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Physiological factors influencing climate-smart agriculture: Daylength-mediated interaction between tillering and flowering in rice

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Abstract

Background Controlling rice tillering and flowering is essential for reducing greenhouse gas emissions from paddy fields, a key objective in climate-smart agriculture. However, the interaction between tillering and flowering remains controversial and poorly understood. In this study, we subjected plants of the rice cultivars 'Saenuri' and 'Odae' to short- and long-day conditions and compared their growth and flowering responses after tiller removal.

Results The effects of tiller removal differed depending on daylength conditions. Under short days, plants in the tiller-removal group flowered earlier than the controls, whereas the opposite trend was observed under long days. This response was associated with changes in florigen gene expression. Under short days, the expression of *Hd3a*, which promotes flowering, increased in the tiller-removal group compared with that in the controls. In contrast, under long days, the expression of *OsMFT1*, a gene that delays flowering and promotes spikelet formation, was significantly upregulated, leading to an increased spikelet number. Notably, spikelets per panicle in the tiller-removal groups increased approximately 3.4-fold in 'Saenuri' and 2.2-fold in 'Odae' under long-day conditions compared with those in their respective controls.

Conclusions These findings highlight the daylength-dependent variability in tillering and flowering interactions, providing new insights into their regulatory mechanisms. This study offers a foundation for optimizing rice growth strategies under varying photoperiod conditions, contributing to climate-smart agricultural practices and improved breeding programs.

Keywords Climate-smart agriculture, Rice, Tillering, Flowering, Interaction

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Introduction

Rice is a staple crop for over half of the global population and plays a crucial role in global food security. However, methane emissions from paddy fields significantly contribute to greenhouse gas accumulation, making rice cultivation an important environmental challenge [1, 2]. These emissions primarily result from anaerobic conditions in waterlogged soils [3] and are largely released through the aerenchyma tissues of rice tillers [4]. To mitigate methane emissions, strategies such as modifying tillering patterns or shortening the growth period (i.e., adjusting flowering time) have been proposed to promote climate-smart rice production [4, 5].

For stable rice production in response to climate change, enhancing resilience to extreme weather events is essential [4, 6]. The impact of these events varies significantly depending on the growth stage, with phenological responses—particularly flowering—playing a critical role in determining stage-specific effects [7].

Since both tillering and flowering are key determinants of rice productivity [8, 9], understanding the environmental factors that regulate these traits is essential. Among these, daylength plays a crucial role, as it not only governs flowering but also influences tillering patterns, thereby shaping overall plant architecture and yield potential [7, 8]. Notably, the optimal daylength for tillering often contrasts with conditions that promote flowering, creating a trade-off between vegetative and reproductive growth phases [9, 10]. Despite extensive research, conflicting results have been reported regarding the interaction between tillering and flowering under different photoperiodic conditions [11, 12, 13].

To better understand these inconsistencies, molecular studies have focused on identifying key genetic and hormonal regulators that govern tillering and flowering. These include cytokinin, auxin, and strigolactone, which mediate shoot branching and tiller development [14, 15, 16]. In addition, studies manipulating flowering-related genes, such as OsRFL and OsSOC1, suggest that tillering and flowering exhibit complex, context-dependent interactions [17, 18]. Some reports have indicated that delayed flowering promotes increased tillering [19, 20], whereas others have suggested the opposite trend, where delayed flowering results in reduced tillering [21, 22]. These discrepancies highlight the complexity of the relationship between tillering and flowering and underscore the need for further investigation [23, 24, 25, 26, 27].

We hypothesized that the inconsistencies among previous studies stem from differences in developmental responses—including tillering, spikelet formation, and flowering—under specific daylength conditions. Although the florigen activation complex (FAC) has been implicated in regulating both flowering and vegetative growth, including tillering [28, 29], the precise interaction between tillering and flowering in response to daylength remains unclear. FAC plays a central role in this interaction, with Hd3a, a florigen gene, binding to 14-3-3 proteins and *OsFD*, a transcription factor in the *bZIP* family, to promote floral induction [28]. In addition to its role as a florigen gene, Hd3a has also been reported to promote lateral branching [20]. Meanwhile, the MOTHER OF FT AND TFL1 (*OsMFT1*) gene is known to delay flowering while extending the growth period, thereby promoting tillering and increasing spikelet number per panicle (SPP) [18, 24, 26]. The regulatory functions of these genes are influenced by photoperiod conditions [20, 22].

In this study, we aimed to elucidate the interaction between tillering and flowering by restricting tillering and growing two rice cultivars under controlled daylength conditions. Our findings provide insights into the photoperiodic regulation of tillering and flowering, helping to reconcile previous discrepancies and inform climate-smart rice management strategies.

Materials and methods

Ethics statement

This study was performed in accordance with Institute-approved guidelines and regulations. The test varieties were provided by SeoYeong Yang of the Rice Production and Physiology Division of the National Institute of Crop Science (NICS). We obtained permission from the NICS to use these varieties (https://www.nics.go.kr/apo/breed.do?m=100000128_homepageSecod=nics).

Experimental materials and design

A pot experiment was conducted using a completely randomized design incorporating two factors of variation, i.e., daylength and tiller removal (TR), at two levels of variation each, i.e., short (SD) and long days (LD) and with or without tillers removed. Two experiments were conducted in a controlled environment facility (ENT Inc, Boocheon, South Korea) at the NICS in Jeonju, South Korea (35°49′19″ N, 127°8′56″ E), where light intensity, temperature, and humidity can be artificially controlled (Figure. S1). Lights were turned on at 0730 h regardless of daylength treatment, such that daylength was adjusted by the lights-off time. Two rice cultivars representing ecotypes with different maturation times were used, namely, early maturing 'Odae' (*Oryza sativa* ssp. *japonica*, IT218242) and mid-late maturing 'Saenuri' (*Oryza sativa* ssp. *japonica*, IT235281).

