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# Identification and validation of a major quantitative trait locus for precise control of heading date in wheat (*Triticum aestivum* L.)

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## Abstract

**Background** Heading date (HD) is a crucial agronomic trait in wheat, significantly influencing both adaptation and yield. Despite having identical genotypes for the major heading genes *Vrn-1* and *Ppd-1*, two Korean wheat cultivars, Jokyoung and Joongmo2008, exhibit substantial differences in heading date. However, the underlying genetic factors responsible for this variation remain unclear. To address this, we aimed to identify major quantitative trait loci (QTLs) associated with narrow-sense earliness under field conditions and develop a practical molecular marker for wheat breeding programs.

**Results** A recombinant inbred line (RIL) population was developed from a cross between the late-heading Jokyoung and the early-heading Joongmo2008 using speed breeding systems. The RILs were genotyped using a 35 K SNP chip, and a genetic map was constructed. A stable QTL for HD (*qDH-3A*) was identified on chromosome 3A, with an average logarithm of the odds (LOD) score of 59.4, explaining 72.6% of the phenotypic variance in HD across three years of field phenotyping. This indicates the robustness of *qDH-3 A* across multiple environments. Additionally, a kompetitive allele-specific PCR (KASP) marker linked to *qDH-3A* was developed and validated. The marker showed significant genotypic differences and effectiveness across diverse genetic backgrounds, including 616 worldwide wheat accessions.

**Conclusions** The successful application of the KASP marker in both the RIL population and broader genetic resources highlights its potential use for marker-assisted selection (MAS) in wheat breeding programs. This study provides valuable insights into the genetic basis of HD in wheat and offers practical tools for developing cultivars better adapted to specific environmental conditions.

**Keywords** Wheat, Heading date, QTL, Plant breeding, Marker

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## Background

Heading date is a critical factor in wheat adaptation and yield potential across various cultivation conditions [1]. In Korea, early-heading cultivars are significantly associated with higher protein content and improved gluten quality, owing to an extended maturation period [2]. Wheat transitions from vegetative to reproductive stages in response to temperature and photoperiod, making these environmental cues essential for regulating heading date [3]. Breeders select suitable genotypes for each region by prioritizing traits such as phenological characteristics (heading date and maturity period) and components of yield [4].

Flowering time in wheat is primarily regulated by three pathways: vernalization, photoperiod, and earliness per se (*Eps*) [5]. The vernalization gene *Vrn-1*, located on chromosomes 5A, 5B, and 5D, is activated by low temperatures [6]. The alleles *Vrn-A1*, *Vrn-B1*, and *Vrn-D1* induce a spring growth habit, whereas the recessive forms (*vrn-A1*, *vrn-B1*, and *vrn-D1*) lead to a winter growth habit. In contrast, the photoperiod-responsive gene *Ppd-1*, located on chromosomes 2A, 2B, and 2D, determines photoperiod sensitivity: *Ppd-1a* alleles confer insensitivity to photoperiod, consequently enabling earlier heading, whereas *Ppd-1b* alleles confer sensitivity [5]. The narrow-sense *Eps* genes have been fine-mapped on chromosomes 1B and 1D, with additional quantitative trait loci (QTLs) identified in several other chromosomes, including 1B, 2D, 4A, 5A, 5B, 6A, 7A, and 7D. However, the specific roles of these genes remain unclear [5, 7–8]. Despite the complexity of the genetic architecture underlying heading date, *Eps* genes hold potential for fine-tuning heading date to adapt to various environmental conditions.

In this study, we aimed to identify the key QTLs and candidate genes that enable precise control of heading date using a recombinant inbred line (RIL) population derived from two Korean wheat cultivars with identical genotypes for *Vrn-1* and *Ppd-1*. We further aimed to develop a practical molecular marker for wheat breeding programs, ultimately supporting the development of wheat cultivars adaptable to diverse environmental conditions.

