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RESEARCH ARTICLE

Morpho-physiological differences and responses to source-sink manipulation in Aus rice varieties

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Abstract

Rice is the staple food crop of Bangladesh, playing a critical role in national food security. This study investigated the morpho-physiological traits and the impact of source-sink manipulations on grain yield in four rice varieties Binadhan-14, Binadhan-19, China IRRI and Kalihatta under field conditions. Various treatments, including partial spikelet and flag leaf removal at different growth stages, were applied to assess their effects on yield components. Among the tested varieties, Binadhan-19 exhibited the highest grain yield under normal conditions, attributed to a greater number of grains per panicle and fewer sterile spikelets. Source-sink manipulations revealed that spikelet removal significantly increased individual grain size and weight, indicating that yield was sink-limited. Conversely, flag leaf removal reduced grain size and weight, emphasizing the importance of source strength for grain filling. These findings highlight that grain yield in rice is co-regulated by both source activity, sink capacity and strategic manipulation of these factors could be a promising approach in breeding programs aimed at enhancing rice productivity.

Keywords: flag leaf; grain yield; morpho-physiological traits; rice; source-sink manipulation

Introduction

Rice (*Oryza sativa* L.) is a major food crop in Bangladesh and many Asian and African countries, cultivated under diverse cultural conditions worldwide. Over the years, rice production has steadily increased, with Bangladesh ranking third among the leading rice-growing countries (1). The country's agriculture sector is tasked with producing food for a population of 163.5 million people, utilizing only 8.75 million hectares of agricultural land (2). However, sustaining rice production is increasingly challenging due to population growth, reduced cultivable land and climate vulnerabilities. To address this, researchers are focused on developing high-yielding varieties and improved management practices, as rice productivity depends on key morphological and physiological processes across growth stages (3).

In rice, yield is significantly and positively associated with morphological characters such as plant height, the number of filled grains per panicle, the percentage of filled grains and grain weight per panicle, which are critical parameters contributing to grain productivity (4, 5). Root morpho-physiology also contributes to the yield superiority of japonica/indica hybrid rice (6). Compared with the "old" rice grown in the last century, modern rice genotypes exhibit improved sink characteristics, such as more spikelets per panicle (7, 8) and source characteristics, such as greater dry matter production (8). Recent studies showed that the rice yield enhancement of hybrid rice is significantly greater than that of conventional rice due to its large sink capacity (9). Further improvement in rice depends on the conserved use of phenotypic characters and genetic variability in rice breeding programs.

Rice yield is a complex trait contributed by the source-sink relationship, where photosynthates are produced in source organs and stored in sink organs. The yield of rice is an integrated result of various processes, including canopy photosynthesis and the conversion of assimilates to grains, maintaining both assimilate supply (source) and utilization by the sink (10, 11). Further, grain yield can be defined as the product of yield sink capacity and filling efficiency. To further increase yield and break the yield ceiling, breeding efforts have expanded the yield sink capacity mainly by increasing the number of spikelets per panicle. As a result, cultivars with large panicles containing more spikelets per panicle (12) and improved rice quality have become available (13). Grain filling is the most significant and critical developmental stage in rice, contributing to higher crop yields in cereals. The degree and rate of grain filling in rice spikelets differ largely with their positions on a panicle (7). In general, earlier flowering superior spikelets, usually located on apical primary branches, fill fast and produce larger and heavier grains. In contrast, later-flowering inferior spikelets, usually located on proximal secondary branches are either sterile or fill slowly and poorly, producing grains unsuitable for human consumption (14). Moreover, yield stability is positively correlated with the grain filling percentage (15).

Manipulation of the source-sink ratio is an effective technique to study the grain filling process in cereals (16). Artificial reduction in grain number per inflorescence is suggested as a method to increase the photo-assimilate supply for developing grains. Conversely, the removal of the flag leaf or a portion of it is expected to reduce the amount of photo-assimilate available to developing grains (17). Rice is also known to rely heavily on assimilates produced before anthesis and stored in vegetative organs to fill grains (18) ensuring an adequate supply of assimilates. Rice genotypes differ widely in yield traits; japonica cultivars typically show higher filled grain percentages than indica and modern varieties have more panicles per plant (19). In hybrids, poor grain filling may result from inefficient assimilate partitioning to grains (20). Additionally, Florets are the primary photosynthate sink and the top three leaves, particularly the flag leaf, are the primary source (21). A large sink size that allows efficient transport of photo-assimilates from leaves and stems to developing spikelets is required to produce high yield and harvest index. Moreover, the capacity to transport photo-assimilates from source to sink (vascular bundles) could also be the basis for photo-assimilate limitations of grain filling (22).

Understanding the relationship between growth and developmental, physiological and yield-related traits and other contributing factors maximizes breeding gains from selection is important. However, the physiological basis of source-sink interactions remains underexplored. This study aims to evaluate morpho-physiological responses and yield traits in Aus rice varieties under source–sink manipulation, focusing on traits influencing grain size, weight and yield potential.

