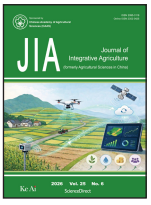
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RESEARCH ARTICLE

Enhancing rice yield by optimizing tillering through the transplantation of seedlings cultivated at a high density on crop straw boards

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Highlights

- High-density seeding and a short seedling period boost middle and low tillering.
- Optimizing the development of middle and low position tillers can further enhance rice yield.
- Properly balancing seeding density with seedling age is vital for achieving a high rice yield.

Abstract

In the face of agricultural labor shortages, reducing labor and costs in rice production while meeting demand or increasing yield is crucial for sustainable agricultural development. Using crop straw boards and raising seedlings at a high-density can reduce labor demand and enhance rice yield. This study investigated the effects of seeding density and transplanting age on tillering patterns, panicle formation rates, and yield to determine the optimal cultivation practices for maximizing rice yield. Two-year field experiments were conducted in Sihong County, Jiangsu Province, China, using the *japonica* rice variety Nanjing 5718. Five seeding densities (150–350 g/tray) and four transplanting ages (10–25 days) were evaluated to assess their impacts on tillering patterns, panicle formation rates, and yield. Innovative crop straw boards were employed to enhance planting efficiency and reduce dependence on soil for raising seedlings. This approach also lessened tillage layer destruction, promoting sustainable practices. The results indicated that increasing seeding density significantly altered tillering and panicle formation patterns by reducing the occurrence and panicle formation rates of lower-position tillers. Although the occurrence of middle- and high-position tillers increased, the overall number of panicles per hill decreased, especially at higher densities, negatively affecting yield. Reducing the transplanting age promoted the emergence and panicle formation of lower-position tillers, thus mitigating these negative effects. Specifically, compared to traditional methods (150 g/tray, 20-day seedlings), the higher seeding density (300 g/tray) and reduced transplanting age (15-day seedlings) increased total panicle number by 3.79–4.73% and yield by 3.38–5.05%. Combining higher seeding densities with reduced transplanting ages offers significant advantages over conventional practices by enhancing resource utilization and improving tillering efficiency. These findings provide actionable recommendations for optimizing rice cultivation practices and contribute to sustainable agricultural development.

Keywords: rice, seeding density, seedling age, crop straw boards, tiller yield formation

1. Introduction

Rice serves as the staple food for more than half of the world's population, but it faces significant production challenges (Deng *et al.* 2019; Xu *et al.* 2020). An aging workforce and a reduction in agricultural labor are exacerbating the urgent need for food security and greater production capacities (Li Z H *et al.* 2018; Zhu *et al.* 2020). As a key indicator of rice yield, the number of tillers is greatly influenced by seeding density and the age of transplanted seedlings (Conway and Toenniessen 1999; Yuan *et al.*

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2007; Alzueta *et al*. 2012; Zhen *et al*. 2019; Zhou *et al*. 2020). However, its reliance on seasonal short-term labor highlights the critical need to reduce dependence on human resources in the mechanized cultivation and transplanting of rice seedlings (Hossen *et al*. 2022; Nawaz *et al*. 2022). Consequently, optimizing seeding density and transplanting age has become critical for enhancing rice yield and can provide key insights into more efficient agricultural practices with reduced labor dependency.

To minimize labor requirements during the initial phases of seedling cultivation and transplanting in mechanized rice systems, previous studies suggested that higher seeding densities in *indica* rice transplanting can reduce the need for seedling trays by 60% (Long *et al*. 2021). Although this approach facilitates labor savings, it intensifies intra-group competition among seedlings, which can impede their early growth and development (Li Y X *et al*. 2018). A critical factor in this scenario is the age at which seedlings are transplanted. Prolonging the transplanting age under high-density conditions leads to a noticeable decline in seedling quality (Wang *et al*. 2019), in which they are more susceptible to damage during transplantation and the duration of the regreening period is increased due to reduced seedling vigor (Li Y X *et al*. 2020). Furthermore, while older seedlings may exhibit an increase in middle to high position tillers (Yu *et al*. 2004; Kariali and Mohapatra 2007; Wang Y *et al*. 2016; Yang *et al*. 2019), this does not compensate for the reduction in low-position tillering which is vital for robust yield outcomes (Cai *et al*. 2014; Tilley *et al*. 2019). Therefore, optimizing the transplanting age is crucial for enhancing the tillering patterns and yield under high-density conditions. Some scholars have noted that promoting tillering by lowering the transplanting age can mitigate the negative effects of high seeding density on rice yield (Abbas and Orang 2003; Liu *et al*. 2017). However, premature transplantation may cause excessive growth of low-position tillers, with subsequent tillers capable of panicle formation dying off due to inferior competition for water and nutrients, thus reducing the total number of panicles and yield (Wang Z *et al*. 2016; Zhao *et al*. 2020; Deng *et al*. 2022). To enable the transplanting of seedlings at a younger age, recent studies suggest that employing crop straw boards in seedling cultivation not only supports high-density seeding by reducing labor but also allows for shortening the transplanting age (Ling *et al*. 2023). Crop straw boards are typically made from agricultural residues such as straw or wheat straw, which are processed through physical and chemical treatments to achieve high porosity and excellent water retention capacity (Ling *et al*. 2021). Their unique structure not only improves the aeration and water-holding properties of seedbed soils but also gradually releases nutrients during decomposition to meet the growth needs of seedlings. In addition, crop straw boards promote healthy root development and enhance plant stress resistance. Although some studies have explored the use of crop straw boards for high-density seedling cultivation, the specific impacts of seeding density and different transplanting ages on rice tillering patterns and panicle formation still require more detailed investigation, particularly in terms of how they interact to affect the final yield and quality of rice.

This study employed crop straw boards as the material for seedling cultivation to explore the optimal seeding density and transplanting age that can enhance rice tillering, with the aim of increasing yield. Using a randomized block design, this study aimed to delineate the complex interactions between seeding density and transplanting age, and how they influence tillering patterns and panicle formation. These variables were comprehensively assessed under varying conditions to identify beneficial leaf positions that support the mechanized cultivation of *japonica* rice through effective tillering management. Furthermore, this detailed investigation will not only optimize yield and efficiency but also provide substantial scientific support for “light simplification” and “reduced labor” cultivation models in the seedling stage of machine-transplanted rice. This approach is expected to advance modern agricultural technologies by enhancing our understanding of plant developmental dynamics in controlled agricultural systems.

