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ARTICLE

Effects of Paclobutrazol Seed Soaking on Non-Structural Carbohydrate and Grain Enrichment in Direct-Seeded Rice

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ABSTRACT: The yield of direct-seeded rice (DSR) was constrained by inadequate grain filling. Recent studies have indicated that paclobutrazol application plays a significant role in enhancing crop agronomic traits and increasing yield. This study aimed to examine the effects of paclobutrazol seed soaking (PSS) on non-structural carbohydrate accumulation and grain enrichment in DSR, potentially providing a theoretical foundation for achieving high-yield DSR cultivation. The experiment utilized two rice varieties, Jiyujing (JYJ) and Jijing305 (JJ305), with seeds soaked in paclobutrazol concentrations of 0 mg L^{-1} and 100 mg L^{-1}. PSS demonstrated increased chlorophyll content, net photosynthetic rate, and leaf area, as well as an extended photosynthetic function period during the filling stage. It also elevated soluble sugar and starch contents in the flag leaf (during the filling stage) and stem sheath (after heading), decreased starch content in the top panicle while increasing it in the middle and lower panicle during the filling stage, and enhanced spikelet per unit area and seed setting rate, thereby improving DSR yield. In conclusion, PSS enhanced the photosynthetic capacity of DSR during the filling stage, coordinated the filling process of superior and inferior grains, maintained source-sink balance, and facilitated stable and orderly filling, ultimately resulting in improved yield.

KEYWORDS: Paclobutrazol; direct-seeded rice; soluble sugar; starch; yield

1 Introduction

Rice serves as a crucial component in maintaining global food security, providing sustenance for over half of the world's population [1]. Consequently, ensuring high and stable rice yields is paramount for safeguarding food security. In rice cultivation, transplanting and direct seeding represent the two most prevalent methods. However, labor and water resource scarcity impede the sustainable development of transplanted rice [2,3]. Direct-seeded rice (DSR) involves sowing seeds directly into the field, eliminating the need for traditional transplanting and seedling cultivation. This method has the potential to reduce labor input by approximately 25% and decrease water consumption by 50% [4,5]. Given its labor-saving and efficient nature, DSR holds promise for promoting sustainable agricultural development and is anticipated to be a significant direction for future rice cultivation practices.

Given the constraints of limited arable land, the primary strategy for enhancing crop yield involves increasing productivity per unit area [6,7]. As the global population continues to expand, improving crop yields becomes increasingly crucial to meet the growing food demand. This challenge is further compounded by issues in the grain filling process. The material enrichment phase of grain filling primarily involves the synthesis and accumulation of starch, and maintaining an adequate material source from stem sheaths and leaves is essential for effective grain filling and yield improvement [8,9]. The yield of DSR is particularly hindered by inadequate grain filling, which impedes overall yield increases [10].

Paclobutrazol, a cost-effective plant growth regulator applied in low doses, has gained widespread use in agriculture due to its significant impact on plant growth, development, and stress resistance [11,12]. The application of paclobutrazol has been demonstrated to mitigate lodging risk, enhance photosynthetic capacity, increase dry matter accumulation, and facilitate the transport of photosynthetic products to the panicle, ultimately resulting in higher yields [12–14]. Rice yield stability is primarily determined by seed setting rate (SSR) and/or TS [15,16]. PSS can enhance the yield of DSR by improving SSR and TS [17]. However, there is a lack of systematic research on PSS effects on grain enrichment.

Grain enrichment in rice primarily involves the translocation of photosynthetic assimilates from leaves and storage materials from stem sheaths to the panicle after heading [18]. This two-year field trial utilized Jiyujing (JYJ) and Jijing305 (JJ305) as test materials to examine the effects of PSS on non-structural carbohydrates and grain enrichment. The study focused on assessing photosynthetic characteristics and non-structural carbohydrate content in flag leaves, stem-sheath non-structural carbohydrate content, panicle starch content, and yield under an appropriate concentration of PSS. The results of this investigation aim to provide a theoretical foundation for achieving high-yield cultivation of DSR.

