride (NPK: 0–0–60) were top-dressed in the middle of the panicle initiation stage. At 20 days after the full heading stage, 150 kg ha^{-1} of urea and 150 kg ha^{-1} of potassium chloride were top-dressed to promote axillary bud sprouting in the main stems. At two days after the harvest of main season rice, 112.5 kg ha^{-1} of urea was top-dressed onto main season rice stubble to accelerate the emerging of tillers as tillering fertilizer for ratooning rice. The

other managements were the same as the general practice. During the harvest of main season rice, the height of the remaining stubble was 40 cm.

2.2. Measuring Items and Methods

2.2.1. Leaf Area Index (LAI)

There were 10 hills in each plot sampled to measure the green leaf area. The measurements were conducted at the booting, full heading, milking, and maturing stages in the main season rice and ratooning rice.

2.2.2. Photosynthesis (Pn) of Functional Leaves

Ten flag leaves in each plot were measured. The Pn was measured through a Li-6400 photosynthetic system at the full heading stage, milking stage, and the wax-maturing stage of the main season rice and ratooning rice.

2.2.3. Net Assimilation Rate (NAR) and Crop Growth Rate (CGR)

On the bases of measurements of leaf area and dry matter production, the NAR and CGR were calculated with the following formula [18]:

$$\text{NAR}(\text{mg cm}^{-2} \text{ d}^{-1}) = \frac{(W_2 - W_1)}{T_2 - T_1} \times \frac{(\ln A_2 - \ln A_1)}{A_2 - A_1}, \text{CGR} = \text{NAR} \times \text{LAI}$$

where W_1 and W_2 represent the biomass weight at sampling time T_1 and T_2 , respectively; A_1 and A_2 represent the leaf area at sampling time T_1 and T_2 , respectively.

2.2.4. Dry Matter Production and ^{14}C -Assimilate Partitioning

At the maturing stage of the main season rice and ratooning rice, 10 hills in each plot were sampled to determine the dry matter production. At the full heading stage of the main season rice and ratooning rice, ^{14}C - NaHCO_3 was fed to the flag leaf, and 5 leaves for each plot were sampled. The irradiation intensity of ^{14}C in the panicle, stem, leaf sheath, and leaves was measured at the maturing stage.

2.2.5. Catalase Activity of Rachis Branches

At the milking and maturing stages in 2019 and full heading, milking, and wax-maturing stages in 2020, the catalase activity of the rachis branches in the main season rice and ratooning rice was measured. Ten panicles from each plot were sampled. After threshing, the rachis branches were clipped and mixed and triturated into plasm under 4 °C, and titration was carried out with potassium permanganate.

2.2.6. Sink Capacity and Yield

For the investigations of the main season rice yield components and ratooning rice yield components, 10 hills of rice plants were sampled in each plot at the maturing stage. The sink capacity was expressed as spikelet m^{-1} . The ratio of the grain number to the maximum leaf area represents the sink/source ratio.

The ratio of grain number to leaf area = the total number of grains per hill/the total green leaf area per hill in booting/heading stage [19].

Ten plants with consistent growth were taken from each plot to test leaf area. Grains were counted after threshing.

2.3. Statistical Analysis

Excel 2007 was used for data processing, and SPSS 23.0 and Origin were used for statistical analyses. The results are the average values for the years 2019 and 2020.

3. Results

3.1. Leaf Area Index

There was little difference in the LAI of the main season rice at the booting stage among different varieties, which was generally higher for hybrid varieties than the two inbred varieties. After the booting stage, the LAI decreased gradually until the maturing stage; all of the varieties (hybrids) preserved a higher LAI because of the fertilizer top-dressing at 20 days after the full heading stage. No significant difference in the LAI among the different varieties was found at different growth stages of the main season rice (Table 1).

Table 1. The leaf area index (LAI) of different varieties for the main season rice and ratooning rice.

Cropping Type	Variety	2019				2020			
		Booting Stage	Heading Stage	Milking Stage	Maturing Stage	Booting Stage	Heading Stage	Milking Stage	Maturing Stage
Main season rice	LLY072	7.71 ± 0.38 a	6.32 ± 0.28 a	5.83 ± 0.48 a	5.04 ± 0.19 a	7.35 ± 0.24 a	6.62 ± 0.40 a	5.98 ± 0.46 a	4.83 ± 0.39 a
	SY9576	7.38 ± 0.25 a	6.98 ± 0.44 a	6.49 ± 0.58 a	5.09 ± 0.37 a	7.22 ± 0.25 a	7.08 ± 0.38 a	6.18 ± 0.44 a	4.95 ± 0.29 a
	XWX10	7.05 ± 0.31 a	6.58 ± 0.41 a	5.90 ± 0.43 a	4.84 ± 0.18 a	7.11 ± 0.22 a	6.73 ± 0.27 a	5.27 ± 0.44 a	4.67 ± 0.42 a
	MH63	7.14 ± 0.37 a	6.37 ± 0.33 a	5.51 ± 0.40 a	4.86 ± 0.32 a	7.16 ± 0.25 a	6.76 ± 0.29 a	5.69 ± 0.57 a	4.88 ± 0.46 a
Ratooning rice	LLY072	1.63 ± 0.08 a	1.44 ± 0.13 a	1.10 ± 0.12 ab	0.92 ± 0.18 a	1.72 ± 0.12 a	1.55 ± 0.08 a	1.24 ± 0.12 a	0.96 ± 0.10 a
	SY9576	1.06 ± 0.18 b	0.93 ± 0.16 b	0.81 ± 0.11 b	0.54 ± 0.08 b	1.19 ± 0.14 b	1.07 ± 0.10 b	0.92 ± 0.13 b	0.65 ± 0.06 b
	XWX10	1.14 ± 0.20 b	1.21 ± 0.10 ab	1.23 ± 0.12 a	0.63 ± 0.10 b	1.24 ± 0.09 b	1.27 ± 0.09 b	1.31 ± 0.11 a	0.79 ± 0.06 ab
	MH63	1.03 ± 0.09 b	1.21 ± 0.08 ab	1.26 ± 0.09 a	0.61 ± 0.07 b	1.20 ± 0.11 b	1.22 ± 0.11 b	1.23 ± 0.06 a	0.63 ± 0.11 b

