Genome-wide association study identified novel genetic loci controlling internode lengths and plant height in common wheat under different nitrogen treatments

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Abstract  Nitrogen is an important nutrient for crop growth and development. Plant height-related traits can be affected by nitrogen supplementation. In this study, we performed a genome-wide association study (GWAS) on plant height, spike length, length of different internodes, and lodging resistance strength at the grain-filling stage based on wheat local varieties subjected to low nitrogen and normal (CK) treatments. GWAS analysis showed that a total of 86 quantitative trait loci (QTLs) were detected, including 13 QTLs for plant height, 10 QTLs for spike length, 19 QTLs for the length of the first internode from the top of the plant, 6 QTLs for the second internode length, 11 QTLs for the third internode length, 13 QTLs for the fourth internode length, and 14 QTLs for the fifth internode length. Compared to the CK treatment, the plant height, spike length, and fourth and fifth internode lengths were significantly affected by the low nitrogen treatment. A total of 18 QTLs responding to low nitrogen level were detected, including three QTLs for the fourth internode length detected on 3A, 6A, and 6D chromosomes, eleven QTLs for the fifth internode length on 1A, 1B, 1D, 2A, 2B, 3A, 3B, 4A, 4B and 7B chromosomes, one QTL for spike length on 3A chromosome, and one QTL for plant height on 5B chromosome. These QTLs will enhance our understanding of the genetic basis of plant height responses to nitrogen deficiency and will benefit genetic reactions to nitrogen fertilization.

Keywords  Wheat · GWAS · Wheat 90K SNP assay · Plant height-related traits · Low nitrogen level

Introduction

Nitrogen is an important nutrient for crop growth and development. Large quantities of nitrogen fertilizer are commonly used to obtain high yields for many crops (Cormier et al. 2016; Peng et al. 2010). In addition, modern breeding programs have mostly aimed at obtaining high yields under a high nitrogen supply (Liu et al. 2021). The high input of nitrogen fertilizers has resulted in low nitrogen use efficiency and has caused a series of environmental problems, such as soil acidification and water eutrophication (Shi...
et al. 2010). To solve these kinds of problems and to improve nitrogen use efficiency, the breeding of new cultivars with improved productivity in low nitrogen environments provides an effective approach to increase nitrogen use efficiency (Marino et al. 2011; Xu et al. 2014).

Plant height is an important agronomic trait in wheat, as it is a key parameter affecting the lodging and grain yield of wheat. A reduction in crop height can be associated with reduced grain yield (Law et al. 1978), and the aim of breeding programs is therefore the identification of variants with reduced height without adversely affecting yield (Wurschum et al. 2015). In general, along with a lower incidence rate of lodging, an appropriate grain number per spike, and an improved harvest index, an appropriate plant height could increase grain yield and quality (Hedden 2003).

Classical genetic studies have indicated that the plant height of bread wheat is a complex trait and that genes located on almost all 21 chromosomes can control plant height (Law et al. 1978; Snape et al. 1977). Most dwarfing genes have now been well characterized. Rht-B1 and Rht-D1, which have been successfully used in wheat breeding programs worldwide, are located on the short arms of chromosomes 4B and 4D, respectively (Borner et al. 2002; Huang et al. 2003). Rht13 on chromosome 7BS has been verified to produce a marked reduction in height (Ellis et al. 2005). In addition, the photoperiod-insensitive alleles of the major photoperiod regulator Ppd-1 have also been reported to exert pleiotropic effects on plant height in wheat (Borner et al. 1993).

Previous studies showed that different nitrogen levels had significant effects on plant height in wheat (Hussain et al. 2006; Yu et al. 2020). With increasing nitrogen levels, the plant height will increase accordingly. Plant height in wheat includes the spike length plus all internode lengths above the ground. The nitrogen response of the components of plant height in wheat is probably different. Understanding which components of plant height have significant responses to different nitrogen levels would be beneficial for wheat breeders to efficiently select related traits.

Quantitative trait loci (QTL) mapping based on linkage analysis is often used to analyze the molecular basis of complex traits. The objectives of previous studies were to map QTLs for agronomic and yield traits, uptake, and utilization efficiency of nitrogen in a recombinant inbred line (RIL) population under different supplemental nitrogen environments (An et al. 2006; Xu et al. 2014; Cui et al. 2016; Zhang et al. 2019; Sun et al. 2012). However, QTLs have rarely been reported from local varieties in environments with different levels of nitrogen supplementation.