2 Materials and Methods

2.1 Experimental Design

Rice (*Oryza sativa L.*) varieties JYJ (Ji90-g4; male parent: Qiuguang, female parent: Hui73) and JJ305 (Ji15-30; male parent: Ji09-2624, female parent: 2010Q4-7) were used. The rice seeds were soaked in paclobutrazol (Sichuan Guoguang Agrochemical Co., Ltd., Chengdu, China) at concentrations of 0 mg L^{-1} and 100 mg L^{-1} (experimental screening to determine the appropriate concentration) for 24 h to sown. The experiment site, experiment time, fertilization method and water management are the same as Gai et al. [17].

2.2 Sampling and Measurements

2.2.1 Photosynthetic Characteristics

Flag leaves from main stems were selected at the early (EF), mid (EF), and late (LF) filling stages for the measurement of leaf area and chlorophyll content. The chlorophyll content was calculated using the formula described by Arnon [19]. At the EF, the net photosynthetic rate was measured using a Li-Cor 6400 gas exchange analyzer. The data on chlorophyll content and net photosynthetic rate reference to Gai et al. [17].

2.2.2 Non-Structural Carbohydrates

Flag leaves from the main stems at EF, MF, and LF, as well as stem sheaths at the heading stage (HD), EF, MF, LF, and mature stages (MA) were selected for analysis. Additionally, the main stem panicles, divided into top, middle, and bottom sections based on their length, were sampled at the EF, MF, and LF stages. After drying, the contents of soluble sugar and starch were determined. The determination method followed the protocol described by Yoshida et al. [20].

2.2.3 Yield

Plants representative of each plot were collected at MA for analysis of the yield components, and the theoretical yield was calculated. The data on yield reference to Gai et al. [17].

2.3 Data Analysis

Data were processed by SPSS 23.0 software. Statistical significance was indeed achieved by *t*-test ($p <$ 0.05). All graphs were constructed with Origin 2021.

3 Results

3.1 Effects of PSS on Photosynthetic Characteristics of Flag Leaves of DSR

The Flag Leaves of DSR exhibited a progressive decrease in chlorophyll levels, net photosynthetic rate, and leaf area (Fig. 1). In comparison to the control (CK), PSS treatment enhanced chlorophyll content, net photosynthetic rate, and leaf area during the grain filling stage.

