BMC Plant Biology

RESEARCH

Open Access

Phenotypic plasticity of flowering time and plant height related traits in wheat

Ying Chen[1†], Hai-Bin Dong[2,3†], Chao-Jun Peng[2,3], Xi-Jun Du[2,3], Chun-Xin Li[2,3], Xue-Lian Han[1], Wen-Xian Sun[1], Yuan-Ming Zhang[1*] and Lin Hu[2,3*]

Abstract

Background Climate changes pose challenges to crop production. However, the causes of phenotypic differences across environments remain unclear.

Results Here, heading date (HD), flowering date (FD), and plant height (PH) were measured along with four environmental factors (day length (DL), growing degree days (GDD), precipitation (PRCP), and photothermal ratio (PTR)) to investigate the genetic basis of phenotypic plasticity of these traits in 616 wheat accessions using genome-wide association studies. Regarding quantitative trait locus-by-environment interactions (QEIs), five known and three candidate genes for HD, six known and seven candidate genes for FD, and four known and eighteen candidate genes for PH were identified. For the genes associated with phenotypic plasticity, 10 genes exhibited responsiveness to alterations in diverse environmental conditions according to transcriptome data; haplotype effects of 33 genes were identified as significantly correlated with the changes in environmental factors; six candidate genes were identified as hub genes in the gene network, possibly influencing other genes and causing the phenotypic plasticity. And over-dominant effects can explain over 50% the genetic variance of phenotypic plasticity. More importantly, one FD/HD candidate gene (*TraesCS4A01G180700*) and two PH candidate genes (*TraesCS5B01G054800* and *TraesCS2A01G539400*) partly explain the phenotypic plasticity for the FD/HD and PH traits, respectively. In addition, the potential utilization of these genes in wheat breeding was discussed.

Conclusions This study elucidated the genetic basis of phenotypic differences caused by environments and provided a foundation for addressing the impact of climate change on crop production.

Keywords Phenotypic plasticity, Wheat, Environmental factors, Genome-wide association study, QEI

†Ying Chen and Hai-Bin Dong are equally contributed to this work.

*Correspondence:
Yuan-Ming Zhang
soyzhang@mail.hzau.edu.cn
Lin Hu
hulin209@163.com
[1]College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, People's Republic of China
[2]Institute of Crops Molecular Breeding, Henan Academy of Agricultural Sciences, Zhengzhou 450002, People's Republic of China
[3]The Shennong Laboratory, Zhengzhou 450002, People's Republic of China

Background

Dramatic changes in the global climate pose a major challenge to food security, and global trends in climate change have negatively affected on global crop yields [1, 2]. Wheat (*Triticum aestivum* L.) is a major global food crop, feeding about 40% of the world's population [3]. Changes in environmental conditions can affect the performance of wheat traits, such as high temperature, drought, and soil salinity [4–5]. And approximately 40% of the annual variation in wheat yield is due to temperature and moisture stress, with wheat yield decreasing by 6% for every degree of temperature increase [4–6]. Henan Province is a major wheat-producing region in China, contributing about 29% of the total wheat production in China [7]. More importantly, wheat breeding has increased wheat yield, which greatly contributes to ensuring food security [7]. It is of great importance to investigate the genetic mechanisms of environmental factors on phenotypic plasticity of wheat in Henan Province. Genotype-by-environment interaction refers to the differential response of genotypes to varying environmental conditions, while quantitative trait locus (QTL)-by-environment interactions (QEIs) describe how specific genetic loci interact with environmental factors to influence trait expression. Genotype-by-environment interaction is an important genetic component, influencing trait phenotypes. However, QEIs were mainly detected in integrated environments, such as different locations or years, in previous studies [8–10]. The performance of a trait is mainly influenced by light, temperature and water environmental factors, including day length (DL), growing degree days (GDD), precipitation (PRCP), and photothermal ratio (PTR) in this study [4–6]. In detail, DL regulates photosynthetic efficiency and act as the primary photoperiodic cue synchronizing flowering initiation through circadian clock gene networks, with longer photoperiods typically accelerating floral transition [11–15]. GDD quantifies heat accumulation, determining developmental phase duration [16–17]. PRCP modulates water availability for wheat. PTR describes the balance between growth and development [18]. Li et al. [19] and Fu and Wang [20] used genome-wide association studies (GWAS) to investigate the effects of various environmental factors on plant height, flowering time, and grain yield in maize, wheat, and oat, and on the general and specific combining ability of plant height and flowering in maize, respectively. However, it is difficult to identify and estimate their dominant effects. To address this issue, Li et al. [21, 22] established a compressed variance component mixed model that considers all possible genetic effects and controls for all possible polygenic backgrounds, providing a powerful tool for detecting QTLs and QEIs.

In this study, we performed the regression analysis of three traits, including flowering date (FD), heading date (HD), and plant height (PH), on four environmental factors, including DL, GDD, PRCP, and PTR, in a maximum correlation window, and used the regression slopes and intercepts as phenotypes in 616 wheat accessions to conduct GWAS to indirectly identify QEIs. Meanwhile, multi-environment joint GWAS analysis was performed to detect QTLs and QEIs. Around these QTLs and QEIs, known and candidate genes and gene-by-environment interactions (GEIs) were identified using transcriptome analysis, gene function annotation, homologous gene analysis, haplotype analysis, and co-expression gene network. Our aim is to reveal the genetic basis of phenotypic differences in different environmental conditions. Thus, this study provides a reference for overcoming the effects of climate change on crop production.

Materials and methods

Plant materials and field trials

The 616 wheat accessions, comprising 351 landraces and 265 cultivars (Supplementary Information), were sourced from the Wheat Institute of the Henan Academy of Agricultural Sciences and employed as association mapping populations. The experimental materials were planted in two environments, namely Anyang and Zhumadian in Henan Province, during the 2016–2017 and 2017–2018 growing seasons. PH: After the milky stage, 10 individual plants were randomly sampled and the length to the top of the spike, excluding awn, was measured and averaged; HD: Number of days after planting until 1 cm of the spike tip was exposed in the flag leaf sheath and this was visible in more than 50% of the plants; FD: The number of days after planting to more than 50% panicle flowering was calculated for the experimental material.

The phenotypic observation used in this study was the average across replicates in each environment. Individual breeding values were estimated via best linear unbiased prediction (BLUP) using the *lme4* package (version 1.1.31) [23] in R. The BLUP method systematically disentangles GEIs, producing reliable estimates of heritable phenotypic variation for individual organisms. The formula for calculating heritability is $h^2 = V_g/(V_g + V_e/l)$, where V_g and V_e are genetic and residual variances, respectively, and l is the number of environments. The statistical analysis of phenotypes across different environments was conducted using the R package *agricolae* (version 1.3-5).

SNP genotyping

Wheat 660 K microarrays were used to sequence 616 wheat accessions, yielding 552,470 original SNPs. Beagle v5.2 [24] was used for imputing missing markers, while Plink v1.9 [25] was employed to filter SNPs based on minor allele frequency (MAF ≥ 0.05). Finally, 429,721 high-quality SNPs were selected for further analysis.