2. Materials and methods

2.1. Experimental site and cultivars

The experiment was conducted at the external research facility of Yangzhou University located in Shiji Township, Sihong County, Jiangsu Province, China, during the years 2021 and 2022 (33°22′N, 118°16′E). The site had previously been used for wheat cultivation. At the start of this study, the topsoil layer (0–20 cm) exhibited a pH of 6.64 and was composed of 23.52 g kg^{-1} organic matter, 1.34 g kg^{-1} total nitrogen, 16.34 mg kg^{-1} available phosphorus, and 127 mg kg^{-1} available potassium. The rice variety chosen for this experiment was Nanjing 5718, a conventional medium-maturing *japonica* rice known for its high quality and flavor that is widely planted in Jiangsu Province. The crop straw boards used in the experiment, measuring 57.5 cm×27.5 cm×2 cm, were supplied by the Jiangsu Academy of Agricultural Sciences. According to local agricultural practices, the normal seeding density was 150 g/tray (3.20 grains cm^{-2}), and the normal seedling age was 20 days. The average temperature, sunshine hours, and precipitation during the two growing seasons at the rice experimental site are shown in Fig. 1.

2.2. Experimental design and management

Rice seedlings were cultivated in plastic trays measuring 58 cm×28 cm×3 cm, with crop straw boards replacing the traditional seedbed soil at the bottom. This study adopted a two-factor split-plot design, with the main plots including five seeding densities of D1 at 150 g/tray (3.20 grains cm^{-2}) as the standard seeding density, followed by D2 at 200 g/tray (4.26 grains cm^{-2}), D3 at 250 g/tray (5.33 grains cm^{-2}), D4 at 300 g/tray (6.39 grains cm^{-2}), and D5 at 350 g/tray (7.46 grains cm^{-2}). Four different ages for transplanting formed the subplots, namely A1, 10 days; A2, 15 days; A3, 20 days; A4, 25 days. To ensure data integrity and effective analysis, each treatment was replicated three times. Uniform conditions were maintained for seedling cultivation, followed by transplantation into the field on June 18 in both 2021 and 2022. Transplantation was conducted using the Yanmar High-

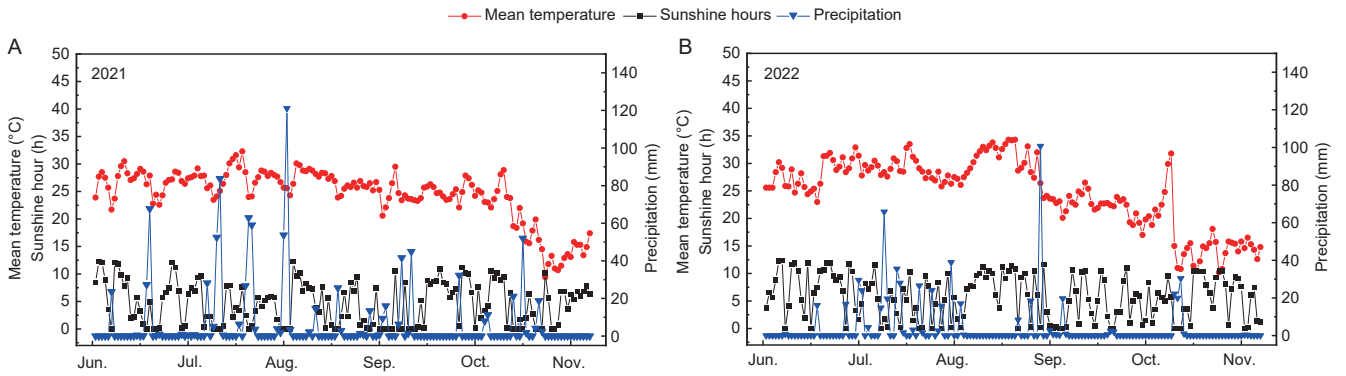


Fig. 1 Daily mean temperature, sunshine duration, and precipitation during the rice growing seasons in 2021 (A) and 2022 (B) at the field site in Sihong County, Jiangsu Province, China.

Speed Transplanter (Model 2ZGQ-60D (G4) (YR60D), Yanmar Agricultural Machinery (China) Co., Ltd.) for dense seedling transplanting, with a planting density of 30 cm×11.8 cm and four seedlings per hill. By adjusting the size of the longitudinal and transverse cutting of the rice transplanter, the average value of each hill during transplanting was four seedlings. Each field experiment plot was 316.8 m^2 (7.2 m×44 m), with three replicates per treatment. The total application of pure nitrogen was 270 kg ha^{-1}, which was delivered as a controlled-release mixed fertilizer (Zhidaodi, Moith Corporation, China) one day prior to seeding or transplanting. The fertilizer's elemental composition was N:P_2O_5:K_2O=30:7:13. All water management and pest control practices adhered to local agricultural guidelines.

2.3. Sampling and measurements

Prior to transplanting, 20 seedlings were randomly selected from each treatment to measure leaf age and seedling height. From each treatment, 100 seedlings were divided into their aboveground parts and initially dried in an oven at 105°C for 30 min to stabilize their biochemical components, followed by drying at 80°C to a constant weight to determine the dry weight. The content of soluble sugars in the aboveground parts of the seedlings was quantified using the anthrone colorimetric method.

After transplanting, rice typically undergoes a phase of yellowing before reverting to green, accompanied by the gradual unfolding of leaves. This period, known as the regreening period, marks the stage at which rice resumes active growth. To investigate tillering occurrence, two adjacent plots, each containing 15 hills with similar growth patterns, were selected from each treatment group for fixed-point, time-based observations. Leaf age was marked every 5 days, and tiller occurrence was monitored every 5 days before internode elongation and every 7 days after internode elongation. In addition, multiple surveys were conducted at the critical leaf stage for effective tillering (i.e., total leaf number on the main stem (*N*) minus the number of internodes (*n*)) and at the heading stage. Each main stem and tiller was labeled using plastic tags to indicate their secondary and leaf positions.

At maturity, the marked plants were individually harvested, and the tillers at different leaf positions were separated. The numbers of tillers and panicles and other panicle characteristics were recorded. The number of grains per panicle, seed-setting rate, and thousand-grain weight of rice were measured to evaluate the yield components under different treatment conditions. The tillering occurrence rate at each leaf position refers to the percentage of the actual number of tillers at that position relative to the total number of observed plants. The tillering panicle formation rate at each leaf position refers to the percentage of the number of panicles formed at that position relative to the actual number of tillers. First- and second-order tillers are represented in fractional form based on the position of the tiller on the mother stem, with "0" indicating the main stem and "1", "2", "3", etc., indicating the leaf positions. First-order tillers are labeled as "*X*/0", where *X* denotes the *X*th leaf of the main stem (0/0). For instance, 3/0 represents a first-order tiller emerging from the third leaf of the main stem. Second-order tillers are labeled as "*Y*/*X*", indicating that the tiller arises from the *Y*th leaf of the *X*/0 mother tiller (Li *et al.* 2011; Xu *et al.* 2014). For example, 1/3 denotes a second-order tiller from the first leaf of the 3/0 tiller. Each main stem and tiller was labeled according to their positions, where the main stem (MS) was marked as 0/0. Lower part tillers (LPT) were marked as 4/0 and included the main stem tillers preceding them. Middle part tillers (MPT) were marked as 5/0 and 6/0. High part tillers (HPT) were marked as 7/0 and included the main stem tillers succeeding them. Secondary tillers (ST) were marked accordingly.

