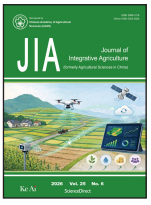
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LETTER

# Improving spikelet production efficiency is crucial for further unleashing yield potential in rice

**Weiyang Zhang[1, 2#], Meijie Jia[1, 2], Shengkai Yang[1, 2], Xiaohan Zhong[1, 2], Haotian Chen[1, 2], Ying Liu[1, 2], Zhiqing Wang[1, 2], Jianhua Zhang[3, 4], Jianchang Yang[1, 2#]**

[1] *Jiangsu Key Laboratory of Crop Genetics and Physiology/Jiangsu Key Laboratory of Crop Cultivation and Physiology/Agricultural College, Yangzhou University, Yangzhou 225009, China*

[2] *Jiangsu Co-Innovation Center for Modern Production Technology of Grain Crops, Yangzhou University, Yangzhou 225009, China*

[3] *Department of Biology, Hong Kong Baptist University, Hong Kong 999077, China*

[4] *State Key Laboratory of Agrobiotechnology, The Chinese University of Hong Kong, Hong Kong 999077, China*

**Highlights**

- Improving spikelet production efficiency (SPE) can further enhance the grain yield and harvest index in rice.
- Higher SPE can enhance post-anthesis photoassimilate production in the shoots of rice.
- Higher SPE can promote the post-anthesis remobilization of non-structural carbohydrate (NSC) from rice stems.

Rice grain yield is a complex agronomic trait determined by four key components: panicles per plant, spikelets per panicle, filled-grain rate, and grain weight. Among these four factors, the number of panicles per plant is often limited by spatial resources and has a certain saturation level; grain weight is mainly controlled by the inherent heritability of the variety itself and relatively stable; the filled-grain rate is mainly regulated by the water, nutrient, temperature, and light conditions post anthesis; while the number of spikelets per panicle is more variable and adjustable, so it still has a relatively large potential for improvement (Zhang 2018; Wang *et al.* 2018; Liu *et al.* 2023). Therefore, developing varieties with a high number of spikelets per panicle, while minimizing the trade-offs with other components, has long been a fundamental objective in the breeding of high-yield and super-high-yield rice (Panigrahi *et al.* 2019; Liu *et al.* 2023).

Spikelet number per panicle is determined during panicle morphogenesis, which involves meristem differentiation, inflorescence patterning, and the differentiation and subsequent degeneration of spikelets. This complex biological process is regulated by numerous genes and plant hormones, and is closely related to the material accumulation in individual above-ground plant parts (shoots) during the vegetative growth stage (Zhang 2018; Zhang *et al*. 2019, 2024; Li *et al.* 2021; Lu *et al.* 2022; Liu *et al.* 2023). Therefore, we introduce a new concept: the spikelet production efficiency (SPE) of rice, which is defined as the ratio between the number of differentiated spikelets per panicle and the dry weight (DW) of vegetative organs (culm, leaves, and leaf sheaths) per individual shoot (for either the main stem or a tiller with at least three fully expanded leaves that has the potential to develop into a productive tiller) at the spikelet differentiation stage. The SPE has units of spikelets $g^{-1}$ DW.

A comparison of representative rice varieties in Jiangsu Province, China from the 1930s to the 1980s revealed that ancient varieties had a total spikelet number of approximately 225 million per hectare, whereas modern varieties exceeded 525 million per hectare. However, the leaf area index (LAI) values of both ancient and modern varieties ranged from 5.5 to 7.0, indicating that the LAI of modern varieties only increased by about 30% despite this dramatic increase in total spikelet number (Ling 2000). Furthermore, in-depth analyses of the data (Wei *et al.* 2016, 2017; Wei 2017; Meng *et al.* 2018) revealed that a 33% increase in spikelet number in the super rice population (from approximately 450 million to around 600 million per hectare) was accompanied by only a 10% increase in population biomass at the initial panicle differentiation stage. These results imply that during the evolution of rice varieties or under high-yielding population conditions, the increase in the spikelet number of the population relies more on the improvement

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[#]Correspondence Weiyang Zhang, E-mail: wyz@yzu.edu.cn; Jianchang Yang, E-mail: jcyang@yzu.edu.cn

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of SPE and relatively less on the increase in population biomass. However, the precise relationship between the SPE and yield formation in rice (especially under high-yielding population conditions) remains unclear.

