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Unravelling consensus genomic regions conferring stem-related traits in wheat via meta-QTL analysis

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Abstract

Background Wheat stem is an important vegetative organ, that is responsible for supporting leaves and spikes, and transporting water, minerals and organic nutrients to spikes through vascular bundles, thereby promoting plant growth and development. Therefore, wheat stems contribute to plant structure and total yield.

Results We constructed a high-density consensus map and performed a meta-analysis using 306 stem-related QTLs. The results revealed 45 meta-QTLs (MQTLs) with a mean confidence interval (CI) 4.50 times lower than that of the original QTL. A total of 25/31 MQTLs (PI < 100 Mb) overlapped with SNP-trait associations reported in genome-wide association studies (GWASs). By associating MQTL interval genes with multiomics datasets and performing coexpression analysis of common genes, we generated a more reliable and concise list of putative candidate genes involved in stem regulation. Furthermore, we identified an ethylene-responsive transcription factor in the form of *TraesCS5B02G236900* haplotype, whose variations may be related to stem-related traits.

Conclusion In this study, comprehensive analysis was used to determine the most stable loci on a high-density consensus map associated with reliable genetic markers, and MQTLs, candidate genes and excellent haplotypes were identified, which laid a foundation for further research on the genetic basis of wheat stem development and promoted the development of wheat molecular breeding.

Keywords Wheat, Meta-QTL, Stem, Candidate genes, Haplotypes

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Background

Wheat (*Triticum aestivum* L.) is a widely cultivated crop that dominates global agricultural production. By the year 2050, wheat yield must increase by 60%, according to conservative estimates, to meet the worldwide demand of the growing human population [1]. Increasing grain yield remains the main objective of wheat breeding. The wheat stem is an important vegetative organ, that contributes to both plant structure and overall yield [2]. For example, Ehdaie et al. (2008) [3] reported that the contribution of stem reserves to grain yield ranged from 19.1 to 53.6% under well-watered conditions and from 36.6 to 65.4% under drought conditions. The stem is responsible for providing support to leaves and spikes and for transporting water, minerals and organic nutrients to spikes via vascular bundles, which in turn facilitate growth and development. Furthermore, the stem stores nutrients, such as water-soluble carbohydrates (WSCs), and starch, that are reallocated during later grain filling [4]. This process ensures that wheat plants have the necessary resources for growth and yield [5]. Thus, understanding the importance of the stem in wheat production is essential.

Lodging can affect the yield and quality of wheat [6], and can be reduced by decreasing plant height. However, a significant reduction in height may result in diminished grain yield [6–8]. Thus, merely shortening plant height is not a viable approach for improving crop lodging resistance [9]. However, enhancing stem-related traits is a preferred strategy for breeding crops with increased resistance to lodging and increased yield [9, 10]. In early studies of wheat stems, many stem traits related to lodging resistance, such as stem strength, plant height, basal internode length, stem diameter, stem wall thickness and pith diameter, were extensively investigated [11]. Shah et al. (2019) [12] reported the anatomical characteristics of stems (vascular bundle number, mechanical tissue layer width, etc.) and biochemical characteristics (lignin and cellulose content, etc.), as well as the effects of other factors on lodging.

Stem phenotype is widely known to be determined by complex quantitative traits that are controlled by many QTLs/genes. Stem-related quantitative trait loci (QTLs) have been identified in wheat using various mapping populations. Several QTLs related to lodging, internode diameter (ID), stem diameter (SD), stem strength (SS), WSC and other related traits have been identified [13–17]. These complex traits are governed by various gene networks that are primarily influenced by environmental conditions [15]. Moreover, QTL mapping results for these traits are subject to several factors, including the experimental conditions, population size and type, genetic map quality and density, and statistical methods utilized [18, 19]. In addition, many QTLs have low phenotypic variance explained (PVE) values and large confidence intervals (CIs), making it difficult to determine important putative candidate genes [19]. This limits the application of marker-assisted selection (MAS) for improving crop breeding [20, 21]. These weaknesses have prompted researchers to conduct meta-analysis to better use these QTLs and obtain reliable, consistent and stable meta-QTLs (MQTLs) [19, 22, 23].

Meta-analysis is a crucial tool that helps to identify stable and consistent QTL/MQTL regions associated with trait variation in different mapping studies by narrowing the confidence interval, thereby facilitating the identification of MAS candidate genes. A more comprehensive and robust statistical understanding of a particular phenomenon can be achieved by comparing/merging data from different sources [24–27]. To date, several meta-analyses have been conducted on different traits for different specializations, enabling the identification of multiple consistent MQTLs, overlapping QTLs and candidate genes. In the field of wheat genetics, meta-analysis has been shown a significant impact on revealing the complex genetic architecture of polygenic quantitative traits. This method plays an important role in identifying consistent QTL regions linked to agriculturally significant traits, such as organ- and tissue-related traits, including root traits [26, 28], leaf traits [29], spike traits, multiple disease-related traits [21, 30, 31], yield and yield-related traits [23, 32], quality-related traits [33–35], abiotic or biotic stress factor-related traits [36–38], and some plant physiology-related traits [39, 40]. However, few studies have entailed meta-analysis of wheat stem-related traits. Therefore, the primary objective of this research was to conduct a meta-analysis and integrate omics datasets to enhance our understanding of the genetic mechanisms that regulate stem-related traits in wheat. To that end, we conducted a meta-analysis of previous QTL studies performed on stem-related traits in wheat to identify novel MQTLs and candidate genes (CGs). Furthermore, the meta-analysis results were integrated with GWAS and transcript omics studies to identify potential genomic regions and CGs affecting wheat stem-related traits. Additionally, we utilized wheat genomic regions that have synteny and collinearity with those in rice and performed haplotype analysis to increase the accuracy of the potential candidate genes. The findings from this study may help identify diagnostic markers and aid in marker-assisted breeding or genomic selection to improve stem-related traits in wheat.