Calculation of environment factors

The environmental data was collected from National Centers for Environmental Information (https://www.ncei.noaa.gov/) and US Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/index.php). GDD (℉) was calculated using $GDD_i = \bar{T}_i - T_{base}$ [16], PTR (h/℉) was calculated using $PTR_i = DL_i/GDD_i$, where T_{base}= 41℉ for wheat, and i is the i-th day after planting (DAP) [18]. The averages of the above four environmental factors in the windows were used in this study.

Genome-wide association study

The 3VmrMLM (version 1.0), BLUPmrMLM (version 5.0.2), and Fast3VmrMLM methods [21, 22, 26] (https://github.com/YuanmingZhang65) were used to perform genome-wide association studies, in which 11 principal components calculated by plink with a variance explanation rate > 1% was used to control for population structure, and the kinship matrix was calculated by each software. The Bonferroni correction threshold ($P = 1.16 \times 10^{-7}$) was used to determine significant QTLs and QEIs, while LOD = 3.0 (the *P*-value threshold is at least 10^{-3}) was used to determine suggested QTLs and QEIs [16, 17].

LD analysis

PopLDdecay v3.41 [27] was used for LD decay analysis, providing access to the extent and patterns of linkage disequilibrium in the genome. The candidate genes within the physical intervals of the identified QTLs were extracted from the IWGSC RefSeq 1.0 (https://www.wheatgenome.org/Resources/Annotations/IWGSC-RefSeq-v1.0-annotation), which was based on the decay of the squared correlation coefficient (r^2) to half of the maximum value.

Identification of candidate genes

Differential expression analysis was based on transcriptome data from public databases [28–29] using the R package *DESeq2* (version 1.38.3) [30] with the criterion of $|\log_2 FC| > 1$ and *P*-value < 0.05. In detail, public RNA-seq data was used to check if the identified candidate genes from GWAS show differential expression between conditions (e.g., heat stress vs. control). Gene annotation was performed using eggNOG-mapper (http://eggnog-mapper.embl.de/) and AgBase (https://agbase.arizona.edu/). Known rice genes were obtained from the China Rice Data Centre (https://ricedata.cn/gene/) and Arabidopsis genes were obtained from TAIR (https://www.arabidopsis.org/). Wheat protein sequences (https://urgi.versailles.inra.fr/, version 1.0) and rice protein sequences (http://rice.uga.edu/, version 7.0) were used to find the homologous genes using the Othofinder [31]. The known wheat genes were collected from WheatOmics 1.0 (http://202.194.139.32/) and the reported literature.

The potential candidate genes that were significant in the haplotype analysis using one-way or two-way ANOVA were considered as candidate genes. Superior haplotype was determined by multi-comparison. The haplotype effect of the gene was the trait average of the accessions with the gene haplotype minus the total average trait value.

Gene network analysis

WGCNA software (version 1.72.1) [32] was used to conduct the gene co-expression network analysis based on the public transcriptome data derived from Choulet et al. [33]. The goodSamplesGenes function was employed to assess and refine the data, subsequently selecting the median absolute deviation of genes that did not equal 0. The pickSoftThreshold function was then utilized to ascertain the soft threshold as 26. Finally, the blockwiseModules function was executed to construct the gene network and identify modules. The hub genes were selected based on the criterion of |KME| ≥ 0.8. STRING (https://cn.string-db.org/) was used to predict the protein and protein interaction based on the protein sequences. The minimum required interaction score was set as 0.40.

Identification of over-dominant loci

The dominance ratio is the absolute ratio of the dominant effect to the additive effect of each QTN, and these effects were obtained from 3VmrMLM and Fast3VmrMLM. The over-dominant locus was defined as the locus with a dominance ratio greater than 1.2.

Result

Phenotypic identification

To investigate the phenotypic plasticity of FD, HD, and PH in this study, 616 wheat accessions were planted in two locations: Anyang (36.05° N, 114.13° E, AY) and Zhumadian (32.93° N, 113.92° E, ZMD) (Fig. 1A), in the 2016–2017 and 2017–2018. Based on variance component estimates using the *lme4* software, the heritability of FD, HD, and PH were 84%, 85%, and 97%, respectively, indicating the high quality of the phenotypic datasets, while the proportions of environmental variances to total phenotypic variances for the three traits were 62%, 57%, and 5%, respectively (Fig. 1B), demonstrating the influence of environmental factors on trait phenotypes. The significantly low environmental variance percentage (5%) and high heritability observed for PH may explain why PH is less influenced by the environment. Furthermore, analysis of variance showed the significant differences of FD, HD, and PH among environments (Fig. 1C). In detail, FD and HD were significantly later in 18 AY than in 17

