

## Research Paper

# Days to heading, controlled by the heading date genes, *Hd1* and *DTH8*, limits rice yield-related traits in Hokkaido, Japan

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A key aspect of rice breeding programs is the optimization of days to heading (DTH) for maximizing grain productivity in cultivation areas. Here, the effects of genotypes for heading date on yield-related traits in rice (culm and panicle length (CL and PL), panicle number (PN), and total number of seeds) were investigated. *Heading date 1* (*Hd1*) and *Days to heading 8* (*DTH8*) are the main controllers of the variation in heading date in the rice population of Hokkaido, Japan. Thus, an F<sub>2</sub> population (n = 192) derived from a cross between Kitaibuki (*Hd1dth8*) and Akage (*hd1DTH8*) was developed. Significant differences in DTH were found among all combinations. Each genotype for heading date showed variations in the yield-related traits without a significant difference. However, DTH exhibited high positive coefficient values (more than 0.709) with the yield-related traits except for PN, which had a negative coefficient value of -0.431. A later heading date resulted in a longer growth duration and a higher yield with a combination of longer PL and CL and lower PN. These results suggest that DTH limits the yield-related traits rather than the genotype for heading date.

**Key Words:** rice, heading date, yield, days to heading (DTH), *Hd1*, *DTH8*.

## Introduction

Heading date in crop species is a limiting factor of species range and cropping season. Variations in the heading date are determined by the response to seasonal cues from changing environmental factors, including day length and temperature (Blümel *et al.* 2015, Fujino *et al.* 2019a, Hill and Li 2016, Hu *et al.* 2019). Expanding the species range is a major goal for crop breeding programs in improving the food supply for the growing worldwide population and under the conditions of global warming. Many genes for the control of heading date in rice have been identified (Gramene, <http://www.gramene.org>), and a genetic network for heading date has been proposed (Hori *et al.* 2016, Tsuji *et al.* 2011). However, it is unclear whether the genotype for heading date affects the yield in agriculture.

Asian cultivated rice, *Oryza sativa* L., originated in the tropics (Choi *et al.* 2017, Fuller 2011). Extensive efforts in rice breeding programs to optimize the heading date have made the stable production of rice possible under various climatic conditions at latitudes ranging from 53°N to 40°S (Fujino *et al.* 2015, 2017, 2019a, 2019b, Lu and Chang 1980, Shinada *et al.* 2014). An earlier heading date, by a

decrease in the photoperiod sensitivity, may have played an important role in expanding the range of rice (Fujino *et al.* 2019a, 2019b, 2019c, Izawa 2007, Shrestha *et al.* 2014, Zheng *et al.* 2016).

Based on a series of genetic analyses for the heading date in rice, QTLs/genes for an extremely early heading date were previously identified. Only varieties with an extremely early heading date were adapted to Hokkaido (41–45°N latitude), Japan, which has a long natural day length of more than 15 hours in summer (Fujino and Sekiguchi 2005a, 2005b, 2008, Fujino *et al.* 2013, 2019a, 2019b, 2019c, Nonoue *et al.* 2008). The loss-of-function alleles at *Oryza sativa Pseudo-Response Regulator37* (*OsPRR37*) and *Grain number, plant height and heading date 7* (*Ghd7*) accounted for the extremely early heading date in EARLY-DUO (Fujino *et al.* 2019a, Gao *et al.* 2014, Koo *et al.* 2013, Xue *et al.* 2008).

In addition to the adaptability to local environmental conditions, genes shaping the adaptability have been selected for stable rice production in modern agriculture. A loss-of-function allele at *Heading date 1* (*Hd1*), *hd1*, was selected for in the early phase of expanding the rice range to northern Japan (Yokoo *et al.* 1980). Rice breeding programs in Hokkaido introduced functional alleles to the *Hd1* locus, *Hd1*, in the Hokkaido rice population. Under long-day conditions, a functional *Hd1* delays the heading date (Hayama *et al.* 2003, Yano *et al.* 2000), whereas a functional *Hd1* promotes an earlier heading date in EARLY-

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DUO (Fujino *et al.* 2019b).