At physiological maturity, three 2.5 m×2.5 m quadrats were randomly selected from each treatment for manual harvesting. After threshing, the grain was dried to a standard moisture level of 14.5% to calculate the final yield. At physiological maturity, five hills from each treatment were randomly chosen to estimate the theoretical yield, calculated as: Number of panicles per unit area×Number of grains per panicle×1,000-grain weight×Seed-setting rate.

2.4. Data processing and statistical analysis

Data processing was performed using Excel 2016 (Microsoft Corporation, Redmond, WA, USA). Statistical analyses, including analysis of variance (ANOVA), were conducted with IBM SPSS Statistics 20.0 (IBM Corp., Armonk, NY,

USA), a statistical analysis software package. Graphical representations were created using Origin 2021 (OriginLab Corporation, Northampton, MA, USA).

3. Results

3.1. Seedling characteristics and the regreening stage

Seeding density and seedling age significantly affected rice seedling growth parameters, including seedling height, shoot dry weight per 100 seedlings, dry weight per unit seedling height, and soluble sugar content. Higher seeding densities and older seedling ages increased seedling height (Fig. 2), with the maximum increases in both years observed under density D5 (up to 3.29 cm in 2021 and 1.88 cm in 2022). Shoot dry weight per 100 seedlings also increased with seeding density and seedling age, particularly at the highest density of D5. Conversely, dry weight per unit seedling height increased until seedling age A3 (20 days) and then decreased, especially under higher densities (D2 to D5). Soluble sugar content decreased with increasing seeding densities and seedling ages, especially under high-density conditions, indicating potential stress responses. In addition, leaf age increased and the regreening period was extended by approximately 2–3 days with higher seeding densities and older seedling ages (Fig. 2), which may affect seedling adaptation and early growth after transplanting.

The analysis of variance results (Table 1) indicated that seeding density (D), seedling age (A), and their interactions had significant effects on the seedling quality parameters (P<0.05 or P<0.01). Both D and A had significant effects (P<0.01) on all measured parameters. The interaction

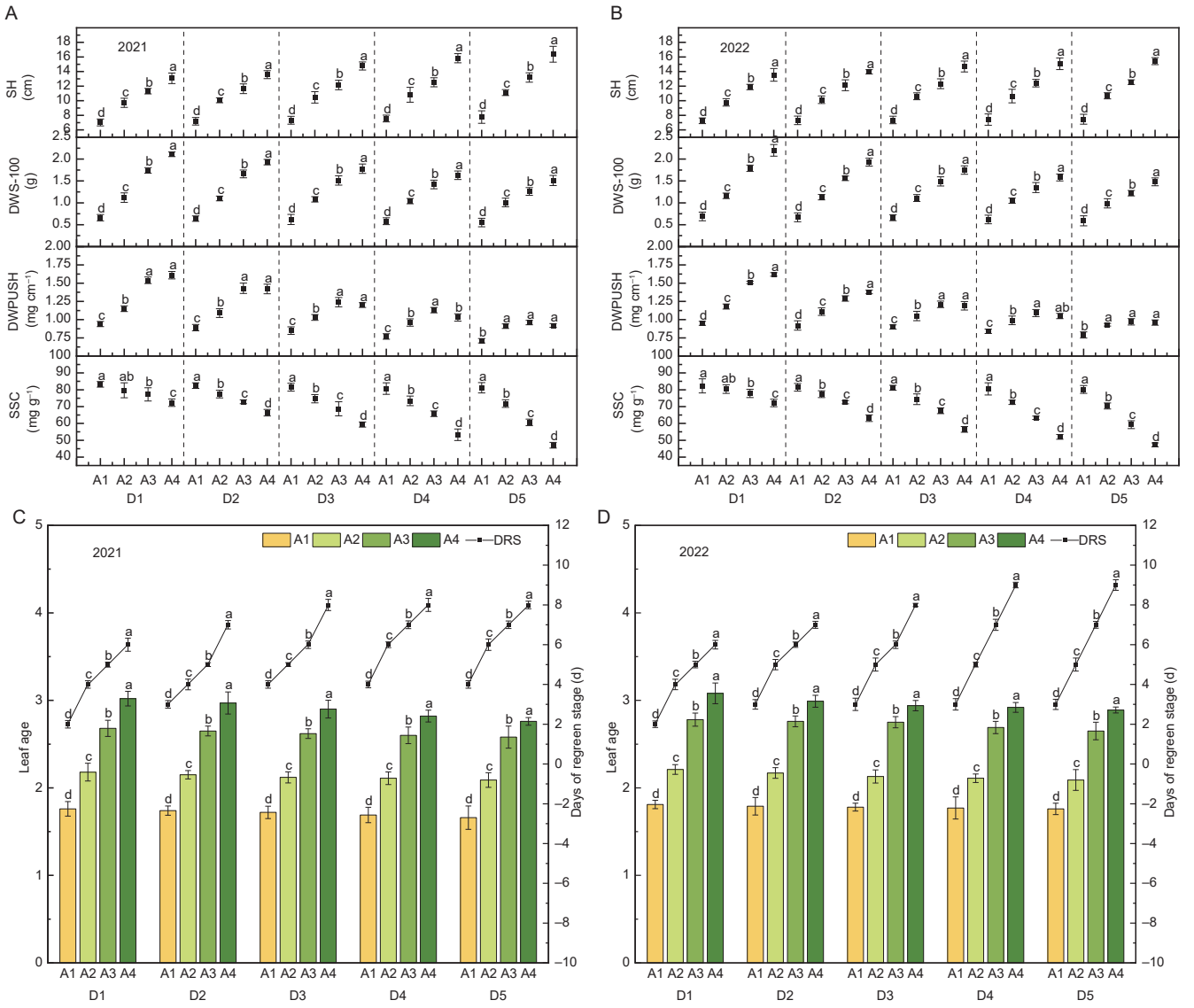


Fig. 2 Seedling characteristics and days of the regreening stage of rice as affected by increases in seeding density and seedling age with crop straw boards for seedling cultivation in 2021 and 2022. SH, seedling height; DWS-100, dry weight of shoots for 100 seedlings; DWPUSH, dry weight per unit of seedling height; SSC, soluble sugar content. A1–A4, different ages for transplanting formed the subplots, 10, 15, 20, and 25 days, respectively. D1–D5, five seeding densities, 150, 200, 250, 300, and 350 g/tray, respectively. Bars represent SE (n=3). Different letters above the columns represent the statistically significant differences at P<0.05 between different treatments.