Results

Characteristics of stem-related QTLs from studies on wheat

A total of 306 QTLs for stem-related traits in wheat were identified in previous studies. The present study investigated 32 different biparental populations, including

16 RILs, 15 DHs, and one F_2 population (Table S1). The size of the population ranged from 92 to 414 individuals. The distribution of QTLs on the chromosomes was uneven, with approximately 30.1% (192/306) on the A sub-genome, 36.9% (113/306) on the B sub-genome and 33.0% (101/306) on the D sub-genome. Chromosomes 2D, 4B and 5A contained 37, 32 and 30 QTLs, respectively, accounting for 32.4% of the total, while chromosome 6A contained only 2 QTLs (Fig. 1a). The analysis of the PVE associated with each of the 306 initial QTLs showed that only 33.99% of the loci had PVE values above 10%, highlighting that many of them were minor QTLs. More than 69.97% of the QTLs had large CIs greater than 10 cM, with a mean value of 19.93 cM (Fig. 1b).

Construction of a high-density consensus genetic map

After combining the seven widely used genetic maps with the R package LRmerge, a consensus genetic map including SSR, DArT, SNP and a few genes was obtained for downstream meta-QTL analysis. This map included 221,599 markers (ranging from 2102 on 4D to 20331 on 2B) with a total length of 10319.86 cM (ranging from 180.09 cM on 2D to 771.64 on 5A). The marker density on individual chromosomes ranged from 7 markers/cM on 4D to 48 markers/cM on 1A, with a mean of 23 markers/cM on the whole genome. Sub-genome 'A' had a genetic length of 3592.39 cM with 24.45 markers/cM, sub-genome 'B' had a length of 3941.58 cM with 25.30 markers/cM, and sub-genome 'D' had a length of 2785.89 cM with 12.21 markers/cM (Fig. 2).

Projected QTL and MQTL for stem traits in wheat

Here, 306 individual QTLs were projected onto the consensus genetic map, and 201 (65.69%) could be successfully projected. A total of 105 QTLs were not projected onto the consensus map for the following reasons: (i) unavailability of common markers between the consensus and initial linkage maps and (ii) large CIs for the initial QTLs. After MQTL analysis, these initial QTLs were classified as 45 MQTL (QTL $\geq$ 2) (Table S2 and Fig. 3). There were marked differences among the different wheat chromosomes. The number of MQTLs per chromosome varied from one (on chromosomes 1A, 5B and 6B) to a maximum of five (on chromosome 5A). The number of clustered QTLs per MQTL ranged from two (in several MQTLs) to nine (in MQTL4A.2) (Table S2). The CIs for the MQTLs ranged from 0.05 (MQTL4A.2) to 27.84 cM (MQTL2B.1). The average MQTL CI (4.43 cM) was 4.50-fold less than that of the original QTL (19.93 cM). The degree to which the CI decreased in MQTLs differed among the different chromosomes; the mean CI for MQTLs on chromosomes 1A and 5B decreased by 14.01 and 9.69 times, respectively, followed by, 8.66 and 5.63 times on chromosomes 4A and 4B, respectively. The mean PVE explained by each MQTL was an average of 9.55% and ranged from 3.40 to 36.40%. The physical length of the MQTLs ranged from 0.97 Mb (MQTL2A.1) to 531.79 Mb (MQTL2B.2), with a mean of 116.28 Mb. A total of 31 MQTLs had a physical length less than 100 Mb, and 12 MQTLs were shorter than 10 Mb (Table S2 and Fig. 3).

MQTLs overlapping GWAS-MTAs

The physical collinearity of the MQTLs identified in the present study was compared with GWAS marker trait associations (GWAS-MTAs) for stem related traits from previous studies. Among the 31 MQTLs (PI < 100 Mb), as many as 25 MQTLs were colocalized with at least one MTA. Some MQTLs colocalized with MTAs identified in more than one GWAS and for more than one

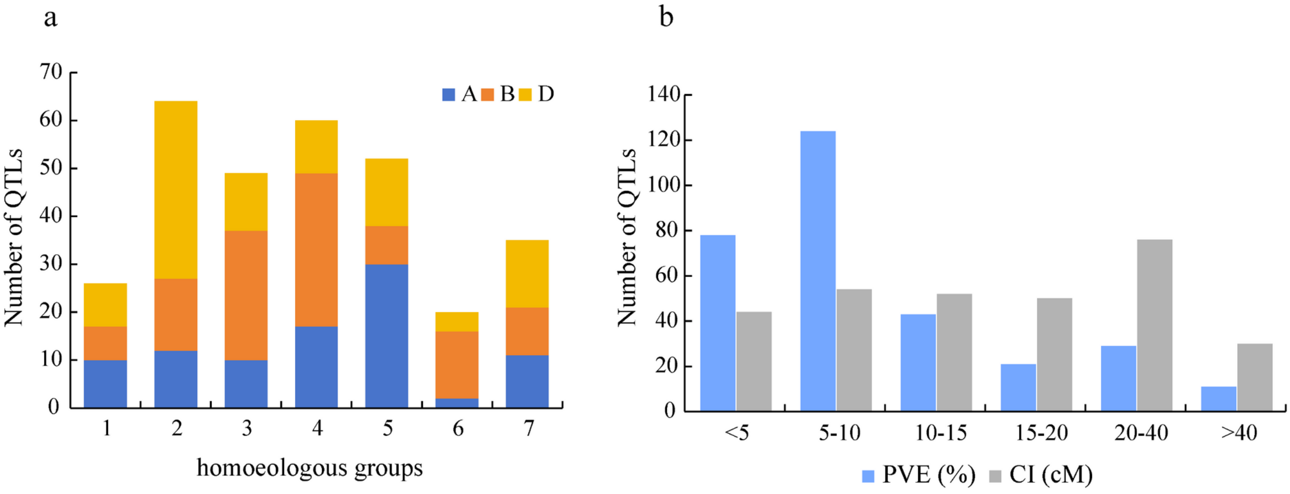

Fig. 1 (**a**) Number of QTLs on seven homoeologous groups (1–7) and three sub-genomes (A, B, D) from the collected QTL studies. (**b**) Supporting confidence intervals and individual PVE estimated from the initial QTLs

