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Note

Development and evaluation of pyramiding lines carrying early or late heading QTLs in the *indica* rice cultivar ‘IR64’

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The heading date is an important trait for determining regional and climatic adaptability in rice. To expand the adaptability of the *indica* rice cultivar ‘IR64’, we pyramided multiple early or late heading quantitative trait locus (QTLs) in the ‘IR64’ genetic background by crossing previously developed near-isogenic lines (NILs) with a single QTL for early or late heading. The effects of pyramiding QTLs were observed in three different climatic zones of the Philippines, Madagascar, and Japan. The early heading pyramiding lines (PYLs) headed 6.2 to 12.8 days earlier than ‘IR64’ while the late heading PYLs headed 18.8 to 27.1 days later than ‘IR64’. The PYLs tended to produce low grain yield compared to ‘IR64’. The low yield was not improved by combining *SPIKE*, which is a QTL that increases the number of spikelets per panicle. Conversely, ‘IR64-PYL(7+10)’ carrying *Hd5* and *Hd1* headed earlier, produced more tillers, and more panicles per m^2 than ‘IR64’, and mitigated the yield decrease in early heading. These results suggest that the effects of pyramided QTLs on heading date were consistent across various environments and PYLs could be used to enhance the adaptation of ‘IR64’ in other rice growing environments.

Key Words: adaptability, heading date, pyramiding lines, quantitative trait loci (QTL), rice.

Introduction

Crop adaptation in an environment is crucial for maximum growth and productivity in the environmental conditions (Chloupek and Hrstkova 2005). Flowering time is an important determinant of regional and climatic adaptability in crops (Izawa 2007). An appropriate flowering time enables crops to fully utilize light and temperature resources in the given environment (Zhang *et al.* 2015).

Rice is a short-day plant that is grown widely in Asia and Africa as a staple food. The *indica* high-yielding variety ‘IR64’ was developed by the International Rice Research Institute (IRRI) in the 1980s. This variety has a wide adaptability and has been distributed in Southeast Asia, South Asia, and West Africa, and was grown in over 10 million hectares of paddy fields by the end of last century (Mackill and Khush 2018). The diverse success was partly due to early maturation (approximately 116 days in the tropics) compared with traditional varieties, which enabled double rice cropping in the tropics (Khush and Virk 2005, Peng and Khush 2003). However, increased versatility is necessary in IR64 to keep up with demand in growing and diverse markets and with producers’ demands in changing climatic conditions. With further earlier heading, three rice crops a year is possible and producers can escape the risks of drought or low temperature stresses at the end of the growing period (Farooq *et al.* 2009, Shavrukov *et al.* 2017). Alternatively, a longer growing period may improve the one-time grain yield and reduce labor costs compared with multiple rice cropping. In general, a longer growth duration contributes to a yield increase through high biomass production when grown in adequate climatic conditions (Zhang *et al.* 2009) and higher temperature regions of the future, where late-season low temperatures are problematic (van Oort and Dingkuhn 2021).

The flowering time (heading date) in rice is controlled by multiple genes that respond to photoperiod and temperature (Yano *et al.* 2001). The progress in rice genomics over the past two decades has elucidated the genetic and molecular

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mechanisms underlying heading date (Hori *et al.* 2016, Matsubara *et al.* 2014). Recently, Wei *et al.* (2016) revealed that 'IR64' obtained early maturity with an insensitivity to photoperiod due to the loss of functional alleles of the quantitative trait loci (QTLs), *Hd1* (Yano *et al.* 2000) and *Ehd1* (Doi *et al.* 2004). Using new plant type (NPT) rice varieties as donors, Fujita *et al.* (2009) detected QTLs for heading date in the 'IR64' genetic background. Fujita *et al.* (2011) developed five near-isogenic lines (NILs) carrying the QTLs in the 'IR64' genetic background. Three NILs showed a three to five day earlier heading than 'IR64' while two NILs showed an eight to ten day later heading than 'IR64' in the tropics. Therefore, we hypothesized that a wider variation in heading date is possible by pyramiding the QTLs in the 'IR64' genetic background to expand the adaptability in other rice-growing environments and contribute to an increase in rice production.