Note: Different letters represent significance at the 0.05 level in the same column in the same year.

The LAI of the ratooning rice was markedly lower than that of the main season rice, and the former was approximately 1/7–1/5 of the latter. The LAI of the hybrids decreased after the booting stage; however, the LAI of the two inbred varieties increased after the booting stage until the milking stage and then decreased.

There was no significant correlation of the LAI between the main season rice and ratooning rice. The results were similar in both years.

3.2. Pn of Functional Leaves

The functional leaf Pn of the ratooning rice was markedly higher than that of the main season rice at the full heading and milking stages in 2019 and 2020 (Table 2). However, the Pn of the ratooning rice was generally lower than that of the main season rice at the wax-maturing stage in 2020. This suggested that the photosynthetic potential of the ratooning rice was higher than that of main season rice under the same ecological conditions and cultivating techniques. Still, the assimilating ability of the ratooning rice tended to decrease at the late stage due to its smaller sink size (less assimilate demand).

Table 2. Comparison of photosynthetic rate between the main season rice and ratooning rice ($\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$).

Cropping Type	Variety	2019		2020		
		Full Heading Stage	Milking Stage	Full Heading Stage	Milking Stage	Wax-Maturing Stage
Main season rice	PLY 210	18.53 ± 0.69 a	14.68 ± 0.99 a	18.4 ± 1.04 a	17.1 ± 1.11 a	16.9 ± 0.98 a
	SY 9576	14.95 ± 0.96 b	10.44 ± 1.10 b	16.3 ± 1.65 ab	17.3 ± 1.35 a	13.7 ± 1.39 b
	XWX 10	18.06 ± 1.33 a	11.95 ± 1.04 ab	15.3 ± 0.78 bc	17.3 ± 0.96 a	17.7 ± 1.31 a
	MH63	16.53 ± 1.96 ab	11.25 ± 1.57 b	13.4 ± 0.66 c	17.2 ± 0.53 a	16.9 ± 1.08 a
Ratooning rice	PLY 210	25.38 ± 1.30 a	18.76 ± 1.12 a	20.6 ± 1.70 a	21.2 ± 1.71 ab	14.6 ± 1.45 ab
	SY 9576	19.18 ± 1.81 c	13.17 ± 1.20 b	20.8 ± 1.18 a	22.2 ± 1.04 ab	12.4 ± 1.31 b
	XWX 10	23.08 ± 1.18 ab	14.82 ± 1.02 b	19.9 ± 1.21 a	24.2 ± 1.82 a	16.1 ± 1.61 a
	MH63	19.86 ± 1.19 bc	15.43 ± 1.33 b	19.2 ± 0.89 a	19.4 ± 1.40 b	14.8 ± 1.95 ab

Note: Different letters represent significance at the 0.05 level in the same column in the same year.

3.3. Dry Matter Production and Partitioning

There were differences in the dry matter accumulation among the different varieties, both for the main season rice and ratooning rice (Table 3).

Table 3. Dry matter accumulation of different varieties at maturing stage (g hill^{−1}).

Cropping Type	Variety	2019			2020		
		Total Weight	Stem and Leaf Sheath Weight	Panicle Weight	Total Weight	Stem and Leaf Sheath Weight	Panicle Weight
Main season rice	LLY072	59.04 ± 2.67 a	15.87 ± 1.21 a	36.05 ± 1.18 a	60.61 ± 1.74 a	16.18 ± 1.18 a	36.51 ± 1.22 a
	SY9576	58.01 ± 2.19 a	15.54 ± 1.02 a	35.20 ± 1.09 a	59.27 ± 2.08 a	15.82 ± 1.02 ab	35.50 ± 1.11 ab
	XWX10	50.69 ± 2.60 b	13.05 ± 0.98 b	31.96 ± 1.48 b	50.58 ± 2.20 b	13.18 ± 0.91 bc	32.45 ± 1.89 ab
	MH63	47.41 ± 2.52 b	12.31 ± 0.97 b	31.52 ± 1.71 b	47.87 ± 2.41 b	12.67 ± 1.15 c	31.74 ± 1.87 b
Ratooning rice	LLY072	22.16 ± 2.25 a	5.33 ± 0.49 a	14.22 ± 1.14 a	22.38 ± 1.94 a	5.23 ± 0.39 a	14.39 ± 1.45 a
	SY9576	15.97 ± 1.39 c	4.34 ± 0.37 ab	10.40 ± 0.59 c	16.67 ± 0.80 b	4.10 ± 0.48 b	10.65 ± 0.86 b
	XWX10	19.79 ± 1.79 ab	4.79 ± 0.38 ab	13.00 ± 0.97 ab	19.68 ± 1.46 ab	4.73 ± 0.54 ab	13.32 ± 1.14 ab
	MH63	17.79 ± 1.55 bc	4.25 ± 0.31 b	11.57 ± 1.16 bc	17.88 ± 1.26 b	4.02 ± 0.39 b	11.52 ± 1.40 ab