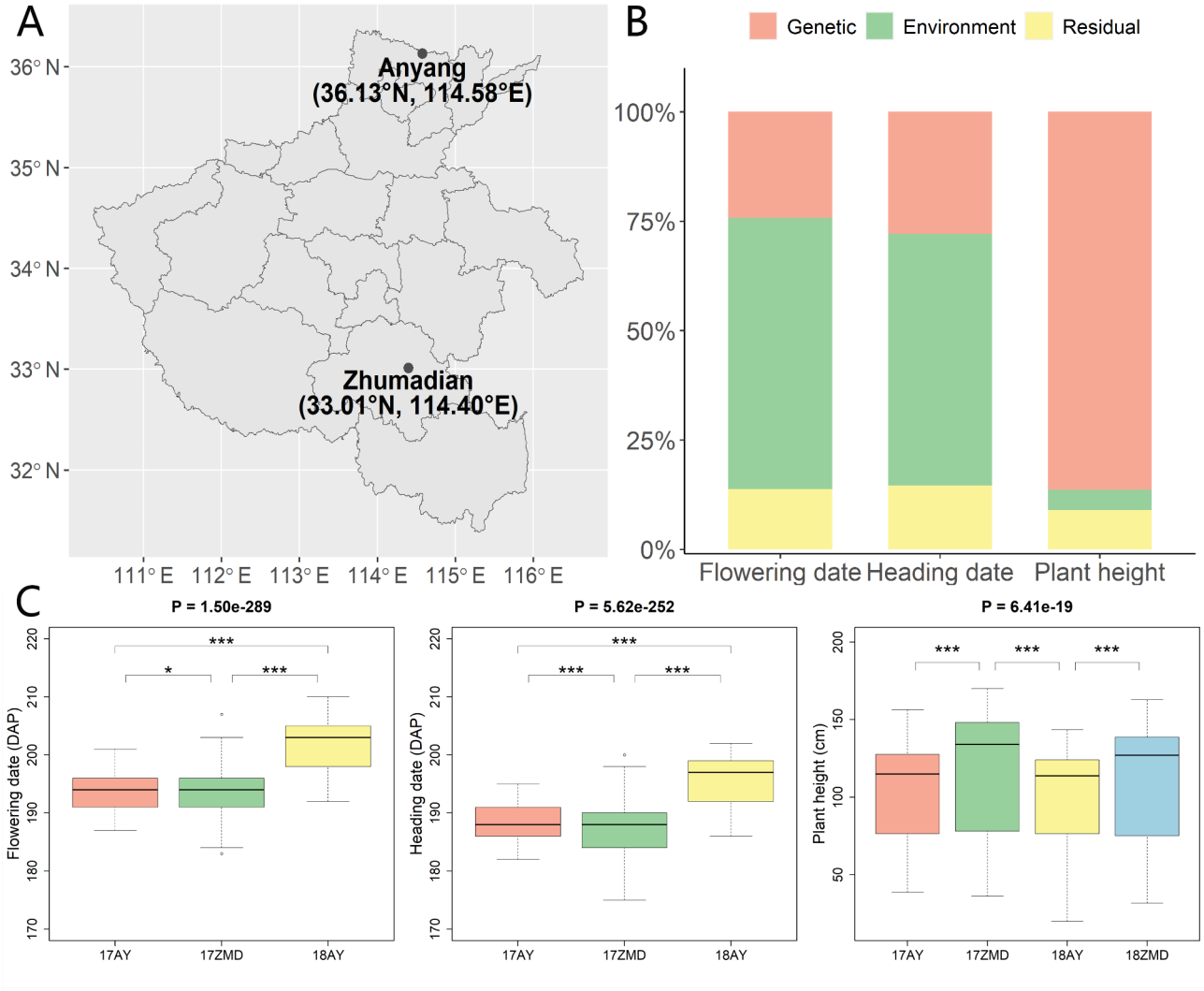

Fig. 1 Phenotypic analysis of wheat accessions across different environments. **A**, Geographic distribution of the two experimental locations. **B**, Phenotypic variance composition. **C**, Variance analysis of flowering date, heading date and plant height

AY and 17 ZMD, while PH was significantly higher in ZMD than in Anyang (Fig. 1C), indicating the phenotypic plasticity of the three traits in different environments.

Determination of environmental factors and critical windows

Based on the method of Fu and Wang [15], critical windows of each trait under different environmental factors were determined and shown in Fig. 2. For example, the significant negative correlation between DL and FD during the critical window (61 to 180 days after planting (DAPs)) suggests that longer daylight exposure in this window accelerates flowering (Fig. 2). Furthermore, the critical windows were found to be consistent with the actual growth periods. The critical windows for FD were close to FD and for HD were almost 10 to 15 days before HD, while the critical windows for PH were almost always in the erecting and jointing stages. In addition, opposite correlation coefficients were observed between PH and an environmental factor and between HD and the same environmental factor (Fig. 2).

Although the heatmaps of HD and FD in Fig. 2 were roughly consistent, their critical windows were not completely consistent because the two traits may have different environmental responses. All environmental factors were found to be significantly correlated with the three traits in the regression analysis of environmental factor on the trait, except for the regression coefficient of DL on PH (P-value = 0.0833), demonstrating the significant influence of environmental factors on trait phenotypes. The regression coefficient and intercept were used as phenotypes to perform GWAS.

Genetic analysis of FD, HD and PH

To investigate the phenotypic plasticity of the three traits, we performed two types of GWAS to identify

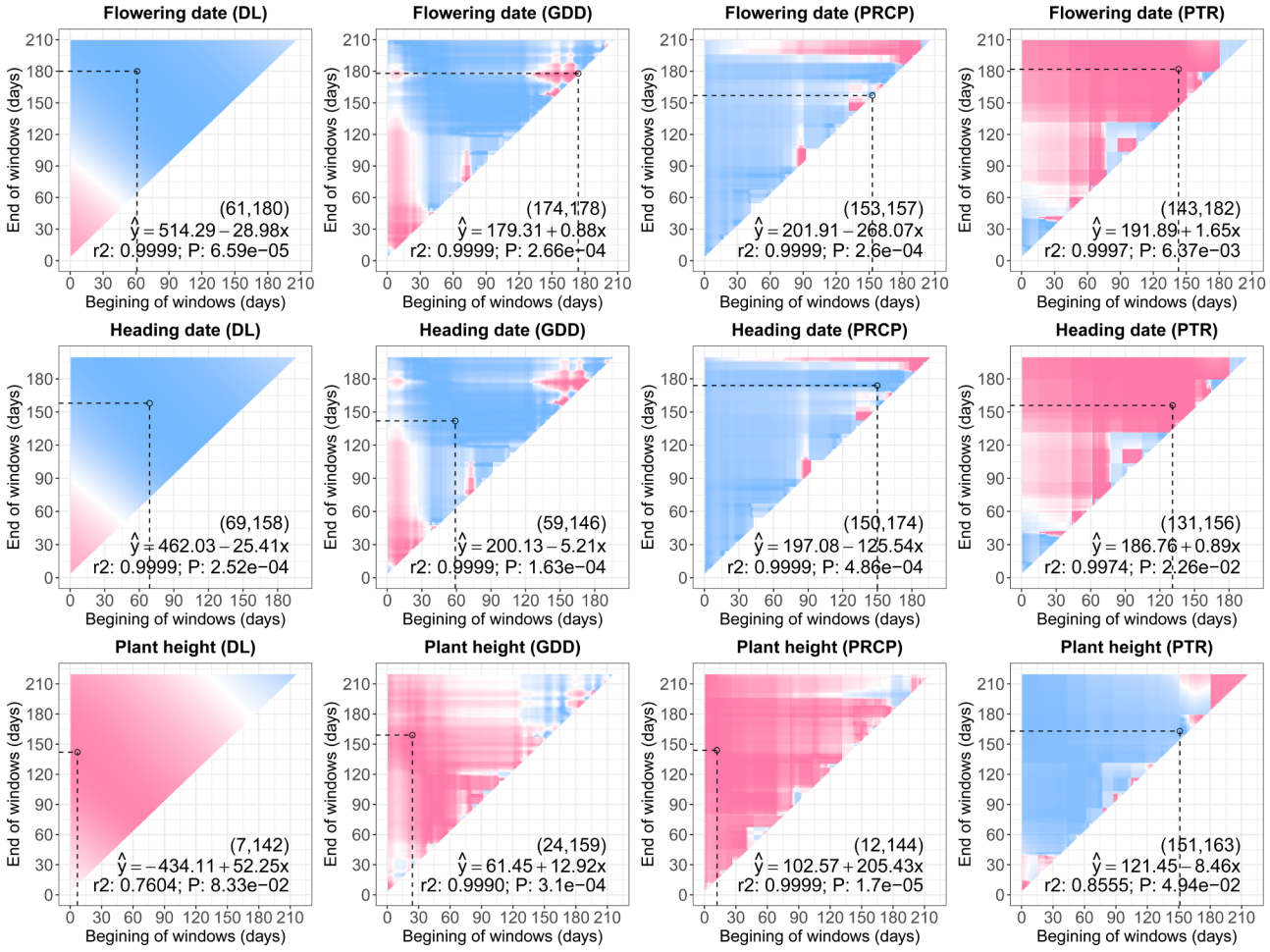

Fig. 2 Heatmap of correlation between traits and environmental factors. DL: day length, GDD: growing degree days, PRCP: precipitation and PTR: photothermal ratio

QEIs. First, the regression coefficient and intercept of the trait on the environmental factor were used as phenotypes to perform GWAS to indirectly identify QEIs. Second, all the phenotypes in all environments were used to perform multi-environment joint analysis to identify QEIs directly. For FD, the indirectly detected QEIs and the directly detected QTNs and QEIs are listed in Tables S1, S2, S3. Around all the QEIs, 6 genes were reported to be associated with FD in previous studies, such as *FUL3-2B* [34], *PhyC-5B/5D* [35], *SVP3-4* [36], and *WPCL1-3D* [37] (Fig. 3A); 7 candidate genes were identified by GO annotation, differential expression, rice or *Arabidopsis* homologous gene, and haplotype analysis (Fig. 3A; Table S4). The candidate gene *TraesCS3B01G070200* was found to be related to DL, PRCP, and GDD and could respond to water stress in transcriptome analysis (Table S4), in which its homologous gene *OsPTR* is affected by circadian, water and salt stress [38–39]. *TraesCS4A01G180700* detected by PRCP could respond to salt, heat, and drought stress in transcriptome analysis (Table S4), where its homologous gene *AtFER* controls flower development in *Arabidopsis* [40]. These two genes with relatively sufficient evidence could contribute to the differential FD in different environments.