Table 1 Analysis of variance results for the effects of seeding density, seedling age, and their interactions on the seedling quality of rice under crop straw board seedling cultivation

Variable	Seedling height (cm)	Dry weight of shoots for 100 seedlings (g)	Dry weight per unit of seedling height (mg cm^{-1})	Seedling soluble sugar content (mg g^{-1})
Year (Y)	NS	NS	NS	NS
Seeding density (D)	**	**	**	**
Seedling age (A)	**	**	**	**
Y×D	NS	NS	NS	NS
Y×A	NS	NS	**	NS
D×A	*	**	**	**
Y×D×A	NS	NS	NS	NS

** and * indicate significant correlations at the 0.01 and 0.05 levels, respectively; NS indicates no significant correlation at the 0.05 level (P>0.05).

between seeding density and seedling age (D×A) had significant effects on seedling height (P<0.05) and other parameters (P<0.01). The interaction between year and seedling age (Y×A) had significant effect (P<0.01) on dry weight per unit seedling height. However, the main effect of year (Y) and other interactions involving year did not show significant effects (P>0.05) on any of the seedling quality parameters.

3.2. Effects of leaf position and emergence rate on tillers and panicles

At the same seeding density, older transplanting ages reduced the emergence rates of lower-position tillers (3/0, 4/0) but increased those of middle- (5/0, 6/0) and upper-position (7/0) tillers (Fig. 3-A). The reduction in lower-position tiller emergence was accompanied by reduced secondary tiller occurrence. These changes became more pronounced at higher seeding densities. For instance, at the lowest density (D1), the emergence rate and panicle formation rate of the 4/0 tiller were 96.13 and 100% at age A1, decreasing to 73.87 and 86.74% at A4; meanwhile, the 6/0 tiller emergence and panicle formation rates increased from 10.71 and 24.72% to 85.52 and 37.15%, respectively. Conversely, at the highest density (D5), the 4/0 tiller emergence and panicle formation rates sharply decreased from 91.24 and 100% at A1 to 11.46 and 58.88% at A4; while the 6/0 tiller rates increased from 66.57 and 31.48% to 100 and 65.64%, respectively. These results indicate that higher seeding densities amplify the effects of transplanting age on tiller emergence patterns. The emergence rates of tillers directly influenced the panicle formation rates at corresponding leaf positions (Fig. 3-B). Consequently, due to changes in the tiller emergence and panicle formation rates, the number of tillers per hill decreased with older transplanting ages, a trend that was exacerbated at higher seeding densities (Fig. 3-C). These findings highlight the importance of considering the interaction between seeding density and transplanting age when developing cultivation strategies.

3.3. Yield components of main stems and tillers

As shown in Fig. 4, under consistent seeding conditions, older transplanting ages reduced the panicle number on lower-position tillers (3/0, 4/0) but increased it on middle-position tillers (5/0, 6/0). Secondary tillers displayed variable patterns. For instance, the panicle number on 1/3 tillers declined with advancing transplanting age; whereas on 1/4 tillers, it initially rose and then fell under low seeding densities (D1 and D2) but consistently declined at higher densities (D3 to D5). Increasing the seeding density resulted in a reduction in the panicle number of lower position tillers, an increase in the panicle number of middle position tillers, and an overall decline in the panicle number of secondary tillers. Both primary and secondary tillers exhibited reductions in the number of grains per panicle as transplanting age and seeding density increased. The grain-setting rate on lower position tillers declined with increasing transplanting age. In contrast, the setting rate on middle position tillers increased, reaching a peak at transplanting age A3, and then decreased. Secondary tillers consistently showed reduced setting rates with age progression. Higher seeding densities further reduced the grain-setting rate at each tiller position. For lower-position tillers, the 1,000-grain weight decreased with older transplanting ages, whereas it increased for the middle, upper, and secondary tillers. Under a constant transplanting age, increasing the seeding density reduced the 1,000-grain weight across all tiller positions.

3.4. Tillering yield and contribution rate

Under the same seeding density conditions, older transplanting ages led to declining yields from secondary tillers in each treatment and shifted the primary yield sources from the main stem and lower-position tillers to the main stem and middle-position tillers (Table 2). This shift became more pronounced with increasing seeding density. According to Figs. 5 and 6, apart from the main stem, high-yielding rice primarily relies on the production from lower and middle position tillers. As shown in Table 2, under the lowest seeding density (D1), the total yield decreased slightly with increasing seedling age from A1 to A4 (from 10.94 to 10.52 t ha^{-1}), but it remained relatively stable. However, the yield and contribution rate of lower position tillers (LPT) decreased significantly; the yield dropped from 4.43 to 2.28 t ha^{-1}, and the contribution rate from 40.62 to 21.24%. In contrast, the yield and contribution rate of middle position tillers (MPT) increased significantly, with the yield rising from 2.11 to 4.53 t ha^{-1} and the contribution rate from 19.35 to 42.21%. Under the highest seeding density (D5), this trend was even more evident. As seedling age increased from A1 to A4, the total yield declined from 10.85 to 9.52 t ha^{-1}. The yield and contribution rate of lower position tillers decreased markedly, with the yield dropping from 3.51 to 0.23 t ha^{-1} and the contribution rate from 33.32 to 2.46%. Conversely, the yield and contribution rate of middle position tillers increased significantly, with the yield increasing from 2.96 to 5.30 t ha^{-1} and the contribution rate from 28.14 to 57.22%.

The analysis of variance results (Table 3) showed that seeding density, seedling age, and their interactions had