With the rapid development of genotyping technologies and computational methods, genome-wide association studies (GWAS) are now becoming a powerful tool for detecting underlying complex natural variation traits in crops. Recently, important QTLs for agronomic traits have been found in crops based on GWAS methods (Lou et al. 2020; Pang et al. 2020; Sansaloni et al. 2020; Zhou et al. 2015; Hu et al. 2016). Furthermore, GWAS has more advantages than RIL population mapping, as it provides higher resolution and allows more variation to be detected without the need to construct populations (Huang and Han 2014). The wheat 90K SNP genotyping assay comprised approximately 90,000 gene-associated SNPs covering the whole genome (Wang et al. 2014). Compared to SSR markers, the 90 K SNP assay is generally more abundant, stable, efficient, and cost-effective (Sun et al. 2017; Gao et al. 2016). In this study, we performed a GWAS using a set of 120 winter wheat cultivars and a 90 K SNP assay to identify QTLs associated with plant height-related traits under normal nitrogen environments and low nitrogen environments, with a focus on QTLs that respond to nitrogen stress.

Materials and methods

Plant Materials and Experimental design

A total of 120 bread wheat cultivars collected from the Yellow and Huai Valley Regions of China, including Henan, Hebei, Shaanxi, and Shandong provinces, were selected as a collection of local varieties (Table S1). These cultivars were planted and harvested in 2017–2018 and 2018–2019. In each cropping season, all the surveyed cultivars were planted in experimental fields of Shandong Agricultural University, Tai’an city (116°36’ E, 36°57’ N). Between the two cropping season, the statistic of temperature and rainfall was similar between 2018 and 2019, according to official data (http://sd.cma.gov.cn). Two
treatments were applied: low nitrogen (LN) and a
normal fertilized control (CK). Hereafter, “2017LN”,
“2017CK”, “2018LN”, and “2018CK” represent the
treatment trials. Each block had four rows with a
length of 1.5 m spaced 25 cm apart.

To analyze the soil nitrogen content, samples were
selected at a depth of 0–40, 40–60 cm using a five-
point sampling method in each block during the seed-
ing stage. The nitrogen content of the soil samples
was measured using the alkali-hydrolyzable nitrogen
method (Fan et al. 2005). The soil nitrogen contents
were the average of the samples. In the depth of
0–40 cm, the soil nitrate nitrogen content in the low
nitrogen environments was 90 mg/kg, while that in
the CK environments was 135 mg/kg. Significant dif-
fferences ($p < 0.01$) existed between the LN and CK
blocks. In the depth of 40–60 cm, there was no differ-
ent soil nitrate nitrogen content (72.5 mg/kg) between
LN and CK blocks. In the LN and CK blocks, urea
were applied about 300 kg/hm$^2$ at elongation stage
of wheat, and no other fertilizer was applied at the
crop growth stages. Crop management was performed
according to the local cultivation practices.

Phenotyping

For each cultivar surveyed, five representative tillers
from different individual plants were investigated.
Plant height and its component traits (Fig. 1), includ-
ing plant height (PH), spike length (SL), length of
the first internode from the top (FIRILT), length of the
second internode from the top (SECILT), length of the
third internode from the top (THILT), length of the
fourth internode from the top (FORILT), length of the
fifth internode from the top (FIFILT), length of the
sixth internode from the top (SIXILT), and the peduncle length (PL), were investigated (Fig. 1). The
lodging resistance strength (LRS) was measured in
the field during the grain filling stage 15 days after
flowering. The strength was recorded when the stem
was pushed down 20 cm above the ground using a
YYD-1 plant culm-strength meter (Hangzhou Wan-
shen Detection Technology Co., Ltd., HangZhou,
China).

In the analysis of variance (ANOVA), the for-
mula $\sigma^2_g + \sigma^2_e + \sigma^2_{ge} + \sigma^2_{er}$ was used to cal-
culate $\sigma^2_g$, $\sigma^2_e$, $\sigma^2_{ge}$ and $\sigma^2_{er}$. The formula $h^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_e + \sigma^2_{ge}/n + \sigma^2_{er}/nr)$ was used to calculate broad-sense heritability ($h^2$), where $\sigma^2_g$, $\sigma^2_e$, $\sigma^2_{ge}$,
and $\sigma^2_{er}$ represent the variance components geno-
type, environment, genotype × environment and error,
respectively, n and r are the numbers of environments
and replications, respectively (Lou et al. 2020; Yang
et al. 2020). The calculation of pairwise correlation
coefficients for these traits was conducted using the
“Performance Analytics” package in R software,
and the boxplot of traits was visualized using the
“ggplot2” package under multiple comparisons meth-
ods and was utilized to compare the same trait in the
different environments using the “LSD.test” (Fisher’s
least significant difference test) method. The formula
$T_{delt,aver} = 100 \times (T_{CK} - T_{LN}) / T_{LN}$ was used to calculate
the trait reaction response to LN; $T_{CK}$ represents the
trait in the CK environment, and $T_{LN}$ represents the
trait in the LN environment.