Furthermore, the gene controlling the cropping season in Hokkaido has been identified. A loss-of-function allele at *Heading date 5 (Hd5)*, *hd5*, accounted for the earlier heading date in the Hokkaido rice population in an early-maturing type (Fujino 2003, Fujino *et al.* 2013). *Hd5* is allelic to *Days to heading 8 (DTH8)*, encoding a putative HAP3 subunit of a CCAAT-box-binding transcription factor (Fujino *et al.* 2013, Wei *et al.* 2010).

Rice breeding programs in Hokkaido had great success in the development of new varieties expressing good eating quality with a unique adaptability to Hokkaido's climate (Fujino *et al.* 2019a, 2019c). The heading date and yield are major determinants for the development of commercial rice. The yield-related traits (panicle length (PL), culm length (CL), panicle number (PN), and total number of seeds (TS)) are indicators of yield in rice. Due to the significance of rice in agriculture, many mappings and molecular cloning of QTLs for heading date and yield have been reported, revealing the natural variations of the traits. Some have shown common associations between heading date and yield; delaying the heading date causes an increase in yield.

The genes and genotype for the heading date established by rice breeding programs in Hokkaido have been investigated (Fujino *et al.* 2019a). However, the genetic base for rice yield in agriculture was still unclear. Pleiotropic effects of the heading date genes on the developmental phase in panicles have been reported (Endo-Higashi and Izawa 2011, Fujino and Ikegaya 2020, Fujino *et al.* 2019a, Wei *et al.* 2010, Weng *et al.* 2014, Xue *et al.* 2008). Furthermore, it was unclear whether the genotype for heading date regulates the yield-related traits as a genetic background. Here, we examined the effects of *Hd1* and *DTH8* on yield in the Hokkaido rice population.

## Materials and Methods

### Plant material

Two *japonica* rice varieties from Hokkaido, Kitaibuki (KT) and Akage (AG), were used as the parental varieties. KT was registered in 1990 in rice breeding programs in Hokkaido. AG is a landrace variety in Hokkaido. To identify the effects of *Hd1* and *DTH8* on the yield-related traits, an F<sub>2</sub> population (n = 192) derived from a cross between KT (*Hd1dth8*) and AG (*hd1DTH8*) was developed.

### Cultivation methods

Seeds of these rice varieties were provided by the Local Independent Administrative Agency Hokkaido Research Organization Hokkaido Central Agricultural Experiment Station (Takikawa, Japan). All plant materials were cultivated in an experimental paddy field at Hokkaido Agricultural Research Center (Sapporo, Hokkaido, Japan, 43°00' N latitude) in 2015 with 15.0 cm spacing between the plants within each row and 30.0 cm spacing between rows. Cultiva-

tion management followed the standard procedures used at Hokkaido Agricultural Research Center. Sowing and transplanting were performed on April 27 and May 21, 2015, respectively.

### Trait evaluation

The heading date was measured for all F<sub>2</sub> plants as days to heading (DTH). DTH is the number of days from sowing to heading of the earliest heading panicle on an individual. As yield-related traits, CL, PL, PN, and TS were evaluated in accordance with Fujino *et al.* (2017). These yield-related traits were measured in plants with the four genotypes homozygous in both *Hd1* and *DTH8*. In addition, the internode length and panicle components were measured according to Fujino and Ikegaya (2020). The phenotypes were averaged for each line/variety and were compared using Tukey–Kramer HSD test among genotypes. Genetic interactions between *Hd1* and *DTH8* on the yield-related traits were calculated by two-way ANOVA.