## Materials and methods

### Plant materials and phenotyping days to heading

A RIL population was developed through a cross between the late- and early-heading hard white wheat cultivars Jokyoung and Joongmo2008, respectively. Jokyoung was developed from a cross between Seri 82, a hard white wheat line from CIMMYT, and the Korean hard white wheat cultivar Keumgang. Joongmo2008 also shares Keumgang as a common parent, derived from a cross between Keumgang and the breeding line (Eunpamil*2/SH3/CBRD). Both Jokyoung and Joongmo2008 were developed through conventional field-based breeding methods. The RIL population was generated using the single-seed descent method as described by Cha et al. [9], combining a speed vernalization (SV) system with a speed breeding (SB) system (Fig. S1).

In total, 175 RILs and 61 Korean wheat cultivars were cultivated in a field located in Miryang, Republic of Korea (35°29'32.9"N, 128°44'33.4"E), during the 2020.11–2021.06, 2021.11–2022.06, and 2022.11–2023.06 seasons. Over 20 seeds were hand-planted per row, with a spacing of 30 cm between rows and 15 cm between plants within rows. Fertilizer application rates were 9.1 kg of N, 7.4 kg of $P_2O_5$, and 3.9 kg of $K_2O$ per 1,000 $m^2$.

A total of 555 worldwide genetic resources reported by Min et al. [10] were cultivated in three years (2018–2020), with detailed information reported by Kang et al. [11].

The heading date of each line and cultivar was recorded when >40% of ears were visible. Days to heading (DH) were calculated as the number of days from the sowing date to the heading date.

### Linkage map construction, QTL analysis, and identification of candidate genes

Genomic DNA was extracted from fresh seedling leaves using the cetyltrimethylammonium bromide method (CTAB) [12]. The RILs were genotyped using the Axiom 35 K Wheat Breeder's Array, which includes 31,926 markers (Affymetrix UK Ltd., United Kingdom). Of these, 4,341 single nucleotide polymorphisms (SNPs) were polymorphic between Jokyoung and Joongmo2008 (Fig. S2). SNPs with >20% missing data or showing significant segregation distortion ($P<0.01$) were excluded. A final set of 2,677 markers was used to construct a genetic map using IciMapping v4.2. The map was constructed through grouping by anchor only, ordering by input order, and rippling by REC, employing the mapping function of IciMapping. QTLs for DH were identified using the BIP function in IciMapping through the inclusive composite interval mapping method. The following parameters were used: Step size = 1 cM, PIN = 0.001, and 1,000 times of permutation ($P<0.05$).

To further validate the reproducibility and robustness of the QTL analysis, additional statistical analyses were conducted using the GAPIT package (version 3.0) and the R/qtl package in RStudio (version 1.4.1717). Association analysis in GAPIT was performed based on the Fixed and random model Circulating Probability Unification (FarmCPU) method [13], with genome-wide significance thresholds adjusted by Bonferroni correction [14]. In R/qtl, the QTL position detected by IciMapping was directly modeled using the makeqtl() and fitqtl() functions to confirm its statistical significance and estimate the proportion of phenotypic variance explained.

Allele-specific markers were used as listed in Table S1 to genotype the *Vrn-1* and *Ppd-1* alleles, the major vernalization and photoperiod response genes [15–17]. Polymerase chain reaction (PCR) was performed in a 30 µL reaction volume, containing 25 ng template DNA, 0.5 µM of each primer, 2.5 µL of 10 mM dNTPs, 3.0 µL of 10X buffer, and 0.3 µL Taq polymerase (Genetbio, Korea). Primer sequences, PCR product sizes, and amplification parameters for each marker are detailed in Table S1.

The candidate genes for the identified QTL were found using the EnsemblePlants database (https://plants.ensembl.org/Triticum_aestivum/Info/Index). Further informati on on these genes was extracted from the UniProt database (https://www.uniprot.org).

#### Kompetitive allele-specific PCR (KASP) assay

The Ax-95079372 marker from the 35 K chip was converted into a KASP marker using the reference sequence and SNP data obtained from the National Center for Biotechnology Information to genotype *qDH-3A*. The KASP marker was designed using the KASP assay design service provided by LGC Genomics (LGC Ltd., Teddington, UK), as detailed in Table S1.