DNA extraction and genotyping

DNA was extracted from multiple young leaf tissues
from different plant of each cultivar using the SDS
method (Cui et al. 2011). DNA quality was checked
by electrophoresis on 1% agarose gels, and DNA
concentration was determined with a Nanophotom-
er (NanoDrop Technologies Co., Ltd., Wilmington,
USA). Genotyping was performed by Beijing EMTD
Technology & Investment Co., Ltd. (Beijing, China;
http://www.emtd.com.cn) using the 90 K wheat genotyping assay (Wang et al. 2014) following the manufacturer’s protocol.

The genotypic clusters for each SNP were determined using Genome Studio version 2011.1 software, filtering out SNPs with a call rate > 0.35. After the filtering out of SNPs with a minor allele frequency of < 5% and SNPs with > 10% missing data, 120 cultivars with 20,689 polymorphism SNPs were retained for further analysis. This processing was implemented in PLINK software (Purcell et al. 2007). The physical maps of all SNPs were obtained from the website (http://wheatgenomics.plantpath.ksu.edu/wpdb/assay?from=singlemessage) and are aligned to the IWGSC reference version 1.0 genome (International Wheat Genome Sequencing et al. 2018). Among the 20,689 SNPs, 8,632 SNPs with known physical positions were retained.

Linkage disequilibrium and population structure analysis

Linkage disequilibrium (LD) among markers was calculated for the A, B, and D genomes in PLINK software. The window size for linkage disequilibrium calculation was set based on the number of SNPs located in each genome. Pairwise linkage disequilibrium was measured using squared allele frequency correlations and was assessed by calculating the squared allele frequency correlation ($r^2$) for pairs of SNP loci (Pang et al. 2020). Principal component analysis (PCA) was conducted using GAPIT with the default parameters to calculate principal components (PCs) (Lipka et al. 2012).

Genome-wide association study

GWAS was implemented by GAPIT packages in R software using the mixed linear model (MLM, PCA + K), which took the population structure and relative kinship into account (Zhang et al. 2010). The kinship matrix (K) was automatically calculated using the VanRaaden method (VanRaaden 2008). The first four principal components of the SNP data were included in the GWAS model. To combine the GWAS results from all environments, a uniform suggestive genome-wide significance threshold ($P$ value = 1.0e−3) was used. Quantile–quantile (Q–Q) plots and Manhattan plots were visualized with the R package “CMplot” (https://github.com/YinLiLin/CMplot). The $R^2$ value was used to evaluate the magnitude of the location’s effects.

Results

LD analysis

A total of 120 cultivars and 8632 SNPs with known physical positions were retained for further analysis. The number of SNPs within 1 MB across each chromosome is shown in Figure S1. Moreover, the number of SNPs across each chromosome is shown in Table S1. These SNPs were distributed on all 21 wheat chromosomes, with 3260, 4310, and 1062 SNPs in the A, B, and D subgenomes, respectively.

LD was estimated by calculating the $r^2$ among all possible pairs of markers for each of the 21 chromosomes. The obtained $r^2$ values were then plotted against the physical distance for each of the three genomes separately (Figure S2) and across the whole genome. When the cutoff threshold for $r^2$ was defined as 0.1, the LD decay distance for the entire genome was greater than 15 MB.

Phenotypic trait analysis among subpopulations under different conditions

We analyzed each phenotypic trait among subpopulations under different conditions. The performance of all traits in the LN and CK environments is displayed in Fig. 2. From Fig. 2, we found that the same traits of subgroups were different. By comparing the same traits under the CK and LN environments within a subgroup (Table S2), we found that the PH and PH components were both greater in the CK treatment than in the LN treatment, except for the SECILT and THILT of the C subgroup. In the ANOVA results, a significant $P$ value of $\sigma^2$ existed among the different environments (Table S3), which illustrated that the environment affected the traits. According to the comparison of all traits in the CK and LN environments, the PH, SL, FORILT, FIFILT, and LRS showed significant differences ($P < 0.001$). The results indicated that the decrease in PH in the LN treatment was mainly caused by decreases in the length of FORILT, FIFILT, and SL in the LN treatment.
Using the ANOVA results and formula of broad sense heritability, we calculated $h^2$ for each trait. The $h^2$ of the tested traits ranged from 0.668 (SIX-ILT) to 0.97 (PH). For four traits (PH, SECILT, THILT, FORILT), $h^2$ was greater than 0.9, whereas $h^2$ for FIRILT, LRS, PL, FIFILT, and SL was 0.884, 0.875, 0.862, 0.810, 0.799 and 0.668, respectively (Table S3).