Fifteen-day-old seedlings of both varieties were transplanted into 1/5000 a Wagner pots at a density of three plants per pot. The soil at the NICS in Jeonju

(35°49′19″ N, 127°8′56″ E) is characterized by a slightly acidic pH (5.7), moderate organic matter content (22 g/kg), and sufficient levels of available phosphorus (122 mg/kg). Exchangeable cations, including Ca (5.2 $cmol_a$), Mg (1.5 $cmol_a$/kg), and K (0.24 $cmol_a$/kg), are generally within the optimal range for paddy soil (https://soil.rda.go.kr/soilmap/crop.do). A composite slow-release fertilizer was applied with 9, 4.5, and 5.7 kg nitrogen, phosphate, and potassium per 1000 m^2, respectively, at a rate based on the area used by three plants (i.e., 0.042 m^2; planting distance: 30 × 14 cm) instead of the entire pot area. The fertilizer used in this study was a slow- and controlled-release fertilizer (Danhanbeon, Chobi, Korea, http://www.chobi.co.kr/company/en_products/). Tillers were removed every 2–3 d starting 7 d after transplanting, and water was continuously applied at a depth of 2–3 cm or more. A plant with tillers removed is shown in Figure S2. These procedures were performed as previously described [8, 29].

Experiment 1: preliminary test of growth and heading responses to tiller removal under short-day conditions

Temperature was set to 22 °C (maximum 28 °C/minimum 18 °C) and daylength was fixed to relatively short conditions (12 h 30 min light/11 h 30 min dark) from sowing to the heading stage [30, 31, 32]. The light intensity was set at 700 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) and the relative humidity was set at 65% [33].

Experiment 2: analysis of growth and heading upon tiller removal under short- and long-day conditions

Before TR, the temperature was set to 28 °C (maximum 33 °C/minimum 23 °C) for 22 d (15 d after sowing and 7 d after transplanting), and to minimize the induction of photosensitivity, daylength was set to 15 h [30, 31, 32], which is slightly longer than that generally used as a LD condition (14 h 30 m light/9 h 30 m dark). The LD condition was set before TR to differentiate the photosensitive response to daylength conditions after TR. Daylength conditions after TR were matched between SD (12 h light/12 h dark) and LD (14 h 30 m light/9 h 30 m dark) [30, 31, 32], and the temperature was set to 28 °C (maximum 33 °C/minimum 23 °C).

After the heading stage date, conditions were adjusted to 25 °C (maximum 30 °C/minimum 20 °C) and LD (14 h light/10 h dark) during the ripening stage. Temperature and daylength were changed again after the ripening stage, as 28 °C is deemed excessively high for the ripening stage, which could present challenges in accurately evaluating grain weight [34]. Additionally, different daylength conditions can affect grain weight; therefore, we set the same daylength condition again for the ripening stage. These conditions were set to observe the effect of temperature and daylength up to the heading stage. The light intensity was set at 700 μmol m^{-2} s^{-1} PAR and the relative humidity at 65%.

Growth and development measurements

For the plant growth analysis, 20 individual plants were analyzed as biological replicates. Plant height was measured from the ground to the top of the apical leaf tip. Stem length was measured from the ground to the uppermost internode. Leaf age is the leaf number formed on the main stem. Leaf age was calculated using the following equation:

$$Leaf\ age = (n-1) + (m \div M)$$

where, n, M, and m are the total number of leaves, including incomplete leaves, length of the second fully expanded leaf from the top, and length of the unexpanded leaf derived from the second leaf sheath, respectively. Leaf age is used as an indirect indicator to assess the transition among growth stages [8]. In both experiments, the heading date was calculated as the number of days (growth period) after transplanting, before panicle emergence from the leaf sheath. Panicle emergence was examined daily from 1300 to 1400. Fifteen plants were used to analyze heading date and growth. These procedures were performed as previously described [8].

RNA extraction and gene expression

For RNA expression analysis, three individual plants of the Saenuri cultivar were used with two leaves collected from each plant. Each leaf sample was further analyzed in triplicated technical replicates. Two plant leaves were sampled, namely the 2nd and 3rd leaves of the main stem and tiller, immediately frozen under liquid nitrogen, and stored at − 80 °C until RNA extraction. The sampling of the 2nd and 3rd leaves has a more relatively stable physiological response because the 1st leaf is still developing. Each treatment had three biological replicates, with each replicate comprising three plants. For each plant, the 2nd and 3rd leaves were sampled and utilized for real-time polymerase chain reaction. Technical replicates were performed thrice per biological replicate to ensure statistical robustness and accuracy. Plant material for RNA extraction was sampled at 10:00. (2.5 h after the lights were turned on) because *Hd3a*, *RFT1*, *Ehd1*, *Ghd7*, and *OsMFT1* reportedly maintain a high expression level for 0–4 h after plant exposure to light [35]. Total RNA was extracted according to the protocol by Chang et al., [36]. cDNA synthesis was performed using a Primescript RT reagent kit with gDNA eraser (TaKaRa Bio, Inc, Kusatsu, Japan). For RT-PCR, SYBR Green (SYBR Realtime PCR Master Mix, Toyobo, Japan) was used as a fluorescent

dye. The analysis was conducted using a Roter-Gene 6000 (Corbett Research, Australia). All experiments were performed in triplicate. Relative expression values were calculated using the reference gene ubiquitin for comparison of Ct values. These values were then normalized to a baseline of 1.0, with the sample collected 1 d prior to the day-length, and TR treatments were used as the reference. Primer sequences are listed in Table S1. The procedures were performed as previously described [8].

Statistical analysis

Statistical analysis was performed using R software (version 4.0.3, R Foundation, Austria). Significant differences were assessed at $p < 0.05$ using a one-sample t-test and ANOVA, followed by Duncan's multiple range test. Before statistical analyses, Levene's test and the Shapiro-Wilk test were performed to assess the homogeneity of variance and normality of the data, respectively. When the assumptions of homogeneity or normality were not met, non-parametric tests, such as the Kruskal-Wallis test, were employed as they are more suitable for small sample sizes ($n = 9$ for RNA expression). Parametric tests, such as ANOVA, were applied if the assumptions were met. This approach allowed us to rigorously assess the effects of high temperature and ozone on plant growth and physiological responses, including dry weight, plant height, leaf age, stomatal conductance, and stress-related gene expression, both before and after the treatments.

To model the development of plant height, leaf age, and tiller number based on the number of growing days from transplanting, we applied Eq. (1) [37]:

$$F = \frac{H_{max} \text{ or } L_{max} \text{ or } T_{max}}{1 + e^{-(t-tm)*rF}} \quad (1)$$

where, H_{max}, $L_{\max}$, and $T_{\max}$ represent the final plant height, final leaf age, and final tiller number, respectively. The term ${}_rF$ denotes the rate of development up to the final value, and t corresponds to the number of days after transplanting. The parameter *tm* indicates the timepoint at which half of the final value is achieved, representing the stage when the growth rate is at its maximum. The coefficients H_{max}, $L_{\max}$, $T_{\max}$, ${}_rF$, and *tm* were determined by nonlinear regression performed using Sigmaplot v11.1. Analyses of phenological development using such models have been widely reported in previous studies [7, 8, 34].