Materials and Methods

Plant materials, experimental design and management practices

The experiment was conducted at the Bangladesh Institute of Nuclear Agriculture (BINA) sub-station in Barishal during April to July 2021. Two BINA-released Aus rice varieties, namely Binadhan-14 and Binadhan-19, along with two local cultivars (Kalihatta and China IRRI) collected from the Barishal region, are traditionally cultivated by farmers for their unique adaptation to local environmental conditions were used as planting materials. The experiment was arranged in a randomized complete block design (RCBD) with two factors and three replications. Each plot size was 3 m × 3 m, with spacing between hills and rows set at 15 cm and 20 cm respectively. Rice seedlings, aged 25 days, were transplanted on May 19, 2021. The soil used was sandy loam with a pH of 6.5, low organic matter content and overall low fertility. Fertilizers were applied according to recommended rates and intercultural operations were performed as needed.

Anatomical features of internode tissues

The first internode was collected at the ripening stage and preserved in a small bottle containing FAA (Formalin-Aceto-Alcohol) solution, stored at 4 °C (23). Peduncle samples were cut with a sharp blade and stained with 1 % safranin for 30 sec, followed by two washes with distilled water. The samples were then placed on glass slides with glycerin. Cross sections of the first internode were observed under an optical microscope at 100× magnification.

Pollen viability study

For the pollen viability study, unopened spikelets were collected from the tips of randomly selected rice panicles across three biological replicates per treatment. Approximately 10 spikelets per replicate were sampled and preserved in a bottle containing FAA solution. Pollen from each spikelet was stained on a glass slide using 1 % potassium iodide, fixed with a cover slip and examined under an optical microscope (4). For each slide, at least 100 pollen grains were counted. Pollen grains that were stained and well-filled were counted as fertile, while those that were unstained, half-stained, shriveled or empty were classified as sterile.

Imposition of source-sink manipulation

Source-sink manipulation treatments were imposed by selectively removing specific source-sink organs with scissors at different growth stages. The manipulations included: (a) lower half spikelet removal at anthesis, (b) lower half spikelet removal at heading, (c) upper half spikelet removal at anthesis, (d) upper half spikelet removal at heading, (e) flag leaf removal at booting, (f) flag leaf removal at heading stage of at panicle development stage of respective four rice varieties. Control plants were grown without any manipulations. All rice varieties were grown and maintained until the maturity stage.

Data collection

Rice was harvested when 80 % of the grains had turned golden yellow. Five hills (excluding border hills) were randomly selected from each experimental plot to record data related to yield and yield attributes. A 1 m^2 area in the middle of each plot was selected to measure the yield of grain and straw. Grains were sun-dried to a moisture level of 14 % and then cleaned. Straws were also properly sun-dried. Finally, both straw and grain yield per plot were recorded and converted to tons per hectare (t/ha). The harvest index, which is the ratio of economic yield to biological yield, was calculated using the following formula (24):

$$\text{Harvest index (\%)} = \frac{\text{Grain yield}}{\text{Biological yield}} \times 100$$

Statistical analysis

Data on yield and yield-contributing characters were compiled, tabulated and analyzed statistically. The data collected were subjected to ANOVA and mean differences were evaluated using Duncan's Multiple Range Test (DMRT) as described (25) using the MSTAT-C statistical software package. Additionally, the chart was designed using Microsoft Excel 2016.

Results and Discussion

Morphological traits

Morphological and yield-associated traits are often used as criteria to evaluate phenotypic variability and as a basis for enhancing the yield potential of rice. In rice, yield is associated with several component traits, including panicle number per unit area, filled grains per panicle and 1000-grain weight (4, 26, 27). Conversely, Variation in panicle structure, spikelet branching and grain formation affects the grain quality, ultimately inhibiting the rice grain yield production (28). Other traits, such as plant height, tillering ability and canopy architecture, are also crucial for grain yield (5). The improvement of rice yield potential is controlled by different mechanisms, including canopy phenotype and total biomass production (29). The rice varieties studied here exhibited a wide range of variability in all the morphological traits, which contributed to differences in yield-related characteristics. These morphological developments were compared from the vegetative to the maturity stage.

Plant height and root structure

Plant height varied significantly among different varieties. The local cultivar China IRRI produced the tallest plants, while Binadhan-14 and Binadhan-19 exhibited the shortest plant heights (Fig. 1A, B and Table 1), consistent with previous findings (27). Interestingly, Binadhan-19 exhibited a profuse root system, which may enhance nutrient uptake and support survival under drought conditions (Fig. 1C). Although all the studied cultivars displayed similar root systems, Binadhan-14 and China IRRI produced slightly longer roots (Fig. 1C). This observation aligns with the results reported in the previous studies (30).

Internode elongation pattern

The contributions of each internode to the culm length are schematically presented in Fig. 2A. All internodes were evenly shortened across all varieties, fitting the dn-type of internode elongation pattern (31). Both the local cultivars China IRRI and Kalihatta produced six internodes, while the BINA-developed rice varieties, Binadhan-14 and Binadhan-19, formed five internodes. Among these internodes, the first internode contributed the most to culm length in all tested cultivars. The third and fourth internodes of China IRRI and Kalihatta were mostly elongated (Fig. 2A, B), potentially increasing culm length. Taller rice varieties tend to be more susceptible to lodging, whereas semi-dwarf types show improved lodging resistance and nitrogen responsiveness, emphasizing the significance of culm length (16).