The average data based on each trait were used to calculate Pearson’s correlation coefficients. PH was positively correlated with SECITL, THILT, and FORILT (Figure S3); SL was negatively correlated with FORILT and FIFILT (Figure S3). PL showed a strong positive correlation with FIRILT (Figure S3), and the LRS showed no correlation with other traits (Figure S3), which indicated that LRS had no significant relationship with the length of internodes (Figure S3).

GWAS of plant height-related traits under low nitrogen and normal environments

To eliminate the influence of the kinship and structure of the population, we performed GWAS for all traits with the MLM method under CK and LN environments, and significant SNPs ($P < 1e-3$), repetitive SNPs in multiple environments (all, E > 3; CK, E = 2; LN, E = 2) and SNPs located within the LD decay distance (15 M) were defined as repetitive QTLs. Manhattan plots and QQ plots for all traits are shown in Fig. 2 and Figure S4. All detected SNPs and QTLs in the CK and LN environments are displayed in Table S4. GWAS analysis showed that a total of 86 QTLs were detected in the LN and CK environments.

Plant height and plant height components

A total of 12 QTLs were detected after analysis of PH (Fig. 2; Table S4), including 7 QTLs in the
CK environment and 6 QTLs in the LN environment, which were mainly distributed on chromosomes 1B, 3A, 3B, 3D, 4B, 6B, 7A, and 7B. Two QTLs, *QPH.sdau-3A.1* (142 MB) and *QPH.sdau-4B* (555–570 MB), were detected in both the CK and LN environments, explaining 8.0–10.6% and 9.2–10% of the phenotypic variation, respectively (Fig. 2; Table S4, PH). Two QTLs, *QPH.sdau-3B.2* (814 MB) and *QPH.sdau-7A.1* (34–49 MB), were detected in the 2017CK and 2018CK environments and explained 9.5–10% and 8.0–8.3% of the phenotypic variation, respectively. No repetitive QTLs were detected with PH in the 2017LN and 2018LN environments.

A total of 10 QTLs mainly distributed on chromosomes 2A, 2B, 3A, 3B, 3D, 5A, 5B, and 7B were associated with SL, including 6 QTLs in the CK environment and 4 QTLs in the LN environment (Fig. 2; Table S4, SL). Among all QTLs, *QSL.sdau-3D* (602 MB) in 3D was detected in the 2017CK and 2018CK environments, while no SNP was detected in the LN environment. The phenotypic variation explained by *QSL.sdau-3D* ranged from 7.9 to 11%.

For FIRILT, 19 QTLs were identified on chromosomes 1A, 1B, 1D, 2A, 3A, 3B, 4B, 5A, 5B, 6A, 6B, 7A and 7B, including 14 QTLs in the CK environment and 8 QTLs in the LN environment (Fig. 2; Table S4, FIRILT). *QFIRILT.sdau-3A.2* (503 MB) and *QFIRILT.sdau-4B* (555–570 MB) were both detected in the 2017CK, 2018CK, 2017LN, and 2018LN environments, explaining 9.8–12.8% and 9.9–13.7% of the phenotypic variation, respectively. *QFIRILT.sdau-7B.2* (606–608 MB) was detected in the 2017CK and 2018CK environments and explained 10.9–12.3% of the phenotypic variation. A total of 6 QTLs for SECITL were identified on chromosomes 1B, 3A, 4A, 4B, 6B, and 7B, including 2 QTLs in the CK environment and 4 QTLs in the LN environment (Fig. 2; Table S4, SECITL). Among all QTLs, the QTL *QSECILT.sdau-4B* (535–570 MB) was detected in the 2017LN and 2018LN environments. The phenotypic variation of *QSECILT.sdau-4B* ranged from 8.6 to 9.9%. For THILT, 11 QTLs were identified on chromosomes 2A, 2D, 3A, 3B, 4B, 6B, 7B and 7D, including 7 QTLs in the CK environment and 6 QTLs in the LN environment (Fig. 2; Table S4, THILT). A total of 13 QTLs for FORILT were identified on chromosomes 1B, 3A, 3B, 5A, 5B, 6A, 6B, 7B and 7D, including 7 QTLs in the CK environment and 7 QTLs in the LN environment (Table S4, FORILT). For FIFILT, 14 QTLs were identified on chromosomes 2A, 3A, 3B, 5A, 5B, 6A, 6B, 7B and 7D, including 11 QTLs in the CK environment and 3 QTLs in the LN environment (Fig. 2; Table S4, FIFILT). From SECITL to FIFILT, no repetitive QTLs were detected in the CK or LN environments. Plant height in wheat is the spike length plus the length of all internodes above the ground, while SIXILT existed in a small number of cultivars; therefore, so it was not suitable to perform GWAS with SIXILT in the present study.