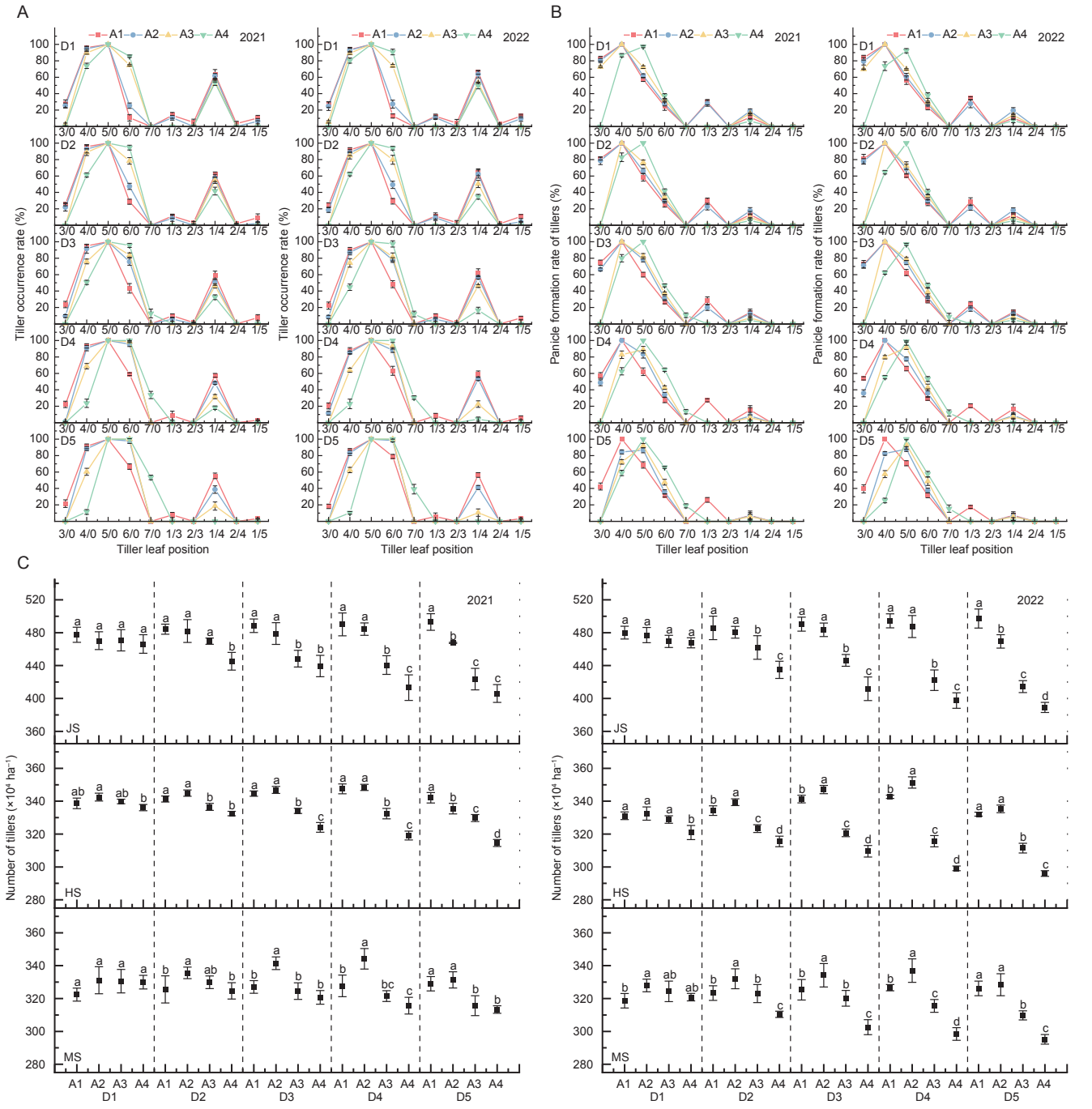


Fig. 3 Tiller and panicle leaf position of rice as affected by increases in seeding density and seedling age with crop straw boards for seedling cultivation in 2021 and 2022. A, tillering occurrence rates at different leaf positions in rice. B, panicle formation rates of tillers at different leaf positions in rice. C, numbers of tillers during the jointing stage (JS), heading stage (HS), and maturation stage (MS). A1–A4, different ages for transplanting formed the subplots, 10, 15, 20, and 25 days, respectively. D1–D5, five seeding densities, 150, 200, 250, 300, and 350 g/tray, respectively. Bars represent SE (n=3). Different letters indicate significant differences between treatments at P<0.05.

significant effects on the total rice yield, the yields at different tiller positions, and their contribution rates (P<0.05 or P<0.01). Specifically, both seeding density and seedling age had significant effects on total yield, the yields of lower position tillers, and the yields of middle position tillers (P<0.01), and significant effects on the yields of high position tillers and secondary tillers (P<0.05). Interactions between year and seeding density, and between year and seedling age, also had significant effects on some indicators.

3.5. Correlation analysis

The correlation analysis revealed that leaf age was significantly negatively correlated with the number of tillers at critical growth stages, while yield was positively correlated with tiller number. In addition, rice yield was positively correlated with the contribution rates of lower position and

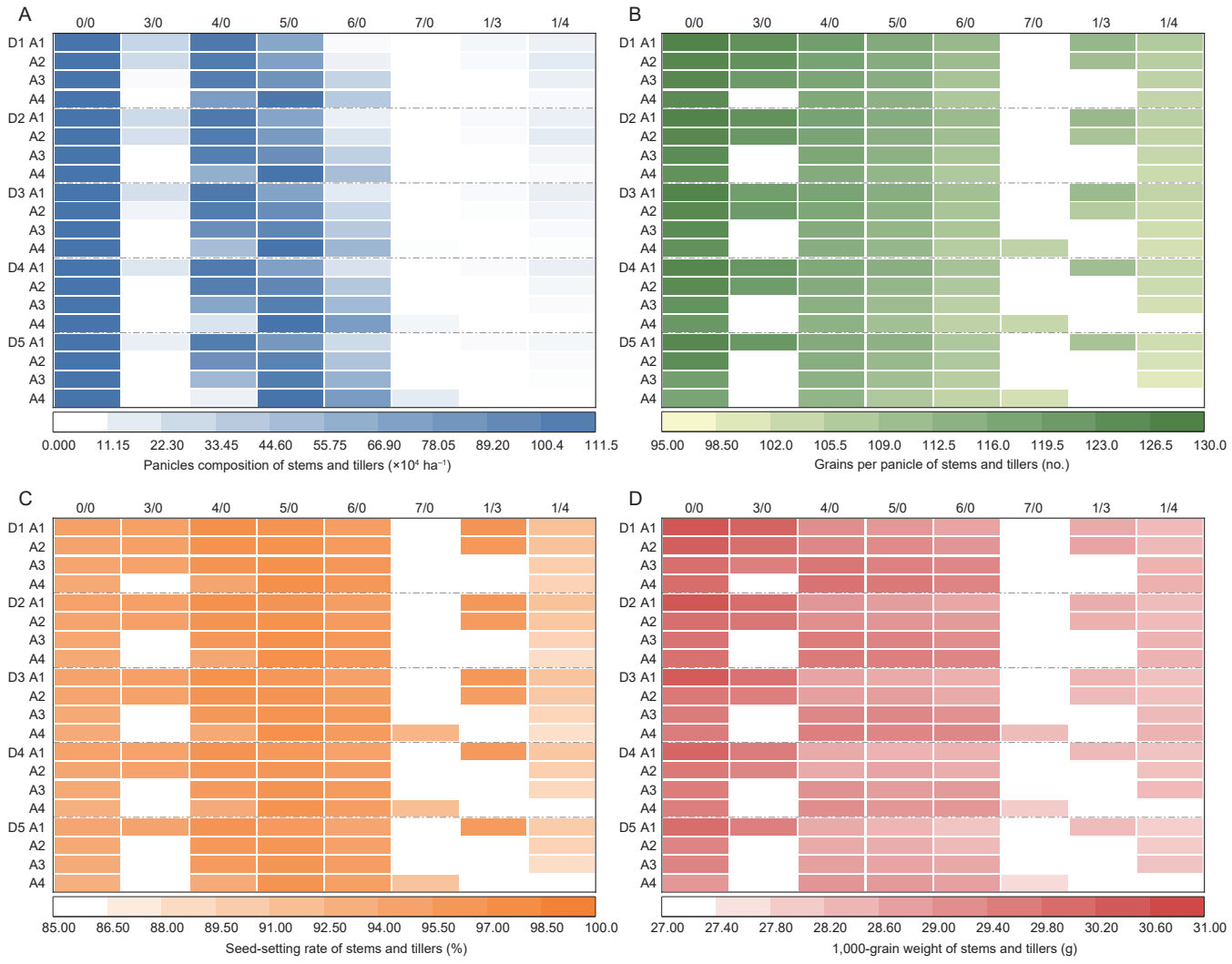


Fig. 4 Yield components of rice in different panicle leaf positions as affected by increases in seeding density and seedling age with crop straw boards used for seedling cultivation in 2021 and 2022. A1–A4, different ages for transplanting formed the subplots, 10, 15, 20, and 25 days, respectively. D1–D5, five seeding densities, 150, 200, 250, 300, and 350 g/tray, respectively.

secondary tillers but negatively correlated with those of middle and upper position tillers (Fig. 6).