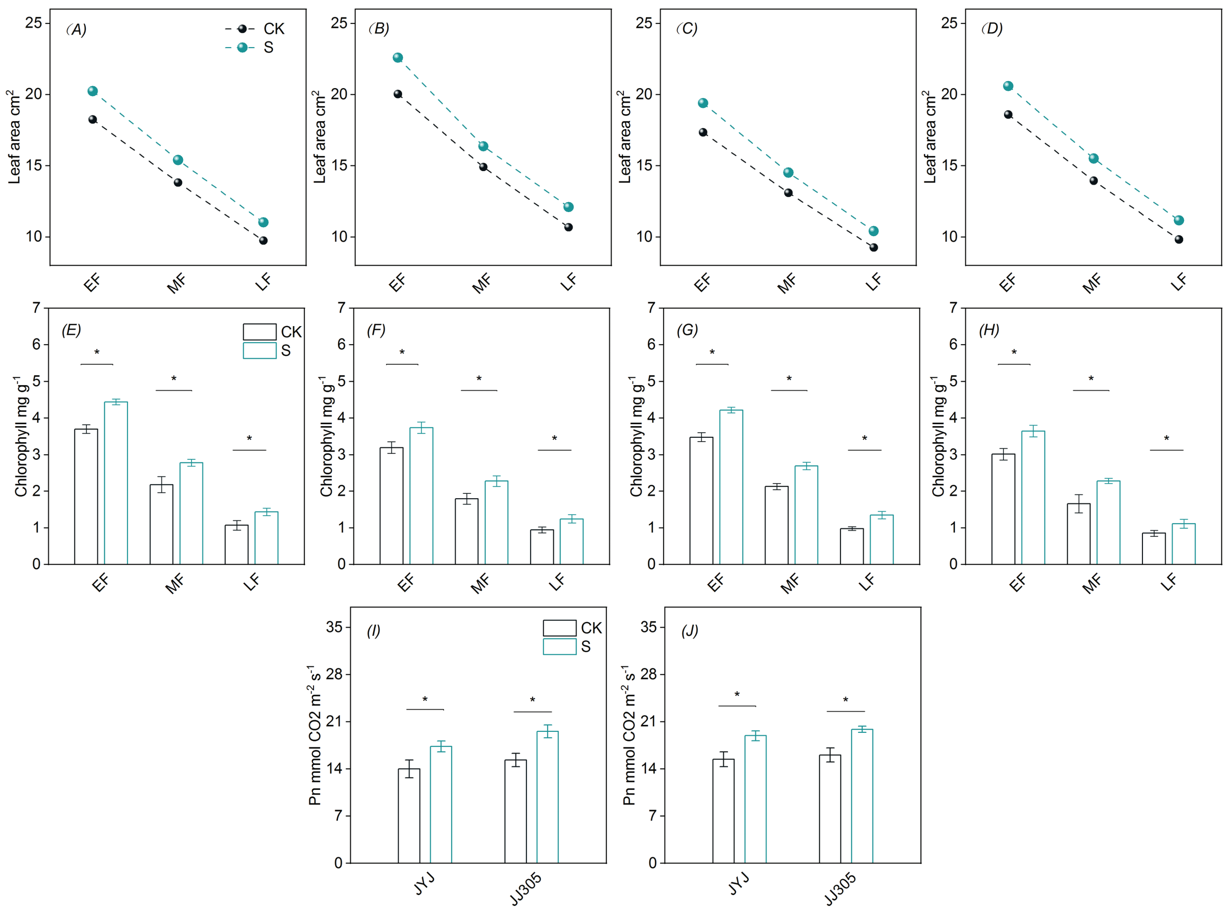

Figure 1: Effects of PSS on photosynthetic characteristics of flag leaves of DSR. A, C, E, G represent rice varieties JYJ; B, D, F, H represent rice varieties JJ305. A, B, E, F, I represent 2021 year; C, D, G, H, J represent 2022 year; * represent $p < 0.05$

3.2 Effects of PSS on Non-Structural Carbohydrate Content in Flag Leaves of DSR

The soluble sugar and starch contents of flag leaves showed a trend of increasing and then decreasing, and reached the maximum in the MF (Fig. 2). PSS increased the soluble sugar and starch contents at the EF, LF, but decreased at the MF.

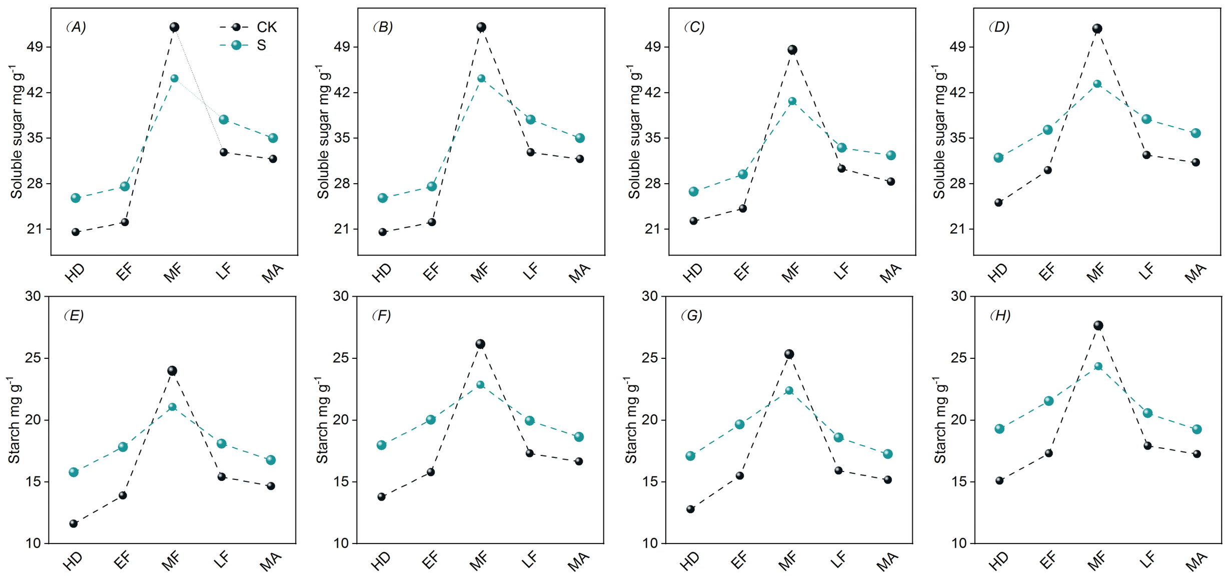

Figure 2: Effects of PSS on non-structural carbohydrate content in flag leaves of DSR. A, E represent 2021 JYJ; B, F represent 2021 JJ305; C, G represent 2022 JYJ; D, H represent 2022 JJ305