Plant height-related traits

Although PL and LRS are not components of PH, they are associated with plant morphology, which is closely related to PH. A total of 13 QTLs were detected with PL on chromosomes 2A, 3A, 3B, 4A, 4B, 5B, 6A and 7B, including 7 QTLs in the CK environment and 9 QTLs in the CN environment and 9 QTLs in the LN environment (Fig. 2; Table S4, PL); however, none of the QTLs were repetitively deactivated. A total of 7 QTLs for LRS were detected on chromosomes 2B, 3A, 3B, 4A, and 6A, including 5 QTLs in the CK environment and 3 QTLs in the LN environment (Fig. 2; Table S4, LRS). Among them, *QLRS.sdau-4A* (630 MB) was detected in the 2017CK, 2018CK, 2017LN, and 2018LN environments, explaining 11.2–12.5% of the phenotypic variation. *QLRS.sdau-2B* (42 MB) and *QLRS.sdau-3B* (657–664 MB) were detected in the 2017LN and 2018LN environments, while *QLRS.sdau-3A.1* (487 MB), *QLRS.sdau-3A.3* (513 MB) and *QLRS.sdau-6A* (614 MB) were detected in the 2017CK and 2018CK environments. *QLRS.sdau-2B* and *QLRS.sdau-3B* explained 12.1–12.5% and 12.1–16.8% of the phenotypic variation, respectively (Table S4, LRS).

GWAS of plant height-related traits in response to nitrogen stress

According to the comparison of the same traits in the CK and LN environments, different nitrogen contents in the soil caused the difference in FORILT, FIVILT, SL, PH, and LRS. T_{delt.aver} was measured as the trait that responded to nitrogen stress. Based on GWAS and T_{delt.aver}, QTLs that responded to nitrogen stress
were detected (Fig. 3; Table 1). A total of 18 QTLs that responded to nitrogen stress were detected.

In total, three QTLs for $T_{\text{delt}_\text{aver}_\text{FORILT}}$ responding to nitrogen stress were detected on 3A, 6A, and 6D (Fig. 3; Table 1). $Q_{\text{delt}_\text{aver}_\text{FORILT}.sdau-3A}$ (657 MB), $Q_{\text{delt}_\text{aver}_\text{FORILT}.sdau-6A}$ (18 MB) and $Q_{\text{delt}_\text{aver}_\text{FORILT}.sdau-6D}$ (17 MB) explained 12.1–12.5% and 12.1–16.8% of the phenotypic variation, respectively (Table 1). A total of 11 QTLs detected for $T_{\text{delt}_\text{aver}_\text{FIFILT}}$ in response to nitrogen stress were detected on 1A, 1B, 1D, 2A, 2B, 3A, 3B, 4A, 5B and 7B (Fig. 3; Table 1). Among them, $Q_{\text{delt}_\text{aver}_\text{FIFILT}.sdau-3A.2}$ (648–658 MB) had the lowest P-value and explained 12.1–12.5% and 12.1–16.8% of the phenotypic variation, respectively (Table 1).
variation, which was considered a main-effect QTL (Table 1). Qdelt_aver_SL.sdau-3A (705 MB) was detected for Tdelt_aver_SL in response to nitrogen stress, which explained 11.3% of the phenotypic variation (Table 1). Qdelt_aver_PH-5B (701 MB) was detected for Tdelt_aver_PH in response to nitrogen stress, which explained 11.3% of the phenotypic variation (Fig. 3; Table 1). Two QTLs, Qdelt_aver_LRS.sdau-3B (150 MB) and Qdelt_aver_LRS.sdau-5B (520 MB), for Tdelt_aver_LRS responded to nitrogen stress and explained 12.0% and 10.4% of the phenotypic variation, respectively (Fig. 3; Table 1) (Fig. 4).