The PCR conditions were as follows: initial denaturation at 95 °C for 20 s; 10 cycles of annealing at an initial temperature of 65 °C, with 1 °C increments per cycle for 25 s. This was followed by 30 additional cycles of annealing at 95 °C for 10 s and 57 °C for 1 min, concluding with extension at 72 °C for 5 min. Fluorescence detection and subsequent data analyses were carried out using a QuantStudio 3 real-time PCR system and the QuantStudio Design & Analysis Software v1.5.1 (Applied Biosystems, Carlsbad, CA, USA).

#### Statistical analysis

T-tests and multi-way analysis of variance were performed using RStudio (version 1.4.1717; RStudio, PBC, Boston, MA, USA).

## Results

#### Differences in heading date despite identical major heading genes

A significant difference in heading date was observed between Jokyoung and Joongmo2008 in this study. Joongmo2008 consistently headed earlier than Jokyoung across all three growing seasons, with differences of three, four, and four days in 2021, 2022, and 2023, respectively (Fig. 1A, Table S2). The distribution of DH in the RIL population ranged from 160 to 175 days in 2021, 156 to 172 days in 2022, and 162 to 181 days in 2023.

Genotypic analysis of the *Vrn-1* and *Ppd-1* loci revealed that both cultivars carried identical alleles for all six genes: *vrn-A1*, *vrn-B1*, and *Vrn-D1* for *Vrn-1*, and *Ppd-A1b*, *Ppd-B1b*, and *Ppd-D1a* for *Ppd-1* (Table 1).

#### Major QTL and candidate genes for fine control of heading date

A linkage map of the Jokyoung × Joongmo2008 RIL population was constructed using 2,677 polymorphic markers from the Axiom 35 K DNA chip (Fig. S3). The total genome length covered was 35,321 cM, with individual chromosome lengths ranging from 876 cM on chromosome 4D to 4,014 cM on chromosome 1B (Table S3).

A single environmentally stable QTL, *qDH-3A*, was identified on chromosome 3A for DH, with no additional QTLs detected on other chromosomes (Fig. 1B; Table 2). The logarithm of the odds (LOD) scores for *qDH-3A* were 61.4, 55.2, and 61.6 in 2021, 2022, and 2023, respectively. This QTL explained an average of 72.6% of the observed variation in DH, with an early heading effect of 3.54–4.85 days contributed by Joongmo2008. The percentage of phenotypic variation explained (PVE) was 78.5%, 67.3%, and 72.0% for 2021, 2022, and 2023, respectively.

The *qDH-3A* QTL was mapped between the SNP markers Ax-94603874 and Ax-95079372, located between 1135.5 cM and 1136.5 cM on chromosome 3A (Fig. 1C). This region corresponds to the physical interval from 737.97 Mbp to 739.52 Mbp, according to the IWGSC RefSeq v1.0 (Fig. 1D).

Both Ax-94603874 and Ax-95079372 exhibited significant differences in DH between Jokyoung- and Joongmo2008-type lines ($P < 0.0001$). In contrast, markers outside the *qDH-3A* region showed no significant differences between SNP alleles ($P > 0.5$) (Fig. 1E).

To validate the robustness of this major QTL, additional analyses were conducted using GAPIT and R/qtl. In GAPIT, the same SNP marker Ax-95079372, located at 739.52 Mbp on chromosome 3A, was identified as significantly associated with heading date across all three years ($-\log_{10}(p) = 67.1$, 51.4, and 58.9 in 2021, 2022, and 2023, respectively) (Table S4). Furthermore, a QTL model was fitted in R/qtl using the makeqtl() and fitqtl() functions targeting the IciMapping-identified interval (1136 cM). The fitted model yielded LOD scores of 55.8, 41.1, and 45.7, and PVE values of 77.0%, 66.1%, and 69.9% in 2021, 2022, and 2023, respectively, with all effects being highly significant ($P < 2.2 \times 10^{-16}$) (Table S5). Thirty-two candidate genes were identified within these two markers (Table S6).