3.3 Effects of PSS on Non-Structural Carbohydrate Content in Stem Sheaths of DSR

The soluble sugar levels in the stem sheaths showed a trend of increasing, decreasing, and increasing again, reached the maximum in the EF (Fig. 3). Compared with CK, PSS increased the soluble sugar content of stem sheaths after the HD.

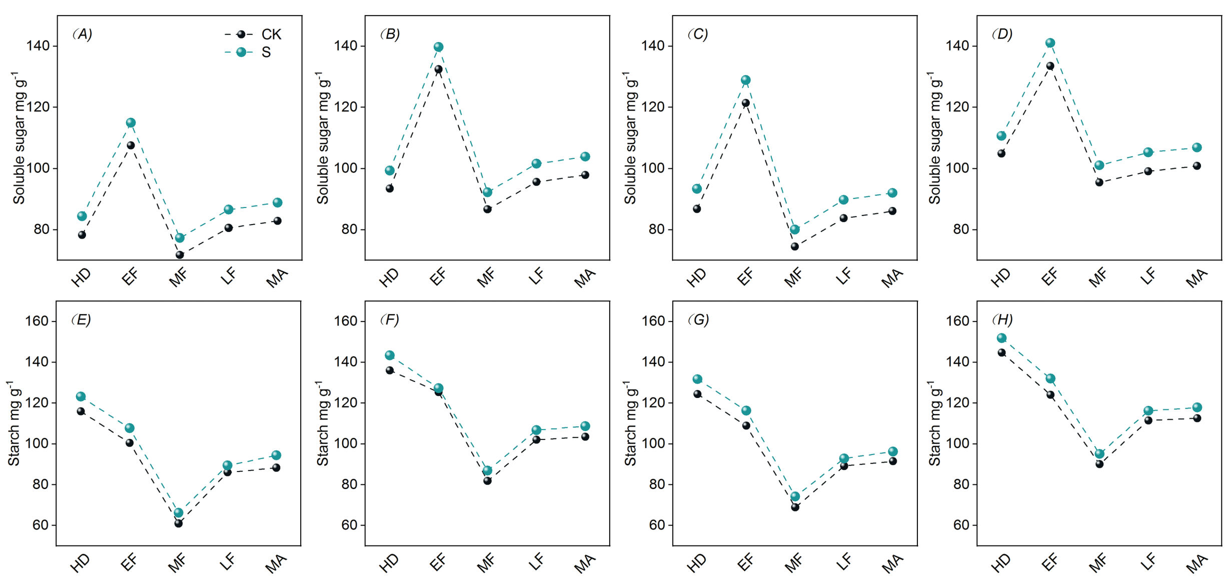

Figure 3: Effects of PSS on non-structural carbohydrate content in stem sheaths of DSR. A, E represent 2021 JYJ; B, F represent 2021 JJ305; C, G represent 2022 JYJ; D, H represent 2022 JJ305

The starch levels in stem sheaths demonstrated an initial decreasing followed by a subsequent increasing, reached the maximum at the HD (Fig. 3). Compared with CK, PSS increased the starch levels in the stem sheaths after the HD.

3.4 Effects of PSS on Starch Content in Panicle of DSR

The starch content in the panicle of DSR exhibited a progressive increase as the reproductive period advanced, with the distribution pattern observed as top panicle > middle panicle > bottom panicle (Fig. 4). In comparison to the CK, PSS treatment resulted in a decrease in starch content in the top panicle, while the middle and bottom panicles showed an increase in starch content.