Discussion

QTLs for plant height

Classical genetic studies indicated that plant height was a complex trait controlled by both Mendelian genes and quantitative genes. Previous genetic studies have identified numerous major QTLs for PH among 21 wheat chromosomes (Yu et al. 2020). Most dwarfing genes have been characterized, and closely linked molecular markers have been developed for marker-assisted selection in wheat breeding programs. Among the dwarfing genes, Rht-B1 and Rht-D1, which have been successfully utilized in wheat breeding programs worldwide, are located on the short arms of chromosomes 4B and 4D, respectively (Wurschum et al. 2015). In addition to Rht-B1 and Rht-D1 genes, other genes associated with PH had been reported in prervious studies such as Rht 8, Rht 13, Rht 22, Rht 24 et al. (Zhang et al. 2017; Wang et al. 2014; Li et al. 2013; Herter et al. 2018). What's more, other QTLs were also identified. Griffiths et al. identify 16 Meta-QTL using four DH population, which distributed in all chromosome except 3D, 4A, 5D, 7A ,7B and 7D chromosomes (Griffiths et al. 2010). Li et al. found a QTL located in 6A chromosome, explained 8–10.4% phenotypic variation (Li et al. 2013). A total of 33 QTL were identified across eight environments, and of these QTL, 17 stable QTL were located on chromosomes 1B, 2D, 3A, 4B, 4D, 5A, 6A, 6D, 7A, and 7B, explaining more than 95% of the observed variation of PH (Guan et al. 2018). Pang conducted a large-scale genome-wide association study using a panel of 768 wheat cultivars that were genotyped with 327 609 SNPs and detected 85 QTLs associated with PH, which distributed in 19 chromosomes except 1D and 3D chromosomes (Pang et al. 2020).

In this study, many QTLs were also detected for PH. The GA-responsive dwarfing gene Rht-1b (Wilhelm et al. 2013; Li et al. 2013) on the short arm of chromosome 4B was not detected, possibly because the materials used in this study are mainly widely used cultivars that maybe possess the Rht-B1b genes. QPH.sdau-7A.1, represented by SNP BS00078359_51, was located to a position similar to Rht 22 (Li et al. 2013), and it can be detected in 2017CK and 2018CK envirnoments. QPH.sdau-7B.1 and QPH.sdau-7B.2 might be similar to Rht 13 on chromosome 7BL (Wang et al. 2014). The FIRILT, SECILT, and THILT internodes may have an association with maturity in reproductive growth. The QTLs QTHILT.sdau-4B, QSECILT.sdau-4B, and QFIRILT. sdau-4B, which could be represented by SNP Bob-White_c5694_1201 located on 4B, were detected for PH, FIRILT, SECILT, and THILT, which could be the same loci reported in a previous study on maturity (Zou et al. 2017).

QTLs for the development of different internodes

The development period of wheat PH is dynamic. Genetic control of PH in bread wheat is complex, and most chromosomes harbor factors that can affect it. Stem elongation occurs in an ordered sequence. When the lower internode elongates to half of its final length, the one above it begins to elongate, then the next, and so on.

In the present study, QTLs were analyzed for PH and the lengths of each internode. When the lower-most internode of wheat (FIFILT) was elongating, the QTLs that were associated with FIFILT were probably activated. As FIFILT reached half of its final length, FORILT began to elongate, and the QTLs that were associated with FORILT were activated. This phenomenon continued with the development of other internodes. In the present study, the lengths of the different internodes were correlated with each other. This means that a certain QTL might not only control a certain length of a particular internode but might also control other internodes. In other words, some QTLs were temporarily activated in the development of one internode, while some QTLs were
consistently activated in the development of several internodes.

According to the QTLs detected in Table S4, we found some QTLs indicating this phenomenon. First, QTLs **QFIFILT.sdau-3A.1, QFORILT.sdau-3A.1, QTHILT.sdau-3A.1, QSECILT.sdau-3A** and **QFIRILT.sdau-3A.1**, which were represented by SNP **wsnp_Ex_c13802_21639096** on 3A, controlled the development of FIFILT, FORILT, THILT, SECILT and FIRILT, respectively. Previous study indicated that a QTL located on 3A mainly affects FIRITL and FIFITL to regulate PH, probably is a similar locus.