Note: The total dry weight of the ratooning rice does not include the stubble of the main season rice; different letters represent significance at the 0.05 level in the same column in the same year.

The total dry weights of ratooning rice of different varieties were much smaller than that of the main season rice at the maturing stage, of which the highest one was approximately 39% of that of the main season rice and only 27.5% for the lowest one.

There also existed distinct differences in the dry matter partitioning between the main and ratooning season rice. In 2019, the flag leaves of four varieties were fed with ¹⁴C-NaHCO₃ at the full heading stage both for the main season rice and the ratooning rice, which were sown by stages to make the main season rice and ratooning rice head at the same time. The results indicated that the ratio of ¹⁴C-assimilate via flag leaf transport to the panicle was higher in ratooning rice than in the main season rice for all tested varieties; the difference was approximately 9–28 percent. However, the ¹⁴C-residue in the stem and leaf sheath was higher for the main season rice than in the ratooning rice (Table 4).

Table 4. Comparison of ¹⁴C-assimilate partitioning between the main season rice and ratooning rice in 2019.

Cropping Type	Variety	Flag Leaf %	Panicle %	Stem and Sheath %
Main season rice	LLY072	9.94 ± 1.08 b	57.07 ± 3.67 b	32.99 ± 2.62 a
	SY9576	9.47 ± 1.15 b	74.23 ± 2.67 a	16.15 ± 1.96 b
	XWX10	14.75 ± 1.56 a	71.28 ± 2.26 a	13.96 ± 1.27 b
	MH63	10.51 ± 1.33 b	53.23 ± 2.16 b	36.22 ± 3.69 a
Ratooning rice	LLY072	5.37 ± 0.78 b	79.42 ± 1.97 a	15.21 ± 1.55 a
	SY9576	7.33 ± 1.17 ab	83.23 ± 2.20 a	8.44 ± 1.15 b
	XWX10	9.61 ± 1.52 a	81.85 ± 2.59 a	8.40 ± 1.34 b
	MH63	7.20 ± 0.78 ab	81.20 ± 2.12 a	10.61 ± 2.77 b

Note: Different letters represent significance at the 0.05 level in the same column in the same year.

There was a significant difference in the partitioning of ¹⁴C-assimilate remaining in the stem and leaf sheath among different internodes of the main season rice (Table 5). The ratio of ¹⁴C-assimilate quantum into the upper first and second internodes was over 90%, while that into the other internodes together was less than 10%; the ratio into the fourth internode was the lowest. This coincides with the ratooning tillers' sprouting ability from the different nodes of the main season rice.

Table 5. ^{14}C -residue in stem and leaf sheath partitioning among different internodes of the main season rice in 2019.

Variety	^{14}C -Assimilate Partitioning Ratio into Different Internodes of Main Culm %					
	Upper 1st Node	Upper 2nd Node	Upper 3rd Node	Upper 4th Node	Upper 5th Node	Upper 6th Node
LLY072	35.71 \pm 2.76 c	55.33 \pm 3.37 a	7.34 \pm 0.36 a	1.70 \pm 0.11 a	-	-
SY9576	41.21 \pm 2.86 c	49.38 \pm 3.99 a	5.68 \pm 0.45 b	1.11 \pm 0.12 b	2.62 \pm 0.16 a	-
XWX10	52.55 \pm 4.06 b	37.95 \pm 2.86 b	4.06 \pm 0.44 c	0.79 \pm 0.11 c	1.53 \pm 0.06 b	3.12 \pm 0.17
MH63	61.60 \pm 3.84 a	33.35 \pm 3.56 b	1.72 \pm 0.33 d	1.50 \pm 0.13 a	2.63 \pm 0.13 a	-

Note: Different letters represent significance at the 0.05 level in the same column in the same year.

3.4. NAR and CGR

The NAR of the ratooning rice was usually higher than that of the main season rice in different growth stages, especially from the booting stage to the heading stage and from the milking stage to the maturing stage (Table 6). The NAR of the ratooning rice was approximately 1.63–2.17 times that of the main season rice. These results were in accordance with different years and varieties. From the full heading stage to the milking stage, the difference in the NAR between the main season rice and ratooning rice was smaller because it also possessed a higher NAR. However, the CGR of the ratooning season rice was much smaller than that of the main season rice because of the smaller LAI of the ratooning rice.

Table 6. Comparison of NAR and CGR between the main season rice and ratooning rice.