The objectives of this study were to develop breeding materials using 'IR64' with modified days to heading. The experiment will be undertaken by pyramiding QTLs for heading date using the NILs in the 'IR64' genetic background. The effects of the pyramided QTLs on heading date and productivity will be evaluated in three different climatic zones. A short growth duration generally decreases grain yield, therefore, we also use *SPIKE*, a QTL that increases the number of spikelets per panicle (Fujita *et al.* 2013), to the QTLs for heading date to evaluate whether *SPIKE* can compensate for the yield decrease.

Materials and Methods

Development of pyramiding lines (PYLs)

Six NILs for heading date and spikelet number per panicle were previously developed by Fujita *et al.* (2011) as 'IR64-NIL7' to 'IR64-NIL11' and 'NIL-*SPIKE*' in the 'IR64' genetic background using more than 200 genome-wide SSR markers (**Fig. 1**). The six NILs were used to develop PYLs according to the procedure summarized in **Supplemental Fig. 1**. 'IR64-NIL7', 'IR64-NIL10', and 'IR64-NIL11' are early heading NILs carrying *Hd5*, *Hd1*, and *qDTH11*[yp7] from each NPT or *temperate japonica* donor variety, respectively. The NILs, 'IR64-NIL8' and 'IR64-NIL9' are late heading NILs carrying *Hd3a* and *qDTH11*[YP6] from each NPT donor variety (**Fig. 1**) (Fujita *et al.* 2011). We first conducted crossings using 'IR64-NIL7', 'IR64-NIL10', and 'IR64-NIL11' as well as between 'IR64-NIL8' and 'IR64-NIL9'. Using DNA markers for the target regions, we selected F_2 or F_3 progenies with the two target segments homozygous for the donor varieties as PYLs; 'IR64-PYL(7+10)', 'IR64-PYL(7+11)', 'IR64-PYL(10+11)', and 'IR64-PYL(8+9)'. In the same way, we then crossed 'IR64-PYL(10+11)' with 'IR64-NIL7' as well as 'NIL-*SPIKE*'. We selected the PYLs with the three target segments homozygous for the donor varieties; 'IR64-PYL(7+10+11)' and 'IR64-PYL(10+11+*SPIKE*)'. Finally, we crossed 'IR64-PYL(7+10+11)' with 'IR64-PYL(10+11+*SPIKE*)', and selected the 'IR64-PYL(7+10+11+*SPIKE*)' that were homozygous with the donor varieties containing the four target segments.

Filed experiments

Field experiments were conducted in the tropical regions in the International Rice Research Institute, Los Baños, Philippines (14°17N, 121°26E), in the wet seasons (WS) of 2018, in farmers' paddy fields in Ankazomiriotra, Madagascar (19°40S, 46°34E) in the rice growing season of 2019–2020, and in the temperate region in the Japan International Research Center for Agricultural Sciences, Tsukuba, Japan (36°05N, 140°08E) in 2020. Rice was grown conventionally in each environment. Seeds were sown in seedling nurseries. The 3- to 4-week-old seedlings were transplanted into the experimental paddy fields with