These cross-platform results consistently support the presence of a major QTL for heading date at the same genomic position on chromosome 3A, confirming the stability and reyliabilit of *qDH-3A*.

#### Development and validation of the *qDH-3A* KASP assay for broad applicability

A KASP marker was designed based on the sequence of the Ax-95079372 SNP chip marker and subsequently validated. The RIL population was initially genotyped using

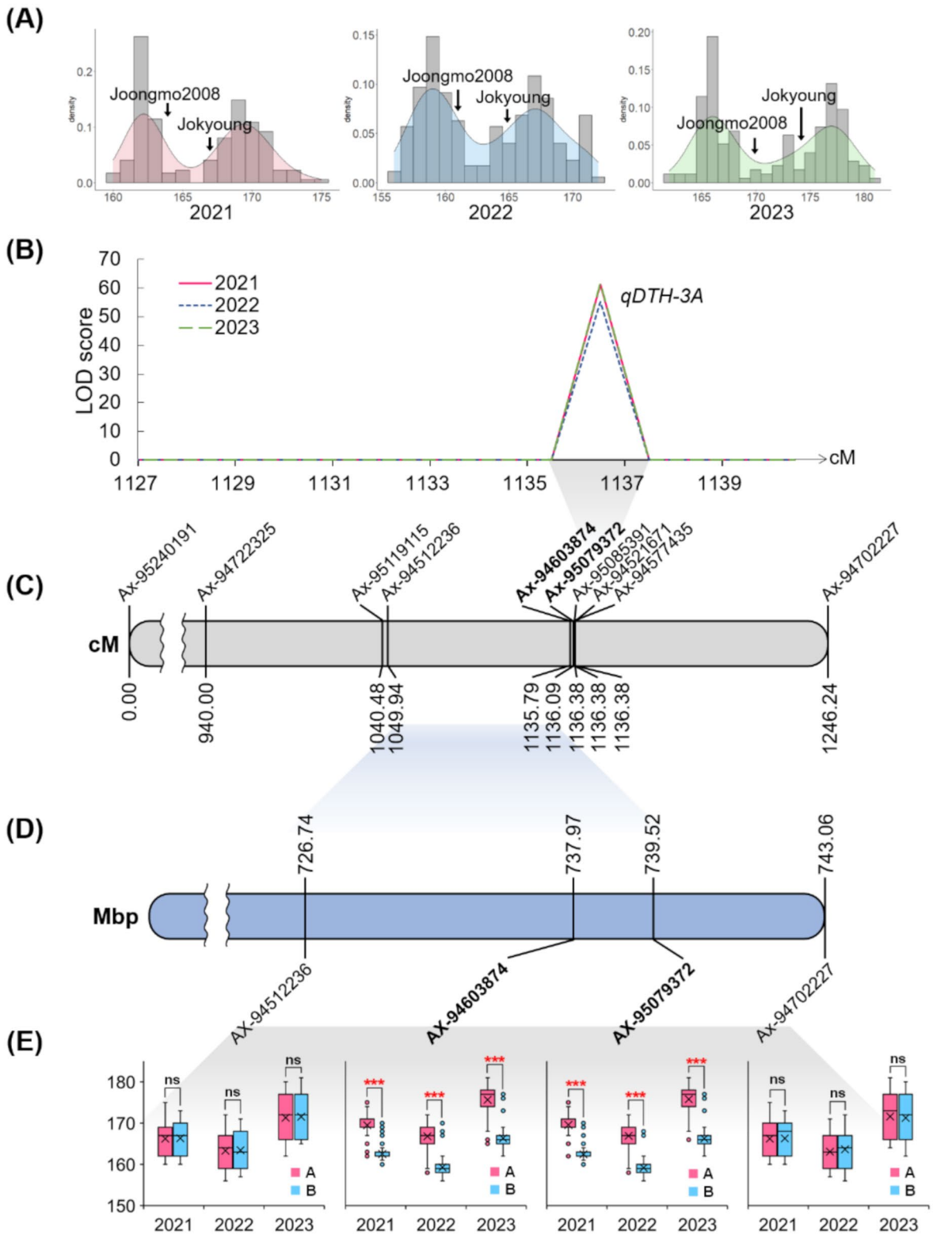


**Fig. 1** QTL analysis for days to heading (DH) on chromosome 3A in the Jokyoung × Joongmo2008 RILs. (**A**) Distribution of DH across three growing seasons. (**B**) QTL mapping for DH on chromosome 3A across three years. (**C**) A genetic map of the *qDH-3A* region in the RIL population. (**D**) A physical map of the *qDH-3A* region based on IWGSC RefSeq v.1.0. (**E**) T-test comparison of DH based on the SNP alleles for each marker (A: Jokyoung-type; B: Joongmo2008-type; ns: $P > 0.05$; ***: $P < 0.0001$)

**Table 1** Genotypes of *Vrn-1* and *Ppd-1* in the two parental lines

| Variety Name | Vrn-A1 | Vrn-B1 | Vrn-D1 | Ppd-A1 | Ppd-B1 | Ppd-D1 |
|---|---|---|---|---|---|---|
| Jokyoung | *vrn-A1* | *vrn-B1* | *Vrn-D1* | *b* | *b* | *a* |
| Joongmo2008 | *vrn-A1* | *vrn-B1* | *Vrn-D1* | *b* | *b* | *a* |

**Table 2** Quantitative trait loci for days to heading detected in the RIL population

| Year | Chromosome | Position (cM) | Left marker | Right marker | LOD | PVE (%) | Add | Left CI | Right CI |
|---|---|---|---|---|---|---|---|---|---|
| 2021 | 3A | 1136 | AX-94603874 | AX-95079372 | 61.39 | 78.47 | 3.54 | 1135.5 | 1136.5 |
| 2022 | 3A | 1136 | AX-94603874 | AX-95079372 | 55.17 | 67.29 | 4.01 | 1135.5 | 1136.5 |
| 2023 | 3A | 1136 | AX-94603874 | AX-95079372 | 61.58 | 72.02 | 4.85 | 1135.5 | 1136.5 |