Number of leaves and tiller per hill

The number of leaves per hill, which influences photosynthetic capacity and grain yield, varied significantly among rice varieties (Table 1). Binadhan-19 produced the highest number of leaves, while China IRRI and Kalihatta had the lowest. This aligns with previous findings linking leaf number to improved grain yield through enhanced photosynthesis (21, 32). Tiller number, a key trait affecting panicle count and grain production, also differed significantly among varieties. Kalihatta had the most tillers per hill, whereas Binadhan-14 had the fewest. Although more tillers often correlate with higher yield, this result contrasts with earlier findings (27). Nevertheless, tiller number is positively associated with plant biomass and yield potential (33). The number of leaves per hill can influence photosynthetic capacity in senescent leaves and is associated with maintaining grain yield (32). This trait was significantly influenced by different varieties (Table 1). Binadhan-19 produced the highest number of leaves per hill, while the lowest number was observed in both China IRRI and Kalihatta. Similar results also found in another research, which reported that the number of leaves significantly contributes to grain yield production in rice by enhancing photosynthetic capacity (21).

Fig. 1. Morphological appearance: (A) flowering stage, (B) ripening stage of rice variety; China IRRI, Kalihatta, Binadhan-14, Binadhan-19, respectively, (C) roots of 4 rice cultivars.

Table 1. Effect of variety on yield and yield contribution characteristics of rice

Variety	Plant height (cm)	Tiller hill^{-1} (nos)	Leaves hill^{-1} (nos)	Panicle length (cm)	Primary branches/panicle (nos)	Grains panicle^{-1} (nos)	Sterile spikelets panicle^{-1}	Yield/m^2(g)
Binadhan-14	103.9b	14.0	65.3b	22.1c	8.7ab	114.0a	11.7bc	472.5^{a}
Binadhan-19	103.4b	14.3	76.3a	22.8c	8.3b	112.7a	8.0c	510.3^{a}
China IRRI	177.5a	13.6	66.3b	27.5a	10.0a	87.7b	34.0a	318.7^{b}
Kalihatta	161.9a	14.6	66.3b	25.3b	9.0ab	79.0b	15.0b	298.8^{b}
CV%	18.42	6.41	22.93	2.04	1.59	22.01	6.62	8.94

Common letters in a column on specific treatment do not differ significantly at 5 % level as per DMRT.

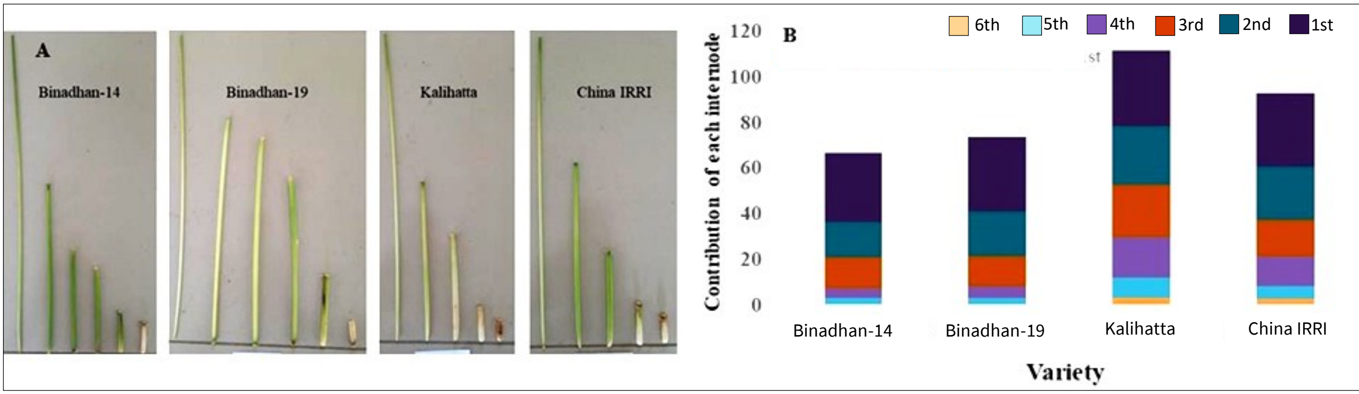

Fig. 2. Internodes elongation pattern: (A) schematic appearance, (B) relative contribution of each internode to culm length.

Tiller number per hill

Tillering in rice is an important agronomic trait, as it affects panicle number per unit land area and overall grain production. Tiller number per hill was significantly influenced by different varieties, ultimately contributing to grain yield (Table 1). The highest number of tillers per hill was observed in Kalihatta, while the lowest was in Binadhan-14. Generally, the variety with highest number of tillers produces higher yield but this result contrasts with previous findings (27). Additionally, the number of tillers has been reported to have a positive association with plant biomass and economic yield in rice (33).