For HD, the indirectly detected QEIs and the directly detected QTNs and QEIs are listed in Tables S5, S6, S7. Around all the QEIs, 5 genes were reported to be associated with HD in previous studies, such as *FUL3-2B* [34], *PhyC-5B/5D* [35], and *TaVRN1-5 A* [41] (Fig. 3B); 3 candidate genes were identified by GO annotation, differential expression analysis, *Arabidopsis* or rice homologous genes and haplotype analysis (Fig. 3B, Table S8). The candidate gene *TraesCS6B01G041100* was found to be related to all four environmental factors and could respond to salt, heat, and drought stress in transcriptome analysis (Table S8). *TraesCS4A01G180700* detected by PRCP in FD could respond to salt, heat, and drought stress in transcriptome analysis (Table S8), where its homologous gene *AtFER* controls flower development in *Arabidopsis* [40]. These two genes with relatively sufficient evidence could contribute to the differential HD in different environments.

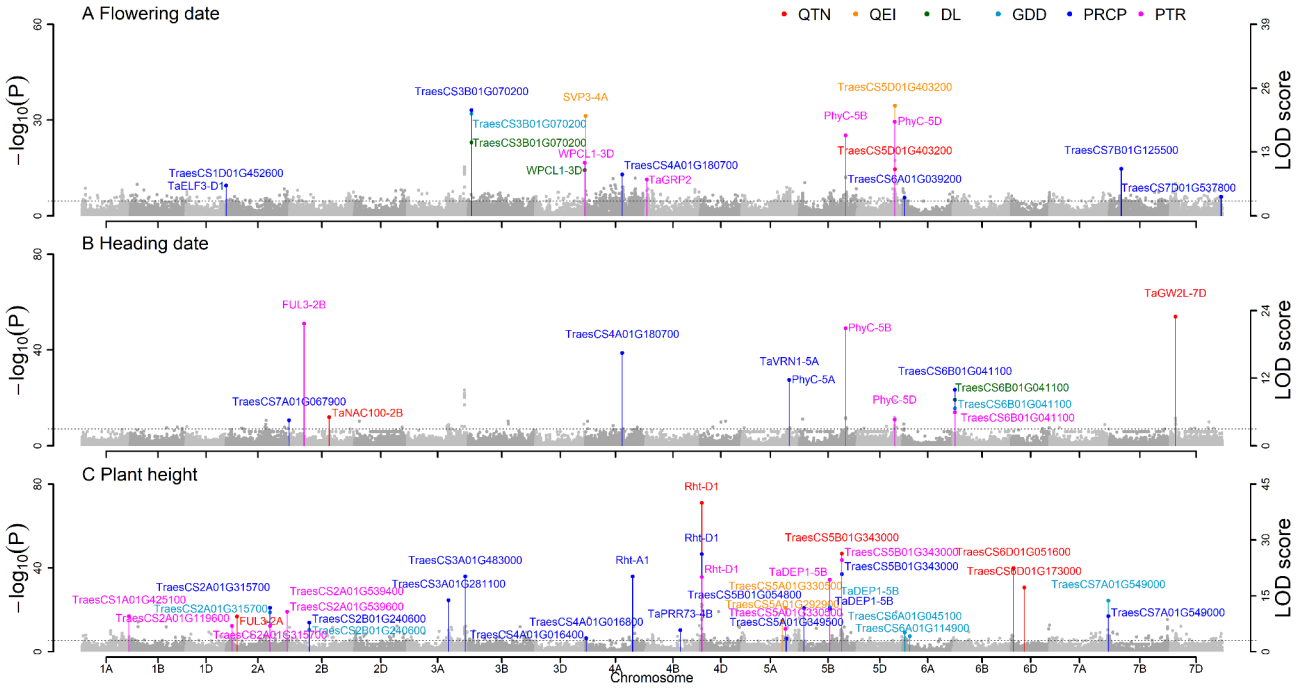

Fig. 3 Manhattan plot of flowering date, heading date and plant height. QTL: main effect QTLs detected by joint analysis across different environments, QEIs: QTL × environment interactions detected by joint analysis across different environments, DL: QEIs related to day length, GDD: QEIs related to growing degree days, PRCP: QEIs related to precipitation and PTR: QEIs related to photothermal ratio

For PH, the indirectly detected QEIs and the directly detected QTNs and QEIs are listed in Tables S9, S10, S11. Around all the QEIs, 4 genes were reported to be related to PH in previous studies, such as *Rht-A1*, *Rht-D1* [42], and *TaDEP1-5B* [43], in which *Rht-D1* was detected 7 times and *TaDEP1-5B* was detected 4 times, and *Rht-D1* greatly contributed to the improvement of PH in Henan Province; 18 candidate genes were identified by GO annotation, differential expression, *Arabidopsis* or rice homologous gene and haplotype analysis (Fig. 3C; Table S12). The candidate gene *TraesCS2A01G315700* was found to be related to GDD, PRCP, and PTR and could respond to heat and drought stress in the transcriptome analysis (Table S12). *TraesCS2A01G539400* detected by PTR could respond to heat stress in the transcriptome analysis, where its homolog *OsHIPP24* was reported to be related to PH in rice [44]. *TraesCS7A01G549000* detected by GDD and PRCP could respond to salt, heat, and drought stress in the transcriptome analysis, where its homolog *ONAC095* was reported to be related to PH in rice and affected by drought, cold, salt, and abscisic acid [45]. In total, 7 candidate genes were found to respond to corresponding environmental conditions in the transcriptome analysis and were related to PH, which may contribute to the differential PH in different environments (Table S12).

Among all the known and candidate genes around QEIs indirectly identified by regression parameters, gene haplotype effect and environmental factors were used to perform correlation analysis. As a result, haplotype effect of 33 genes were found to be significantly correlated with environmental factors, including three known genes for FD, two known genes for HD and three known genes for PH (Fig. 4). The results demonstrated that environmental factors influence the performance of gene haplotypes, resulting in the differences of traits in different environments. Furthermore, the superior haplotypes of these genes remained largely consistent across different environments, despite variations in their haplotype effects. For example, the *TraesCS4A01G180700* haplotype, indicated by the 'blue line', consistently outperformed other haplotypes in different environments. However, it is noteworthy that a small subset of superior haplotypes did not maintain their advantageous status in all environments, indicating their instability. For instance, the superior haplotype of *TraesCS5A01G391700* exhibited environment-dependent performance, reflecting its conditional adaptability.