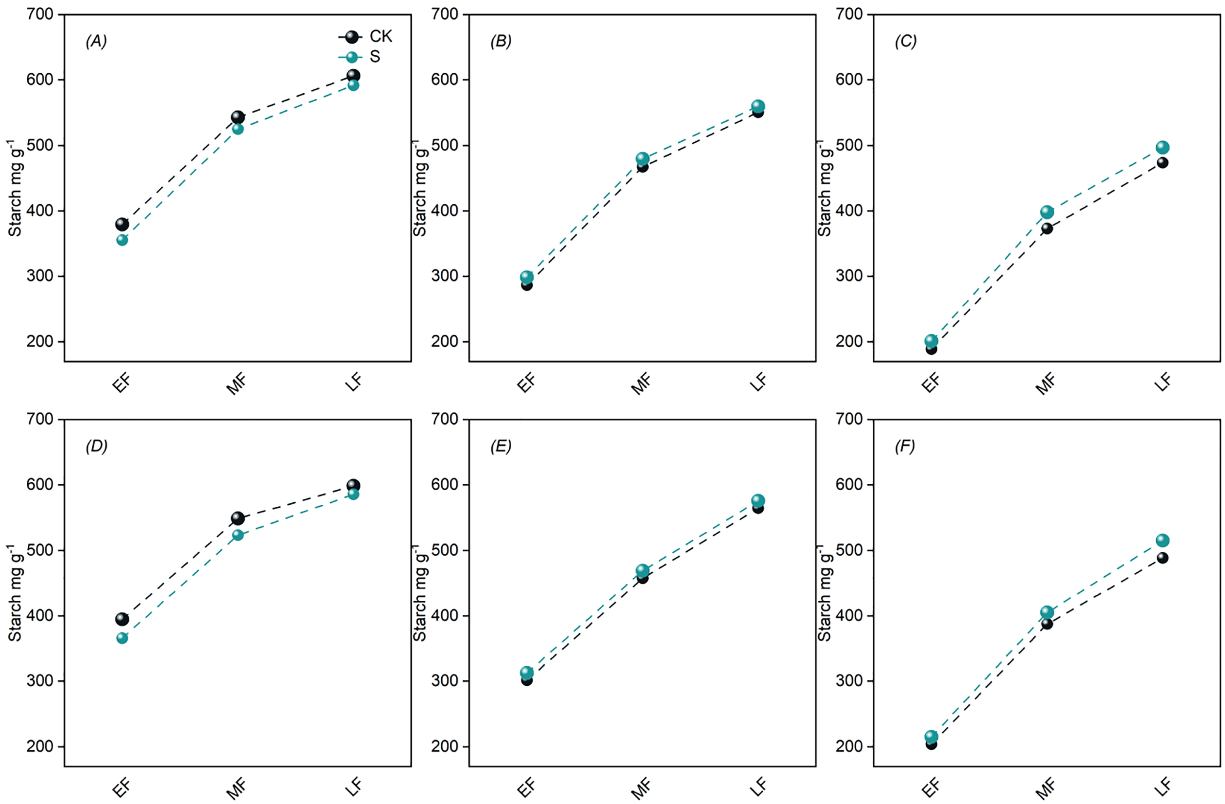

Figure 4: Effects of PSS on starch content in panicle of DSR. A, B, C represent 2022 JYJ; D, E, F represent 2022 JJ305. A, D represent top panicle; B, E represent middle panicle; C, F represent bottom panicle

3.5 Effects of PSS on Yield in DSR

PSS increased the yield of DSR (Fig. 5). Compared with CK, PSS increased the SSR and TS, but decreased the thousand-grain weight (TGW).

3.6 Correlation Analysis of Starch Content in Panicle with SSR and TGW

Correlation analysis revealed distinct relationships between starch content in different panicle positions at the LF stage, SSR, and thousand-grain weight (Fig. 6). Starch content in the top panicle exhibited a negative correlation with SSR and a positive correlation with TGW. Conversely, starch content in the middle panicle demonstrated a positive correlation with SSR and a negative correlation with TGW. Notably, starch content in the bottom panicle showed a significant positive correlation with SSR and a negative correlation with TGW.