This study compared multiple rice varieties, including commonly-used production varieties with no significant differences in total panicle number or individual shoot vegetative-organ DW at the spikelet differentiation stage but significant differences in SPE, and found that rice varieties in high-yielding rice populations with higher SPE also had higher grain yield and harvest index (HI) values (Appendices A–C). Furthermore, the number of spikelets per panicle, total spikelet number, grain yield, and HI were all extremely significantly and linearly positively correlated with SPE (Fig. 1-A, B, E, and F). However, for the same indicators (especially total spikelet number, grain yield, and HI), the positive correlation coefficients with SPE were all greater than those with the vegetative-organ DW per shoot (single main stem or tiller) during the spikelet differentiation stage (Appendix D). Notably, the negative correlations between SPE and vegetative-organ DW per shoot with the filled-grain rate and 1,000-grain weight were not very strong (Fig. 1-C and D; Appendix D), indicating that increasing rice SPE and/or vegetative-organ DW per shoot is unlikely to significantly compromise the filled-grain rate and/or 1,000-grain weight. Moreover, in practical rice production, excessive biomass accumulation coupled with slender individual shoots during panicle development often impedes the establishment of high-yielding populations and elevates the risk of lodging, both of which are detrimental to grain yield and harvest index (HI) (Ling *et al.* 2000). These results indicate that enhancing the capacity of rice to produce spikelets per unit of biomass (i.e., SPE) is an important approach to further unlock the yield potential, which is especially crucial in high-yielding populations.

The well-established material foundation for rice grain yield predominantly hinges on the direct provision of photoassimilates generated after anthesis. Moreover, the non-structural carbohydrate (NSC) stored in stems (culms and sheaths) prior to anthesis assume a vital role in buffering and compensating for potential yield fluctuations (Yang and Zhang 2018). The results of this study showed that under high-yielding population conditions, SPE was significantly positively correlated with post-anthesis leaf photosynthetic rate (LPR), shoot dry-matter (SDM) accumulation, and the NSC remobilization rate from stems. Moreover, the positive correlation coefficients of SPE with these parameters were all higher than those of individual shoot vegetative-organ DW in rice (Fig. 1-G–I; Appendices E–I). Therefore, we speculate that the higher population spikelet number (sink) in rice driven by higher SPE has a stronger ability to actively "extract" photoassimilates (i.e., NSC) from the photosynthetic production system, which promotes the transport of more NSC to the sink. The "pulling force" generated by a large sink capacity can effectively improve photosynthetic production efficiency, so it is conducive to increases in both grain yield and HI in rice, especially under high-yielding population conditions.

In summary, improving SPE is a vital strategy for further unlocking the yield potential and raising HI in rice, particularly