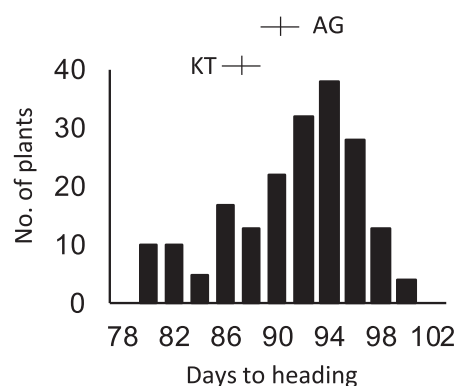
### DNA analysis

Total DNA was isolated from young leaves using the CTAB method (Murray and Thompson 1980). The genotypes of *Hd1* and *DTH8* were determined using the primers for functional nucleotide polymorphisms in these genes (Fujino *et al.* 2013, 2019a). PCR and electrophoresis were performed as described previously (Fujino *et al.* 2004, 2005).

## Results

### Variation in heading dates by *Hd1* and *DTH8*

There was a significant difference ( $p < 0.001$ , *t*-test) in DTH between the parental varieties (Fig. 1, Table 1). The DTH of KT was  $87.7 \pm 0.7$  days, whereas that of AG was  $91.5 \pm 0.9$  days. A wide and continuous variation was observed in the frequency distribution of DTH among the F<sub>2</sub> populations, ranging from 80 to 100 days (Fig. 1).



**Fig. 1.** Frequency distribution of days to heading among the F<sub>2</sub> populations (n = 192) derived from a cross between Kitaibuki (KT) and Akage (AG). Vertical and horizontal bars show the mean and range of days to heading, respectively, in the parents.

**Table 1.** Average days to heading (DTH) among nine genotypes for heading date

Genotype		No. of plants	DTH		
<i>DTH8</i>	<i>Hd1</i>		Range		
			Minimum	Maximum	
A	A	14	96.4 ± 2.1d	92	100
A	H	26	94.4 ± 2.7cd	90	100
A	B	19	91.3 ± 3.0bc	86	96
H	A	21	96.0 ± 1.9d	92	100
H	H	44	92.1 ± 3.3bc	82	98
H	B	25	89.2 ± 3.7b	80	94
B	A	13	90.5 ± 2.7bc	86	96
B	H	17	84.7 ± 3.1a	80	92
B	B	13	80.9 ± 1.0a	80	82

A, B, and H in genotype indicate the Akage (*DTH8hd1*), Kitaibuki (*dth8Hd1*) and heterozygous alleles, respectively. DTH is expressed as mean ± standard deviation. Different letters indicate significant differences at  $p < 0.05$ .

According to the genotypes of *Hd1* and *DTH8*, plants in this population were classified into nine genotypes with significantly different DTH (**Table 1**).

Fifty-five plants in the four classes homozygous in both the *Hd1* and *DTH8* alleles were selected and used for further analysis of the associations between DTH and yield-related traits. First, the effects of *Hd1* and *DTH8* on the heading date were examined (**Table 1**). The genotype *Hd1DTH8* was defined as a wild type (WT) with DTH of 91.3. *hd1* delayed DTH by 5.4 days in comparison to WT, whereas *dth8* significantly decreased DTH by 10.2 days in comparison to WT. *hd1dth8* decreased DTH by 0.6 days in comparison to WT, suggesting that *hd1* and *dth8* epistatically controlled DTH.

### Comparison of the yield-related traits among the genotypes for heading date

To elucidate the role of genotypes for heading date on the yield-related traits, means of the four traits, PL, CL, PN, and TS, were compared among the four genotypes of *Hd1* and *DTH8* (**Table 3**). No abnormality in the yield-related traits evaluated in this experiment was observed in

**Table 3.** Coefficient in the yield-related traits among the four genotypes for heading date in the F<sub>2</sub> population

	DTH	PL	CL	PN	TS
DTH	1				
PL	0.763212	1			
CL	0.825262	0.770695	1		
PN	-0.42837	-0.33047	-0.42183	1	
TS	0.90472	0.740094	0.77523	-0.36027	1

DTH: days to heading, CL: culm length, PL: panicle length, PN: panicle number, TS: total number of seeds.

All values indicate significant differences at  $p < 0.05$ .

genotypes with the recessive alleles of genes for heading date, *hd1* and *dth8* with EARLY-DUO, *ghd7*, and *ospr37* (Fujino *et al.* 2019a).