Cropping Type	Items	Variety	2019			2020		
			Booting–Full Heading Stage	Full Heading–Milking Stage	Milking–Yellow Maturing Stage	Booting–Full Heading Stage	Full Heading–Milking Stage	Milking–Yellow Maturing Stage
Main season rice	NAR ($\text{gm}^{-2} \text{d}^{-1}$)	LLY072	3.94 \pm 0.39 a	4.96 \pm 0.36 a	1.48 \pm 0.10 ab	4.10 \pm 0.67 a	4.75 \pm 0.41 a	1.55 \pm 0.21 ab
		SY9576	3.32 \pm 0.30 a	4.71 \pm 0.51 a	1.34 \pm 0.06 bc	3.72 \pm 0.42 a	4.79 \pm 0.53 a	1.39 \pm 0.17 bc
		XWX10	3.88 \pm 0.32 a	4.50 \pm 0.46 a	1.68 \pm 0.08 a	3.96 \pm 0.40 a	4.57 \pm 0.50 a	1.46 \pm 0.19 a
		MH63	3.10 \pm 0.38 a	4.56 \pm 0.68 a	1.18 \pm 0.14 c	3.57 \pm 0.33 a	4.64 \pm 0.81 a	1.20 \pm 0.23 c
	CGR ($\text{gm}^{-2} \text{d}^{-1}$)	LLY072	26.85 \pm 2.21 a	30.13 \pm 2.75 a	8.04 \pm 0.91 ab	28.64 \pm 2.66 a	29.93 \pm 2.87 a	8.38 \pm 0.91 a
		SY9576	23.84 \pm 2.14 ab	31.72 \pm 2.71 a	7.76 \pm 0.86 ab	26.60 \pm 2.09 ab	31.76 \pm 2.98 a	7.74 \pm 0.86 ab
		XWX10	26.44 \pm 1.97 a	28.08 \pm 2.53 a	9.02 \pm 1.21 a	27.40 \pm 1.76 a	27.42 \pm 2.73 a	7.26 \pm 1.21 ab
		MH63	20.94 \pm 1.92 b	27.09 \pm 2.65 a	6.12 \pm 1.03 b	24.85 \pm 1.77 b	28.88 \pm 2.93 a	6.34 \pm 1.03 b
Ratooning rice	NAR ($\text{gm}^{-2} \text{d}^{-1}$)	LLY072	8.16 \pm 0.28 a	5.66 \pm 0.41 a	2.77 \pm 0.16 a	8.81 \pm 0.41 a	5.43 \pm 0.39 a	3.03 \pm 0.34 a
		SY9576	6.61 \pm 0.33 b	5.03 \pm 0.38 a	2.64 \pm 0.19 a	6.87 \pm 0.36 b	4.92 \pm 0.44 a	2.43 \pm 0.26 a
		XWX10	8.18 \pm 0.40 a	5.68 \pm 0.32 a	2.90 \pm 0.28 a	8.33 \pm 0.35 a	5.47 \pm 0.38 a	2.97 \pm 0.29 a
		MH63	6.74 \pm 0.42 b	5.43 \pm 0.49 a	2.01 \pm 0.19 b	6.92 \pm 0.46 b	5.37 \pm 0.53 a	1.96 \pm 0.21 b
	CGR ($\text{gm}^{-2} \text{d}^{-1}$)	LLY072	12.53 \pm 0.68 a	7.19 \pm 0.71 a	2.80 \pm 0.33 a	14.40 \pm 0.73 a	7.57 \pm 0.71 a	3.33 \pm 0.33 a
		SY9576	6.58 \pm 0.59 b	4.38 \pm 0.58 b	1.78 \pm 0.37 b	7.76 \pm 0.42 c	4.90 \pm 0.58 b	1.91 \pm 0.37 b
		XWX10	9.61 \pm 0.76 ab	6.93 \pm 0.98 a	2.74 \pm 0.45 a	10.45 \pm 0.69 b	7.06 \pm 0.98 a	3.12 \pm 0.45 a
		MH63	7.55 \pm 0.62 b	6.71 \pm 1.06 a	1.88 \pm 0.42 b	8.37 \pm 0.66 c	6.58 \pm 1.06 a	1.82 \pm 0.42 b

Note: Different letters represent significance at the 0.05 level in the same column in the same year.

3.5. Catalase Activity of Rachis Branches

The catalase activity of rachis branches may reflect the assimilation transfer intensity from the source to the sink in one aspect. Under the same ecological conditions, the ratooning rice exhibited higher catalase activity in its rachis branches than the main season rice in all tested varieties (Table 7).

Table 7. Comparison of rachis branches' catalase activity ($\text{mg g}^{-1} \text{min}^{-1}$) between the main season rice and ratooning rice.