Panicle architecture

The rice panicle comprises of primary branches, secondary branches and spikelets on these branches. The development of rice panicles is a complex process and panicle number per unit area is a critical yield component in rice. During the panicle initiation stage, the studied varieties-initiated panicle growth at different times, but no significant differences were observed (Fig. 3A). Among the rice cultivars, China IRRI produced the longest panicles with more primary branches, whereas Binadhan-19 had shorter panicles with a higher number of grains per panicle (Fig. 3B, C and Table 1). These results suggest that longer panicles do not necessarily produce the highest grain number in rice. Rice panicle architecture is highly diverse and varies significantly among genotypes, with the complex branching architecture and grain number determining panicle density (12) which depends on factors such as the main stem, tillers, cultivar types, crop conditions and environmental factors (34).

Grains and sterile spikelets per panicle

Grain number per panicle, a key determinant of rice yield, varied significantly among the tested varieties (Table 1). Binadhan-14 had the highest number of filled grains, while Kalihatta had the lowest, consistent with studies linking grains per panicle to yield (12). However, a high spikelet number doesn't always translate to higher yield due to poor grain filling. Sterile spikelets also differed significantly; China IRRI showed the highest sterility, while Binadhan-19 had the lowest (Table 1). These results underscore the role of panicle architecture and spikelet fertility in influencing yield potential and varietal performance (35).

Physiological traits

Identifying physiological traits responsible for greater biomass or yield production is crucial for genetic improvements in rice productivity. In this study, we examined the differences in vascular bundles and sclerenchyma cells in the uppermost internodes among different rice cultivars. The vascular bundle system in the culms provides stronger mechanical support in shorter rice plants (36, 37). The number of vascular bundles in the 1st internode increased along with the enlargement of the cavity diameters. The highest number of large vascular bundles and the largest pith cavity were observed in China IRRI, followed by Binadhan-19, Binadhan-14 and Kalihatta (Fig. 4A, B). These results suggest that increased meristematic activity and cell proliferation contribute to enhanced plant growth and better dry matter accumulation. Similar results were also reported in a study conducted earlier (23).

Fertile spikelets per panicle are among the most important yield components in rice. For the pollen viability study, unopened spikelets were collected from the tip of each cultivar at the flowering stage. The maximum fertile pollen was recorded in Kalihatta, which was almost similar to Binadhan-14 and Binadhan-19, while the lowest pollen fertility was found in China IRRI. A comparison of pollen fertility (Fig. 5A, B) and sterile spikelet production (Table 1) for each cultivar suggests that pollen fertility is crucial for grain

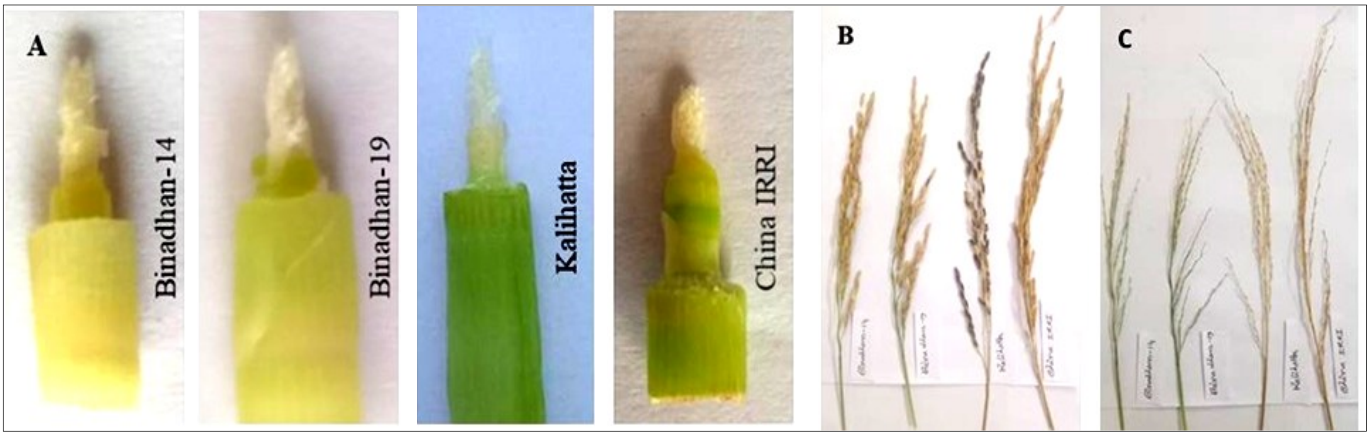

Fig. 3. Panicle characterization: (A) panicle initiation, (B) panicle at maturity stage, (C) schematic representation of rachis branches of 4 rice cultivars.