The variation in PL in the four genotypes for heading date was 12.2–20.5 cm (**Table 2**). PL increased by 0.6 cm and *dth8* decreased by 3.8 cm in *hd1* in comparison to WT (17.4). PL epistatically exhibited a 0.2-cm increase in *hd1dth8* (**Supplemental Table 1**). The variation in CL was 51.5–92.5 cm. CL increased by 9.1 cm in *hd1* and decreased by 16.4 cm in *dth8* in comparison to WT (75.5). *hd1dth8* epistatically exhibited a 0.4-cm decrease in CL (**Supplemental Table 1**). The variation in PN was 10–32. PN decreased by 0.9 in *hd1* and increased by 6.2 in *dth8* in comparison to WT (16.7). *hd1dth8* additively exhibited a 2.5 increase in PN (**Supplemental Table 1**). In TS, WT increased by 8.1 in *hd1* and decreased by 46 in *dth8* in comparison to WT (87.4). *hd1dth8* epistatically exhibited a 5.4 decrease in TS.

*Hd1dth8* exhibited the earliest heading date with the smallest standard deviation, 80.9 ± 1.0 in DTH. PL, CL, TS, and PN in the *Hd1dth8* genotype were significantly smaller than those in the other genotypes (**Table 2**). Although there were no significant differences in yield-related traits among the three genotypes for heading date, *Hd1DTH8*, *hd1DTH8*, and *hd1dth8*, DTH had high positive coefficient values for PL, CL, and TS of more than 0.709 (**Fig. 2, Table 3**), whereas PN had a negative coefficient for DTH of -0.431.

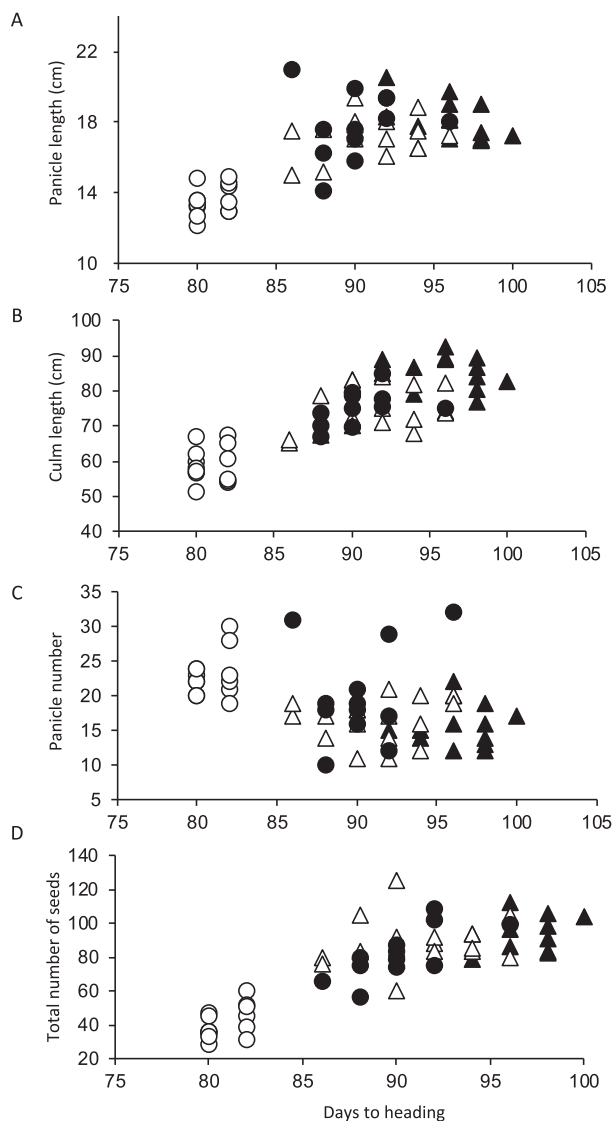
**Table 2.** Differences in yield-related traits among genotypes for heading date