4. Discussion

4.1. Effects of high-density crop straw board cultivation on seedling quality and tillering dynamics

Seedling quality strongly influences tillering and panicle formation in rice (Virk *et al.* 2020). This study demonstrates that increasing seeding density and adjusting transplanting age significantly affect key seedling traits such as height, shoot dry weight per 100 plants, dry weight per unit seedling height, and soluble sugar content (Fig. 2). With higher seeding densities and older seedling ages, seedlings tend to be more elongated, but they develop weaker stems due to intensified competition for light, water, and nutrients (Lampayan *et al.* 2015; Liu *et al.* 2015). This competition-driven elongation raises the risk of mechanical damage during transplanting, potentially reducing survival rates and early growth vigor (Zhang *et al.* 2008; Li *et al.* 2012). Dense nursery beds further limit water and nutrient availability per seedling, which restricts carbohydrate accumulation and lowers the soluble sugar content (Li W *et al.* 2020). This reduction in sugar suggests heightened stress, which is often accompanied by elevated abscisic acid (ABA) that can suppress tiller emergence (Liu *et al.* 2011a). Insufficient nutrient uptake may also compromise chlorophyll synthesis, thereby reducing photosynthetic efficiency and slowing growth (Simkin *et al.* 2022). Consequently, for seedlings under high density, older age treatments require more time to regreen after transplanting (Fig. 2-C and D), which delays tillering initiation. Such delays shift primary tillers from lower nodes (3/0, 4/0) to higher nodes (5/0, 6/0, 7/0) and reduce secondary tillering (Fig. 3-A), potentially causing canopy unevenness and reducing the yield (Kariali and Mohapatra 2007; Chang *et al.* 2019; Niinemets 2023).

By contrast, optimized seeding density and transplanting age can produce moderately tall, robust seedlings with greater dry matter and a higher sugar content (Lampayan *et al.* 2015; Liu *et al.* 2015). Such vigorous seedlings typically develop extensive root systems that enhance water and

Table 2 Yields and contribution rates of tillers in different positions as affected by increases in seeding density and seedling age with crop straw boards used for seedling cultivation in 2021 and 2022

Year	Seeding density[1)]	Seedling age[2)]	Total yield (t ha^{-1})	Yield at each position[3)]					Yield contribution rate[3)]				
				MS (t ha^{-1})	LPT (t ha^{-1})	MPT (t ha^{-1})	HPT (t ha^{-1})	ST (t ha^{-1})	MS (%)	LPT (%)	MPT (%)	HPT (%)	ST (%)
2021	D1	A1	10.94 ab	4.01 a	4.43 a	2.11 d		0.35 ab	36.78 a	40.62 a	19.35 d		3.21 ab
		A2	11.07 a	3.94 ab	4.25 a	2.43 c		0.44 a	35.62 a	38.40 a	22.01 c		3.96 a
		A3	10.77 b	3.86 ab	3.36 b	3.40 b		0.26 b	35.50 a	30.89 b	31.25 b		2.36 b
		A4	10.52 c	3.82 b	2.28 c	4.53 a		0.10 c	35.60 a	21.24 c	42.21 a		0.95 c
		Mean	10.82 a	3.91 a	3.58 a	3.12 e		0.29 a	35.87 b	32.79 a	28.71 e		2.62 a
	D2	A1	10.97 a	3.99 a	4.27 a	2.29 d		0.34 a	36.65 a	39.14 a	20.97 d		3.15 a
		A2	11.09 a	3.87 ab	3.98 b	2.77 c		0.36 a	35.22 a	36.21 b	25.22 c		3.25 a
		A3	10.58 b	3.81 b	3.22 c	3.60 b		0.15 b	35.36 a	29.95 c	33.40 b		1.41 b
		A4	10.32 c	3.76 b	1.78 d	4.79 a		0.06 b	36.16 a	17.13 d	46.09 a		0.62 b
		Mean	10.74 a	3.86 ab	3.31 b	3.36 d		0.23 b	35.85 b	30.61 b	31.42 d		2.11 b
	D3	A1	10.95 a	3.96 a	4.04 a	2.44 d		0.33 a	36.72 a	37.47 a	22.58 d		3.07 a
		A2	11.10 a	3.82 ab	3.46 b	3.46 c		0.21 b	34.83 b	31.55 b	31.53 c		1.95 b
		A3	10.22 b	3.77 b	2.69 c	3.89 b		0.09 c	36.08 ab	25.79 c	37.23 b		0.90 c
		A4	10.15 b	3.72 b	1.40 d	4.92 a	0.04 a	0.04 c	36.76 a	13.89 d	48.67 a	0.37 a	0.37 c
		Mean	10.60 b	3.82 bc	2.90 c	3.68 c	0.01 c	0.17 c	36.10 ab	27.18 c	35.00 c	0.09 c	1.57 c
	D4	A1	10.88 b	3.92 a	3.75 a	2.62 d		0.33 a	36.88 a	35.27 a	24.67 d		3.12 a
		A2	11.13 a	3.80 ab	3.16 b	3.86 c		0.12 b	34.78 b	28.92 b	35.27 c		1.07 b
		A3	10.05 c	3.71 bc	1.97 c	4.32 b		0.06 bc	36.89 a	19.66 c	42.96 b		0.56 bc
		A4	9.71 d	3.63 c	0.49 d	5.38 a	0.13 a		37.70 a	5.12 d	55.80 a	1.37 a	
		Mean	10.44 c	3.77 c	2.34 d	4.04 b	0.03 b	0.13 c	36.56 ab	22.24 d	39.67 b	0.34 b	1.19 c
	D5	A1	10.85 a	3.87 a	3.51 a	2.96 d		0.17 a	36.75 a	33.32 a	28.14 d		1.61 a
		A2	10.65 a	3.73 ab	2.55 b	3.97 c		0.07 ab	36.13 a	24.75 b	38.53 c		0.72 ab
		A3	9.75 b	3.58 bc	1.48 c	4.53 b		0.03 b	37.17 a	15.39 c	47.08 b		0.29 b
		A4	9.52 c	3.46 c	0.23 d	5.30 a	0.28 a		37.32 a	2.46 d	57.22 a	3.02 a	
		Mean	10.19 d	3.66 d	1.94 e	4.19 a	0.07 a	0.07 d	36.84 a	18.98 e	42.74 a	0.75 a	0.65 d
2022	D1	A1	10.89 a	4.07 a	4.37 a	2.11 d		0.35 b	37.33 a	40.09 a	19.39 d		3.20 b
		A2	10.98 a	3.97 ab	4.19 a	2.45 c		0.47 a	35.87 ab	37.84 a	22.10 c		4.28 a
		A3	10.56 b	3.85 bc	3.45 b	3.24 b		0.22 c	35.74 b	32.08 b	30.15 b		2.01 c
		A4	10.29 c	3.75 c	2.17 c	4.47 a		0.11 d	35.76 b	20.63 c	42.62 a		1.00 d
		Mean	10.68 a	3.91 a	3.54 a	3.07 e		0.29 a	36.18 c	32.66 a	28.56 e		2.62 a
	D2	A1	11.02 a	4.03 a	4.13 a	2.41 d		0.35 a	36.86 ab	37.85 a	22.03 d		3.25 a
		A2	11.04 a	3.90 ab	3.79 b	2.92 c		0.41 a	35.46 b	34.43 b	26.55 c		3.70 a
		A3	10.42 b	3.79 bc	3.12 c	3.54 b		0.13 b	35.79 ab	29.53 c	33.45 b		1.26 b
		A4	9.87 c	3.70 c	1.47 d	4.77 a		0.06 b	37.06 a	14.72 d	47.77 a		0.58 b
		Mean	10.59 a	3.85 ab	3.13 b	3.41 d		0.24 b	36.29 c	29.13 b	32.45 d		2.20 a
	D3	A1	11.05 a	3.99 a	3.86 a	2.62 d		0.34 a	36.92 ab	35.72 a	24.19 d		3.13 a
		A2	11.06 a	3.85 ab	3.33 b	3.43 c		0.24 b	35.46 b	30.67 b	31.61 c		2.21 b
		A3	10.20 b	3.74 bc	2.67 c	3.83 b		0.11 c	36.12 b	25.76 c	36.90 b		1.05 c
		A4	9.50 c	3.66 c	1.00 d	4.95 a	0.03 a	0.02 c	38.20 a	10.43 d	51.75 a	0.36 a	0.24 c
		Mean	10.45 b	3.81 bc	2.71 c	3.71 c	0.01 c	0.18 c	36.68 bc	25.64 c	36.11 c	0.09 c	1.66 b
	D4	A1	11.05 a	3.96 a	3.52 a	2.86 d		0.35 a	37.08 b	32.88 a	26.79 d		3.27 a
		A2	11.10 a	3.83 ab	3.15 b	3.69 c		0.13 b	35.48 c	29.19 b	34.20 c		1.23 b
		A3	9.94 b	3.71 bc	1.78 c	4.39 b		0.04 bc	37.32 b	17.91 c	44.18 b		0.45 bc
		A4	9.23 c	3.59 c	0.44 d	5.10 a	0.10 a		39.04 a	4.80 d	55.48 a	1.13 a	
		Mean	10.33 c	3.77 cd	2.22 d	4.01 b	0.03 b	0.13 c	37.23 ab	21.2 d	40.16 b	0.28 b	1.24 b
	D5	A1	11.01 a	3.92 a	3.29 a	3.20 d		0.15 a	37.09 bc	31.19 a	30.31 d		1.41 a
		A2	10.77 b	3.80 ab	2.39 b	4.14 c		0.07 ab	36.66 c	23.02 b	39.92 c		0.69 ab
		A3	9.65 c	3.66 b	1.24 c	4.64 b		0.01 b	38.26 ab	13.00 c	48.54 b		0.13 b
		A4	8.96 d	3.49 c	0.09 d	5.11 a	0.17 a		39.44 a	1.03 d	57.68 a	1.95 a	
		Mean	10.10 d	3.72 d	1.75 e	4.27 a	0.04 a	0.06 d	37.86 a	17.06 e	44.11 a	0.49 a	0.56 c