Cropping Type	Variety	2019			2020	
		Milking Stage	Maturing Stage	Full Heading Stage	Milking Stage	Wax-Maturing Stage
Main season rice	LLY072	51.9 ± 4.0 a	9.2 ± 0.8 c	32.7 ± 3.2 a	29.1 ± 1.9 a	17.6 ± 2.0 b
	SY9576	46.8 ± 3.1 a	15.1 ± 2.4 b	32.4 ± 2.5 a	26.5 ± 1.7 a	24.0 ± 1.7 a
	XWX10	35.2 ± 3.4 b	21.6 ± 2.4 a	32.8 ± 4.3 a	29.65 ± 2.4 a	18.7 ± 1.6 b
	MH63	34.8 ± 1.9 b	8.0 ± 1.2 c	33.7 ± 5.0 a	29.2 ± 2.6 a	20.8 ± 1.9 ab
	Average	42.2	13.5	32.9	28.6	20.3
Ratooning rice	LLY072	69.7 ± 3.9 a	10.5 ± 1.7 b	39.3 ± 1.8 b	36.7 ± 2.4 a	19.4 ± 1.5 c
	SY9576	51.0 ± 4.2 b	21.0 ± 2.2 a	46.2 ± 3.0 a	34.4 ± 1.8 a	28.8 ± 2.1 a
	XWX10	44.8 ± 4.7 b	10.5 ± 1.9 b	40.3 ± 3.0 ab	35.5 ± 2.5 a	27.3 ± 1.1 ab
	MH63	51.2 ± 4.0 b	26.3 ± 2.4 a	39.3 ± 1.9 b	34.9 ± 1.9 a	24.4 ± 1.5 b
	Average	54.2	17.1	41.3	35.4	25.0

Note: Different letters represent significance at the 0.05 level in the same column in the same year.

3.6. Sink Capacity and Yield

The sink capacity of the main season rice was much higher than that of the ratooning rice, the former being approximately 2.4–3.6 times the latter. The filled sink percentage was approximately 9.0–19.4 percent higher in the ratooning rice than in the main season rice; the grain yield of the main season rice was 2.22–3.36 times higher than that of the ratooning season rice (Table 8). The sink capacity of the main season rice was sufficient, and the source size was large enough (the max. LAI was over 7).

Table 8. Sink characteristics and yields of the main season rice and ratooning rice for different varieties.

Cropping Type	Variety	2019				2020			
		Sink Capacity (Spikelet m^{-2})	Filled Sink Percentage (%)	1000 Grain Weight (g)	Yield (kg ha^{-1})	Sink Capacity (Spikelet m^{-2})	Filled Sink Percentage (%)	1000 Grain Weight (g)	Yield (kg ha^{-1})
Main season rice	LLY072	$40,087 \pm 1526$ a	74.9 ± 1.1 a	25.2 ± 0.26 c	7552 ± 217 a	$42,589 \pm 887$ a	74.7 ± 0.9 a	25.3 ± 0.20 b	8058 ± 159 a
	SY9576	$40,567 \pm 721$ a	71.4 ± 1.2 bc	24.7 ± 0.20 c	7158 ± 139 ab	$41,715 \pm 1075$ a	76.8 ± 1.1 a	24.7 ± 0.22 b	7929 ± 191 a
	XWX10	$33,420 \pm 895$ b	74.4 ± 1.0 ab	27.0 ± 0.17 a	6719 ± 151 b	$34,829 \pm 1040$ b	71.6 ± 1.1 b	27.2 ± 0.26 a	6783 ± 165 b
	MH63	$33,423 \pm 1926$ b	70.0 ± 1.3 c	25.8 ± 0.17 b	6029 ± 177 c	$36,208 \pm 1157$ b	71.7 ± 1.1 b	25.3 ± 0.16 b	6554 ± 196 b
Ratooning rice	LLY072	$16,095 \pm 1038$ a	85.0 ± 1.5 b	24.1 ± 0.36 bc	3297 ± 104 a	$15,488 \pm 1272$ a	88.8 ± 1.5 ab	24.3 ± 0.36 bc	3342 ± 93 a
	SY9576	$11,433 \pm 612$ c	90.8 ± 1.5 a	23.7 ± 0.26 c	2460 ± 89 c	$11,571 \pm 535$ b	85.8 ± 1.5 bc	23.8 ± 0.26 c	2363 ± 73 d
	XWX10	$13,943 \pm 368$ b	88.1 ± 0.8 ab	24.6 ± 0.26 b	3022 ± 79 b	$14,384 \pm 805$ a	85.0 ± 1.4 c	24.6 ± 0.20 ab	3008 ± 97 b
	MH63	$11,937 \pm 744$ c	86.7 ± 1.1 ab	25.7 ± 0.26 a	2660 ± 80 c	$12,006 \pm 972$ b	90.7 ± 0.7 a	25.2 ± 0.26 a	2744 ± 68 c

Note: Different letters represent significance at the 0.05 level in the same column in the same year.

The grain/leaf area ratio in the main season rice was 0.47–0.58, significantly higher in the hybrid rice than in the conventional rice; the same results were shown in 2019 and 2020. The grain/leaf area ratio in the ratooning rice was 0.9–1.16, much higher than that of the main season rice, but no significant difference was found among the varieties except for XWX10 in 2020.

Specific leaf weight (SLW) represents the leaf weight per unit leaf area (Table 9). Among the four tested varieties, MH63 had the lowest SLW. The SLW differed in two aspects between the main season rice and ratooning rice: (1) The SLW of the ratooning rice was higher than that of the main season rice at various growth stages, both in 2019 and 2020, with a range of difference of 0.06–0.65 mg cm⁻²; (2) the SLW of ratooning rice increased from milking to maturing, and the reverse occurred for the main season rice.

Table 9. Grain number/leaf area ratios and specific leaf weights of the main season rice and ratooning rice.