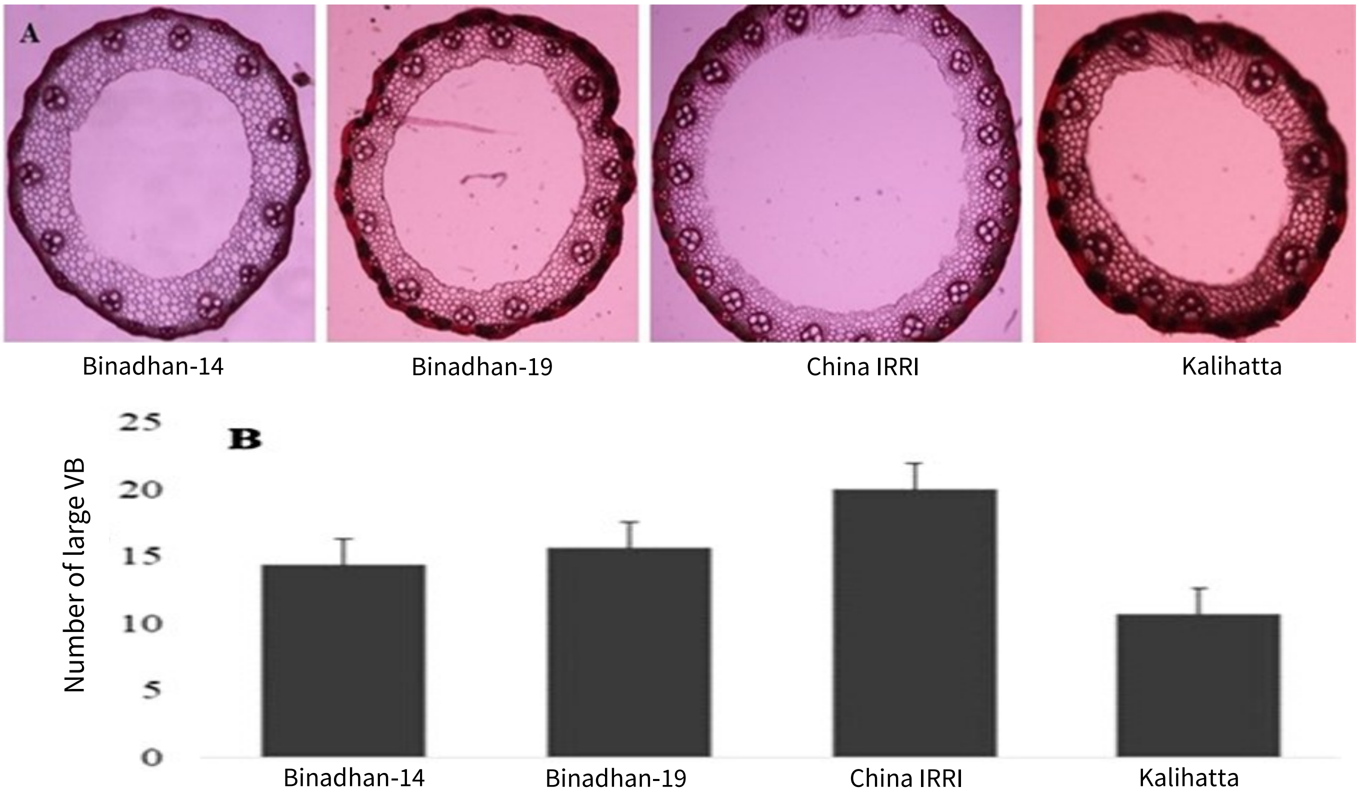

Fig. 4. Anatomical observations. (A) Cross-section of the 1st internode. (B) The number of large vascular bundles.