this KASP marker (Fig. 2A). The results aligned with the Axiom chip data, with all RILs clearly distinguished by the KASP marker. Lines carrying the Jokyoung-type (allele 'G') and Joongmo2008-type (allele 'A') were plotted along the x- and y-axes, respectively.

The developed *qDH-3A* KASP marker was further tested on a broader set of genetic resources, effectively distinguishing between 'G' and 'A' alleles (Fig. 2B). A significant difference was observed between lines carrying the 'G' and 'A' alleles when DH was compared according to genotype. Cultivars with the 'G' allele exhibited an average delay in DH of 2.1 days in 555 genetic resources and 2.6 days in 61 Korean cultivars, compared to those with the 'A' allele (Fig. 2C).

Given the highly significant differences in DH related to *Vrn-D1* and *Ppd-D1* genotypes ($P < 0.001$), interactions between *Vrn-D1*, *Ppd-D1*, and *qDH-3A* genotypes were evaluated (Table S7). The *qDH-3A* genotype showed significant differences in DH among genetic resources harboring the *vrn-D1* or *Ppd-D1a* alleles. In contrast, no significant difference was observed in genetic resources carrying the *Vrn-D1* or *Ppd-D1b* alleles (Fig. 2D and E).

## Discussion

### Effects of the major QTL *qDH-3A* on heading date

We evaluated the effects of the vernalization-related gene *Vrn-1* and photoperiod-related gene *Ppd-1* on heading timing in wheat, as these genes significantly affect this trait [18]. The parental lines Jokyoung and Joongmo2008 shared identical genotypes for all six alleles of *Vrn-1* and *Ppd-1*, indicating that these alleles did not substantially affect heading date. This suggests that *qDH-3A* may play a more critical role in fine-tuning DH regulation.