[1)] D1–D5, 150, 200, 250, 300, and 350 g/tray, respectively.
[2)] A1–A4, different ages for transplanting formed the subplots, 10, 15, 20, and 25 days, respectively.
[3)] MS, main stem (0/0); LPT, low-position tiller (3/0,4/0); MPT, middle-position tiller (5/0,6/0); HPT, high-position tiller (7/0); ST, secondary tiller.

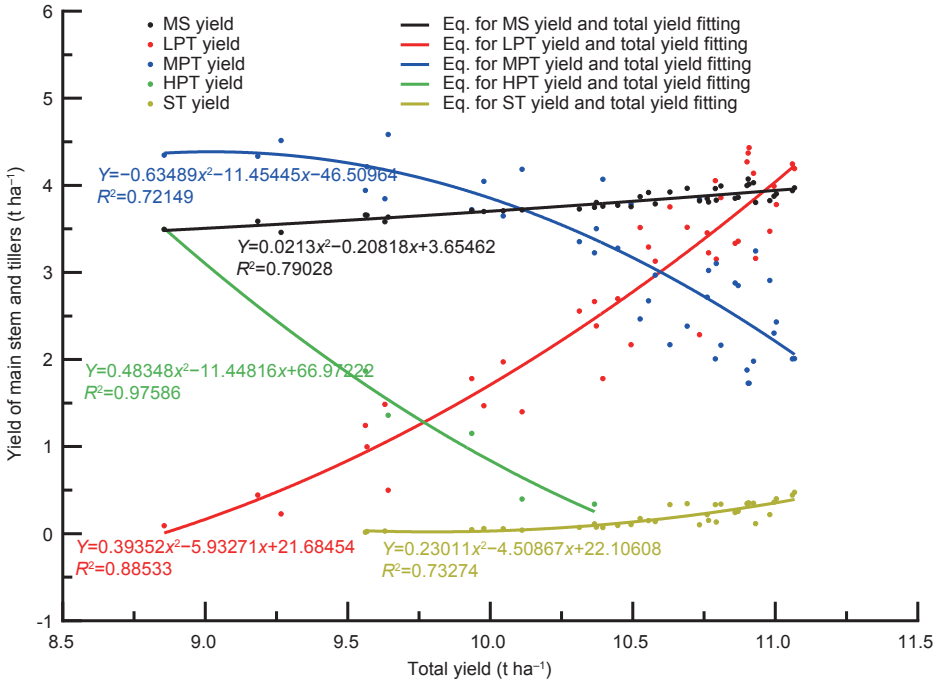


Fig. 5 Relationships between total yield and the tiller position yield equations under increased seeding density and seedling age in 2021 and 2022. MS, main stem (0/0); LPT, low-position tiller (3/0,4/0); MPT, middle-position tiller (5/0,6/0); HPT, high-position tiller (7/0); ST, secondary tiller.

nutrient uptake, support lower-position tiller growth (Pasuquin *et al.* 2008), and promote cytokinin synthesis for tiller bud outgrowth (Liu *et al.* 2009, 2011b). Our findings indicate that these improvements increase the effective tiller numbers and panicles, thereby boosting yield.