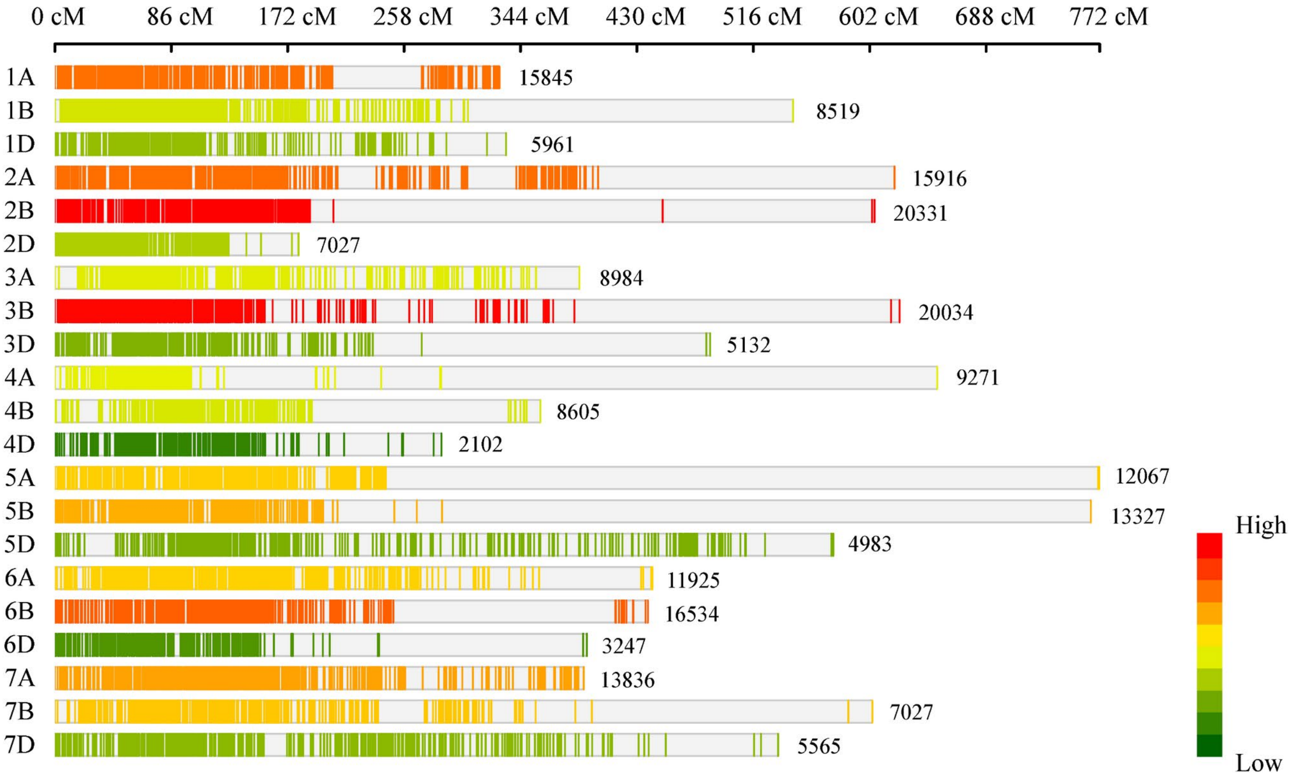

Fig. 2 Marker distribution on consensus genetic maps for meta-analysis. From red to green, the marker density, genetic length, and number of markers on the chromosome were from high to low

stem-related trait. For example, MQTL1A colocalized with 12 MTAs identified in four different GWASs. Two important genes related to wheat plant height were found in MQTL regions, namely *Rht-D1/Rht1* (MQTL4D.1), *TaARF12* (MQTL2D.4), and *TB-D1* (MQTL4D.1) (Table S2 and Table S3).

Gene expression analysis and haplotype analysis

As many as 926 putative HC CGs were identified, and these CGs were five core MQTLs (QTL ≥ 2; CI < 2 cM; PI < 30 Mb) (Table S4). In addition, multiple genes related to grain yield and disease, such as *TaPGS1* (MQTL1D.2), *TaSnRK210-4B* (MQTL4B.1), *TaGL3*, *TaNAC2-5A* (MQTL5A.5), *TaMlo-A1* (MQTL5A.1), *Lr67/Yr46/Sr55/Pm46/Ltn3* (MQTL4B.3), and *Sr45* (MQTL1D.1), were found in the MQTL regions (Table S2). To characterize and analyze the candidate genes in more detail, expression analysis was performed on several tissues. Of the 926 gene models, 274 exhibited tissue-specific expression (TPM > 2) (Table S4) with 57 genes being more highly expressed in stems than in other tissues and organs (Table 1, Table S5 and Fig. 4).

Haplotypes were identified for *TraesCS5B02G236900* using the WheatUnion database. *TraesCS5B02G236900* has four haplotypes (*Hap-I/II/III/IV*), and we validated these four haplotypes through the use of stem-related data from 86 accessions. *Hap-I* was the major haplotype (42/86) and was significantly longer than *Hap-II/IV* (SIL), *Hap-II/III* (TIL) and *Hap-II/II/IV* (FIL). Moreover, the expression of *Hap-II* was related to the shortest stem internode and was significantly shorter than that of *Hap-I* (SIL), *Hap-I/III* (TIL) and *Hap-I/II/IV* (FIL). These results suggested the potential of the *TraesCS5B02G236900* alleles in the modification of stem-related traits (Table S6 and Fig. 5).