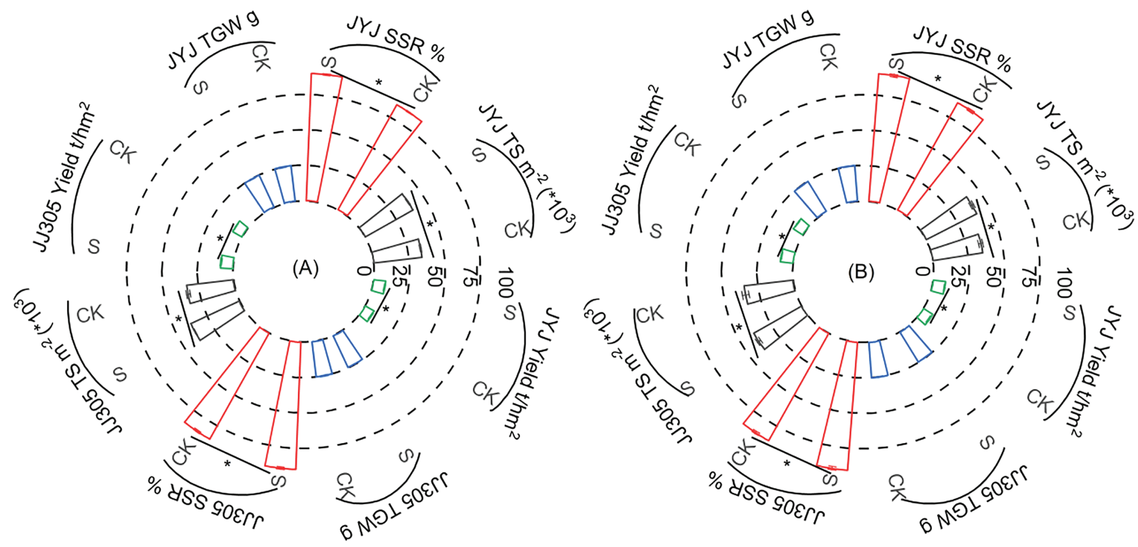

Figure 5: Effects of PSS on yield and yield components in Direct-Seeded Rice. 2021: A; 2022: B. JYJ: Jiyujing; JJ305: Jijing305. The spikelet per unit area: TS; seed setting rate: SSR; thousand-grain weight: TGW; *represent $p < 0.05$