Results

Daylength-mediated effects of tiller removal on plant growth and development

This study examined main stem growth and development, with and without tillers, under varying daylength conditions. The data showed that under LDs, $H_{\max}$ in the TR group exhibited a trend of increase in both cultivars compared to that in the control group. However, under SDs, which are known to promote flowering [8], $H_{\max}$ decreased in the TR group for 'Saenuri' but remained unchanged for 'Odae' (Fig. 1a, b; Table 1). Under SDs, $H_{\max}$ in the TR and control groups was 89.9 cm and 89.8 cm for 'Odae,' and 72.4 cm and 75.3 cm for 'Saenuri,' respectively. Furthermore, under LDs, ${}_rF$ was lower in the TR group than in the control. However, t_m in plant height was longer in the TR group (Fig. 1a, b; Table 1). However, under SDs, ${}_rF$ was higher in the TR than in the control group; concomitantly, t_m was shorter for 'Saenuri,' whereas in 'Odae,' it differed slightly compared with that observed under LDs.

The $L_{\max}$ of the main stem was higher in the TR group than in the control for both varieties across the experimental conditions (Fig. 1c, d; Table 1). Evidently, under SD conditions, it was slightly lower in the TR in both cultivars; however, it differed between the two cultivars under LDs. In contrast, t_m was longer in the TR groups under all conditions for both cultivars. Under SD conditions, 'Odae' exhibited a slight increase in $L_{\max}$ from 13.0 to 13.6 in the TR group, with t_m extending from 5.6 to 7.0 d. Conversely, under LD conditions, $L_{\max}$ increased more significantly from 14.2 to 17.1, and t_m extended from 9.3 to 14.5 d. For 'Saenuri,' $L_{\max}$ similarly increased from 13.1 to 13.8 in the SD TR treatment, with t_m slightly increasing from 6.2 to 6.4 d. Under LD conditions, $L_{\max}$ increased from 16.9 to 18.6, and t_m extended from 14.3 to 16.0 d. ${}_rF$ declined under LDs compared to that under SDs in both cultivars, with 'Odae' showing a reduction from 0.081 to 0.066 and 'Saenuri' from 0.090 to 0.054 in the the control. Interestingly, ${}_rF$ remained consistent or slightly increased under the TR treatments, suggesting that TR may have mitigated the impact of LDs on leaf development. Additionally, $T_{\max}$ was lower under SDs than under LDs for both cultivars (Fig. 1e, f; Table 1).

Differences in growth at the heading stage, i.e., after vegetative growth was completed, in response to TR as per daylength are shown in Fig. 2. Similar to the results described for plant height (Fig. 1a, b), stem length was greater in the TR than in the control group under LDs, whereas no difference was observed under SDs (Fig. 2a, b). Panicle length was only slightly greater in the TR treatment under SDs but showed a substantial increase under LDs (Fig. 2c, d).

Overall, the TR treatment increased vegetative growth of the main stem under LDs; however, under SDs, growth was either smaller or did not significantly differ between the TR and control treatments (Figs. 1 and 2; Table 1).