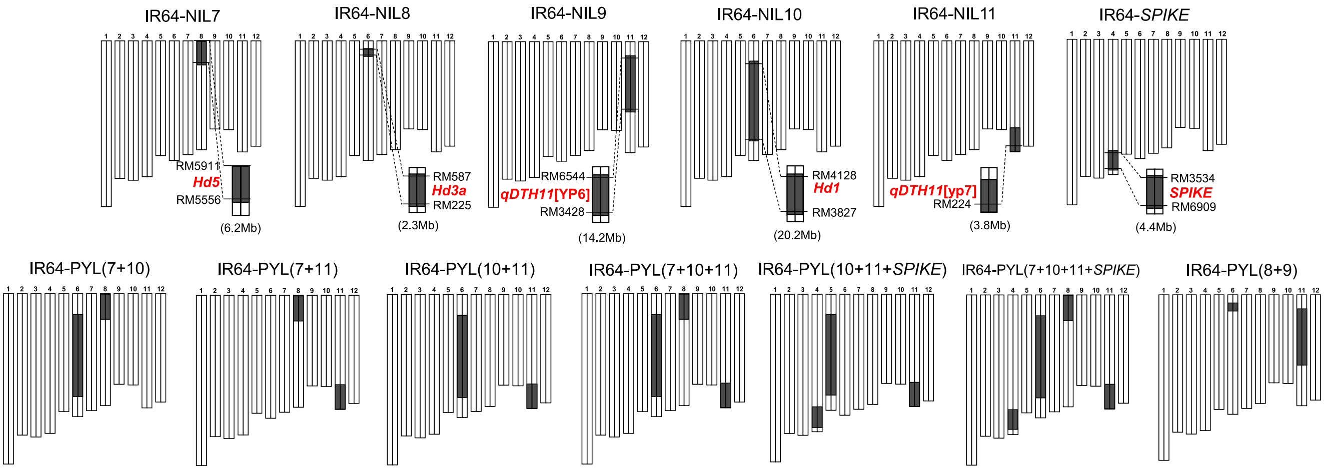

Fig. 1. Graphical genotypes of the near-isogenic lines (NILs) for heading quantitative trait locus (QTLs) and *SPIKE* and also the pyramiding lines (PYLs). The bars represent chromosomes. Chromosome numbers are provided above each bar. The white bars denote regions homozygous for 'IR64' and the black segment denotes a region homozygous for the donors. Mega-base (Mb) in the parentheses shows the size of the introgression segment.

one or two seedlings per hill. The planting densities were: in Los Baños, 20 hills m^{-2} in plots of 7 rows with 21 hills; In Ankazomiriotra, 25 hills m^{-2} in 4 rows with 20 hills; and in Tsukuba, 18.5 hills m^{-2} with a plot size of 4 rows with 13 hills. To evaluate the yield, the experimental plots were arranged in a randomized complete block design with four and three replicates in Ankazomiriotra and Tsukuba, respectively. Chemical fertilizers were applied at a rate of: In Los Baños, 150 kg N ha^{-1}, 45 kg P_2O_5 ha^{-1}, and 45 kg K_2O ha^{-1}; in Ankazomiriotra, 60 kg N ha^{-1}, 40 kg P_2O_5 ha^{-1}, and 29 kg K_2O ha^{-1}; and in Tsukuba, 48 kg N ha^{-1}, 64 kg P_2O_5 ha^{-1}, and 32 kg K_2O ha^{-1}. A total of 14 lines were grown in Tsukuba and 12 lines were grown in Los Baños and Ankazomiriotra. In Los Baños and Ankazomiriotra the excluded lines were ‘IR64-PYL(7+10+11+*SPIKE*)’ and ‘NIL-*SPIKE*’.

Evaluation of days to heading, aboveground biomass, and grain yield

Days to heading was defined as the number of days from sowing to the first panicle heading in each plant. Ten to twenty plants were evaluated for each line in each experiment. In Ankazomiriotra and Tsukuba, six hills were sampled from each plot at the soil surface. The samples were dried at 70°C for 72 h, and weighed to determine the aboveground biomass at heading. At maturity, the number of panicles was counted for 14 hills in Ankazomiriotra and 10 hills in Tsukuba. The hills were then harvested, and the yield and yield components were determined according to the methods described by Takai *et al.* (2021). In Ankazomiriotra, the yield and yield components were not obtained for the late heading lines of ‘IR64-NIL8’, ‘IR64-NIL9’, and ‘IR64-PYL(8+9)’ because farmers accidentally harvested and consumed them. In Tsukuba, the number of tillers was counted using nine hills of ‘IR64’ and ‘IR64-PYL(7+10)’ for the periods from transplanting to heading.

Statistics

Statistical analysis was performed using SPSS 23.0 software (IBM). In all analyses a probability value less than 0.05 was considered statistically significant ($P < 0.05$).

Results

Genotypes of PYLs

A total of seven PYLs were developed, and the genotype of each PYL is provided in **Fig. 1**. Using DNA markers for the target segments, we confirmed that ‘IR64-PYL(7+10)’, ‘IR64-PYL(7+11)’, and ‘IR64-PYL(10+11)’ carried the donor alleles for two of the three QTLs (*Hd5*, *Hd1*, and *qDTH11*[yp7]) that accelerate heading, respectively. We also confirmed ‘IR64-PYL(7+10+11)’ carried the donor alleles for the three QTLs. Both ‘IR64-PYL(10+11+*SPIKE*)’ and ‘IR64-PYL(7+10+11+*SPIKE*)’ carried *SPIKE* as well as the two and three early heading QTLs from the donor varieties, respectively. Similarly, ‘IR64-PYL(8+9)’ carried the donor alleles for *Hd3a* and *qDTH11*[YP6] that delayed heading.