Wheat homologs of known rice genes in MQTL regions

We also collected cloned homologous genes controlling stem-related genes in rice. The results revealed 77 rice genes associated with stem-related traits, and these genes belonged to the following families: cytochrome P450; YT521-B homology (YTH) family protein; epidermal patterning factor (EPF) and EPF-LIKE (EPFL) genes; E3 ubiquitin ligase; TCP family transcription factor; GRAS-domain protein, phytochrome-interacting bHLH factors-LIKE (PIF); WRKY transcription factor; APETALA-2-like transcription factor gene; F box and so on. Finally, a total of 91 wheat homologs of these 77 rice genes were detected in the wheat MQTL regions (Table S7).

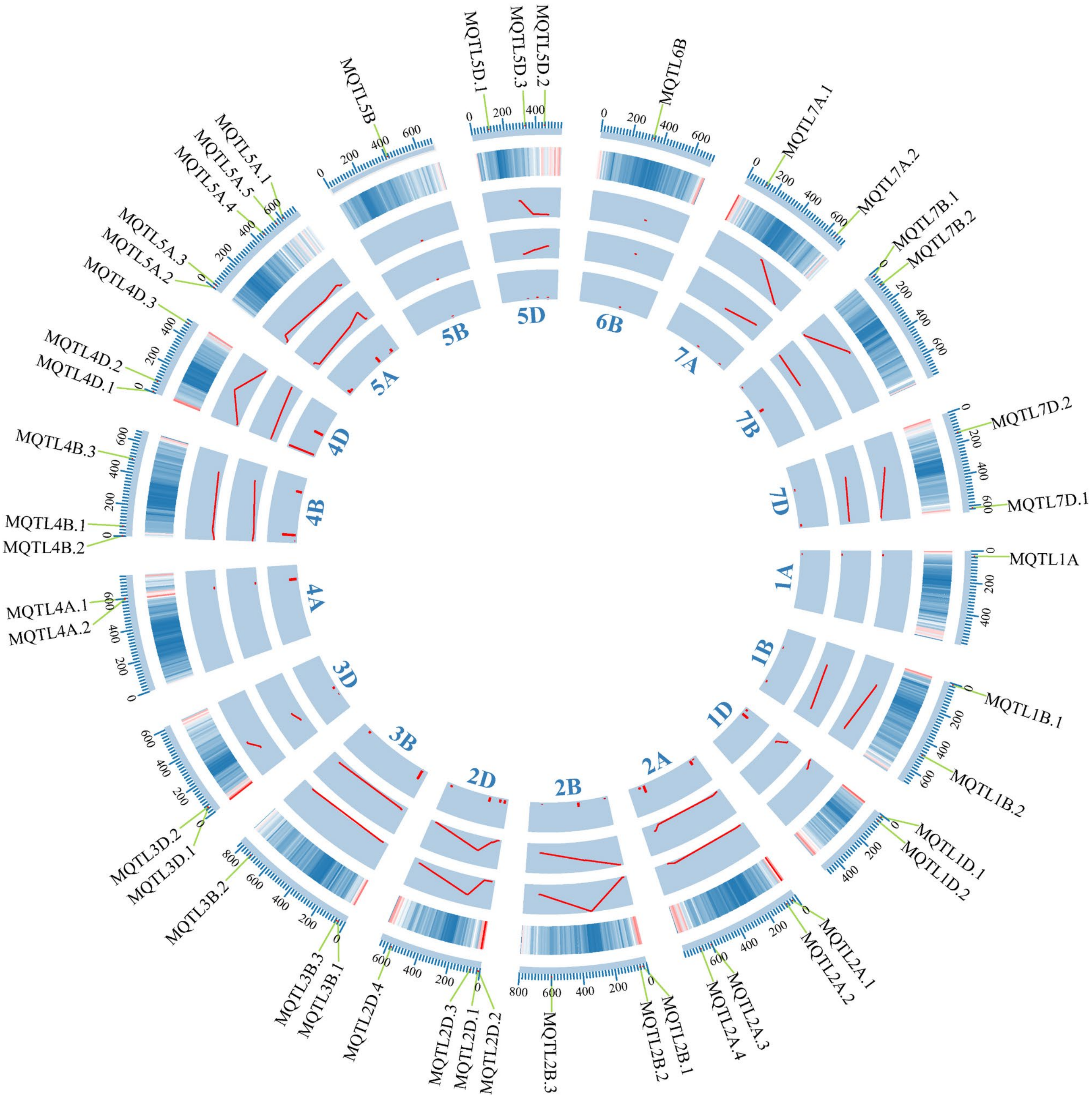

Fig. 3 The chromosome distribution of 45 MQTLs. The circles from outside to inside represent the physical position (Mb), density of high confidence genes, LOD value, CI and PVE, respectively

Discussion

Stem architecture revealed by meta-analysis

Meta-analysis can provide more accurately reveal genomic regions associated with target traits in different genetic backgrounds, population types and environments [19, 22, 32]. In recent years, meta-analysis has been conducted on complex traits of major crops [18, 19, 41]. Here, we conducted a meta-analysis using 306 initial QTLs reported in previous studies and identified 45 MQTLs (QTL ≥ 2) (Table S1). Among the 32 biparental mapping populations, 31 were permanent populations (Table S1). These lines are genetically stable and more useful for phenotyping across different years and diverse environmental conditions [32]. From the breeding perspective, meta-analysis is useful for identifying the most stable and reliable MQTLs, and decreasing the QTL CI using large initial QTLs across different populations and environments, which consequently increases the accuracy and efficiency of candidate gene prediction [33, 41, 42]. Here, there were at least two initial QTLs, and