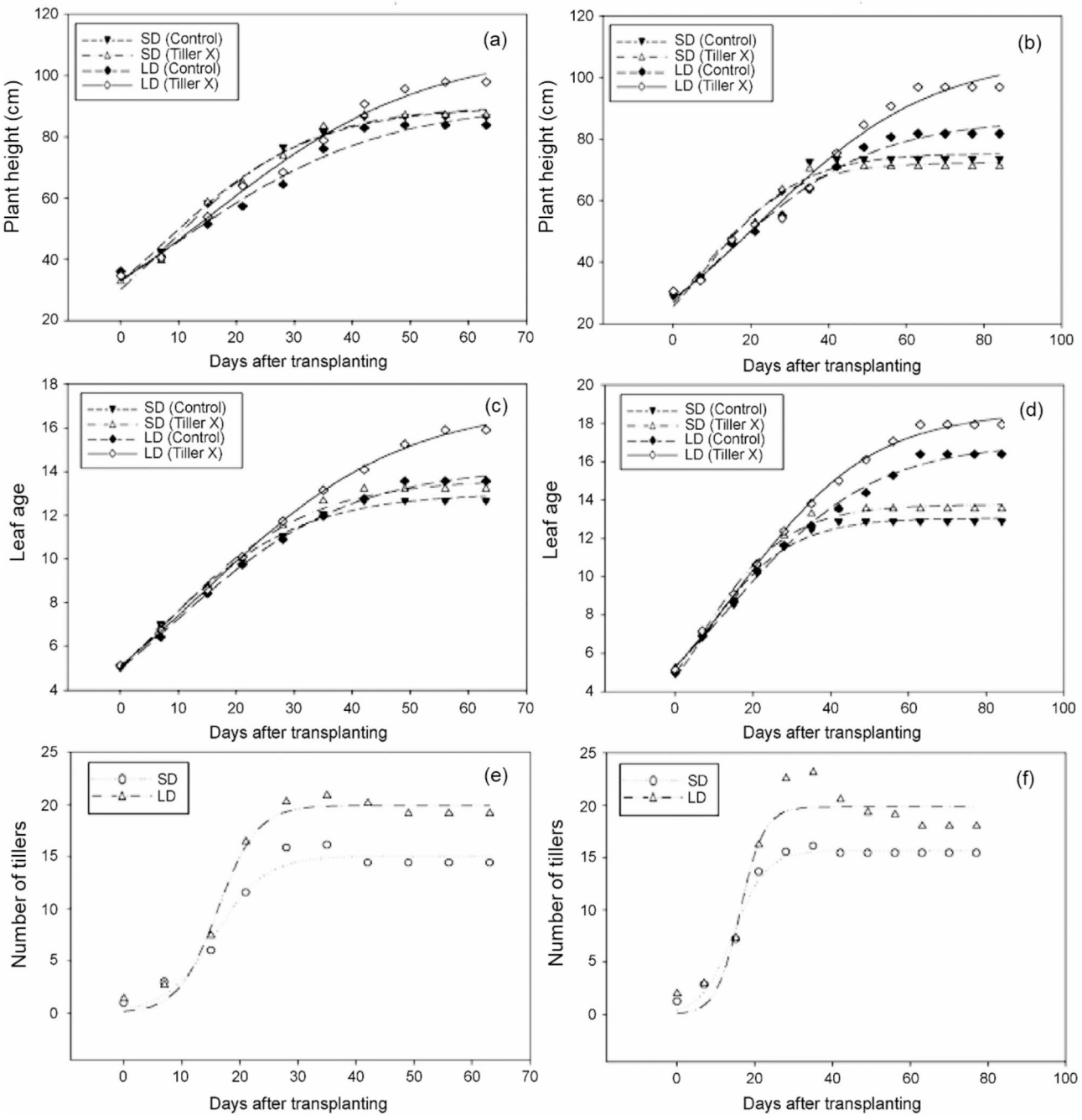

Fig. 1 Logistic model of rice plant height, leaf age, and tiller development from sowing to heading stage date after transplant for tiller removal treatments according to daylength. (**a**) 'Odae,' plant height; (**b**) 'Saenuri,' plant height; (**c**) 'Odae,' leaf age; (**d**) 'Saenuri,' leaf age; (**e**) 'Odae,' tiller number; (**f**) 'Saenuri,' tiller number. SD: short day. LD: long day. Tiller X refers to tiller removal (TR) treatment. Curves were fitted to a logistic equation, as in Table 1. Growth data collected from 20 biological replicates for each treatment ($n = 20$)

Effect of tiller removal on heading response and yield components

When other relevant factors, such as fertilization, are controlled, tiller development is generally enhanced as a result of the longer growth duration [10, 11, 13]. Under the SD conditions used in Experiment 1, days to heading (DTH) was shortened in the TR compared with that in the control group for both cultivars (Figure S3). Furthermore, in Experiment 2, we evaluated DTH under two daylength conditions (Fig. 3). Under SDs, DTH was shortened in the TR group compared with that in the control group, similar to the results of Experiment 1. Conversely, DTH was longer in the TR than in the control group under LDs (Fig. 3). Under

Table 1 Parameters of the logistic function used to describe plant height, leaf age, and tiller development from sowing to heading stage date after transplanting for the TR treatments according to daylength

Varieties	Treatment		Plant height (cm)				Leaf age (ea)				Tiller number (ea)			
			H_{max}†	r_F††	t_m†††	R^2	L_{max}†	r_F	t_m	R^2	T_{max}†	r_F	t_m	R^2
'Odae'	SD	Control	89.8 (1.74)	0.078 (0.007)	7.2 (0.89)	0.98	13.0 (0.14)	0.081 (0.005)	5.6 (0.51)	0.99	15.1 (0.49)	0.232 (0.051)	15.7 (1.04)	0.96
		Tiller X	89.9 (1.71)	0.082 (0.007)	8.3 (0.86)	0.98	13.6 (0.19)	0.079 (0.005)	7.0 (0.65)	0.99	-	-	-	-
	LD	Control	91.0 (3.89)	0.057 (0.008)	9.7 (1.90)	0.97	14.2 (0.17)	0.066 (0.003)	9.3 (0.54)	0.99	19.9 (0.47)	0.294 (0.056)	16.2 (0.66)	0.98
		Tiller X	108.3 (4.29)	0.054 (0.006)	15.4 (1.84)	0.98	17.1 (0.21)	0.058 (0.002)	14.5 (0.54)	0.99	-	-	-	-
'Saenuri'	SD	Control	75.3 (1.27)	0.081 (0.008)	8.1 (1.06)	0.97	13.1 (0.10)	0.090 (0.005)	6.2 (0.52)	0.99	15.7 (0.23)	0.239 (0.029)	14.6 (0.56)	0.98
		Tiller X	72.4 (1.03)	0.084 (0.008)	6.4 (0.94)	0.97	13.8 (0.13)	0.089 (0.006)	6.4 (0.63)	0.98	-	-	-	-
	LD	Control	86.4 (1.89)	0.053 (0.004)	13.8 (1.25)	0.98	16.9 (0.23)	0.054 (0.003)	14.3 (0.79)	0.99	19.9 (0.77)	0.324 (0.123)	16.2 (1.21)	0.91
		Tiller X	107.0 (4.41)	0.046 (0.005)	22.6 (2.41)	0.98	18.6 (0.17)	0.058 (0.002)	16.0 (0.54)	0.99	-	-	-	-

Data values are calculated using a logistic model with standard errors in ( )

Tiller X refers to the TR treatment. SD: short day, LD: long day

† *Hmax* is the final plant height, *Lmax* is the final leaf age from the main stem, and *Tmax* is the final number of tillers

†† *rF* is the rate of development up to the final plant height, leaf age, and tiller number

††† t is the number of days after transplantation; *tm* is the time point at which the plant reached half of its final height, leaf age, and tiller number