Climate conditions at experimental fields

Daylength from sowing to heading was the shortest in Los Baños (13.0 to 12.0 h), intermediate in Ankazomiriotra (13.5 to 12.2 h), and the longest in Tsukuba (14.6 to 12.8 h) (**Supplemental Fig. 2**). The mean temperature during the growing period was the highest in Los Baños at around 28°C, intermediate in Ankazomiriotra with a constant temperature of approximately 23.3°C, and the lowest in Tsukuba at approximately 21.8°C with a gradual increase until heading in mid-August (13.2°C to 29.5°C) followed by a gradual decrease during grain filling until maturity (29.5°C to 14.3°C). The average solar radiation during the growing period in Ankazomiriotra was 21.3 and in Tsukuba was 15.1 MJ m^{-2} d^{-1}. Solar radiation records were not available in Los Baños.

Variation in heading date among NILs and PYLs

The ‘IR64’ headed 82.1, 86.1, and 99.3 days after sowing in Los Baños, Ankazomiriotra, and Tsukuba, respectively (**Fig. 2**). Wide variations were observed for days to heading among NILs and PYLs. The days to heading ranged from 69.3 to 100.9 in Los Baños, from 75.7 to 106.7 in Ankazomiriotra, and 93.1 to 126.4 in Tsukuba (**Fig. 2**). Thus, the earliest PYL headed 12.8, 10.4, and 6.2 days earlier than ‘IR64’ while the latest PYL headed 18.8, 20.6, and 27.1 days later than ‘IR64’ in Los Baños, Ankazomiriotra, and Tsukuba, respectively. The differences were based on the effects of pyramiding the two heading QTLs. The ‘IR64-PYL(7+10)’, ‘IR64-PYL(7+11)’, and ‘IR64-PYL(10+11)’ headed earlier than the parental NILs, whereas ‘IR64-PYL(8+9)’ headed later than the parental NILs. However, additional variations by the three QTLs was not observed; ‘IR64-PYL(7+10+11)’ did not head earlier than ‘IR64-PYL(7+10)’, ‘IR64-PYL(7+11)’, and ‘IR64-PYL(10+11)’ in any experimental field.

Biomass, yield, and yield components among NILs and PYLs

Days to heading was closely correlated with aboveground biomass at heading in both Ankazomiriotra ($r = 0.88$) and Tsukuba ($r = 0.95$) (**Fig. 3**). In contrast, no significant correlation was observed between days to heading and grain yield in either experimental field (**Fig. 4**). ‘IR64’ produced 3.5 and 5.0 t ha^{-1} of grain yield in Ankazomiriotra and Tsukuba, respectively (**Table 1**). NILs and PYLs with early heading tended to produce low grain yield compared to ‘IR64’ at both experimental fields. Similarly, the late heading lines showed significantly lower grain yield than ‘IR64’ in Tsukuba. This result is probably due to the low temperature during the grain filling period. *SPIKE* did not improve the grain yield in the PYLs for early heading in either experimental field. Despite the low yield tendency compared to ‘IR64’, in Ankazomiriotra,