Discussion

In this study, FD, HD and PH were found to have significant differences in different environments with different DL, GDD, PRCP, and PTR, resulting in their phenotypic plasticity (Fig. 1). To dissect the genetic basis of the phenotypic plasticity, the regression parameters of FD, HD and PH on DL, GDD, PRCP, and PTR were used to indirectly identify QEIs, while multi-environment joint analysis was used to directly identify QTNs and QEIs (Tables

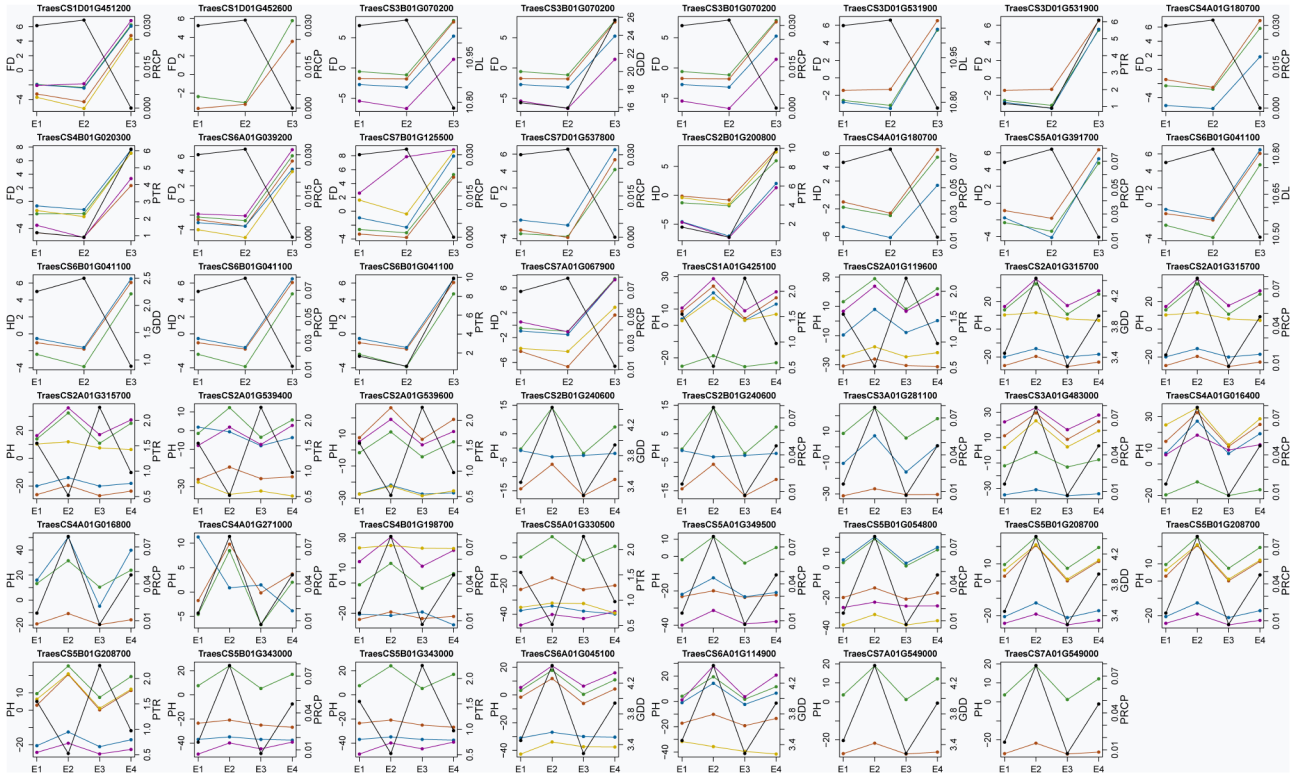

Fig. 4 Correlation analysis between the effect of gene haplotypes and the environmental conditions in each environment. Black lines are the phenotypic value, colorful lines are the effect of gene haplotypes. HD: heading date, FD: flowering date, and PH: plant height. DL: day length, GDD: growing degree days, PRCP: precipitation and PTR: photothermal ratio

S1-S3, S5-S7 and S9-S11). Around these QEIs, 15 known and 27 candidate genes were found to be associated with the three traits, of which 10 candidate genes may respond to the changes of environmental factors in the transcriptome analysis and may contribute to the phenotypic difference in different environments (Fig. 3; Tables S4, S8 and S12). Meanwhile, in the correlation analysis between gene haplotype effect and environmental factor, haplotype effect of 33 genes were found to be significantly associated with environmental factors (Fig. 4). These genes would be used to decipher the genetic basis of the phenotypic plasticity of the three traits.

Genetic basis of the phenotypic plasticity of the three traits

Phenotypic plasticity was observed in the different environments. In detail, FD and HD were found to be significantly later in 18 AY than in 17 AY and 17 ZMD (Fig. 1C), while GDD was significantly lower in 18AY than in 17AY and 18ZMD, and PTR was significantly higher in 18AY than in 17AY and 18ZMD (Table S13). To dissect the phenotypic plasticity of FD and HD, the main environmental factors for plant growth are light, temperature, and water, so that DL, GDD, and PRCP were used to represent the environmental conditions, while PTR was used to represent the environmental condition because it describes the balance between growth and development [25]. As a result, four pieces of evidence were provided to explain the phenotypic plasticity as follows. First, GDD and PTR were found to be significantly correlated with FD and HD (Fig. 2). Then, transcriptome analysis revealed that *TraesCS3B01G070200* and *TraesCS4A01G180700* for FD and *TraesCS6B01G041100* for HD were up-regulated under heat stress (Tables S4 and S8). Next, the rice homology gene (*OsPTR*) of *TraesCS3B01G070200* was affected by circadian, water, and salt stress [38–39], and the homology gene (*AtFER*) of *TraesCS4A01G180700* controls flower development in *Arabidopsis* [40] (Tables S4 and S8). Finally, the haplotypes of 9 FD genes (e.g., *TaELF3-D1* [46], *WPCL1-3D* [35],, *TaGRP2* [47]) and 5 HD genes (e.g., *TaVRN1-5 A* [41], *FUL3-2B* [34]) were significantly correlated with the changes of environmental factors (Fig. 4). In summary, the later FD and HD in 18 AY can be inferred from the changes of environmental factors and the response of the above known and candidate genes.

PH was found to be significantly higher in ZMD than in AY (Fig. 1C), while there are the more GDD and PRCP and the less PTR in ZMD than in AY (Table S13). To dissect the phenotypic plasticity of PH, four pieces of evidence were provided as follows. First, GDD, PRCP, and PTR were found to be significantly correlated with PH (Fig. 2). Then, transcriptome analysis revealed that 7

candidate genes for PH could respond to the changes in environmental conditions, the up/downregulated expression of these genes might contribute to the higher PH in ZMD, such as the upregulated expression of the *TraesCS2A01G539400* under heat stress (Table S12). Next, six out of seven genes have homology with rice genes known to be related to PH (Table S12). For example, *TraesCS2A01G539400* is the homolog of *OsHIPP24*, which has been demonstrated to cause plants to become shorter in rice [44], possibly leading higher PH in ZMD via the upregulation of *TraesCS2A01G539400*. Finally, the haplotype effect of 20 PH-related genes was significantly correlated with changes in environmental factors, including three known PH genes (*Rht-A1* [42], *TaPRR73-4B* [48], *TaDEP1-5B* [44]) and 16 candidate PH genes (Fig. 4). In summary, the shorter PH in 18AY can be attributed to changes in environmental factors and the response of known and candidate genes.