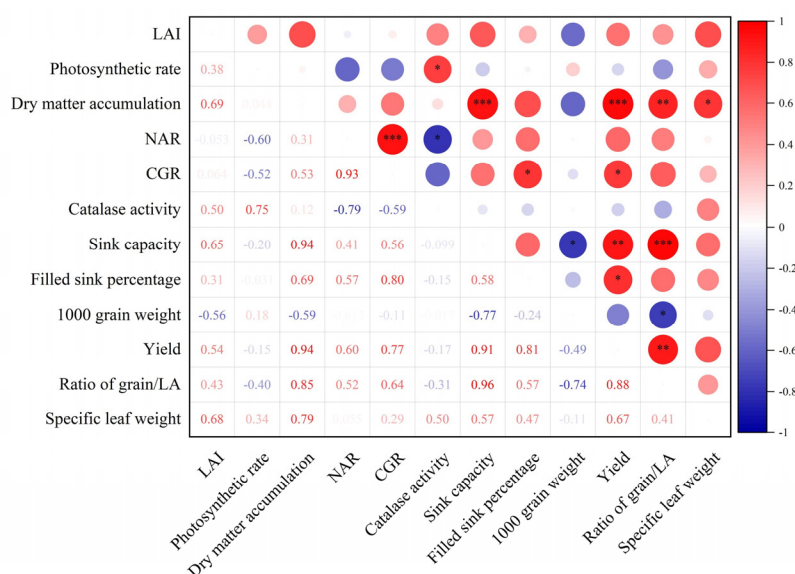
Cropping Type	Variety	2019					2020				
		Ratio of Grain/L.A. (Grain cm ⁻²)	Specific Leaf Weight (mg cm ⁻²)				Ratio of Grain/L.A. (Grain cm ⁻²)	Specific Leaf Weight (mg cm ⁻²)			
			Booting Stage	Full Heading Stage	Milking Stage	Maturing Stage		Booting Stage	Full Heading Stage	Milking Stage	Maturing Stage
Main season rice	LLY072	0.52 ± 0.01 b	2.82 ± 0.04 a	3.12 ± 0.05 a	3.11 ± 0.07 a	2.91 ± 0.04 ab	0.58 ± 0.02 a	2.76 ± 0.03 a	3.08 ± 0.03 a	3.10 ± 0.04 a	2.89 ± 0.04 a
	SY9576	0.55 ± 0.01 a	2.78 ± 0.02 a	2.93 ± 0.05 b	3.03 ± 0.05 a	2.85 ± 0.04 bc	0.58 ± 0.04 a	2.73 ± 0.03 a	2.91 ± 0.02 b	3.03 ± 0.07 ab	2.83 ± 0.05 a
	XWX10	0.47 ± 0.02 c	2.72 ± 0.02 b	2.86 ± 0.04 bc	2.92 ± 0.04 b	2.93 ± 0.04 a	0.49 ± 0.03 b	2.75 ± 0.04 a	3.02 ± 0.06 a	2.94 ± 0.05 b	2.90 ± 0.04 a
	MH63	0.47 ± 0.01 c	2.64 ± 0.03 c	2.82 ± 0.04 c	2.85 ± 0.04 b	2.80 ± 0.05 c	0.51 ± 0.00 b	2.61 ± 0.04 b	2.83 ± 0.03 c	2.83 ± 0.04 c	2.87 ± 0.04 a
Ratooning rice	LLY072	0.99 ± 0.10 a	3.32 ± 0.03 a	3.41 ± 0.04 a	3.23 ± 0.04 a	3.33 ± 0.11 b	0.90 ± 0.04 b	3.26 ± 0.07 a	3.29 ± 0.08 a	3.22 ± 0.04 a	3.28 ± 0.04 b
	SY9576	1.09 ± 0.14 a	3.01 ± 0.06 b	3.43 ± 0.04 a	3.31 ± 0.04 a	3.50 ± 0.05 a	0.98 ± 0.14 ab	3.04 ± 0.08 b	3.36 ± 0.04 a	3.29 ± 0.05 a	3.43 ± 0.05 a
	XWX10	1.16 ± 0.11 a	3.07 ± 0.03 b	3.37 ± 0.05 a	3.27 ± 0.05 a	3.45 ± 0.04 ab	1.14 ± 0.08 a	3.01 ± 0.08 b	3.28 ± 0.07 a	3.21 ± 0.04 a	3.49 ± 0.04 a
	MH63	0.99 ± 0.12 a	2.85 ± 0.04 c	2.98 ± 0.08 b	2.91 ± 0.03 b	3.02 ± 0.05 c	0.99 ± 0.06 ab	2.81 ± 0.05 c	3.01 ± 0.11 b	2.96 ± 0.05 b	3.04 ± 0.05 c

Note: Different letters represent significance at the 0.05 level in the same column in the same year.