QTLs that influence heading date have been identified on chromosome 3A [5]. Martinez et al. identified a QTL that affects earliness per se on the short arm of chromosome 3A by evaluating near-isogenic lines under different vernalization and photoperiod conditions [19]. Our study builds on these findings by using an RIL population derived from parents with identical *Vrn-1* and *Ppd-1* genotypes. This likely enhanced our ability to detect *qDH-3A* with maximized LOD scores and PVE values. Our results identified *qDH-3A* as a fine-tuning QTL for heading date.

Interactions between *Vrn-D1*, *Ppd-D1*, and *qDH-3A* genotypes suggest that *qDH-3A* may exert different effects on heading date depending on the *Vrn-D1* background. In our study, *qDH-3A* significantly influenced heading date in RILs carrying the spring-type *Vrn-D1* and photoperiod-insensitive *Ppd-D1a* alleles, indicating that *qDH-3A* could serve as an effective selection criterion within this genetic background. However, heading date differences associated with *qDH-3A* were only observed in those with the winter-type *vrn-D1* and photoperiod-insensitive *Ppd-D1a* alleles in a broader set of genetic resources. This variation suggests that the effect of *qDH-3A* on heading date may not be consistent across different genotypic backgrounds. In addition, its influence may be limited to specific *Vrn-1* or *Ppd-1* contexts. Although *qDH-3A* shows promise for fine-tuning heading date in wheat, especially within *Vrn-D1* or *Ppd-D1* genotypes, its application in breeding may require careful consideration of the genetic background to achieve predictable outcomes.

### Linkage map and candidate genes for *qDH-3A*

The linkage map in this study showed a relatively long length compared to those in other studies; it covered 4,000–5,500 cM using 50 K–35 K SNP chip arrays [20–22]. This may be due to the low genetic diversity resulting from the use of the same parental cultivar, Keumgang, in both the Jokyoung and Joongmo2008 pedigrees [23]. As a result, only a final set of 2,677 markers was used for genetic map construction.

The presence and stability of *qDH-3A* as a major QTL was confirmed not only by IciMapping but also through cross-validation using GAPIT and R/qtl analysis. All approaches consistently identified the same genomic region on chromosome 3A across three years, supporting its robustness. Although GAPIT also detected weaker signals on chromosomes 1D and 4B, these loci showed opposite effect directions, suggesting possible interactions, which require further investigation.

Among the 32 candidate genes identified within *qDH-3A*, *TraesCS3A02G525200* may control DH in the RIL population. This gene encodes PIN-LIKES 2, a protein that regulates auxin-dependent plant growth by