A gene network was constructed using the WGCNA software and STRING to measure the contribution and relationship of the above known and candidate genes to the phenotypic differences. As a result, 6 candidate genes were determined as hub genes ($|KME| \geq 0.8$) in the gene co-expression network using WGCNA, including *TraesCS1A01G425100*, *TraesCS2A01G539600*, *TraesCS5A01G292900*, and *TraesCS5A01G330500* for PH, *TraesCS6B01G041100* for HD, and *TraesCS7D01G537800* for FD (Table S14). To elucidate the relationship of the above known and candidate genes, the co-expression network showed that five candidate genes and one known gene *WPCL1-3D* for FD were assigned to the 'Grey' module; eleven candidate genes and one known *SVP1-6B* for PH were assigned to the 'Grey' module, and two known genes *Rht-A1* and *Rht-D1* and one candidate gene *TraesCS2A01G539400* for PH were assigned to the 'Turquoise' module (Figure S1). The protein and protein interactions predicted by STRING showed that *TraesCS6A01G039200* was interacted with *TaELF3-D1* for FD and *TraesCS5B01G054800* was interacted with *Rht-A1* and *Rht-D1* for PH, respectively (Figure S1). These findings suggest PH candidates likely participate in gibberellic acid signaling pathways, given their co-regulation with *Rht* genes and DELLA domain interactions, FD candidates might share photoperiod regulatory mechanisms with *WPCL1-3D* through ELF3-mediated circadian networks [35, 4246]. Moreover, it is speculated that environmental factors may cause the changes of the six hub genes and further affect the gene network, leading to phenotypic differences in different environments.

In conclusion, there were four main reasons for the phenotypic differences of the three traits in different environments. First, the different environmental conditions could lead to phenotypic differences. Then, the 10 candidate genes related to environmental responses in the transcriptome analysis were up-/down-regulated in different environments, causing phenotypic differences. Next, environmental conditions could influence the haplotype effects of 33 known and candidate genes to cause phenotypic differences. Finally, environmental factors may influence phenotypic differences in different environments based on the gene network analysis. It should be noted that these genes need further experimental validation.

Key genes affecting phenotypic plasticity

As described in Ravet et al. [40], *AtFER*, homologous to *TraesCS4A01G180700*, controls flower development in *Arabidopsis*. In our differential expression analysis, the expression of the FD and HD candidate *TraesCS4A01G180700* was up-regulated by salt, heat and drought (Tables S4 and S8), indicating that environmental changes may regulate its expression and influence flower development to cause phenotypic plasticity of FD and HD across environments.

In Chen and Xiong [44], *OsHIPP24* was reported to affect plant development and height in rice. In our differential expression analysis, the expression of the PH candidate gene *TraesCS2A01G539400*, which is homologous to *OsHIPP24*, was up-regulated under heat stress (Table S12), while ZMD has more GDD than AY due to its relatively lower latitude, indicating that more GDD in ZMD may up-regulate the expression of *TraesCS2A01G539400* and cause higher PH than AY (Table S13).

Meanwhile, *OsPIL1* was identified as a key regulator of internode elongation and induced rice plant shortening in response to drought stress in Todaka et al. [49]. In our differential expression analysis, the expression of the PH candidate gene *TraesCS5B01G054800*, which is homologous to *OsPIL1*, was down-regulated in response to drought in wheat (Table S12), while ZMD has more PRCP than AY, indicating that more PRCP in ZMD may up-regulate the expression of *TraesCS5B01G054800* and cause higher PH than AY (Table S13).

In summary, the higher PRCP and greater GDD in ZMD likely upregulate the expression of *TraesCS5B01G054800* and *TraesCS2A01G539400*, resulting in the increase of PH in ZMD compared to AY (Fig. 1; Table S13). This demonstrates how environmental factor variations influence gene expression, driving phenotypic plasticity across different environments. In addition, further experimental validation of *TraesCS2A01G539400* and *TraesCS5B01G054800* is required in the future.

The likely designs for further experimental validation of *TraesCS2A01G539400* and *TraesCS5B01G054800* are as follows. The wild-type and mutant (e.g. obtained by CRISPR-Cas9) lines were used to measure their phenotypes and to validate stress-responsive expression patterns using qRT-PCR expression profiling under high and

low PRCP for *TraesCS5B01G054800* and under high and low GDD for *TraesCS2A01G539400*.

Influence of over-dominant effect on phenotypic plasticity

Of all the QEIs indirectly identified by IIIVmrMLM and FastIIIVmrMLM for the three traits, over 70% of QEIs for each trait were over-dominant loci with dominance ratios greater than 1.2, highlighting the prevalence of over-dominant loci associated with phenotypic plasticity (Tables S1, S5 and S9). In the genetic variance of phenotypic plasticity, over-dominant components accounted for more than 50% for each trait, suggesting that over-dominance may explain most of the genetic variation influencing phenotypic plasticity (Table S15). Our findings indicate that over-dominance is the primary genetic effect driving phenotypic plasticity in wheat and may underlie the significant phenotypic differences observed across environments (Fig. 1C). This conclusion is in agreement with Semel et al. [50], where over-dominant loci were shown to contribute significantly to plant yield and fitness. Furthermore, heterozygous genotypes may exhibit greater environmental sensitivity, and heterozygosity may destabilize plant phenotypes [51–52].

Inspiration for wheat breeding

Genetic improvement is a critical approach to ensure food security in the face of significant climate change [6]. The phenotypic variation in different environments is largely caused by GEIs, as environmental factors are significantly correlated with the haplotype effects of 33 known and candidate genes in Fig. 4. We found that the superior haplotypes of most genes still perform well in different environments. These genes can be utilized in wheat breeding. In addition, some genes that interact with environmental conditions should be used with caution in wheat breeding. One is that their superior haplotypes were changed in different environments, and another is that the genes were significantly up-/down-regulated in different environmental conditions. Of course, in certain regions with regular environmental changes, the phenotypic plasticity-related genes can be used to breed environmentally adaptive cultivars to maximize the effects of genes in response to environmental conditions.

All the QTLs detected by the BLUP values and joint analysis were stable in different environments, and 8 known and 8 candidate genes were found around these QTLs (Table S16 and S17). Among the 16 genes, the superior haplotypes of 12 genes were identified, including one gene for FD, 4 genes for HD, and 7 genes for PH, which can be utilized to improve FD, HD, and PH in wheat breeding (Table S18).

Effect of environmental factors on wheat flowering and heading date

Three candidate GEIs were detected by both HD and FD, involving two environmental factors PRCP and PTR, confirming the similar impact of environmental factors on FD and HD (Tables S4, S8). The vernalization was one of the main factors influencing the FD and HD in wheat [53]. However, the environmental conditions related to vernalization like vernalization time, temperature and accumulated temperature were not significantly correlated with FD and HD in different environments. Therefore, environmental factors related to vernalization were not used in QEI detection. However, we identified some vernalization related genes in this study, such as known vernalization gene *TaVRN1-5A* in wheat [41] and candidate gene *TraesCS5D01G403200* homologous to vernalization gene *VIP4* in *Arabidopsis* [54].