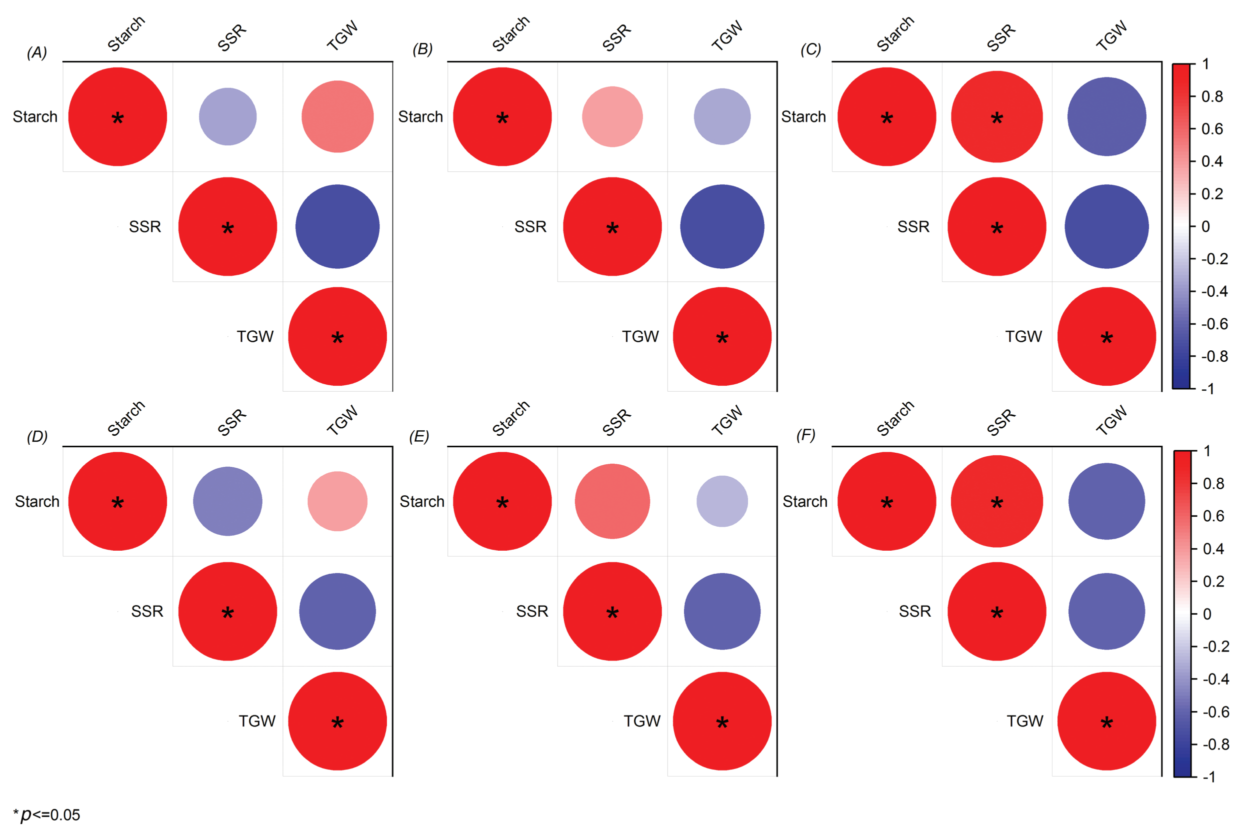

Figure 6: Correlation analysis of starch content in the panicle at LF with SSR and TGW A, B, C represent JYJ; D, E, F represent JJ305. A, D represent top panicle; B, E represent middle panicle; C, F represent bottom panicle; * represent $p < 0.05$

4 Discussion

4.1 Effects of PSS on Material Production of Flag Leaves in DSR

The flag leaf plays a crucial role in rice grain filling, contributing over 50% of the organic matter accumulated in the rice panicle through its photosynthetic products [21–23]. Flag leaf senescence is closely linked to yield, with premature senescence during the filling process potentially shortening the functional period of leaves and limiting the production and transfer of photosynthetic products to the panicles, thus affecting overall yield. Consequently, extending the lifespan of rice flag leaves represents a significant strategy for enhancing rice yield. Previous research has shown that paclobutrazol application increases chlorophyll content, net photosynthesis, antioxidant enzyme activity, and soluble sugar levels [24,25]. In this study, PSS demonstrated the ability to delay leaf senescence and improve flag leaf area, chlorophyll content, and net photosynthetic rate during the filling stage (Fig. 1). This enhancement enabled leaves to maintain higher photosynthetic capacity, ensuring sustained material synthesis and supply in the later stages, thereby providing a sufficient material basis for high DSR yield.

The filling period represents a crucial stage for grain utilization of carbohydrates, directly influencing grain filling and final yield [26,27]. Carbohydrates, the primary products of photosynthesis in plants, are categorized into structural and non-structural types [28]. Non-structural carbohydrates play a vital role in plant growth and development, ensuring normal physiological functions [29]. In this study, PSS increased soluble sugar and starch content in the flag leaves of DSR at the EF and LF stages, providing a sufficient material foundation for grain filling and ultimately promoting grain enrichment (Fig. 2). However, PSS was observed to reduce soluble sugar and starch content in flag leaves at the MF stage (Fig. 2). Two possible explanations for this phenomenon are proposed. Firstly, the plumpness in the stem sheath of DSR may have decreased from EF to MF, with PSS promoting the transfer of materials from leaf to stem sheath, enriching the stem sheath to improve lodging resistance (Fig. 3). Secondly, the grain filling process of DSR from EF to MF requires a significant amount of organic material, and PSS may facilitate the transfer of material from the 'source' to the 'sink' (Fig. 4).