** $P < 0.01$

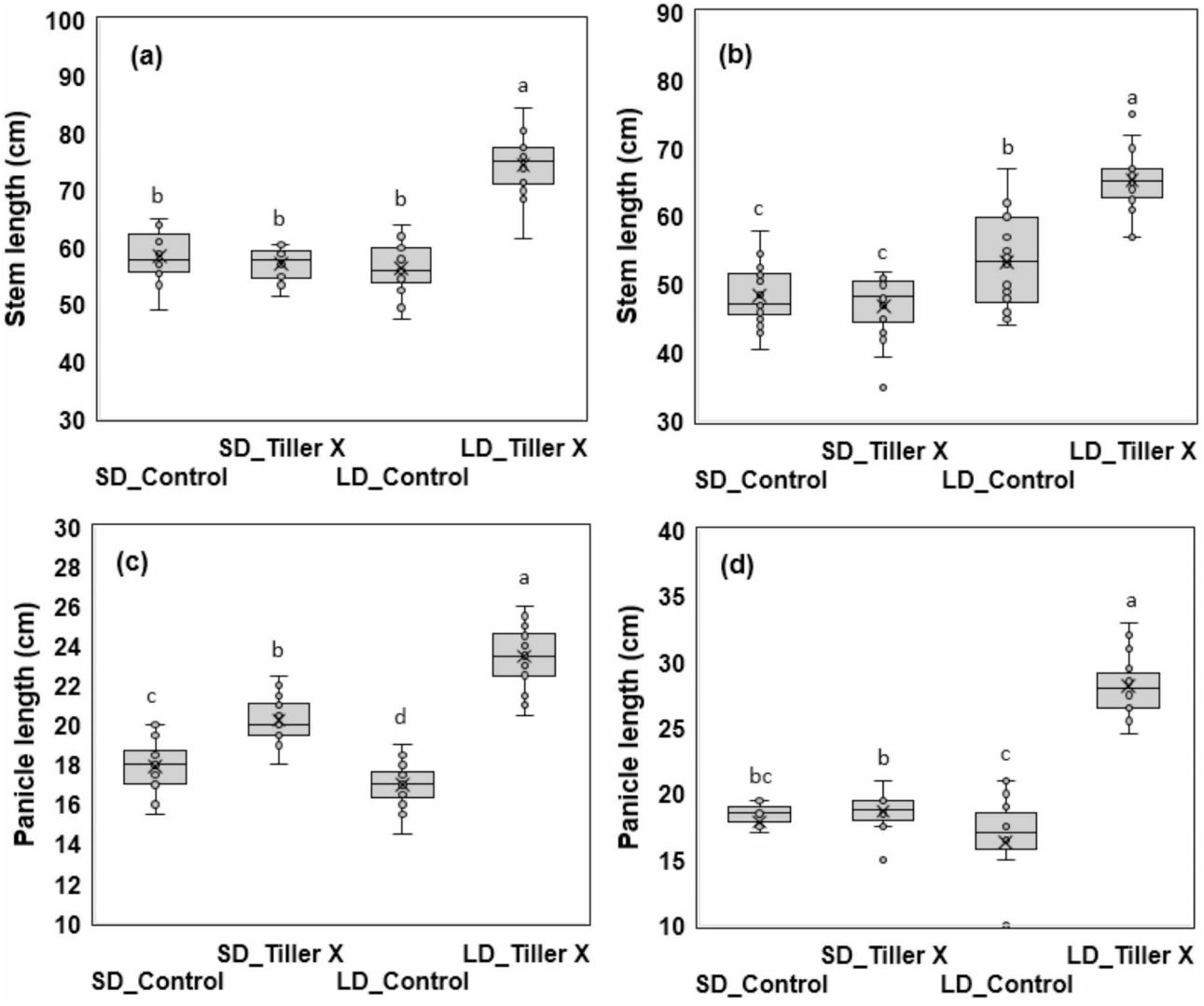

Fig. 2 Boxplot graph of the differences in growth with tiller removal and daylength conditions at heading date. (**a**) 'Odae, stem length; (**b**) 'Saenuri, stem length; (**c**) 'Odae' panicle length; (**d**) 'Saenuri panicle length. SD: short day. LD: long day. Tiller X refers to tiller removal treatment. Letters above bars indicate significant differences ($P < 0.05$) according to Duncan's multiple range test. Growth data collected from 20 biological replicates for each treatment (n = 20)

SD conditions, TR reduced the heading date by 3 d in both 'Odae' and 'Saenuri.' In contrast, under LD conditions, TR delayed the heading date by 5 d in 'Odae' and approximately 2 d in 'Saenuri.'. The ANOVA revealed that no significant difference was observed in DTH due to TR, although it showed a highly significant difference as a result of the interaction between daylength and TR (Table S3).

Among yield components, spikelet number per panicle (SPP) showed the largest change associated with TR and daylength treatments (Table 2). In particular, SPP was lower under short than under LDs for both control and TR groups. SPP showed a greater daylength-mediated variation in the TR than that in the control group. In the 'Saenuri' cultivar, SPP was the lowest (62.2) and highest (235.0) in the TR group under short and LDs, respectively, with a 3.78-fold difference between the two extreme values. The proportion of ripened grain slightly decreased in the TR treatment, particularly under SDs, in which case SPP increased significantly. Furthermore, 1000-grain weight did not significantly differ between the experimental groups for either cultivar (Table 2). Similar results were found for Experiment 1 (Table S2).

Florigen- and spikelet formation-related gene expression

Florigen *Hd3a* expression levels significantly increased under LDs compared with that under LDs at 3 and 7 d after treatment (DAT, Fig. 2a). At 7 DAT under SDs, *Hd3a* levels were 102.4, 79.0, and 75.8 in the main stem of the TR (TMS), control (CMS), and tillers of the control (CT, Fig. 4a) groups, respectively. Additionally, the

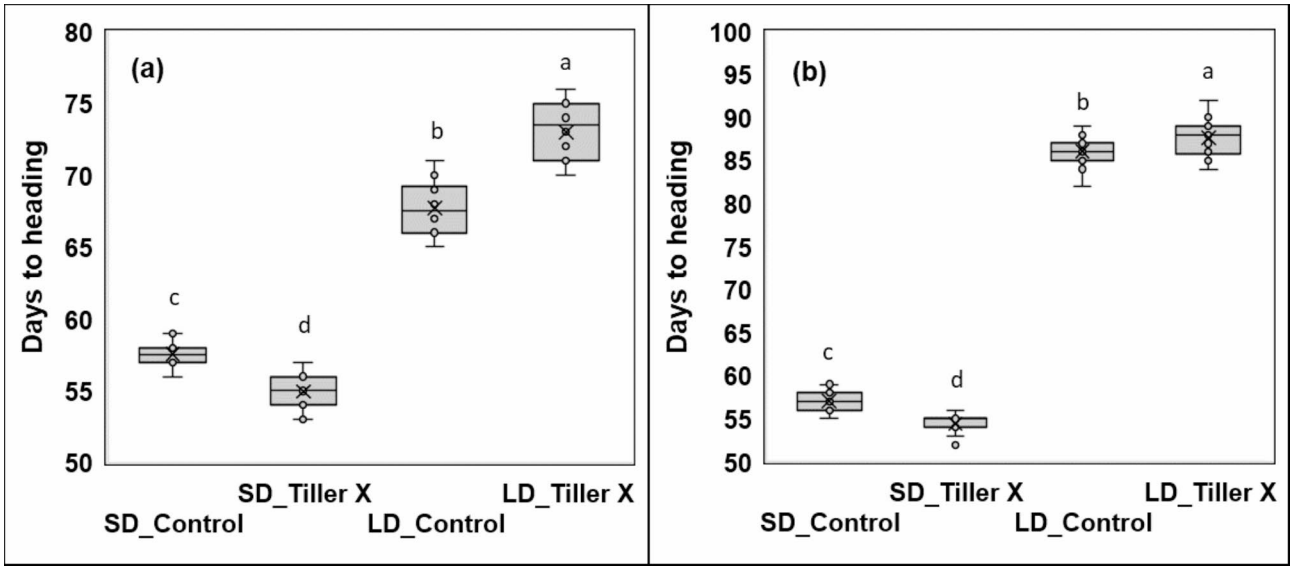

Fig. 3 Boxplot graph of days to heading upon tiller removal and under contrasting daylength conditions. (**a**) 'Odae,' (**b**) 'Saenuri.' SD: short day. LD: long day. Tiller X refers to tiller removal treatment. Days to heading data collected from 20 biological replicates for each treatment ($n = 20$). Letters above bars indicate significant differences ($P < 0.05$) according to Duncan's multiple range test