Conclusion

All four environmental factors were significantly correlated with the three traits with the exception of the effect of DL on PH. 6 known and 7 candidate genes for FD, 7 known and 3 candidate genes for HD, and 5 known and 18 candidate genes for PH were detected around QTLs and QEIs. One FD/HD candidate gene (*TraesCS4A01G180700*) and two PH candidate genes (*TraesCS5B01G054800* and *TraesCS2A01G539400*) partly explain the phenotypic plasticity for the FD/HD and PH traits, respectively. The observed phenotypic differences across environments can be attributed to four main reasons: (1) the environmental conditions differed across the various environments, (2) transcriptome analysis showed that 10 candidate genes were up-/down-regulated in response to the disparate environmental factors, (3) the environmental conditions may have influenced the haplotype effects of 33 genes, and (4) the environmental conditions resulted in alterations to the gene network, with 6 candidate genes acting as hubs. Moreover, over-dominant effects may be a crucial factor in phenotypic plasticity.

Abbreviations

AY	Anyang
BLUP	Best linear unbiased prediction
DAP	Day after planting
DL	Day length
FD	Flowering date
GDD	Growing degree days
GEI	Gene-by-environment interaction
GWAS	Genome-wide association study
HD	Heading date
LD	Linkage disequilibrium
PH	Plant height
PRCP	Precipitation
PTR	Photothermal ratio
QEI	Quantitative trait locus-by-environment interaction
QTL	Quantitative trait locus
ZMD	Zhumadian

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06489-8.

Supplementary Material 1

Supplementary Material 2

Supplementary Material 3

Acknowledgements

We would like to thank Jinbang Li, Chunlin Yang, Yuhong Cheng, Zhensheng Guo, Dongmei Cheng and Wei Zhu for the help in obtaining phenotypic data at each planting site. And we sincerely thank the Editor and anonymous reviewers for their constructive comments and valuable suggestions, which have significantly improved the quality of this manuscript.

Author contributions

L.H., and Y.M.Z. conceived and managed the research and revised the manuscript. Y.C. analyzed datasets. H.B.D., C.J.P., X.J.D., C.X.L., and L.H. measured the phenotypes of these traits and genotypes of molecular markers. Y.C., H.B.D., X.L.H., and W.X.S. wrote the draft. All authors reviewed the manuscript.

Funding

This work was supported by the National Natural Science Foundation of China (32270673; 32470657; 32200500) and Basic Research Project of the Henan Academy of Agricultural Sciences (2024JC01).

Data availability

The datasets that support the findings in this study are available in the Supplementary Material of this manuscript. The variation data reported in this paper have been deposited in the Genome Variation Map (GVM) (https://ngdc.cncb.ac.cn/gvm/) in National Genomics Data Center, Beijing Institute of Genomics, Chinese Academy of Sciences and China National Center for Bioinformation, under accession number PRJCA030529.

Declarations

Ethics approval and consent to participate

All relevant international, national and institutional guidelines and legislation were compiled or adhered to in the production of this study.

Consent for publication

Not application.

Competing interests

The authors declare no competing interests.

Received: 7 January 2025 / Accepted: 31 March 2025
Published online: 14 May 2025

References

1. Lobell DB, Field CB. Global scale climate-crop yield relationships and the impacts of recent warming. Environ Res Lett. 2007;2:014002.
2. Bowerman AF, Byrt CS, Roy SJ, Whitney SM, Mortimer JC, Ankeny RA, et al. Potential abiotic stress targets for modern genetic manipulation. Plant Cell. 2023;35(1):139–61.
3. Langridge P, Alaux M, Almeida NF, Ammar K, Baum M, Bekkaoui F, et al. Meeting the challenges facing wheat production: the strategic research agenda of the global wheat initiative. Agronomy. 2022;12:2767.
4. Lobell DB, Gourdji SM. The influence of climate change on global crop productivity. Plant Physiol. 2012;160(4):1686–97.
5. He Y, Fang J, Xu W, Shi P. Substantial increase of compound droughts and heatwaves in wheat growing seasons world-wide. Int J Climatol. 2022;42:5038–54.
6. Mao H, Jiang C, Tang C, Nie X, Du L, Liu Y, et al. Wheat adaptation to environmental stresses under climate change: molecular basis and genetic improvement. Mol Plant. 2023;16(10):1564–89.
7. Zhang Y, Xu W, Wang H, Dong H, Qi X, Zhao M, et al. Progress in genetic improvement of grain yield and related physiological traits of Chinese wheat in Henan Province. Field Crops Res. 2016;199:117–28.
8. Hayashi E, You Y, Lewis R, Calderon MC, Wan G, Still DW. Mapping QTL, epistasis and genotype × environment interaction of antioxidant activity, chlorophyll content and head formation in domesticated lettuce (*Lactuca sativa*). Theor Appl Genet. 2012;124(8):1487–502. https://doi.org/10.1007/s00122-012-1803-0
9. Weng X, Haque T, Zhang L, Razzaque S, Lovell JT, Palacio-Mejía JD, et al. A pleiotropic flowering time QTL exhibits gene-by-environment interaction for fitness in a perennial grass. Mol Biol Evol. 2022;39(10):msac203.
10. Krause MD, Piepho HP, Dias KOG, Singh AK, Beavis WD. Models to estimate genetic gain of soybean seed yield from annual multi-environment field trials. Theor Appl Genet. 2023;136(12):252.
11. Dowla MANNU, Edwards I, Hara GO, Islam S, Ma W. Developing wheat for improved yield and adaptation under a changing climate: optimization of a few key genes. Engineering. 2018;4(4):514–22.
12. Cao S, Luo X, Xu D, Tian X, Song J, Xia X, et al. Genetic architecture underlying light and temperature mediated flowering in Arabidopsis, rice, and temperate cereals. New Phytol. 2021;230(5):1731–45.
13. Takagi H, Hempton AK, Imaizumi T. Photoperiodic flowering in Arabidopsis: multilayered regulatory mechanisms of *CONSTANS* and the florigen *FLOWERING LOCUS* T. Plant Commun. 2023;4(3):100552.
14. Distelfeld A, Li C, Dubcovsky J. Regulation of flowering in temperate cereals. Curr Opin Plant Biol. 2009;12(2):178–84.
15. Hernando CE, Murcia MG, Pereyra ME, Sellaro R, Casal JJ. Phytochrome B links the environment to transcription. J Exp Bot. 2021;72(11):4068–84.
16. McMaster GS, Wilhelm WW. Growing degree-days: one equation, two interpretations. Agr for Meteorol. 1997;89(3):351–6.
17. Rao D, Singh R. Heat use efficiency of winter crops in Haryana. J Agrometeorol. 1999;1:143–8. https://doi.org/10.54386/jam.v1i2.343..
18. Liu B, Heins RD. Photothermal ratio affects plant quality in `freedom' Poinsettia. J Am Soc Hortic Sci. 2002;127(1):20–6.
19. Li X, Guo T, Wang J, Bekele WA, Sukumaran S, Vanous AE, et al. An integrated framework reinstating the environmental dimension for GWAS and genomic selection in crops. Mol Plant. 2021;14(6):874–87.
20. Fu R, Wang X. Modeling the influence of phenotypic plasticity on maize hybrid performance. Plant Commun. 2023;4(3):100548.
21. Li M, Zhang YW, Xiang Y, Liu MH, Zhang YM. IIIVmrMLM: the R and C++ tools associated with 3VmrMLM, a comprehensive GWAS method for dissecting quantitative traits. Mol Plant. 2022;15(8):1251–3.
22. Li M, Zhang YW, Zhang ZC, Xiang Y, Liu MH, Zhou YH, et al. A compressed variance component mixed model for detecting QTNs and QTN-by-environment and QTN-by-QTN interactions in genome-wide association studies. Mol Plant. 2022;15(4):630–50.
23. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Softw. 2015;67:1–48.
24. Browning BL, Tian X, Zhou Y, Browning SR. Fast two-stage phasing of large-scale sequence data. Am J Hum Genet. 2021;108(10):1880–90.
25. Chang CC, Chow CC, Tellier LC, Vattikuti S, Purcell SM, Lee JJ. Second-generation PLINK: rising to the challenge of larger and richer datasets. GigaScience. 2015;4:7.
26. Li HF, Wang JT, Zhao Q, Zhang YM. BLUPmrMLM: A fast MrMLM algorithm in genome-wide association studies. Genomics Proteomics Bioinformatics. 2024;22(3):qzae020.
27. Zhang C, Dong SS, Xu JY, He WM, Yang TL. PopLDdecay: a fast and effective tool for linkage disequilibrium decay analysis based on variant call format files. Bioinformatics. 2019;35(10):1786–8.
28. Liu Z, Xin M, Qin J, Peng H, Ni Z, Yao Y, Sun Q. Temporal transcriptome profiling reveals expression partitioning of homeologous genes contributing to heat and drought acclimation in wheat (*Triticum aestivum* L). BMC Plant Biol. 2015;15:152.
29. Da Ros L, Bollina V, Soolanayakanahally R, Pahari S, Elferjani R, Kulkarni M, et al. Multi-omics atlas of combinatorial abiotic stress responses in wheat. Plant J. 2023;116(4):1118–35.
30. Love MI, Huber W, Anders S. Moderated Estimation of fold change and dispersion for RNA-seq data with DESeq2. Genome Biol. 2014;15(12):550.
31. Emms DM, Kelly S. OrthoFinder: solving fundamental biases in whole genome comparisons dramatically improves orthogroup inference accuracy. Genome Biol. 2015;16(1):157.
32. Langfelder P, Horvath S. WGCNA: an R package for weighted correlation network analysis. BMC Bioinformatics. 2008;9:559.