Table 1 Summary of the five core MQTLs detected in the present study

MQTL	MQTL CI/ Projected QTL CI/PI	R^2 (%)	QTL Number	Flanking Marker	Traits	Putative candidate gene
MQTL1A	1.18/9.87/3.67	8.96	5	AX-110,475,080/AX-112,288,837	SID/SVB/SPD	
MQTL2A.1	1.37/11.00/0.97	5.28	4	wsnp_Ex_c2939_5423698/Excalibur_c15740_1106	Solid/SID	TraesCS2A02G071600; TraesCS2A02G072400
MQTL2D.1	1.48/12.00/17.36	9.45	6	AX-111,987,092/Xgpw332	SVB/Solid/WSC/SWT	TraesCS2D02G049500; TraesCS2D02G037300; TraesCS2D02G062600; TraesCS2D02G065800; TraesCS2D02G047700; TraesCS2D02G034600; TraesCS2D02G064900; TraesCS2D02G043500; TraesCS2D02G065400; TraesCS2D02G064500; TraesCS2D02G052200; TraesCS2D02G062500; TraesCS2D02G037400; TraesCS2D02G032700; TraesCS2D02G065100; TraesCS2D02G063300; TraesCS2D02G038700; TraesCS2D02G036100; TraesCS2D02G065500; TraesCS2D02G064400; TraesCS2D02G041600; TraesCS2D02G037100; TraesCS2D02G061200; TraesCS2D02G056100
MQTL4A.2	0.45/16.54/21.73	7.01	9	BS00021738_51/AX-94,426,335	SID/Solid/SW/WSC	TraesCS4A02G314800; TraesCS4A02G296600; TraesCS4A02G315500; TraesCS4A02G299400; TraesCS4A02G299800; TraesCS4A02G316100; TraesCS4A02G320400; TraesCS4A02G298700; TraesCS4A02G327300; TraesCS4A02G322300; TraesCS4A02G297700; TraesCS4A02G328900; TraesCS4A02G316000; TraesCS4A02G316200; TraesCS4A02G297900; TraesCS4A02G312200; TraesCS4A02G321500; TraesCS4A02G311300; TraesCS4A02G323700; TraesCS4A02G298100; TraesCS4A02G325800
MQTL5B	0.91/2.33/12.41	5.24	3	BS00009789_51/Kukri_c22967_1272	Lodging	TraesCS5B02G238300; TraesCS5B02G238900; TraesCS5B02G240900; TraesCS5B02G238400; TraesCS5B02G238600; TraesCS5B02G235200; TraesCS5B02G241800; TraesCS5B02G236900; TraesCS5B02G240600; TraesCS5B02G239300;

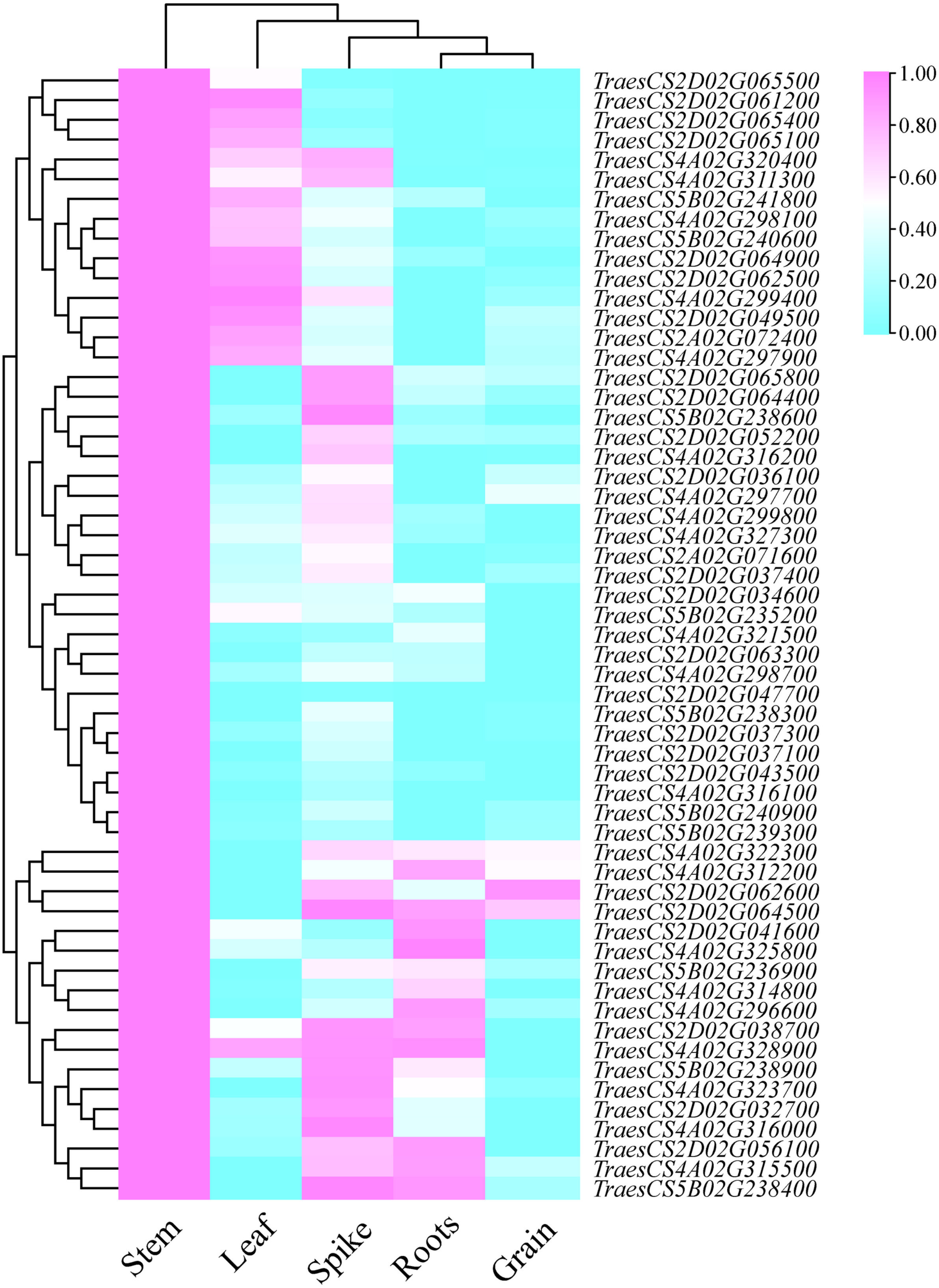

Fig. 4 Expression characteristics of 57 putative candidate genes in five tissues. The transcriptome data was downloaded from expVIP (http://www.wheat-expression.com), and TPM value was used to characterize the expression level based on normalized scale method