Genotype	No. of plants	Trait														
		DTH			PL			CL			PN			TS		
		Average	Minimum	Maximum	Average	Minimum	Maximum	Average	Minimum	Maximum	Average	Minimum	Maximum	Average	Minimum	Maximum
<i>DTH8hd1</i>	13	96.5 ± 2.2a	92.0	100.0	18.0 ± 1.2b	16.5	20.5	84.6 ± 5.6c	74.0	92.5	15.8 ± 3.1b	12	22	95.5 ± 10.7b	79	112
<i>Dth8Hd1</i>	18	91.1 ± 3.0b	86.0	96.0	17.4 ± 1.1b	15.0	19.4	75.5 ± 6.8b	65.0	85.0	16.7 ± 3.1b	11	21	87.4 ± 14.0b	60	125
<i>dth8hd1</i>	11	90.5 ± 2.4b	86.0	96.0	17.6 ± 1.7b	14.1	19.9	75.1 ± 5.1b	67.0	85.0	19.2 ± 6.5ab	10	32	82.0 ± 15.1b	56	108
<i>dth8Hd1</i>	13	80.9 ± 1.0c	80.0	82.0	13.6 ± 0.8a	12.2	14.9	59.1 ± 5.1a	51.5	67.5	22.9 ± 3.1a	19	30	41.4 ± 9.4a	28	60

DTH: days to heading, PL: panicle length, CL: culm length, PN: panicle number, TS: total number of seeds.

Values in the traits are expressed as mean ± standard deviation.

Different letters indicate significant differences at  $p < 0.05$ .



**Fig. 2.** Associations of days to heading with the yield-related traits of the four genotypes for heading date, *dth8Hd1* (open circle), *dth8hd1* (closed triangle), *DTH8Hd1* (open triangle), and *DTH8hd1* (closed circle). (A) panicle length, (B) culm length, (C) panicle number, and (D) total number of seeds.

### Variation of the component traits in CL and TS

CL and TS were compared among the four genotypes for heading date. In CL, variations in the internode length were in the ranges of 28.0–42.5 in I, 17.5–27.0 in II, 4.0–20.5 in III, and 0–10.5 in IV (**Supplemental Table 2**). The lengths of the II, III, and IV internodes were regulated additively by *Hd1* and *DTH8*, whereas that of I was regulated epistatically (**Supplemental Table 1**). *dth8* significantly decreased the internode lengths of I–III, whereas *hd1* significantly increased the internode length of specifically IV. High positive coefficient values were observed between DTH and the internode length of more than 0.646 (**Supplemental Fig. 1, Supplemental Table 3**).

TS was expressed as the sum of seeds on the primary

branches (Pb) and secondary branches (Sb). *dth8* had significantly smaller numbers of both Pb and Sb, decreasing TS. The variations in Pb and Sb were 4–12 and 3–22, respectively (**Supplemental Table 4**). Pb increased by 1.4 in *hd1* and decreased by 3.1 in *dth8* in comparison to WT (8.3). Pb epistatically decreased by 0.2 in *hd1dth8*. For Sb, *hd1* and *dth8* decreased by 0.2 and 8.3, respectively, in comparison to WT (13.9). Sb epistatically decreased by 1.2 in *hd1dth8*.

Similar to the numbers of Pb and Sb, the numbers of seeds on the Pb (SPb) and Sb (SSb) depended on the genotype for heading date. The variations in SPb and SSb were 18–68 and 8–64, respectively (**Supplemental Table 3**). SPb increased by 8.4 in *hd1* and decreased by 21.6 in *dth8* in comparison to WT (48.1). SPb epistatically decreased by 2.5 in *hd1dth8*. For SSb, *hd1* and *dth8* decreased by 0.4 and 24.6, respectively, in comparison to WT (39.4). SSb epistatically decreased by 3.6 in *hd1dth8*.