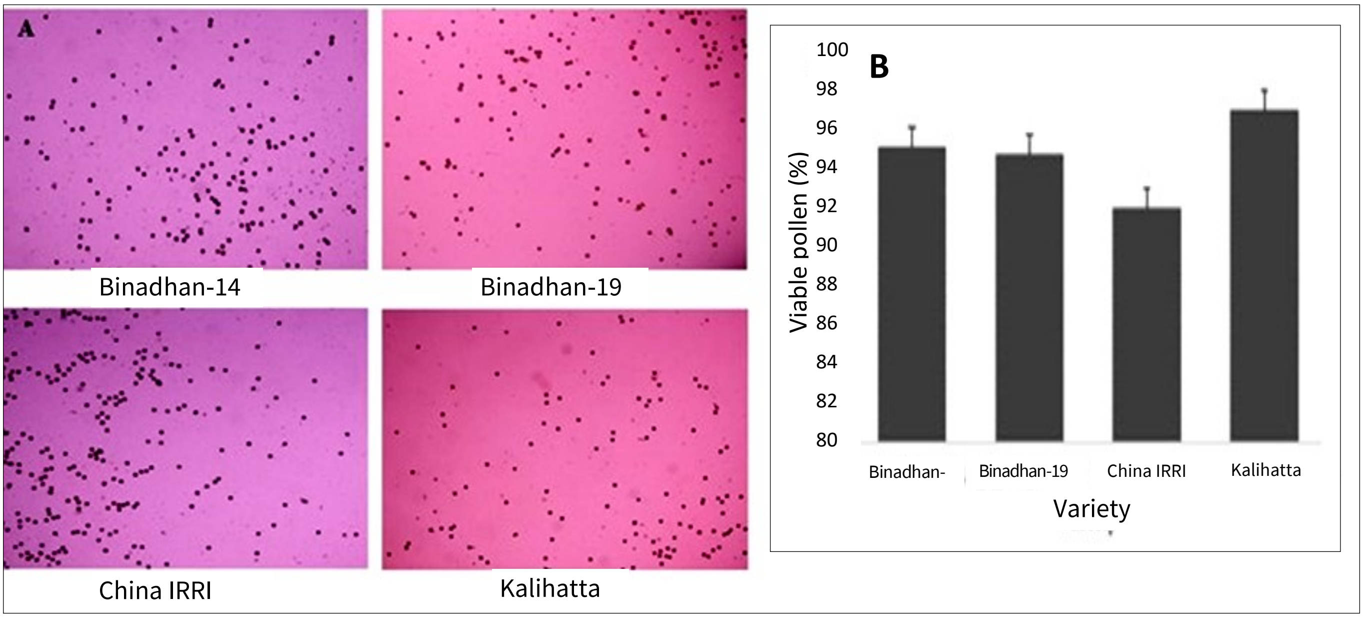

Fig. 5. Pollen viability of rice spikelets: (A) stained and non-stained pollens, (B) percentage of viable pollen.

production in rice which Similar to the previous research (38).

Rice yield and its relationship with dry matter accumulation

Grain yield in rice is significantly influenced by the variety. In this study, the highest grain yield per square meter was recorded in Binadhan-19, while the lowest was observed in Kalihatta. Effective dry matter allocation per spikelet from heading to maturity plays a crucial role in achieving higher grain yield. Poor grain filling can be attributed to inadequate partitioning of assimilates to the grain, a phenomenon reported in earlier studies (39). Furthermore, grain yield is generally correlated with total dry mass production. An earlier study reinforced that grain yield increases with increased total dry matter production (4), supporting the idea that greater dry matter production during grain filling contributes to better grain filling (8). Normally, a positive correlation exists between dry weight and grain weight per plant; however, in this study, an unexpected observation was made where grain yield decreased with increased total dry matter production (Fig. 6). This suggests that there may be a negative correlation between grain yield and total dry mass production in certain cases. The findings suggest that Binadhan-19 showed superiority in grain yield production is mainly due to its higher number of filled grains per panicle and an increased percentage of viable pollen. This underscores the importance of optimizing dry matter allocation and partitioning to maximize grain yield, especially under varying environmental conditions.

Effect of source-sink manipulation

Rice grain yield is influenced by both the supply of assimilates (source) and the grain's capacity to utilize these assimilates (sink) (11). The duration of grain filling is a crucial phase that determines rice grain

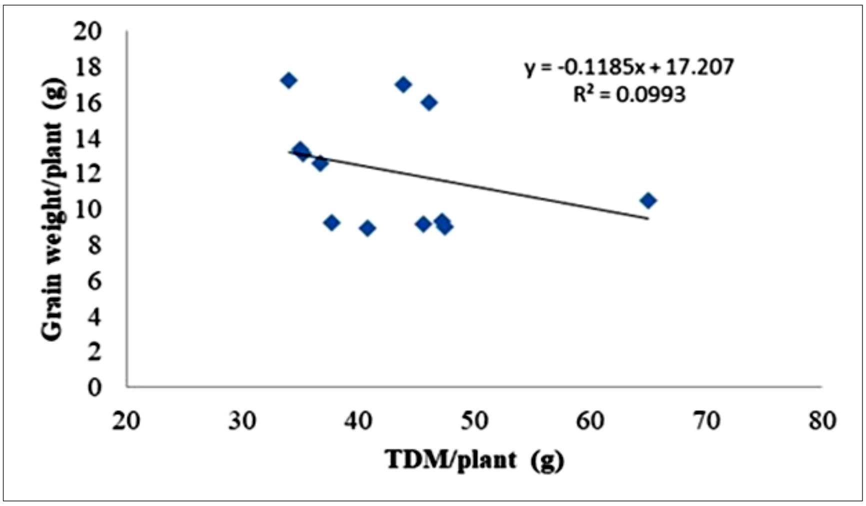

Fig. 6. Relationship between total dry matter (TDM) production and grain weight per plant.

yield (40). A sufficient source supply during this phase, whether from pre-heading non-structural carbohydrate (NSC) reserves or from post -heading photosynthates, is essential to adequately fill the sink and achieve high yield and good quality rice (41).

Grain length

Grain length was significantly affected by source-sink manipulations across all rice varieties studied. For Binadhan-14, various treatments such as lower and upper half spikelet removal at different growth stages, as well as flag leaf removal, showed notable changes in grain length compared to the control (Table 2). For instance, lower half spikelet removal at anthesis and at heading increased grain length to 9.67 and 9.79, respectively, while flag leaf removal at booting and heading resulted in grain lengths of 9.40 and 9.50, respectively. Similarly, grain length was significantly altered for Binadhan-19, China IRRI and Kalihatta under different treatments, indicating a direct influence of source-sink manipulation on this trait. These findings are consistent with earlier studies (21).