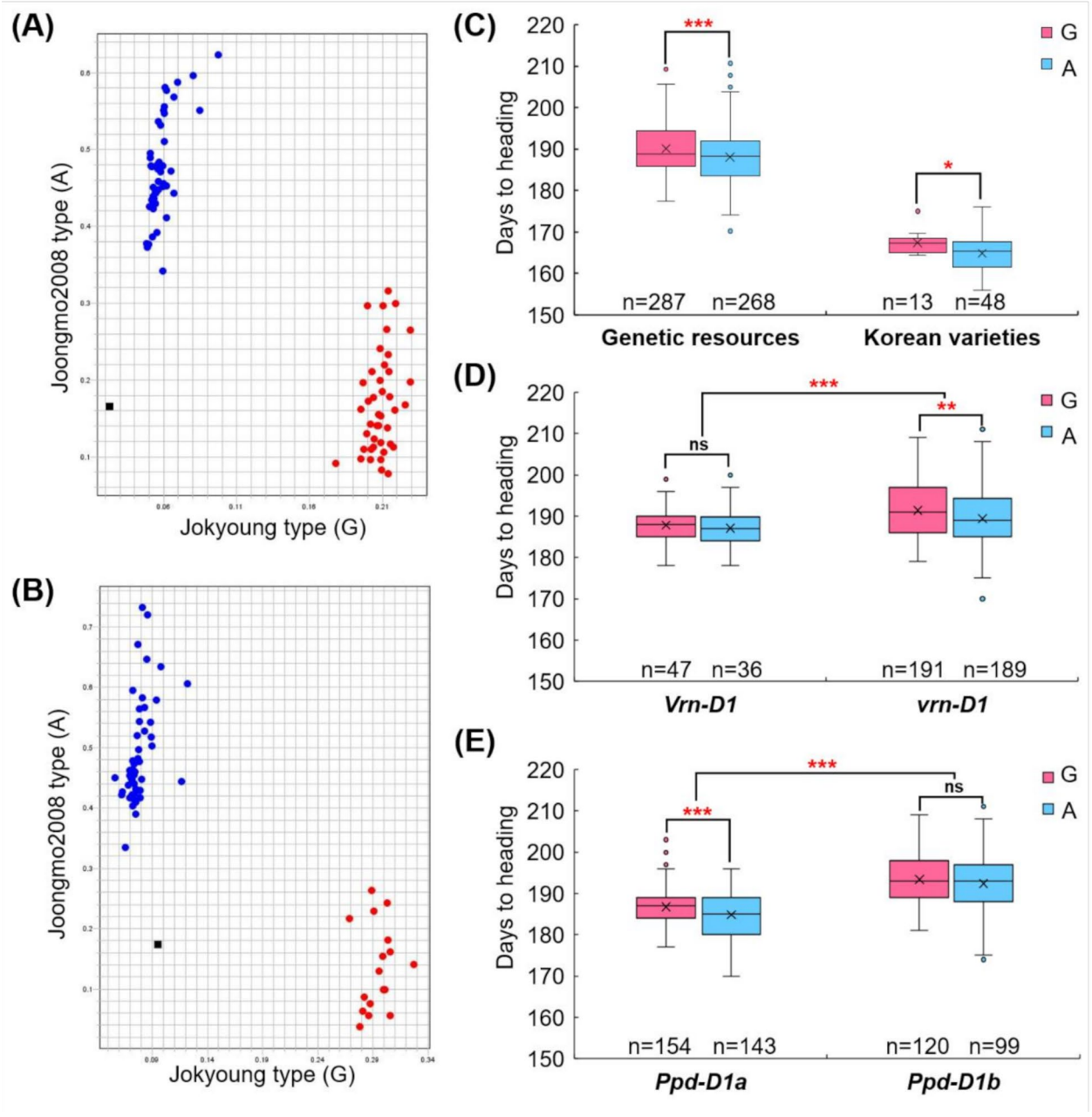


**Fig. 2** Validation of the effect of *qDH-3A* using diverse genetic resources. Development and validation of the *qDH-3A* KASP assay in (**A**) Jokyoung × Joongmo2008 RILs and (**B**) a broader set of genetic resources. Effects of the *qDH-3A* genotype on DH in (**C**) cultivars from different origins, and genetic resources grouped according to (**D**) *Vrn-D1* and (**E**) *Ppd-D1* alleles

determining cellular sensitivity to auxin [24]. Auxin is a crucial hormone involved in various growth functions, including cell elongation and organ development [25]. *TraesCS3A02G525200* controls auxin distribution to coordinate the transition from vegetative to reproductive growth, consequently impacting heading date via the shoot apical meristem and flowering initiation. Another candidate gene, *TraesCS3A02G523600*, encodes a cyclin N-terminal domain-containing protein, which is associated with cell cycle regulation [26]. Cyclins are essential for cell division and growth, and thus may contribute to developmental timing, including heading and flowering. However, its direct involvement in flowering time regulation remains to be clarified through further functional analysis. Together, these candidate genes are hypothesized to fine-tune heading date by integrating internal developmental cues and environmental signals,

although additional studies are needed to validate their roles.

Given that both Jokyoung and Joongmo2008 share Keumgang as a common parent, the observed heading date variation may be partially attributed to allelic differences derived from the other parental lines. Although direct evidence is lacking, it is plausible that the early-heading allele of *qDH-3A* in Joongmo2008 originated from Keumgang, while the late-heading allele in Jokyoung may have come from Seri 82. Further haplotype-based analysis and identification of the causal gene(s) will be needed to clarify the genetic origin of *qDH-3A*.