Table 2 Changes in yield components upon tiller removal according to daylength from sowing to heading stage date

Varieties	Treatment		Panicle number (ea)	Spikelet number per panicle (ea)	Ripened Grain (%)†††	1000-Grain weight (g)†††
'Odae'	**SD**	**Control**	13.0 ± 0.4a	56.9 ± 3.0c	95.6 ± 0.7a	28.1 ± 0.4a
		Tiller X	1.0 ± 0.0b	74.1 ± 1.8b	84.3 ± 1.9b	28.1 ± 0.3a
	LD	**Control**	13.5 ± 0.6a	58.2 ± 3.7c	95.6 ± 0.6a	28.4 ± 0.7a
		Tiller X	1.0 ± 0.0b	127.1 ± 8.1a	78.5 ± 1.4 c	28.4 ± 0.6a
'Saenuri'	**SD**	**Control**	13.8 ± 0.4a	59.3 ± 2.1b	93.8 ± 2.8a	28.9 ± 0.5a
		Tiller X	1.0 ± 0.0b	62.2 ± 1.8b	72.6 ± 0.9c	30.3 ± 0.6a
	LD	**Control**	14.0 ± 0.4a	69.1 ± 1.9b	89.7 ± 2.6a	28.0 ± 1.0a
		Tiller X	1.0 ± 0.0b	235.0 ± 6.5a	79.7 ± 3.0b	28.3 ± 0.2a
Analysis of variance (ANOVA)						
Variety (V)			ns	***	***	ns
Daylength (D)			ns	***	ns	ns
Tiller (R)			***	***	**	ns
Interaction (V*D)			ns	***	ns	ns
Interaction (V*R)			ns	***	***	ns
Interaction (D*R)			ns	***	***	ns
Interaction (V*D*R)			ns	***	***	ns

Data are presented as Mean ± Standard Error

SD: short day, LD: long day

Tiller X refers to the TR (tiller removal) treatment

ns: non-significant ($P \geq 0.05$), *, **, ***: significant at $P < 0.05$, 0.01, and 0.001

Letters indicate significant differences ($P < 0.05$)

† Number of days from sowing to heading date (main stem)

†† Final leaf age from the main stem; final tiller number was the highest up to the heading date

expression of *Hd3a* in the main stem of the TR group tended to increase under SDs and increased over time after TR treatment. However, under LDs, *Hd3a* expression decreased compared with that of its level before daylength treatment, with no discernible difference between TR groups.

OsMFT1 gene reportedly increases SPP and is associated with delayed flowering [38]. Similar to that of the heading and SPP responses induced by daylength and TR treatments, *OsMFT1* expression differed considerably between daylength conditions. Particularly, the *OsMFT1* expression level was higher in the CMS and CT than that

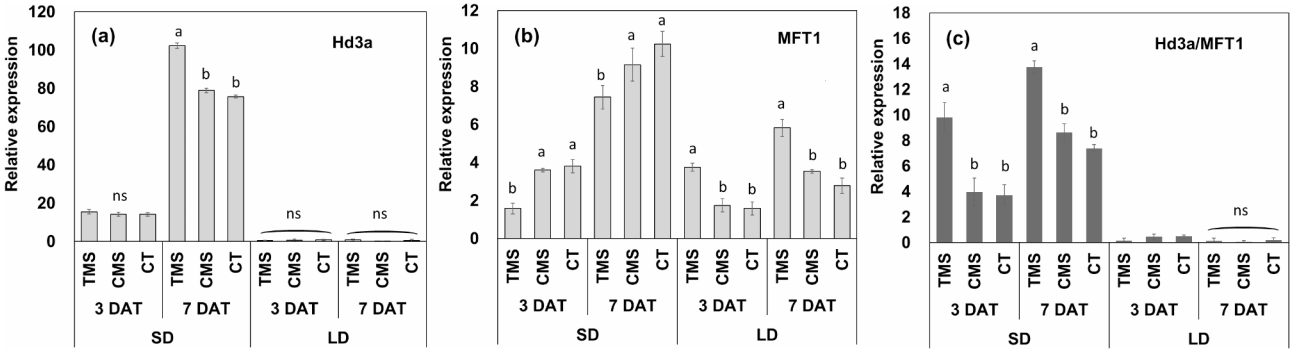

Fig. 4 Changes in (**a**) *Hd3a*, (**b**) *OsMFT1*, and (**c**) *Hd3a/MFT1* mean relative expression levels in 'Saenuri' rice plants in the tiller removal treatment groups according to daylength conditions, compared with that of the relative expression level before treatment (standard). TMS: tiller removal main stem. CMS: control rice plant-main stem. CT: control rice plant-tiller. DAT: days after treatment. SD: short day. LD: long day. Values represent the mean of three biological replicates ($n=3$), each analyzed in triplicate technical replicates. Letters above bars indicate significant differences ($P<0.05$) according to Duncan's multiple range test. "ns" indicates non-significant ($P\geq0.05$). Vertical lines on bars represent SE ($n=9$)

in the TMS groups under SDs; however, the opposite trend was observed under LDs (Fig. 4b).

At 7 DAT under SD conditions, the expression of *Hd3a* relative to *OsMFT1* (*Hd3a/MFT1*) increased under the TR treatments, with values of 13.8, 8.6, and 7.4 for TMS, CMS, and CT, respectively. Contrastingly, at 3 DAT under LD conditions, the expression of *Hd3a* relative to *OsMFT1* decreased under the TR treatments, with values of 0.2, 0.5, and 0.5 for TMS, CMS, and CT, respectively (Fig. 4c). These results indicate that the expression levels of the two genes vary depending on daylength conditions.

Other flowering-related genes were analyzed together (Figure S4). Therefore, for example, *RFT1*, which is another florigen gene controlling flowering under SDs and LDs [32] showed relative expression levels of 61.1, 55.5, and 55.1 in the TMS, CMS, and CT groups, respectively, under SDs (Figure S4a). Similarly, the relative expression levels of *Ehd1*, which enhances the expression of *Hd3a* and *RFT1* under SD conditions [10], were 20.1, 19.2, and 14.7 in the TMS, CMS, and CT groups, respectively (Figure S4b). Simultaneously, the relative expression levels of *Ghd7* under LDs, which suppresses the expression of *Hd3a* and *RFT1* under such conditions [32], were 1.9, 1.7, and 1.4 in the TMS, CMS, and CT groups, respectively (Figure S4c).