4.2 Effects of PSS on Non-Structural Carbohydrates in the Stem Sheath of DSR

Non-structural carbohydrates stored in nutrient organs prior to flowering play a crucial role in crop grain filling and significantly impact crop yield [30,31]. In this study, PSS increased the soluble sugar and starch content of stem sheaths at the HD, providing a solid foundation for grain filling (Fig. 3). During the filling period, organic matter from the stem sheaths is translocated to the panicle, resulting in an elevated center of gravity and an increased risk of lodging [32,33]. Zhang et al. demonstrated that increasing the content of non-structural carbohydrates in the stem sheath during the EF stage was beneficial for enhancing rice's resistance to lodging [34]. In this study, PSS increased the contents of soluble sugar and starch in the stem sheath at the EF stage, while the starch content in the stem sheath at the MF and LF stages was higher (Fig. 3). These findings were conducive to the plumpness of the stem sheath and the improvement of lodging resistance in DSR, which was closely related to the enhancement of photosynthetic capacity and material transport of flag leaves under PSS (Fig. 1 and 2).

4.3 Effects of PSS on Grain Enrichment in DSR

Paclobutrazol application has demonstrated significant importance in enhancing crop agronomic characteristics and increasing yield. Xing et al. showed that the use of paclobutrazol led to a higher SSR, ultimately resulting in a higher yield of rice [35]. In this study, PSS increased the yield of DSR (Fig. 5). SSR, a crucial factor influencing yield, depends on panicle development and grain filling processes [36].

In this study, PSS increased TS in DSR, consequently elevating the demand for photosynthetic products and enhancing their absorption, thereby contributing to improved grain filling (Fig. 5).

The degree of rice grain enrichment is closely associated with its position within the rice spikelet. Generally, grains in the upper and middle parts of the spikelet flower earlier, fill more rapidly, enrich more effectively, and possess higher weights. Conversely, grains in the lower part of the spikelet flower later, fill more slowly, enrich less effectively, and weigh significantly less [37,38]. Grain enrichment primarily involves the synthesis and accumulation of starch, which constitutes approximately 80% of the dry mass of rice grains [9,39]. Xiang et al. found that uniconazole seed soaking decreased the starch content in superior grains and increased it in inferior grains [40]. In this study, PSS decreased starch content in the top panicle but increased it in the middle and bottom panicles, and increased the SSR; starch content in the top panicle negatively correlated with SSR, while starch content in the middle panicle positively correlated with SSR; notably, starch content in the bottom panicle showed a significant positive correlation with SSR (Figs. 4–6). These findings suggest that PSS can coordinate the filling process of superior and inferior grains, thereby promoting grain enrichment. PSS increased the SSR of DSR, thus increasing the number of filled grains per panicle, reducing ineffective tillering, and increasing effective panicles (data not shown). Additionally, this study found that PSS decreased the TGW of DSR, although the difference between treatments was not statistically significant (Fig. 5). This could be attributed to a decrease in the average distribution of organic matter to individual grains due to an increase in sink (Fig. 5). Furthermore, PSS decreased the starch content in the top panicle; starch content in the top panicle positively correlated with TGW, while starch content in middle and bottom panicles negatively correlated with TGW (Figs. 4 and 6). These results indicate that PSS had a minimal negative effect on the seeds in the top panicle.

With a soil half-life exceeding 6 months, residual paclobutrazol may negatively impact plants and pose potential risks to both environmental and human health. PSS can mitigate its direct release into the natural ecosystem and reduce its residual presence in the environment. Si et al. showed that when the concentration of PSS was 10 mg kg^{-1}, no paclobutrazol was detected in storage roots of sweet potato [41].

5 Conclusions

PSS enhanced the photosynthetic capacity of DSR during the filling stage, maintaining a balance between source and sink, and promoting stable and systematic filling, thereby improving yield. This study further substantiates the agricultural application value of PSS, suggesting a potential novel approach for achieving high-yield cultivation of DSR.

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Author Contributions: Yanqiu Geng and Liying Guo conceived and designed the experiments, Dongsheng Gai, Weiyang Liu, Yong Liu, Pengcheng Fu and Xuanhe Liang performed the experiments, Weiyang Liu, Yong Liu and Xuanhe Liang statistically analyzed the data and made illustrations, Qiang Zhang and Dongsheng Gai wrote the paper. Xiwen Shao reviewed and edited the paper. All authors reviewed the results and approved the final version of the manuscript.

Availability of Data and Materials: The data that support the findings of this study are available from the corresponding author upon reasonable request.

Ethics Approval: Not applicable.

Conflicts of Interest: The authors declare no conflicts of interest to report regarding the present study.

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