Grain width

Grain width was also significantly impacted by source-sink manipulations. For Binadhan-14, treatments such as lower half spikelet removal at anthesis and heading, upper half spikelet removal at anthesis and flag leaf removal resulted in changes in grain width ranging from 2.09 to 2.18 (Table 2, Fig. 7). Similar trends were observed in Binadhan-19, China IRRI and Kalihatta. For example,

Table 2. Effects of source-sink manipulations on seed attributes among different rice varieties

Variety	Source-sink manipulation	Grain length (mm)	Grain width (mm)	Individual grain weight (mg)	Increase or decrease (%) in individual grain weight over control
Binadhan-14	Lower half spikelet removal at anthesis	9.67a	2.18a	28.7a	21.67
	Lower half removal at heading	9.79a	2.17a	29.3a	24.15
	Upper half spikelet removal at anthesis	9.72a	2.15a	27.8a	17.79
	Upper half spikelet removal at heading	9.76a	2.15a	28.1a	9.06
	Flag leaf removal at booting	9.40b	2.09a	19.2b	−18.64
	Flag leaf removal at heading	9.50b	2.11a	20.8b	−11.86
	Control	9.84a	2.07a	23.6ab	–
	CV%	1.94	7.37	17.37	23.07
Binadhan-19	Lower half spikelet removal at anthesis	9.70a	2.18a	26.5b	18.30
	Lower half removal at heading	9.71a	2.12b	27.2a	21.42
	Upper half spikelet removal at anthesis	9.65ab	2.15ab	25.7c	14.73
	Upper half spikelet removal at heading	9.73a	2.20a	26.1b	16.51
	Flag leaf removal at booting	9.43c	2.05c	21.0de	−6.25
	Flag leaf removal at heading	9.46c	2.09bc	20.0e	−10.71
	Control	9.54b	2.04c	22.4d	–
	CV%	2.60	2.64	2.36	24.45
China IRRI	Lower half spikelet removal at anthesis	7.62ab	2.54a	26.93b	16.07
	Lower half removal at heading	7.68ab	2.54a	27.77a	19.69
	Upper half spikelet removal at anthesis	7.77a	2.26b	26.17b	12.80
	Upper half spikelet removal at heading	7.74a	2.49a	26.88b	15.86
	Flag leaf removal at booting	7.44c	2.11c	19.30d	−16.81
	Flag leaf removal at heading	7.23d	2.02c	19.90d	−14.22
	Control	7.50bc	2.19c	23.2c	–
	CV%	2.67	4.22	2.21	18.95
Kalihatta	Lower half spikelet removal at anthesis	8.84a	3.27a	38.74a	17.75
	Lower half removal at heading	8.79a	2.51bc	39.10a	18.84
	Upper half spikelet removal at anthesis	8.66ab	2.50c	35.99b	9.39
	Upper half spikelet removal at heading	8.76a	2.46c	36.97ab	12.37
	Flag leaf removal at booting	8.02c	2.85b	26.30d	−20.06
	Flag leaf removal at heading	8.00c	2.53c	28.60d	−13.07
	Control	8.47b	2.24d	32.9c	–
	CV%	2.34	4.78	2.32	20.12

Common letters in a column on specific treatment do not differ significantly at 5 % level as per DMRT.