3.7. Correlation of Sink–Source Characteristics

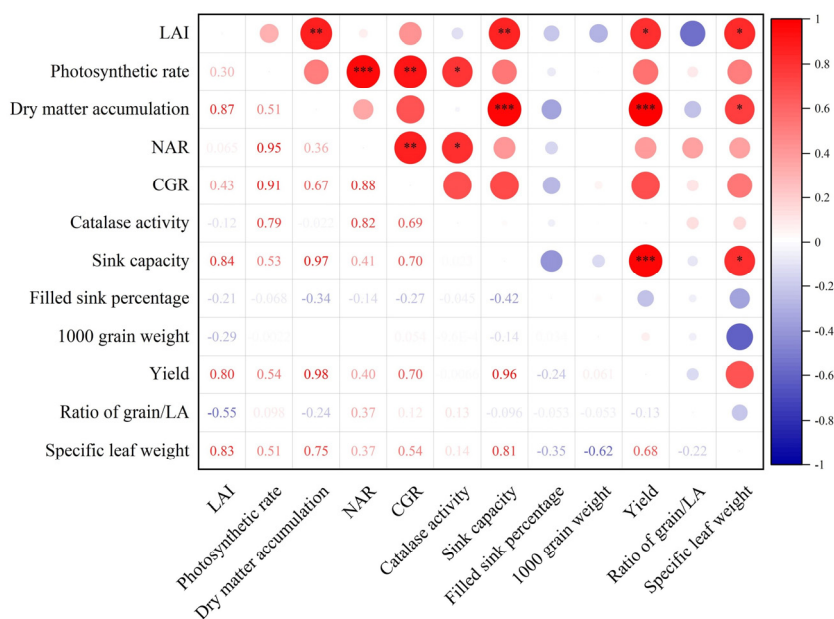
In the main season rice, photosynthetic rate is positively correlated to catalase activity (* $p < 0.05$) (Figure 1). Dry matter accumulation is positively correlated to sink capacity (** $p < 0.001$), yield (** $p < 0.001$), ratio of grain/L.A. (** $p < 0.01$), and specific leaf weight (* $p < 0.05$). There is a positive correlation between NAR and CGR (** $p < 0.001$). CGR is positively correlated to filled sink percentage and yield (** $p < 0.01$). Sink capacity is positively correlated to yield (** $p < 0.01$) and ratio of grain/L.A. (** $p < 0.001$). Yield is positively correlated to ratio of grain/L.A. (** $p < 0.01$).

In the ratooning rice, LAI is positively correlated to photosynthetic rate, sink capacity (** $p < 0.01$), yield, and specific leaf weight (* $p < 0.05$). Photosynthetic rate is positively correlated to NAR (** $p < 0.001$), CGR (** $p < 0.01$), and catalase activity (* $p < 0.05$). Dry matter accumulation is positively correlated to sink capacity (** $p < 0.001$), yield (** $p < 0.001$), and specific leaf weight (* $p < 0.05$). There is a positive correlation between NAR and CGR (** $p < 0.01$). Sink capacity is positively correlated to yield (** $p < 0.001$) and specific weight (* $p < 0.05$) (Figure 2).



* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Figure 1. The correlation analysis of sink–source characteristics of the main season rice.



* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Figure 2. The correlation analysis of sink–source characteristics of the ratooning rice.

4. Discussion

4.1. Comparison of Source–Sink Characteristics between the Main Season Rice and Ratooning Rice under the Same Ecological Conditions

The source–sink characteristics of rice are being studied closely, and significant progress has been made. It is known that many factors influence the source–sink characteristics of ratooning rice, except genotype [20], fertilization [21], the stubble height of the main season rice [22], and community size [23]; furthermore, climatic factors such as temperature, light, photoperiod, and rainfall do influence on source–sink characters [24]. Therefore, it is thought that the comparison of source–sink characters between the main season rice and ratooning rice should be made under the same ecological conditions. Therefore, we

conducted this study using sowing-by-stages to synchronize the heading date of ratooning rice from the last cropping and main season rice in the late season and make both crops under the same ecological and cultivation conditions during their key growing cycles.

The results of the research indicated that the leaf area index (LAI) of the ratooning rice was approximately $1/7$ – $1/5$ that of the main season rice; the source activity (Pn and NAR) was significantly higher; the assimilate transport efficiency from source to sink was significantly higher; the sink capacity was much lower; the activity of transport organs (catalase activity of rachis branches) was higher; and the sink/source ratio (grain/leaf area) in the ratooning rice was much higher. It was suggested that the ratooning tillers of the conventional varieties generated more slowly than those of the hybrids. Therefore, increasing the colony LAI of ratooning rice is very important to exert the advantages of individual productivity in high-yield practices. These results were essentially in agreement with those of many other surveys. Furthermore, the performances of source–sink characteristics in different varieties were almost the same in different years. It may be concluded that their physiological characteristics mainly affect rice varieties' source–sink characteristics.

4.2. Cultivation Techniques for High-Yielding Ratooning Rice According to Source–Sink Characteristics

The source–sink theory has had great importance in the research of crop yield formation since it was put forward by Mason and Maskell in 1928. In the study of ratooning rice yield formation, a few researchers also tried to reveal the yield differences between the main season rice and ratooning rice with source–sink theory. As for source/sink characteristics, it has been known that ratooning rice possesses fewer and smaller leaves, usually 2–4 short and narrow leaves [25], but it has significantly higher leaf photosynthesis compared with the main season rice [26]. This study also verified that the ratooning rice's photosynthesis and net assimilation rate from heading to 10 days after heading were over 30% and 2–5 times higher than those for the main season rice. This suggested that ratooning rice has a higher source intensity.