4.2. Yield formation and transplanting strategies in optimized high-density seedling production

With regard to yield formation, the panicle number, grains per panicle, and grain weight at various tiller positions are key contributors (Okamura and Aoki 2024). We found that higher seeding densities generally reduce the number of lower-position panicles while increasing those in middle and upper positions (Fig. 3-B), largely due to resource competition that can damage basal growth points (Li *et al.* 2003; Zheng *et al.* 2020). Although middle-position tillers partially compensate at later stages, they usually produce fewer grains per panicle compared to lower-position tillers (Li *et al.* 2006). Meanwhile, reducing the transplanting age helps seedlings recover more quickly (Fig. 2), but excessively young seedlings might be too small for efficient transplanting (Liu *et al.* 2017). An overabundance of lower-position tillers may also limit nutrient availability for the later-emerging tillers (Tian *et al.* 2018), leading to higher mortality during drainage periods and fewer effective panicles (Ye *et al.* 2022).

Balancing the lower- and middle-position tillers is thus crucial for maximizing yield. In this study, moderate seeding density combined with an optimal transplanting age (D4A2) achieved higher panicle numbers at both the lower and middle positions, resulting in the greatest total yield (Table 2; Fig. 3). Furthermore, our results show that with increasing seedling age and density, grain number decreases on both

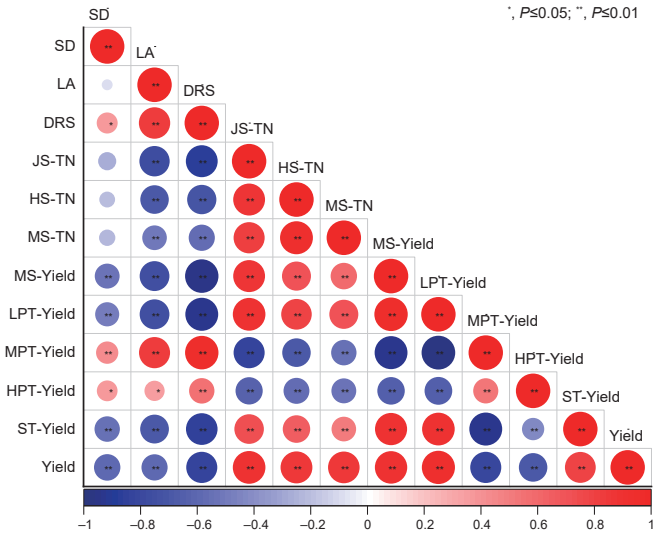


Fig. 6 Correlation analysis of rice yield. $R_{0.05}$=0.677 and $R_{0.01}$=0.733. SD, seedling density; LA, leaf age; DRS, days of the regreening stage; JS-TN, jointing stage tillering number; HS-TN, heading stage tillering number; MS-TN, mature stage tillering number; MS-Yield, main stem yield; LPT-Yield, low-position tillering yield; MPT-Yield, middle-position tillering yield; HPT-Yield, high-position tillering yield; ST-Yield, secondary tillering yield. * and ** indicate significant correlation at P<0.05 and P<0.01, respectively.

the main stem and tillers, and lower-position tillers exhibit notably reduced seed-setting rates under high-density, older-seedling conditions (Fig. 4). In contrast, the middle- and upper-position tillers may initially increase in grain number but eventually decline, indicating dynamic yield shifts among

Table 3 Analysis of variance results for the effects of seeding density, seedling age, and their interactions on rice yield and yield contribution rates in different positions under crop straw board seedling cultivation

Variable	Total yield (t ha^{-1})	Yield at each position (t ha^{-1})[1)]					Yield contribution rate (%)[1)]				
		MS	LPT	MPT	HPT	ST	MS	LPT	MPT	HPT	ST
Year (Y)	**	NS	**	NS	*	NS	**	**	**	NS	NS
Seeding density (D)	**	**	**	**	**	**	**	**	**	**	**
Seedling age (A)	**	**	**	**	**	**	**	**	**	**	**
Y×D	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS
Y×A	**	NS	NS	*	**	NS	NS	NS	NS	**	NS
D×A	**	NS	**	**	**	**	**	**	**	**	**
Y×D×A	NS	NS	NS	NS	**	NS	NS	NS	NS	**	NS

[1)] MS, main stem (0/0); LPT, low-position tiller (3/0,4/0); MPT, middle-position tiller (5/0,6/0); HPT, high-position tiller (7/0); ST, secondary tiller.
** and * indicate significant correlations at the 0.01 and 0.05 levels, respectively; NS indicates no significant correlation at the 0.05 level (P>0.05).

tiller positions. The correlation analysis (Fig. 6) revealed a negative relationship between leaf age and tiller numbers at critical growth stages, while yield was positively correlated with the contributions of lower-position and secondary tillers. These findings underscore the importance of maintaining balanced tillers at various nodes. Although this study focused on seeding density and transplanting age, other agronomic practices — such as balanced fertilization and canopy management — also warrant exploration (Song *et al.* 2014; Liu *et al.* 2019).

In summary, high-density seedling cultivation and prolonged seedling growth significantly affect rice production outcomes, although the responses may vary with climate and soil conditions. Climate change, for instance, can alter light and water availability, further influencing seedling vigor. In addition, the timing of fertilization during the seedling stage and after transplanting is crucial for mitigating the impacts of high-density cultivation on seedling quality. Consequently, optimizing both seeding density and transplanting age is vital for achieving balanced tiller development and maximizing yield. Future research should explore how integrating balanced fertilization, canopy management, and other agronomic measures with refined seeding parameters could further enhance the yield contributions from different tiller positions without compromising overall productivity.

5. Conclusion

This study demonstrates that combining higher seeding densities with reduced transplanting ages significantly enhances *japonica* rice yield by improving seedling quality, tillering dynamics, panicle formation, and yield components. Utilizing crop straw boards and mechanized transplanting systems, we found that increasing the seeding density altered tillering patterns by reducing lower-position tiller occurrence and increasing middle-position tillers. However, reducing the transplanting age mitigated these effects and promoted balanced tiller emergence and panicle formation. Specifically, this study identified the optimal seeding density as 300 g/tray (6.39 grains cm^{-2}) and the optimal transplanting age as 15 days. This treatment showed the best performance in terms of higher total panicle numbers and yield, with total panicle numbers increasing by 3.79 to 4.73% and yield by 3.38 to 5.05% compared to traditional methods. Although this study primarily focused on seeding density and transplanting age, these strategies should be important considerations for future research and practice in maintaining high yields in densely planted *japonica* rice fields. These findings indicate that optimizing seeding density and transplanting age is crucial for maximizing rice yield while reducing labor and costs. This approach enhances resource utilization, improves tillering efficiency, and supports sustainable agricultural practices by reducing labor demand and dependence on soil for raising seedlings. In the context of agricultural labor shortages and future climate challenges, adopting these optimized cultivation practices offers significant advantages for rice farmers and contributes to sustainable agriculture development. However, this study has some limitations. The applicability of these findings under different seedling-raising methods and field environments needs further verification.

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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

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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