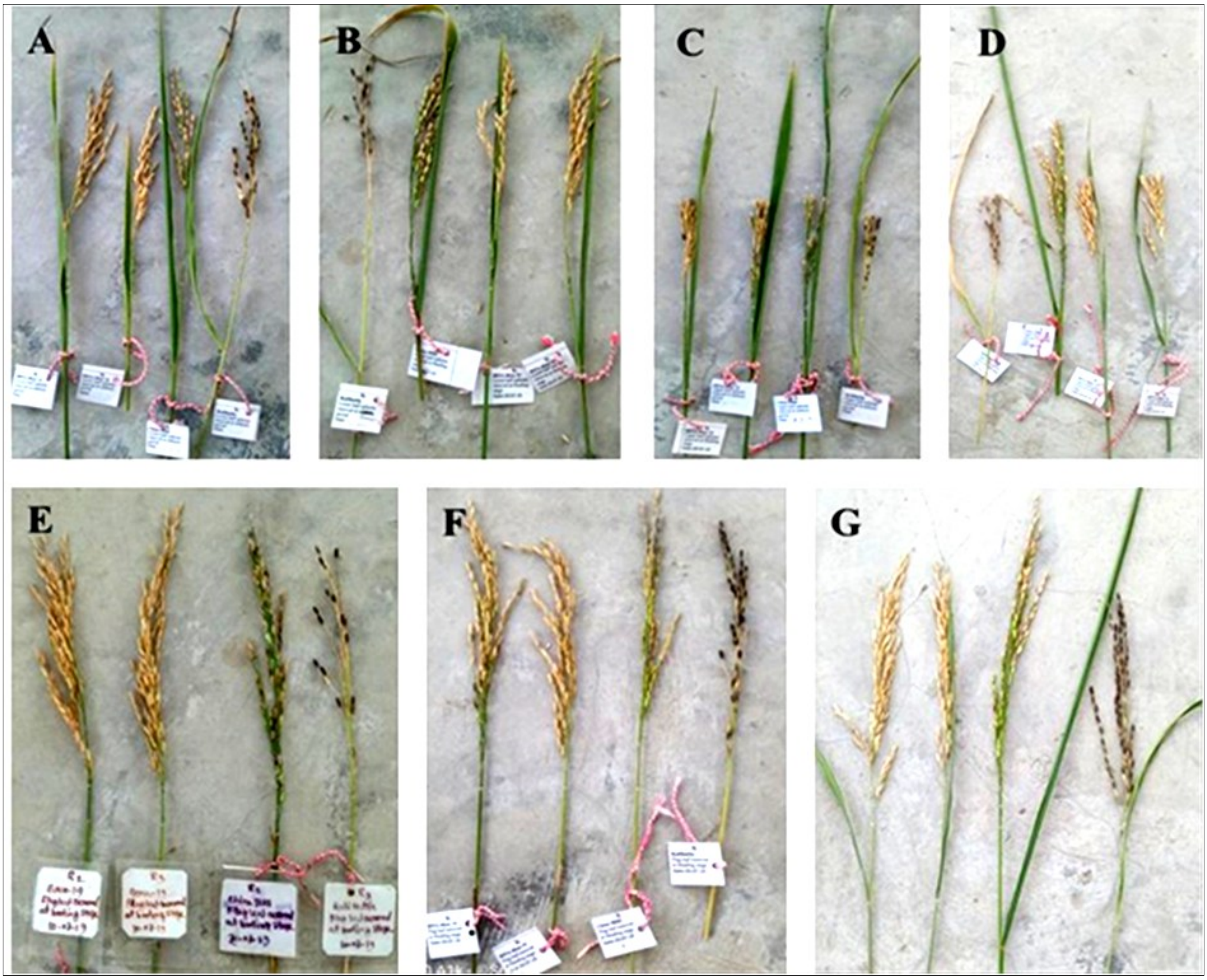

Fig. 7. Source-sink manipulations at different growth stages: (A) lower half spikelet removal at anthesis, (B) lower half spikelet removal at heading, (C) upper half spikelet removal at anthesis, (D) upper half spikelet removal at heading, (E) flag leaf removal at booting, (F) flag leaf removal at heading of Binadhan-14, Binadhan-19, China IRRI and Kalihatta rice, respectively.

grain width for China IRRI ranged from 2.02 to 2.54 across different treatments. This suggests that source-sink manipulations can significantly affect grain width, which results align with previous studies (21).

Individual grain weight

Individual grain weight directly contributed to rice yield production (42) which is significantly affected by source-sink manipulations as well. For Binadhan-14, treatments such as lower and upper half spikelet removal and flag leaf removal led to increases or decreases in grain weight ranging from -19.2 to 29.3 compared to the control (Table 2, Fig. 7). For Binadhan-19, changes in individual grain weight varied from 20.0 to 27.2 across different treatments. China IRRI and Kalihatta also showed significant differences in grain weight under various source-sink manipulations. These findings highlight the impact of assimilate supply on grain weight supported by previous research (21, 43). Additionally, grain weight percentage was significantly affected by source-sink manipulations, with all treatments showing notable changes. For Binadhan-14, grain weight percentage changes ranged from -18.64 to 24.15 depending on the treatment. Similar effects were seen in Binadhan-19, China IRRI and Kalihatta, indicating that source-sink balance plays a crucial role in determining grain weight. For instance, Kalihatta exhibited changes in grain weight percentage ranging from -20.06 to 18.84 across different treatments. These findings align with earlier studies (21), who suggested that increased grain weight in response to higher assimilate supply is indicative of source-limited conditions.

Overall, the data demonstrate that source-sink manipulations significantly affect grain length, width, individual grain weight and grain weight percentage, highlighting the critical role of source-sink dynamics in enhancing rice yield and grain quality. However, the study is limited using a small number of varieties and the absence of biochemical validations, which should be addressed in future research.

Conclusion

The study revealed that all the parameters related to morphological traits and grain yield production showed significant differences under normal growth conditions, highlighting the importance of rice varieties and their yield-contributing traits. Microscopic observation indicated that the number of vascular bundles is crucial for the translocation of assimilates from source to sink, while pollen fertility plays a significant role in determining spikelet number, both of which ultimately contribute to rice yield. Among the rice cultivars studied, Binadhan-19 produced the highest grain yield. Additionally, manipulations involving spikelet number and flag leaf significantly affected grain yield by influencing grain size and individual grain weight. The individual grain length, width and weight were significantly affected by both the variety and the treatments applied. The increase in grain size observed in spikelet removal treatments may be attributed to an enhanced supply of photo-assimilates from the source to a limited sink. Grains with increased weight in response to a higher supply of assimilates suggest a source-limited condition. This indicates that sink manipulation treatments have the potential to produce heavier grains if a greater supply of assimilates is provided. Therefore, strategic manipulation of source–sink dynamics could serve as a promising approach for developing new plant ideotypes in breeding programs aimed at enhancing grain yield potential in rice.

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Authors' contributions

MBA and AKH conceived and designed the project. STP, MSR and AS conducted the experiments and performed the statistical analysis. MBA, STP and NN wrote the original manuscript and AKH revised the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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