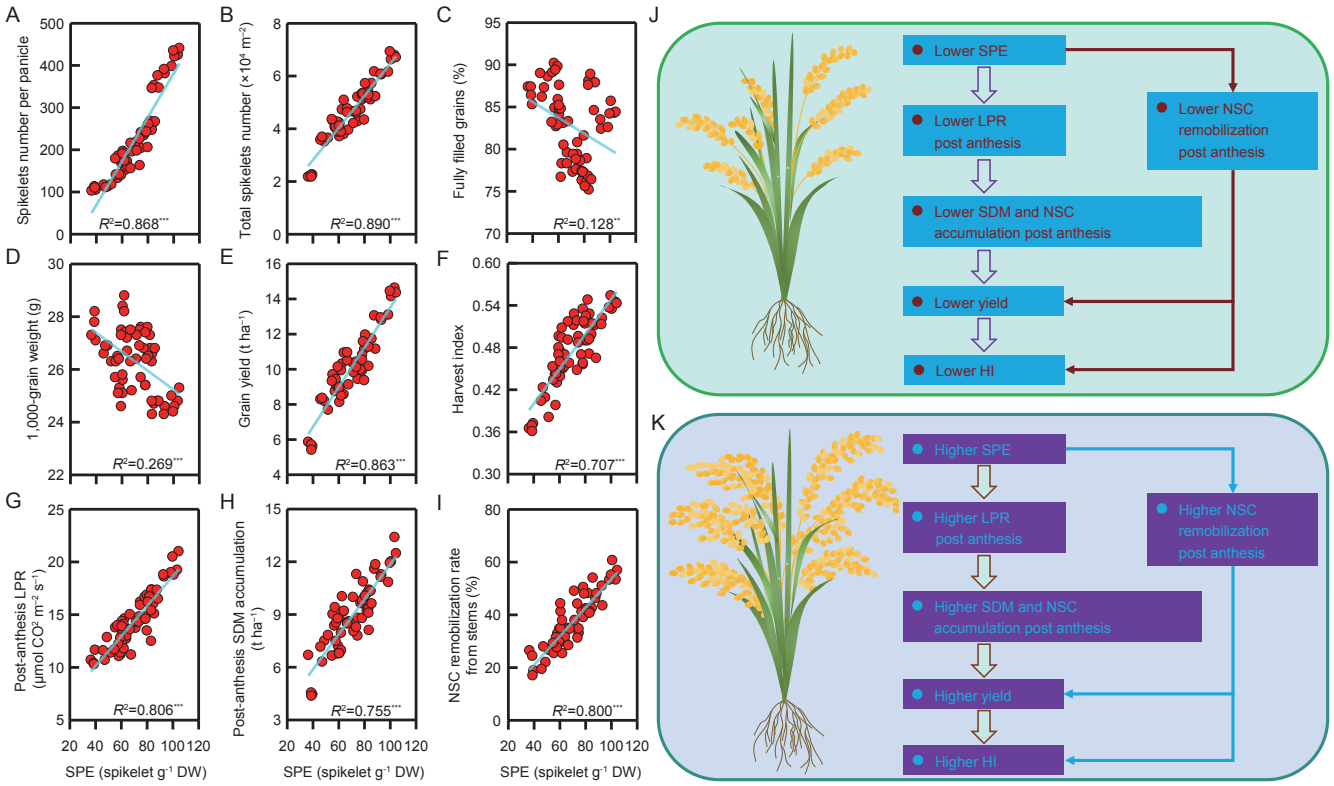



**Fig. 1 Correlation of spikelet production efficiency (SPE) with grain yield, yield components, harvest index (HI), post-anthesis leaf photosynthetic rate (LPR), shoot dry-matter (SDM) accumulation, and non-structural carbohydrate (NSC) remobilization rate.** *** and ** indicate significances at $P$=0.001 and $P$=0.01 ($n$=60, i.e., 15 rice varieties×4 study years), respectively. Arrows in J and K denote promotional effects.

under high-yielding population conditions. Achieving this positive impact by a higher SPE is mainly attributed to its notable enhancement of the production of photoassimilates after anthesis and synergistic improvement in the NSC remobilization rate from the stems in rice after anthesis (Fig. 1-J and K). Therefore, a higher SPE can serve as a new key criterion for breeding super-high-yield rice varieties and developing cultivation strategies. A systematic investigation into the mechanisms underlying rice SPE and its role in enhancing yield potential and HI is warranted, as it may provide novel insights for breeding and cultivation strategies.

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## Declaration of competing interest

The authors declare that they have no conflict of interest.

## Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used generative AI tools to assist in improving the clarity and readability of the language. All content generated was carefully reviewed and revised by the authors as necessary, and the authors take full responsibility for the final content of the article.

**Appendices** associated with this paper are available at https://doi.org/10.1016/j.jia.2026.03.041

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