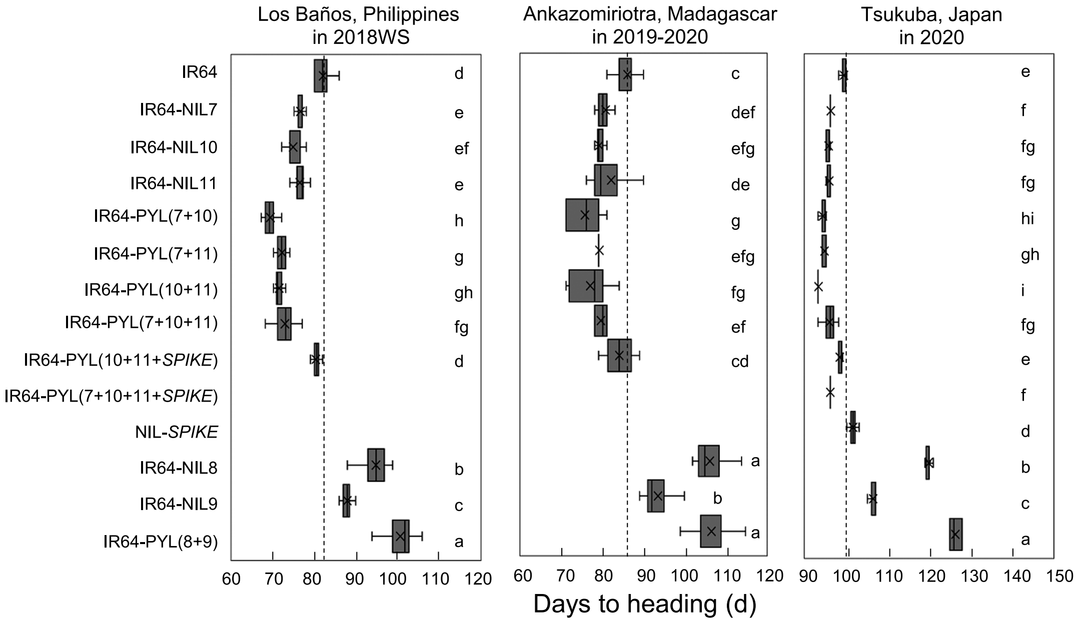

Fig. 2. Comparisons of days to heading among NILs and PYLs with the ‘IR64’ background in Los Baños, Philippines in 2018WS, Ankazomiriotra, Madagascar in 2019–2020, and Tsukuba, Japan in 2020. Days to heading in each line is represented by a box plot. The dotted line exhibits days to heading of ‘IR64’. Different letters indicate significant differences ($P < 0.05$, Tukey’s HSD test).

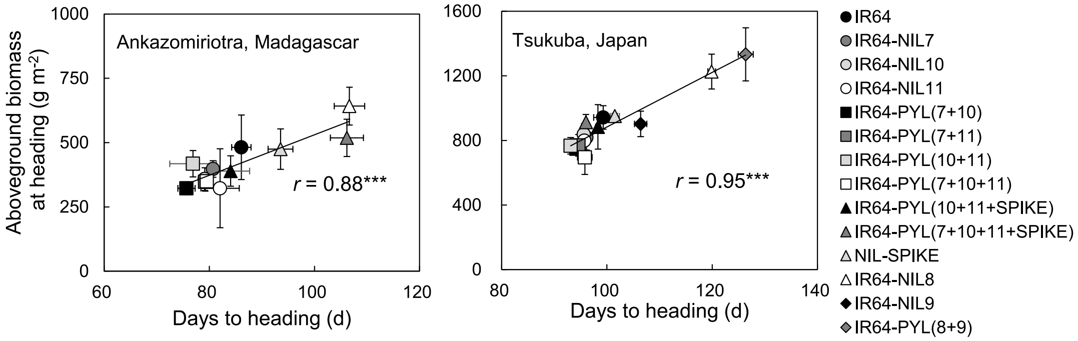

Fig. 3. Relationship between days to heading and aboveground biomass at heading among NILs and PYLs grown in Ankazomiriotra, Madagascar and Tsukuba, Japan. Bars represent standard deviation. *** denotes significance at the 0.1% level.

‘IR64-PYL(7+10)’ headed earliest and did not decrease in grain yield among NILs and PYLs (**Fig. 4**). To elucidate why ‘IR64-PYL(7+10)’ maintained the yield levels, we investigated the yield components and identified the greatest number of panicles in ‘IR64-PYL(7+10)’. The higher number of panicles resulted in a similar number of spikelets m^{-2} to the other NILs and PYLs (**Table 1**). The high number of panicles were derived from vigorous tillering. ‘IR64-PYL(7+10)’ had already produced more tillers than ‘IR64’ at 12 days after transplanting and maintained this difference until the heading stage (**Fig. 5**).

Discussion

Using the PYLs developed in this study, we demonstrated that pyramiding two heading QTLs expanded the variation in days to heading in the ‘IR64’ genetic background in three different experimental fields. The results suggest that PYLs could be used to expand the adaptation of ‘IR64’ into new rice-growing environments.