| Trait | QTL | SNP | Chromosome | Position | P-value | Effect | R² |
|-------|-----|-----|------------|----------|---------|--------|----|
| delt_aver_FORILT | Qdelt_aver_FORILT.sdau-3A | Excalibur_c49745_628 | 3A | 18,464,438 | 3.32 E−04 | 0.117 | 0.121 |
| delt_aver_FORILT | Qdelt_aver_FORILT.sdau-6A | Ra_c29107_289 | 6D | 17,503,572 | 8.02 E−04 | 0.094 | 0.105 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-1A | Excalibur_c58154_84 | 1A | 12,314,552 | 8.97 E−04 | 0.602 | 0.106 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-1B | Tdurum_conf_30712_430 | 1B | 111,368,423 | 4.70 E−05 | 1.477 | 0.164 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-1D | wsnp_Ex_c64327_63176640 | 1D | 19,267,156 | 5.39 E−04 | 0.793 | 0.116 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-2A | Excalibur_c1001_586 | 2A | 178,472,510 | 1.29 E−05 | 2.144 | 0.191 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-2A | BobWhite_rep_c49432_162 | 2A | 185,122,040 | 1.29 E−05 | 2.144 | 0.191 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-2B | TA005635-0459 | 2B | 161,406,179 | 1.54 E−04 | 1.202 | 0.140 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-3A.1 | Excalibur_c46600_919 | 3A | 648,027,721 | 6.28 E−09 | 2.997 | 0.363 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-3A.2 | Excalibur_c1001_586 | 3A | 648,260,665 | 6.28 E−09 | 2.997 | 0.363 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-3B | BobWhite_c17879_519 | 3A | 658,905,380 | 6.28 E−09 | 2.997 | 0.363 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-4A | Excalibur_c24511_1196 | 4A | 613,812,680 | 9.15 E−04 | 1.153 | 0.106 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-5B | JD_c947_819 | 5B | 72,100,553 | 7.93 E−04 | 0.661 | 0.109 |
| delt_aver_FIVILT | Qdelt_aver_FIVILT.sdau-7B | Excalibur_rep_c92684_316 | 7B | 741,244,806 | 1.13 E−04 | 1.504 | 0.147 |
| delt_aver_SL | Qdelt_aver_SL.sdau-3A | Excalibur_c24354_465 | 3A | 705,309,554 | 5.43 E−04 | 0.118 | 0.113 |
| delt_aver_PH | Qdelt_aver_PH.sdau-5B | Excalibur_c25348_659 | 5B | 701,155,513 | 6.95 E−04 | 0.046 | 0.096 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-3B | Excalibur_c17989_527 | 3A | 195,819,414 | 9.58 E−04 | 0.843 | 0.105 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-5B | wsnp_Ex_c32079_40793255 | 2A | 196,521,584 | 9.58 E−04 | 0.843 | 0.105 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-2B | TA005635-0459 | 2B | 161,406,179 | 1.54 E−04 | 1.202 | 0.140 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-3B | Excalibur_c23723_141 | 2B | 161,409,259 | 8.65 E−04 | 0.971 | 0.107 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-4A | Kukri_c41361_186 | 3A | 432,734 | 3.95 E−04 | 0.692 | 0.122 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-5B | Excalibur_c46600_919 | 3A | 648,027,721 | 6.28 E−09 | 2.997 | 0.363 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-3B | Excalibur_c1001_586 | 3A | 648,260,665 | 6.28 E−09 | 2.997 | 0.363 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-5B | BobWhite_c17879_519 | 3A | 658,905,380 | 6.28 E−09 | 2.997 | 0.363 |
| delt_aver_LRS | Qdelt_aver_LRS.sdau-7B | GENE-1167_104 | 3B | 684,256,078 | 8.45 E−04 | 0.713 | 0.108 |

**Table 1** All QTLs responding to nitrogen stress were associated with PH-related traits, including R² and P-value.
Fig. 4  Manhattan plot of significant SNPs for PH-related traits under LN stress
in this study (Zhang et al. 2017). In the nearby area, there existed a cytochrome P450 family protein gene TraesCS3A01G152100. Like the maize Dwarf3 gene (Winkler and Helentjaris 1995), encoding a protein of the cytochrome P450 superfamily, is involved in gibberellin biosynthesis. The gene TraesCS3A01G152100 maybe the candidate genes were represented as this QTL. In this study, this QTL not only control the length of FIRITL and FIFITL, but also control length of all internode. Second, QTHILT.sdau-4B, QSECILT.sdau-4B and QFIRILT.sdau-4B, which were represented by SNPs BobWhite_c5694_1201 and BobWhite_c4311_148 on 4B, controlled the development of THILT, SECILT, and FIRILT, respectively, similar to QTHILT.sdau-7B.2, QSECILT.sdau-7B and QFIRILT.sdau-7B.2, which were represented by SNP RAC875_c7123_1703. This QTL in 4B also was reported to control the length of FIRITL, SECITL, THIITL, and FOURITL, probably is a similar locus (Zhang et al. 2017). In the nearby area, the function of genes TraesCS7D01G498800 (Glyceral-3-phosphate acyltransferase) were reported to be involved in the regulation of plant height in Arabidopsis. (Bai et al. 2021) QFIFILT.sdau-7D.2, QFORILT.sdau-7D.1 and QTHILT.sdau-7D.1, which were represented by SNP IAAV9104, controlled the development of FIFILT, FORILT, and THILT, respectively. Third, QFIFILT.sdau-3B.2 and QFORILT.sdau-3B.2, which were represented by SNP BS00091867_51, controlled the development of FIFILT and FORILT, respectively, similar to QFIFILT.sdau-6B and QFORILT.sdau-6B, which were represented by SNP Excalibur_c2737_197. Furthermore, QFORILT.sdau-3A.1 and QTHILT.sdau-3A.1, which were represented by SNP wsnp_Ex_c13802_21639096, controlled the development of FORILT and THILT, respectively, similar to QTHILT.sdau-3A.2 and QFORILT.sdau-3A.2, which were represented by SNP Excalibur_c81897_420. In addition, QTHILT.sdau-3B and QFORILT.sdau-3B.2, which were represented by SNP TA004228-0191; QTHILT.sdau-6B and QFORILT.sdau-6B, which were represented by SNP Excalibur_c36771_136; QFORILT.sdau-7B and QTHILT.sdau-7B.1, which were represented by SNP Kukri_c41117_824; QFORILT.sdau-7D.2 and QTHILT.sdau-7D.2, which were represented by SNP Tdurum_contig61255_86; and QFORILT.sdau-7D.2 and QSECILT.sdau-6B, which were represented by SNP Tdurum_contig11126_182, controlled the development of THILT and SECILT, respectively. The QTLs for each internode were activated dynamically during the development of the corresponding internode. This study provides an understanding of the genetic basis of the development of internodes.