33. Choulet F, Alberti A, Theil S, Glover N, Barbe V, Daron J, et al. Structural and functional partitioning of bread wheat chromosome 3B. Science. 2014;345(6194):1249721.
34. Li C, Lin H, Chen A, Lau M, Jernstedt J, Dubcovsky J. Wheat *VRN1*, *FUL2* and *FUL3* play critical and redundant roles in Spikelet development and Spike determinacy. Development. 2019;146(14):dev175398.
35. Mizuno N, Kinoshita M, Kinoshita S, Nishida H, Fujita M, Kato K, et al. Loss-of-function mutations in three homoeologous *PHYTOCLOCK 1* genes in common wheat are associated with the extra-early flowering phenotype. PLoS ONE. 2016;11(10):e0165618.
36. Li K, Debernardi JM, Li C, Lin H, Zhang C, Jernstedt J, Korff MV, Zhong J, Dubcovsky J. Interactions between SQUAMOSA and SHORT VEGETATIVE PHASE MADS-box proteins regulate meristem transitions during wheat Spike development. Plant Cell. 2021;33(12):3621–44.
37. Mizuno N, Nitta M, Sato K, Nasuda S. A wheat homologue of *PHYTOCLOCK 1* is a candidate gene conferring the early heading phenotype to Einkorn wheat. Genes Genet Syst. 2012;87(6):357–67.
38. Ouyang J, Cai Z, Xia K, Wang Y, Duan J, Zhang M. Identification and analysis of eight peptide transporter homologs in rice. Plant Sci. 2010;179(4):374–82.
39. Fang Z, Xia K, Yang X, Grotemeyer MS, Meier S, Rentsch D, et al. Altered expression of the *PTR/NRT1* homologue *OsPTR9* affects nitrogen utilization efficiency, growth and grain yield in rice. Plant Biotechnol J. 2013;11(4):446–58.
40. Ravet K, Touraine B, Boucherez J, Briat JF, Gaymard F, Cellier F. Ferritins control interaction between iron homeostasis and oxidative stress in *Arabidopsis*. Plant J. 2009;57(3):400–12.
41. Yan L, Loukoianov A, Tranquilli G, Helguera M, Fahima T, Dubcovsky J. Positional cloning of the wheat vernalization gene *VRN1*. Proc Natl Acad Sci U S A. 2003;100(10):6263–8.
42. Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, Flintham JE, et al. 'Green revolution' genes encode mutant Gibberellin response modulators. Nature. 1999;400(6741):256–61.
43. Zhang Y, Liang Z, Zong Y, Wang Y, Liu J, Chen K, Qiu JL, Gao C. Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nat Commun. 2016;7:12617.
44. Chen G, Xiong S. *OsHIPP24* is a copper metallochaperone which affects rice growth. J Plant Biol. 2021;64:145–53.
45. Huang L, Hong Y, Zhang H, Li D, Song F. Rice NAC transcription factor ONAC095 plays opposite roles in drought and cold stress tolerance. BMC Plant Biol. 2016;16(1):203.
46. Wang J, Wen W, Hanif M, Xia X, Wang H, Liu S, et al. *TaELF3-1DL*, a homolog of *ELF3*, is associated with heading date in bread wheat. Mol Breed. 2016;36:161.
47. Xiao J, Xu S, Li C, Xu Y, Xing L, Niu Y, et al. O-GlcNAc-mediated interaction between *VER2* and *TaGRP2* elicits *TaVRN1* mRNA accumulation during vernalization in winter wheat. Nat Commun. 2014;5:4572.
48. Zhang W, Zhao G, Gao L, Kong X, Guo Z, Wu B, Jia J. Functional studies of heading date-related gene *TaPRR73*, a paralog of *Ppd1* in common wheat. Front Plant Sci. 2016;7:772.
49. Todaka D, Nakashima K, Maruyama K, Kidokoro S, Osakabe Y, Ito Y, et al. Rice phytochrome-interacting factor-like protein *OsPIL1* functions as a key regulator of internode elongation and induces a morphological response to drought stress. Proc Natl Acad Sci U S A. 2012;109(39):15947–52.
50. Semel Y, Nissenbaum J, Menda N, Zinder M, Krieger U, Issman N, Pleban T, Lippman Z, Gur A, Zamir D. Overdominant quantitative trait loci for yield and fitness in tomato. Proc Natl Acad Sci U S A. 2006;103(35):12981–6.
51. Fridman E. Consequences of hybridization and heterozygosity on plant Vigor and phenotypic stability. Plant Sci. 2015;232:35–40.
52. Liu N, Du Y, Warburton ML, Xiao Y, Yan J. Phenotypic plasticity contributes to maize adaptation and heterosis. Mol Biol Evol. 2021;38(4):1262–75.
53. Xu S, Chong K. Remembering winter through vernalisation. Nat Plants. 2018;4(12):997–1009.
54. He Y, Doyle MR, Amasino RM. PAF1-complex-mediated histone methylation of *FLOWERING LOCUS C* chromatin is required for the vernalization-responsive, winter-annual habit in Arabidopsis. Genes Dev. 2004;18(22):2774–84.

Publisher's note