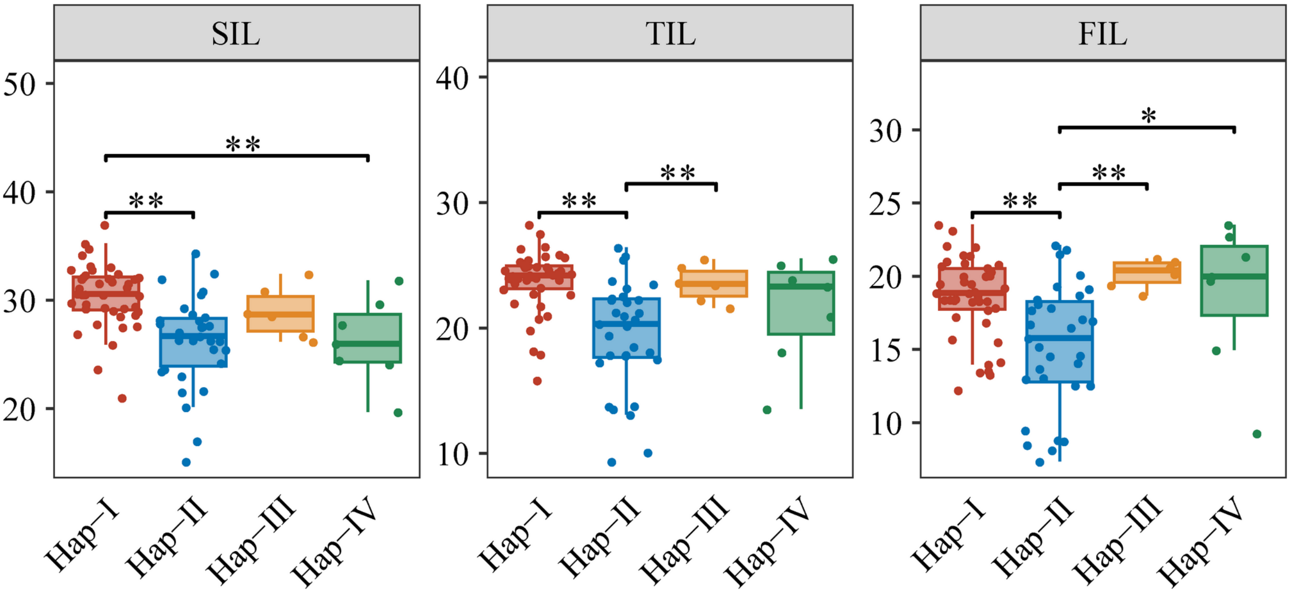

Fig. 5 Haplotypes distribution of *TraesCS5B02G236900*. SIL: second internode length, TIL: Third internode length, FIL: Fourth internode length. *, $P < 0.05$;**, $P < 0.01$

some MQTLs, such as MQTL4A.2, contained more QTL clusters; these included nine initial QTLs from multiple genetic backgrounds. Moreover, the average CI of the MQTLs was 4.50-fold less than that of the initial QTLs. The MQTLs with reduced CIs differed among the different intervals, for example, compared with the mean CIs of the initial QTLs, the CIs for MQTL4A.2, MQTL2D.4, MQTL1A and MQTL2A.1 decreased by 36.75, 14.08, 8.37 and 8.03 times, respectively (Table S2). These results indicate that associated markers must be closely linked to MQTLs, thus facilitating the transfer of MQTLs during breeding and enabling improved CG prediction [23].

Validation of MQTLs in GWASs

Compared with QTL mapping, GWASs based on high-throughput sequencing or array technology represent another high-precision method for identifying genomic regions of quantitative traits [43]. Here, 31 MQTLs (PI < 100 Mb) were compared with the significant signals determined through various GWAS analysis models. A total of 25 MQTLs were colocalized with MTAs from at least one previous GWAS (Table S3). This was notably the case for MQTL1A and MQTL2D.1. MQTL1A consisted of five initial QTLs validated by 11 MTAs identified for various traits, such as third internode length [44], basal second internode diameter [45], and WSC [46]. Similarly, MQTL2D.1 consisted of six initial QTLs validated by five MTAs identified from various traits, including main shoot length, second internode length, third internode length, fourth internode length [44] and basal second internode diameter [45]. The results indicated that the impact of these genomic regions on stem-related genes may be less limited by genetic background. This comparison enabled the identification of common significant common loci, highlighting the reliability of our MQTL results.