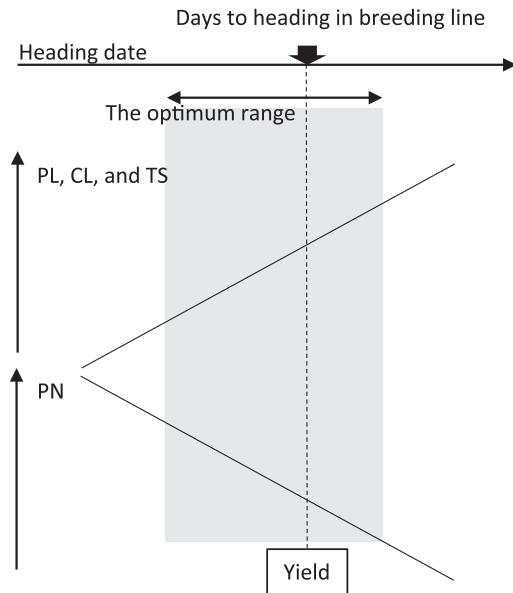
Pb and SPb had higher coefficients for DTH than Sb and SSb (**Supplemental Fig. 2, Supplemental Table 5**). TS also had a high positive coefficient value for DTH (0.826).

## Discussion

Optimization of the heading date to maximize yield in agriculture has been shown in differentiated rice populations from different environments. Rice breeding programs generate novel genotypes other than those in natural populations for exploring the adaptability beyond native species ranges and produce stable rice production (Fujino *et al.* 2019a, Hua *et al.* 2019, Huang *et al.* 2018). *Hd1* and *DTH8* generated a variation in the heading date within the Hokkaido rice population (Fujino and Sekiguchi 2005a, Fujino *et al.* 2013, 2019a, 2019c). Here, the effects of *Hd1* and *DTH8* on yield were examined.

*Hd1* and *DTH8* generated a significant variation in heading date within the growth period in Hokkaido (**Tables 1, 2**). There were no significant differences in the yield-related traits among the genotypes. However, higher coefficient values were found between DTH and yield-related traits (**Supplemental Tables 3, 5**). DTH positively increased PL, CL, and PL, and negatively increased PN (**Table 3**). *Hd1* and *DTH8* may have roles additively and epistatically on the regulation of the yield-related traits and exhibit opposite but different degrees of effects on these traits (**Table 2, Supplemental Table 1**). Variations in DTH in each genotype were similar. DTH showed high positive coefficients with yield-related traits, suggesting that it limits yield rather than the genotype for heading date.

Genes for yield-related traits have epistatic effects on each other (Ando *et al.* 2008, Takai *et al.* 2014, Xu *et al.* 2015). In addition, they may be involved in the pleiotropy of DTH. The genetic role of yield makes their control difficult and complex in rice breeding programs. Previously, associations of DTH with yield-related traits have been demonstrated using series of NILs (Fujino and Ikegaya



**Fig. 3.** Model of the selection during rice breeding programs in Hokkaido. Days to heading (DTH) of the breeding line is within the optimum range (black and bold arrow) of DTH in Hokkaido. The breeding line whose yield is limited by DTH is selected, which is more favorable than those of the current commercial varieties.

2020, Fujino *et al.* 2019a). The higher coefficient values in these studies indicate that the significance of genes/QTLs for the heading date plays a role not only in the control of heading date but also in the regulation of yield.

**Fig. 3** shows the model for the selection of desirable lines in rice breeding programs in Hokkaido is proposed. Desirable lines may exhibit a heading date within the optimum range to produce rice grain with good eating quality. A later heading date produces a maximum growth duration and a higher yield with a combination of longer PL and CL and lower PN. The total seed number is determined as panicle architecture depending on the DTH.

During the process of rice breeding programs in Hokkaido, exotic germplasm may generate novel phenotypes (Fujino *et al.* 2015, 2017, Shinada *et al.* 2014). Genes controlling the heading date were under selection for their unique adaptability to environmental conditions and stable rice production (Fujino *et al.* 2019a). In addition, this study confirmed that the genes for heading date may regulate not only an optimized heading date but also maximize the fitness to agriculture. The pleiotropy of DTH may clarify the yield complex in modern rice breeding programs to develop new rice varieties. Current genomic tools may facilitate rice breeding programs for future demands.

### Author Contribution Statement

Conceived and designed the experiments: KF. Performed the experiments, analyzed the data, and wrote the manuscript: KF.

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