Discussion

Rice is grown over a wide range of latitudes globally; therefore, the plant grows under different daylength conditions depending on the specific location, ranging from approximately 12 h in low-latitude regions to 13–14.5 h in high-latitude regions [8, 26, 27]. Even within the same region, rice is exposed to varying daylength conditions depending on the planting season and climate change [39]. Given that daylength is a key environmental factor influencing both tillering and flowering, understanding its role in developmental trade-offs is crucial.

Tillering is greatly affected by temperature and daylength [24]. Generally, SDs and high temperatures lead to earlier flowering due to the restriction of tillering imposed by the shortened vegetative growth period [27, 40]. However, despite these well-established effects, the precise interaction between tillering and flowering remains unclear and, in fact, controversial. This uncertainty arises because tillering and floral induction are developmentally linked, as both processes are regulated by environmental cues and hormonal signaling pathways [24, 27].

Floral induction is essential for flowering [31, 32], and as it initiates a shift toward reproductive growth, it serves as a key regulator of the vegetative growth period [41–42]. Since tillering primarily occurs during vegetative growth, floral induction has a direct impact on tiller development [43]. Specifically, FLOWERING LOCUS C (FLC) and FRIGIDA (FRI), two floral repressors in the vernalization pathway, reportedly regulate tillering in *Arabidopsis thaliana* [43, 44], and similar findings have been reported in other species [45, 46].

Since the initial discovery of the *MOC1* gene as a crucial regulator of rice tillering, several studies have investigated both physiological and molecular aspects of this process [47, 48]. For instance, correlations between nitrogen-dependent vegetative growth (e.g., tiller and leaf development) and flowering time have been explored [24, 47], highlighting the intricate regulatory network governing rice development.

Several studies have reported a negative relationship between tillering and flowering [13, 14, 23, 27]. FAC activation triggers the expression of *OsMADS14* and *OsMADS15*, key genes involved in floral formation and development [28]. However, FAC components, such as *OsFD*-like transcription factors, also participate in lateral branching in the axillary meristem and leaf development [20, 49], suggesting that *Hd3a* function is not limited to

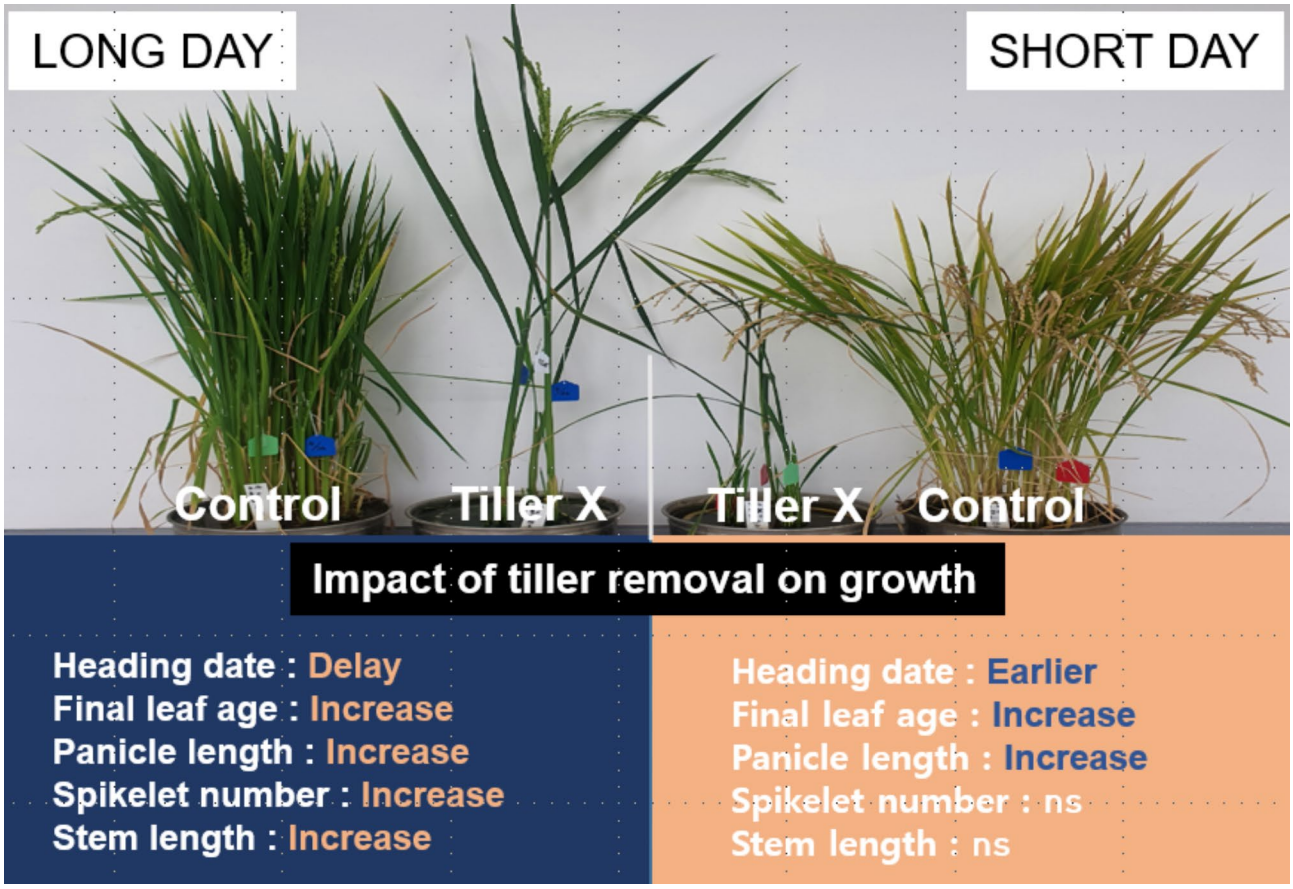

Fig. 5 Changes in plant growth and phenology responses to daylength conditions and tiller removal

flowering induction but also influences tillering patterns. Additionally, *OsLUX*-overexpressing mutants display reduced photoperiod sensitivity and a prolonged juvenile phase, leading to an increased number of tillers and delayed heading [19].