CGs available from MQTLs and their roles in stem

MQTLs are considered potential targets for mining CGs associated with the traits in question. Furthermore, MQTL regions have been shown to be strongly correlated with gene density in the genome, as revealed by earlier MQTL studies [18, 32]. Here, several well-known important genes including three genes for stem-related traits, namely, the genes *Rht-1/Rht-D1* [47], *TaARF12* [48] and *TB-D1* [49] were accurately identified among the MQTLs (PI < 100 Mb) (Table S2). These genes play important roles in plant stem development. The introduction of the gibberellin-insensitive dwarf (*Rht*) genes *Rht-B1b*, *Rht-D1b*, and *Rht* has led to the green revolution in modern wheat cultivars. Since the 1960s, wheat production has rapidly increased worldwide [47]. Kong et al. (2023) [48] edited the auxin response factor *TaARF12* and found that the transgenic plants produced shorter plant heights, thicker stems and larger spikes. Changes in plant morphology increase grain per spike, grain size and final grain yield in the field, with *TEOSINTE BRANCHED1* (*TB1*) being an important regulator of plant architecture, that restricts height and stem elongation in wheat; thus, the variant alleles that alter the expression or function of *TB1* could be used as a new source of genetic diversity for optimizing the architecture of wheat in breeding programs [49]. The important genes mined in the MQTL (PI < 100 Mb) included five genes related to grain yield-related traits, namely, *TaPGS1* (1D) [50], *TaSnRK2.10* (4B) [51], *TaPSTOL* (5 A) [52], *TaGL3* (5 A) [53], and *TaNAC2* (5 A) [54], and three disease-related traits, namely, *Sr45* (1D) [55], *Lr67/Yr46/Sr55/Pm46/Ltn3* (4B) [56] and *TaMlo* (4B) [57].

Gene mining from five core MQTLs, namely, MQTL1A, MQTL2A.1, MQTL2D.1, MQTL4A.2, and MQTL5B, fulfilled the criteria of narrower physical intervals (< 30 Mb), shorter CIs (< 2 cM) and a greater quantity of initial QTLs (a range of three to nine) (Table 1); notably, these MQTLs will be highly favorable for future MAS in stem-related traits, and for isolating key genes by the map-based cloning approach in wheat [37, 58]. Furthermore, we mined 57 DEGs from five core MQTLs based on gene expression models and found that these DEGs exhibited tissue-specific expression (Table S5), and 91 homologs of these rice genes were detected among the MQTLs (Table S7). Some CGs are associated with specific gene superfamily, such as F-box, cytochrome P450, E3 ubiquitin and bHLH genes. These gene clusters are quite common in plant genomes and play important roles in plant growth and development [27, 32, 59–61]. In rice, *D2/D11* encodes the cytochrome P450 protein, which affects plant height, and *d2* mutants exhibit inhibition of elongation in the second internode [59, 60]. *OsBUL1* encodes an atypical HLH protein, and the resulting mutant was found to exhibit reduced plant height due to reduced internode length [61]. In addition, *TraesCS4A02G325800* encodes a hydroxyproline-rich glycoprotein (HRGP). Previous studies have shown that extensins are one of the major classes present in plant cell walls [62, 63], and exhibit significantly reduced cell elongation in stem internodes and largely improved lodging resistance in rice [64].

Ethylene-responsive transcription, is associated with plant height, cellulose and lignin content, and secondary cell wall thickening and strength in rice peduncles [65–67]. *TraesCS5B02G236900*, an ethylene-responsive transcription factor, has four haplotypes (*Hap-I/II/III/IV*). *Hap-I* and *Hap-II* were significantly longer or shorter, respectively, than the other haplotypes for different traits (SIL/TIL/FIL) (Table S6). In fact, wheat breeding has exploited variable haplotypes associated with agricultural traits, and different haplotype combinations have different functions [44]. Thus, different haplotypes or haploid blocks have important value in improving polyploid crops [68]. Lodging is a serious concern that can affect the yield and quality of wheat [6]. With ideal phenotypes, especially short basal internode lengths, wheat plants not only are resistant to lodging but also have great yield potential [15, 45]. Hence, the basal internode length associated with *Hap-II* was significantly shorter than that associated with the other haplotypes, suggesting that this superior haplotype may play an important role in future lodging resistance breeding.

Materials and methods

Bibliographic search and QTL data collection

The QTL studies related to stem-related traits, such as lodging, stem diameter (SD), stem strength (SS), stem weight (SW), stem wall thickness (SWT), stem vascular bundles (SVB), stem pith diameter (SPD), stem internode length (SL), stem thickness-diameter-ratio (STDR), stem wall area (SWA), stem node number (SNN), and both solid and water-soluble carbohydrates (WSC), were collected from the PubMed and China National Knowledge Infrastructure (https://www.cnki.net/). The following information was collected and compiled from individual studies: (i) mapping population type and size, (ii) peak position and confidence intervals (CIs), (iii) flanking markers and genetic positions, (iv) logarithm of odds (LOD) score, and (v) phenotypic variation explained (PVE) or R^2 value. In cases, where no information was available on the peak position of the QTL, the mid-position of the flanking marker was taken as the position. Additionally, when the CI for the QTL was missing, the CI (95%) was estimated using the following population-specific equations developed through different simulations: (i) for F_2 and BC populations: $CI\ (95\%) = 530/(R^2 \times N)$; (ii) for doubled haploid (DH) populations, $CI\ (95\%) = 287/(R^2 \times N)$; and (iii) for recombinant inbred line (RIL) populations, $CI\ (95\%) = 163/(R^2 \times N)$, where 163, 530 and 287 are the population-specific constants obtained from different simulations [69–71]. For a small number of QTLs with missing LOD values, a LOD score of 3.0 was assumed for the purpose of analysis.

Construction of a consensus map

The R package LPmerge [72] was used to construct the consensus map by merging the marker data from the following linkage maps: (I) the Wheat Consensus SSR 2004 map [73], (II) the Wheat Composite 2004 map (http://wheat.pw.usda.gov), (III) the Integrated 2013 durum wheat map [74], and (IV) four SNP maps developed using the following different SNP arrays: the Illumina 9 K iSelect Beadchip Array [75], the AxiomR, Wheat 660 K SNP array [76], the Illumina iSelect 90 K SNP Array [77], and the Wheat 55 K SNP array [78]. Marker information or maps from several other independent studies were also utilized for developing the consensus map.