### Expected roles of *qDH-3A* in wheat breeding

The developed *qDH-3A* KASP marker demonstrated a significant difference in DH between genotypes in both the RIL population and diverse genetic resources. This suggests that the marker is effective not only in biparental populations but also in cultivars with varied genetic backgrounds. This broad applicability indicates that the *qDH-3A* marker can be a powerful tool for marker-assisted selection (MAS) in wheat breeding programs.

The use of this marker in breeding programs presents considerable advantages, especially in regions where optimizing heading dates is critical for yield and quality. Breeders can select the appropriate allele of *qDH-3A* to better synchronize heading dates with local climates, consequently improving wheat adaptation to environmental stresses. Strong positive correlations were observed between DH and grain number per spike (GN) in 2021 ($r = 0.793^{***}$) and 2022 ($r = 0.709^{***}$), respectively (Table S8), suggesting that GN should be considered when introducing the early-heading allele of *qDH-3A*. In contrast, spike number (SN) and thousand-grain weight (TGW) did not show significant or remarkable correlations with DH in 2021. Furthermore, DH exhibited a low positive correlation with SN ($\leq 0.430^{***}$) and a low negative correlation with TGW ($\geq -0.346^{***}$), suggesting that SN and TGW may not be strongly influenced by *qDH-3A*. Further studies are needed to investigate the allelic effects of *qDH-3A* on yield and its components across diverse genetic backgrounds. Additionally, to ensure global applicability and reliable use of this QTL, more extensive research is needed to understand its interactions with diverse heading date-related genes across various environments.

Future research could focus on fine-mapping the *qDH-3A* locus to pinpoint the specific gene(s) responsible for its regulatory effect on DH. Identifying the underlying gene(s) would not only deepen our understanding of the genetic control of heading date but also facilitate the development of more precise, gene-specific markers. These markers could significantly enhance the accuracy of MAS by enabling more targeted selections for DH, thus improving the efficiency of wheat breeding programs across various environmental conditions.

## Conclusion

In this study, we identified a stable and major QTL, *qDH-3A*, associated with HD using a RIL population derived from Korean wheat cultivars with contrasting heading behaviors. The QTL explained a significant proportion of phenotypic variation across multiple years, confirming its robustness under field conditions. A KASP marker closely linked to *qDH-3A* was developed and validated across diverse genetic backgrounds, demonstrating its potential utility for marker-assisted selection in wheat breeding programs. The application of this marker can support the selection of optimal alleles for heading date, particularly in regions where environmental adaptation is crucial for yield and quality. Future research aimed at fine-mapping and identifying the causal gene(s) underlying *qDH-3A* will provide deeper insights into the genetic regulation of HD and facilitate the development of gene-based markers for more precise breeding.

#### Abbreviations

| | |
|---|---|
| HD | Heading date |
| QTL | Quantitative trait loci |
| RIL | Recombinant inbred line |
| LOD | Logarithm of the odds |
| PVE | Phenotypic variation explained |
| KASP | Kompetitive allele-specific PCR |
| PCR | Polymerase chain reaction |
| MAS | Marker-assisted selection |
| SV | Speed vernalization |
| SB | Speed breeding |
| DH | Days to heading |
| SNP | Single nucleotide polymorphisms |

## Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06646-z.

Supplementary Material 1

#### Acknowledgements

Not applicable.

#### Author contributions

JKC, JHL, and SWK designed the experiments. JKC, HP, YK, SML, BJJ, and WJK developed and investigated the RIL population. JKC, HP, and SGJ analyzed the genomic data. CC and YK investigated the genetic resources. JKC prepared the manuscript. All the authors have discussed and agreed to participate in this manuscript.

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#### Data availability

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Ethics approval and consent to participate**
Not applicable.

**Consent for publication**
Not applicable.

**Competing interests**
The authors declare no competing interests.

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