Conversely, some studies have reported a positive correlation between tillering and flowering [22, 50]. For instance, tiller number increases with flowering when *OsRFL*, a regulator of the flowering activator *OsSOC1*, is overexpressed. Conversely, *OsRFL* knockdown results in restricted secondary tiller and panicle branch development, along with delayed flowering [22]. Similarly, reduced expression of *OsWDRa* or *OsTRx1*, components of the COMPASS-like complex, via RNA interference led to a decrease in secondary branch and grain numbers under both LD and SD conditions, accompanied by delayed heading [29].

These contrasting results suggest that photoperiod may play a crucial role in determining the nature of the tillering–flowering interaction. In our study, when tillers were removed, heading occurred earlier under SDs but was delayed under LDs (Figs. 3 and 5, S3). This aligns with previous studies showing that restricting tiller development can accelerate floral induction under SD conditions [28]. One possible explanation is that under SD conditions, *Hd3a* predominantly promotes floral induction rather than lateral branching in the axillary meristem [28].

To investigate this hypothesis, we analyzed the expression of florigen genes (*Hd3a* and *RFT1*) in the main stem and tillers under different treatment conditions (Fig. 4a). We found that under SD conditions, the relative expression of both florigen genes increased over time and were significantly higher in the main stems of TR plants than in controls (Fig. 4a, S4a). This increase in gene expression provides insight into the accelerated heading observed in the TR treatment with SDs.

Interestingly, cultivar-specific responses were observed in H_{max} under SD conditions. Specifically, H_{max} decreased in the TR group for 'Saenuri' but remained unchanged for 'Odae' (Fig. 1a, b), suggesting that genotypic differences may influence the photoperiodic regulation of tillering and flowering. Although this study highlights these contrasting responses, further research is needed to elucidate the genetic and physiological mechanisms underlying these differences.

Under LD conditions, *Hd3a* played a less prominent role than under SD conditions, while SPP increased markedly in the TR group (Table 2). For 'Saenuri' under SDs, the SPP of the TR group (62.2) was slightly higher than that in the control group (59.3). However, under LD conditions, the TR group exhibited a considerable increase in SPP (235), at 3.4 times higher than that in the control (69.1). Such an increase in SPP has been associated with delayed heading, similar to the effects of excessive nitrogen supply [50].

To further investigate this, we analyzed the expression of *OsMFT1*, a gene involved in spikelet and branch formation that also suppresses flowering [38]. Under LD conditions, *OsMFT1* expression was significantly lower in the TR group than in CMS and CT groups (Fig. 4b). Consistent with this, the SPP of the TR group was higher under LD conditions. Thus, the observed phenotypic differences in heading date and SPP correlated with *OsMFT1* expression patterns.

Meanwhile, as presented in Table 2, the number of ripened grains exhibited a slight decline in the TR group, which is likely attributed to the increased spikelets per panicle (SPP). A higher SPP necessitates a greater sink capacity, potentially leading to a lower ripened grain ratio, a phenomenon that has been previously documented [51, 52]. The response differed between cultivars under varying photoperiod conditions. In Odae, the increase in SPP was more pronounced under long-day (LD) conditions, resulting in a further reduction in the number of ripened grains (Table 2). Conversely, despite the more substantial increase in SPP under LD conditions, Saenuri displayed a slight increase in ripened grain number compared to short-day (SD) conditions. This discrepancy may be attributed to additional factors beyond SPP, as previous studies have indicated that pre-heading vegetative growth, particularly the source capacity for assimilate production and translocation, significantly influences ripened grain formation [53].

In summary, under SD conditions, which promote floral induction, *Hd3a* likely plays a more prominent role in accelerating flowering in the main stem rather than promoting tillering in the TR treatment. This resulted in earlier heading (Fig. 3). In contrast, under LD conditions, the difference in SPP between TR and control groups was significantly greater than under SD conditions, and *OsMFT1* expression followed the same trend. Notably, *OsMFT1* expression patterns were opposite to those of *Hd3a* and *RFT1* under SDs (Fig. 4; Figure S4). These findings suggest that under LD conditions, the substantial increase in SPP in the TR treatment contributed to delayed flowering, whereas under SD conditions, heading occurred earlier due to enhanced florigen expression.

Conclusions

Our findings underscore the importance of climate-smart crop production strategies for optimizing rice growth and productivity under variable daylength conditions. This study demonstrated that under LD conditions, reduced tillering led to increased vegetative growth and delayed heading, whereas under SD conditions, reduced tillering accelerated heading. These results clarify that the variability in tillering and flowering—often associated with conflicting findings in previous studies—is strongly influenced by daylength. Furthermore, our findings suggest a novel breeding and management approach that targets daylength-dependent interactions between tillering and flowering, offering a potential strategy to enhance rice adaptability to climate change and optimize growth timing in diverse environments.

Abbreviations

FAC	Florigen activation complex
NICS	National Institute of Crop Science
PAR	Photosynthetically active radiation
SD	Short day-length
LD	Long day-length
DTH	Days to heading
SPP	Spikelet number per panicle
TR	Tiller removal treatment group
TMS	Main stem of the TR treatment
CMS	Main stem of the control
CT	Tillers of the control

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06430-z.

Supplementary Material 1: **Figures S1**: Controlled environment facility; **Figures S2**: Architecture of a 'Saenuri' rice plant; **Figure S3**: Number of growing days from sowing to heading stage in the two rice cultivars for control and tiller removal treatments; **Figure S4**: Changes in (a) RFT1, (b) Ehd1, and (c) Ghd7 mean relative expression levels in 'Saenuri' rice plants for the tiller removal treatment under contrasting daylength conditions; **Table S1**: List of primer sequences of Oryza sativa used for qRT-PCR; **Table S2**: Changes in rice plant growth and development traits after tiller removal; Table S3: Analysis of variance (ANOVA) for growth duration, stem length, and panicle length caused by tiller removal under contrasting daylength conditions

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Author contributions

H.S.L. and J.Y.S. conceived and supervised the project. H.S.L. designed the experiments. H.S.L. and J.H.K. conducted the gene expression analysis and field experiments. H.S.L, S.Y.Y, S.H.J, and J.K.B. analyzed the data and drafted the manuscript. All authors discussed the results and contributed to the paper.

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Data availability
All data and analyses are included in the main manuscript or Supporting Information. The source data for Figs. 1, 2, 3, 4 and 5; Tables 1 and 2, Figures S1–S4, and Tables S1–S3 are provided as Source Data files.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
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Competing interests
The authors declare no competing interests.

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