On the other hand, the grain-setting percentages reached or exceeded 85%, which was much higher than that of the main season rice, and the SLW of the ratooning rice increased from milking to maturing, while the reverse occurred for the main season rice.

Furthermore, the assimilate transport intensity was higher in the ratooning rice than in the main season rice. Therefore, it can be concluded that the limiting factor for high-yielding ratooning rice is its small sink capacity; one of the effective measures to enhance the yield for ratooning rice is to increase the panicle number or/and spikelets per panicle. The sink capacity of the ratooning rice was too small to store more assimilates from the functional leaves; a rather large amount of assimilate was deposited in the leaves, increasing leaf weight. A good relationship exists between increasing sink capacity and increasing source supply in ratooning rice because leaf development and spikelet differentiation are synchronous.

It has been known that young panicle differentiation of ratooning rice occurs approximately 15 days after flowering of the main season rice [13]; the nutrition for panicle differentiation of the ratooning rice is mainly from its main season rice plants, which means improving the nutritional status of the main season rice at the late growth stage may provide more assimilate for the ratooning bud sprouts and increase the spikelet number per panicle [27]. However, at the late growth stage of main season rice, the reutilization rate of the assimilated products from the main season rice to the ratooning rice is usually lower. According to an isotope-tracing experiment [28], approximately 0.8–5.9% of the ^{14}C -assimilate from flag leaf of the main season rice could be used for ratooning rice, of which only 0.2–1.4% was transported to panicles of the ratooning rice. This implies that most yield-forming substances of ratooning rice should be assimilated. Thus, to improve the nutritional status of the main season rice at the late growth stage and promote its ratoon tiller sprouting, it is necessary to increase the assimilative capacity of the ratooning rice. In high-yielding practices for ratooning rice, it is very popular to top-dress sprout-promoting

fertilizer and seedling-promoting fertilizer. Sprout-promoting fertilizer is usually applied 10–15 days before the main season rice is harvested to increase the living axillary buds and promote their differentiation; seedling-promoting fertilizer is usually applied at harvest or immediately after the harvest of the main season rice to promote the growth and development of ratooning tillers and increase their spikelets per panicle.

4.3. *The Differences in Source–Sink Characteristics among Ratooning Tillers from Different Nodes of Main Season Rice*

Under high stubble cutting of the main season rice, more than 90% of ^{14}C -assimilate deposited in the stem and leaf sheath of the mother culm was reallocated into the upper first and second internodes and less than 10% into the other internodes. Thus, the ratooning tillers from the upper second nodes (no dormant bud for the first node) of the mother culm usually have better economic characteristics because of their priority in the assimilate supply from the mother plant, followed by the upper third ratooning tillers, especially under the situation of the upper second nodes being removed or damaged by harvest practices; the upper second and third ratooning tillers contribute 70–80% of the grain yield for ratooning rice. A previous study indicated that the source–sink characteristics of ratooning tillers from different nodes would vary with changes in nutrient supply from the mother plant [29]. Under different cutting height treatments and in vitro cuttage treatments, the plant height, leaf number and leaf area, panicle length, and spikelets per panicle of ratooning tillers were all increased from the upper nodes to the lower nodes, both in vivo and in vitro; however, the increments were bigger in vitro than in vivo. To carry on an objective appraisal of source–sink characteristics among ratooning tillers from different nodes of the main season rice, innovations in research methods are necessary, and integrated methods should be adopted, including the conventional method (keep all dormant buds in vivo), bud-picking method (keep a given bud and pick others), and the in vitro method (cuttage of different nodes in vitro).

5. Conclusions

Ratooning rice had a higher seed-setting rate but a slightly smaller weight for 1000 grains than main season rice, but a higher leaf weight and a double grain-to-leaf ratio. Taking the value of each physiological characteristic of the main season rice to be 1, the LAI of ratooning rice was $1/7$ – $1/5$ of that; the dry matter weight per hill of ratooning rice was $1/4$ – $1/3$, and the grain yield of ratooning rice was approximately $1/3$ – $2/5$. The photosynthetic rate was higher, and the crop growth rate was lower. Still, the net assimilation rate was higher in the ratooning rice than in the main season rice. This was particularly true during the booting stage, from the full heading stage and from milking to the yellow maturing stage. As for assimilation outcomes from the flag leaf, 53–74% of assimilate was translocated to the panicle. Approximately 14–36% remained in the stems and sheaths in the main season cropping. Still, more than $4/5$ of the assimilates were translocated to the panicle during ratooning. The percentage of residue in the stems and sheaths was lower than that of the main season cropping plants. The catalase activity of the rachis branches of the ratooning rice was higher than that of the main season rice. The LAI, dry matter weight, crop growth rate, thousand grain weight, and yield of ratoon rice were all lower than those of the main season rice. The grain yield of ratooning rice was determined by the interaction of source and sink capacity while that of main season rice was mainly increased by enhancing sink capacity. Choosing varieties with heavier 1000 grain weight, exerting the advantages of higher photosynthetic rate and net assimilation rate of ratooning rice, promoting leaf area, and improving the transportation capacity of carbohydrate are the main approaches to increase the grain yield of ratooning rice.

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