Many genetic and molecular studies have elucidated the mechanisms underlying rice heading date and revealed that the combination of *Ghd7*, *Hd5/Ghd8*, and *Hd1* resulted in high natural variation in rice (Zhang *et al.* 2015, 2019). We also identified that pyramiding two QTLs among *Hd5*, *Hd1*, *qDTH11[yp7]* accelerated heading in the ‘IR64’ genetic background. However, pyramiding the three QTLs did not accelerate heading. Previous studies reported that flowering time was not always determined by additive effects of multiple genetic factors (Lin *et al.* 2000, Reeves and Coupland 2001). The results, therefore, imply an interaction among *Hd5*, *Hd1*, and *qDTH11*[yp7], although the mechanisms involved remains unclear. Or there may be other masked QTLs or genes on heading date in the donor

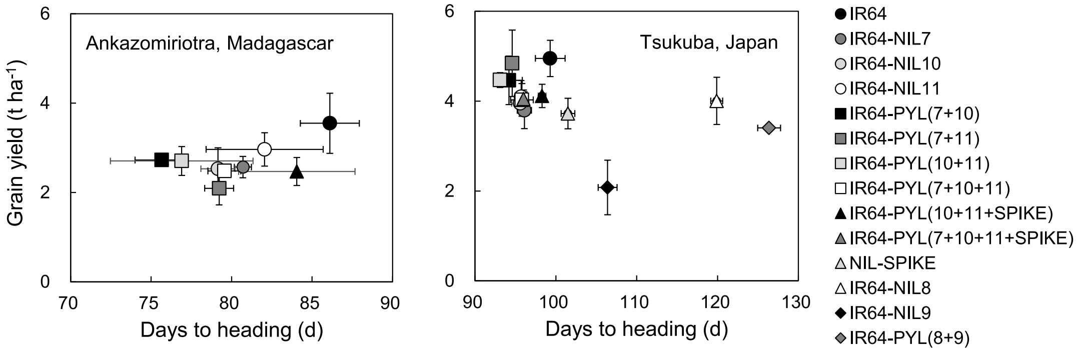

Fig. 4. Relationship between days to heading and grain yield among NILs and PYLs grown in Ankazomiriotra, Madagascar and Tsukuba, Japan. Bars represent standard deviation.

Table 1. Grain yield and yield components for the near-isogenic lines (NILs) and pyramiding lines (PYLs) for days to heading in the 'IR64' genetic backgrounds grown in Ankazomiriotra, Madagascar and Tsukuba, Japan

Lines	Grain yield[a] (t ha^{-1})	No. of panicles (m^{-2})	No. of spikelets (panicle^{-1})	No. of spikelets (m^{-2})	Filled spikelets (%)	Single-grain weight (mg)
Ankazomiriotra, Madagascar in 2019–2020						
IR64	3.5 a[b]	215 b	60 a	13,046 a	85.5 ab	31.7 a
IR64-NIL7	2.6 ab	207 b	53 ab	10,820 a	78.7 b	30.2 b
IR64-NIL10	2.5 ab	267 ab	39 c	10,450 a	82.4 ab	29.6 bc
IR64-NIL11	3.0 ab	227 ab	51 ab	11,551 a	84.7 ab	30.2 b
IR64-PYL(7+10)	2.7 ab	289 a	37 c	10,752 a	90.0 a	28.3 c
IR64-PYL(7+11)	2.1 b	201 b	46 bc	9,099 a	76.0 b	30.3 ab
IR64-PYL(10+11)	2.7 ab	234 ab	47 bc	11,095 a	83.4 ab	29.4 bc
IR64-PYL(7+10+11)	2.5 b	270 ab	38 c	10,240 a	82.3 ab	29.5 bc
IR64-PYL(10+11+*SPIKE*)	2.5 b	222 ab	46 bc	10,308 a	83.7 ab	28.6 c
Tsukuba, Japan in 2020						
IR64	5.0 a	254 ef	106 abc	26,934 bc	69.2 abc	26.8 abc
IR64-NIL7	3.8 ab	270 de	83 defgh	22,510 cde	66.0 abcd	25.6 cdef
IR64-NIL10	4.0 ab	312 bcd	69 gh	21,554 cde	68.5 abc	26.8 abc
IR64-NIL11	4.1 ab	273 e	87 defg	23,735 cde	66.8 abc	26.0 bcdef
IR64-PYL(7+10)	4.5 ab	344 ab	67 h	23,268 cde	72.0 ab	26.9 ab
IR64-PYL(7+11)	4.8 a	354 a	74 fgh	26,226 bcd	71.9 ab	26.2 bcde
IR64-PYL(10+11)	4.5 ab	306 cd	74 fgh	22,689 cde	73.2 ab	27.1 a
IR64-PYL(7+10+11)	4.0 ab	278 cde	76 efgh	21,111 de	70.3 ab	27.1 a
IR64-PYL(10+11+*SPIKE*)	4.1 ab	226 f	90 cdef	20,248 e	78.4 a	25.9 cdef
IR64-PYL(7+10+11+*SPIKE*)	4.0 ab	227 f	93 cde	21,087 de	73.2 ab	26.2 abcd
NIL-*SPIKE*	3.7 ab	220 f	119 a	26,280 bcd	56.4 bcde	25.2 efg
IR64-NIL8	4.0 ab	285 cde	120 a	34,058 a	48.2 cde	24.5 g
IR64-NIL9	2.1 c	231 f	98 bcd	22,748 ce	36.6 e	25.2 fg
IR64-PYL(8+9)	3.4 b	269 de	116 ab	31,373 ab	45.3 de	24.4 g