QTL projection and meta-analysis

All individual QTLs were projected onto the consensus map using the Biomercator v4.2.3 software [79]. Following the projection, a meta-analysis was performed. Two different approaches were used, one involving cases, where the number of QTLs on an individual chromosome was ≤ 10 [24], and the other including cases, where this number was > 10 [25]. The model with the lowest Akaike information criterion (AIC) value was chosen as the best fit in the first approach. In the second approach, the best model was chosen from among the following four models: the AIC model, corrected AIC (AICc and AIC3) model, Bayesian information criterion (BIC) model, and average weight of evidence (AWE) model. The MQTLs were named based on their genetic positions; for instance, MQTLs mapped on chromosome 1A were designated MQTL1A.1, MQTL1A.2, and so on. The PVE and LOD scores of an MQTL were calculated as the means of the PVE and LOD scores, respectively, on which the MQTL was based. The nucleotide sequences of the flanking markers of each MQTL were done using BLASTN searches against the wheat reference genome sequence to determine their physical positions in the genome. The flanking markers within target MQTLs were searched by WheatOmics (http://202.194.139.32/) to determine the physical locations. If their physical locations of the flanking markers were not found, the sequences of the flanking markers were identified via searches of the GrainGenes database (https://graingenes.org/GG3/) or the DArT database (https://www.diversityarrays.com/).

Validation of MQTLs using GWAS for stem-related traits

We collected GWAS studies on wheat stem-related traits to validate MQTLs. The method of obtaining the physical positions of MTAs is similar to that used for obtaining the physical positions of MQTLs. Given that wheat has a relatively high linkage disequilibrium decay distance (about 5 Mb), the MTAs found through GWAS within 5 Mb genomic regions close to MQTL MQTLs were considered as co-located [32].

Expression analysis of gene models identified from the MQTL regions

The preferred criteria for the determination of MQTLs, were as follows: (1) the MQTL was generated through the projection of at least two overlapping QTLs; and (2) the physical interval was less than 30 Mb in the bread wheat Chinese Spring reference genome. High-confidence genes within each highly refined MQTL were subsequently listed and subsequently called putative candidate genes according to WheatOmics based on IWGSC_v1.1_HC_gene annotated genomic features. The transcriptomic data for multiple tissues of bread wheat var. Chinese Spring from the expVIP platform (http://www.wheat-expression.com/) were obtained to identify the d ifferential expression characteristics of putative candidate genes within the target MQTLs. The transcriptomic data included five tissues, namely, roots, stems, leaves, spikes and grains. The expression levels of candidate genes were evaluated by transcripts per million (TPM) values.

Haplotype analysis of *TraesCS5B02G236900* across the WheatUnion database

TraesCS5B02G236900 was subjected to haplotype analysis using WheatUnion (http://wheat.cau.edu.cn/WheatUnion/?language=en). The upstream and downstream extension lengths were set to 2000 bp. We used previously generated stem-related trait phenotypic data [44]. Furthermore, we studied the relationships among haplotypes for stem-related traits, including second internode length (SIL), third internode length (TIL) and fourth internode length (FIL). ANOVA was performed to investigate significant differences among haplotypes at $P < 0.05$.

Homologous relationship

Homology-based candidate gene mining revealed a close evolutionary relationship between the genomes of Poaceae species [80]. Homology analysis of wheat with the model crop rice was suitable for broadening our understanding of wheat genes. Therefore, candidate genes within the MQTL region were mined using a wheat-rice orthologous comparison strategy. Similarly, validated rice genes associated with different stem traits have been identified in the available literature. The homology genes in wheat were identified using the Triticease-Gene Tribe (http://wheat.cau.edu.cn/TGT/) based on IWGSCRefSeqv1.1. The genes located within the MQTL region were considered important candidate genes affecting wheat stem-related traits.

Conclusions

The discovery of MQTLs as potential targets for the mining of CGs associated with these traits, facilitated by this study, has highlighted their significant role in wheat stem regulation. A total of 45 MQTLs were identified, and their average confidence intervals were significantly reduced. Most MQTLs were found to overlap with SNP-trait correlations identified by GWAS. This further supports the credibility of the MQTL approach in elucidating the genetic basis of quantitative traits. In this meta-analysis, a putative candidate gene influencing stem regulation was identified, and the superior haplotype was shown to potentially affect internode length, an insight that was discovered through extensive genetic analysis. Overall, the identification of MQTLs, candidate genes, and advantageous haplotypes provides a robust framework for further investigation into the genetic basis of wheat stem development, and may be beneficial for the development of wheat breeding.

Abbreviations

CG	Candidate genes
CI	Confidence interval
FIL	Fourth internode length
GWAS	Genome-wide association studies
HRGP	Hydroxyproline-rich glycoprotein
ID	Internode diameter
LOD	Logarithm of odds
MAS	Marker-assisted selection
MQTLs	Meta-QTLs
PVE	Phenotypic variance explained
QTL	Quantitative trait loci
SD	Stem diameter
SIL	Second internode length
SL	Stem internode length
SNN	Stem node number
SPD	Stem pith diameter
SS	Stem strength
STFR	Stem thickness-diameter-ratio
SVB	Stem vascular bundles
SW	Stem weight
SWA	Stem wall area
SWT	Stem wall thickness
TB1	TEOSINTE BRANCHED1
TIL	Third internode length
WSC	Water-soluble carbohydrates

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06597-5.

Supplementary Material 1

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Author contributions
YPM and LW designed the research, LW, FLJ, JRY, HY, MS, KZ, FYYH collected relevant literature data and conducted the data analysis, YPM and LW wrote the manuscript, YPM, FLJ, XL, MH, BJ, LH, SZN, XJC, XC discussed and interpreted the data. LQZ and DCL revised the manuscript. All authors read and approved the manuscript.

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Data availability
All data generated or analysed during this study are included in this published article and its supplementary information files.

Declarations

Ethics approval and consent to participate
The use of plant parts in the present study complies with international, national and/or institutional guidelines.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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