[a] Data represented by means; n = 3 to 4 replications. [b] Different letters indicate significant differences ($P < 0.05$, Tukey's HSD test) in each environment.

segments or in the IR64 genetic background.

Our study also observed that the absolute differences in days to heading between the earliest PYLs and 'IR64' reduced (12.8 > 10.4 > 6.2 days) in the order of Los Baños, Ankazomiriotra, and Tsukuba. In contrast, the differences between the latest PYL and 'IR64' increased (18.8 < 20.6 < 27.1 days) in the order of Los Baños, Ankazomiriotra, and Tsukuba. These results suggest that shorter day lengths and higher air temperatures in the tropical region can enhance the effects of the pyramided QTLs on early heading, while longer daylengths and lower air temperatures of the temperate region can enhance the effects on late heading.

Contrary to our expectation, *SPIKE* did not improve grain yield in the pyramiding lines with early heading. While *SPIKE* increased the number of spikelets per panicle (Fujita *et al.* 2013), it also decreased the number of panicles per plant, depending on soil fertility (Takai *et al.* 2017, 2019). In this study, 'IR64-PYL(10+11+*SPIKE*)' and

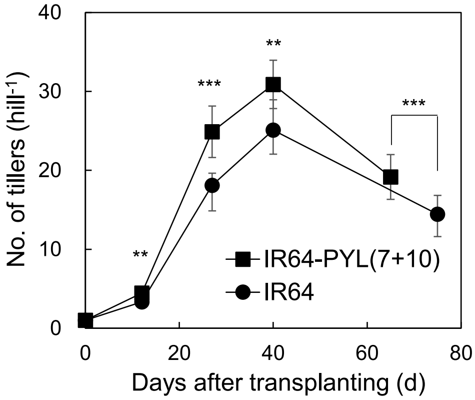

Fig. 5. Changes the number of tillers per hill in 'IR64' and 'IR64-PYL(7+10)' between transplanting and heading when grown in Tsukuba, Japan. Bars represent standard deviation. ** and *** denote significance at the 1% and 0.1% level analyzed with Student's t-test.

'IR64(7+10+11+*SPIKE*)' decreased the number of panicles m^{-2} compared with 'IR64-PYL(10+11)' and 'IR64-PYL(7+10+11)', respectively. This decrease caused no increase in the number of spikelets m^{-2} (**Table 1**). These results suggest that *SPIKE* may not be useful in combination with early heading QTLs. Conversely, 'IR64-PYL (7+10)' headed earlier, produced more tillers, and thus more panicles m^{-2} than 'IR64'. This result indicates the pleiotropic effect of heading QTLs on rice tillering. Previous studies have reported pleiotropic effects with some flowering genes (Tsuji *et al.* 2015, Wang *et al.* 2020). It should be noted that pyramiding *Hd5* and *Hd1* promoted tillering greater than single *Hd5* or *Hd1*. Although further studies are necessary, an enhancement of the flowering signal by the two QTLs may further induce the outgrowth of tiller buds. Consequently, pyramiding *Hd5* and *Hd1* could be useful in mitigating yield decreases due to early heading.

Author Contribution Statement

TT, DF, KS, and NK designed the study. TT, PL, DF, KS, NMR, YT, and EVM performed the experiments. TT and EVM analyzed the data. TT wrote the paper.

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