QTLs responded to low nitrogen level

Nitrogen is one of the most important inputs, and it is commonly the most deficient nutrient in soils (Humbert et al. 2013). PH in wheat is a complex trait; its components include SL and each internode length. As shown in Fig. 5, THILT, FORILT, and FIFILT accounted for approximately 30% of the PH length. Combined with the development period of wheat (White and Edwards 2008), the growth of these three internodes during the period of vegetative growth
leads to reproductive growth. FORILT and FIFILT showed a significant difference between the CK and LN environments in our study. Combined with the different nitrogen contents in the soil, we could infer that in the period of vegetative growth to reproductive growth, internode lengths were affected by the nitrogen content to some degree. Moreover, the PH in the LN environment was shorter than that in the CK environment, and the LRS in the LN environment was stronger than that in the CK environment. It could be presumed that under a degree of low nitrogen level, the PH was reduced, and the stem became stronger. As lodging has occurred frequently in recent years, an appropriate reduction in nitrogen could increase the lodging resistance.

In this study, three QTLs for FORILT in response to nitrogen stress were detected on 3A, 6A, and 6D chromosomes. Among them, the nearby area of 6A loci has been reported to LN stress and N use efficiency and it maybe a same QTL. A total of 11 QTLs for FIFILT were detected on 1A, 1B, 1D, 2A, 2B, 3A, 3B, 4A, 5B and 7B chromosomes and among them the loci on 4A was similar to qPhdv-4A (Zhang et al. 2017). One QTL for SL was detected on 3A; one QTL for PH was detected on 5B; and two QTLs were detected for LRS. QTLs were detected on chromosome 3A for FORILT, FIFILT, while in the nearby area QYd-3A has been reported to increase yield in LN, probably is a similar locus (Cui et al. 2014). Qdelt_aver_LRS.sdau-5B, which was detected for LRS, had the lowest P-value and was located at 520,552,412 bp on chromosome 5B. TraesCS5B01G334500 (UDP-glycosyltransferase) was found near this location (upstream within 5 MB) and is considered a key gene for LRS in response to low nitrogen level. UDP-glycosyltransferase, a key enzyme that may be involved in starch synthesis, is directly limited by the carbohydrate supply and has been shown to be impacted by N supply (Jiang et al. 2004).

Conclusion

In this study, we performed GWAS for plant height with spike length, the length of the first internode to the five internodes from the top during harvest, and the lodging resistance strength at the seedling stage based on local varieties in a low nitrogen and CK environments. GWAS analysis showed that a number of QTLs were detected, including 13 QTLs for PH, 10 QTLs for SL, 19 QTLs for FIRILT, 6 QTLs for SECILT, 11 QTLs for THILT, 13 QTLs for FORILT, and 14 QTLs for FIFILT. Compared to the normal environment, the of PH, FORILT, FIFILT, and SL were significantly shorter and the LRS was significantly stronger under the low nitrogen environment. GWAS was performed to detect QTLs that responded to nitrogen stress. In total, three QTLs for FORILT in response to nitrogen stress were detected on 3A, 6A, and 6D, and 11 QTLs for FIFILT were detected on 1A, 1B, 2A, 2B, 3A, 3B, 4A, 5B and 7B. In addition, one QTL for SL was detected on 3A, one QTL for PH was detected on 5B, and there were two QTLs for LRS. These QTLs may greatly deepen the understanding of the genetic basis of trait responses to nitrogen stress. The present study provided an opportunity for the detection of QTLs induced by nitrogen fertilization as well as direct evidence to dissect traits that responded to nitrogen stress induced by environmental factors.

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Author’s contribution Piyi Xing performed the experiments and prepared the manuscript. Xia Zhang and Dandan Li performed partial experiments. Yinguang Bao and Honggang Wang performed partial experiments and revised the manuscript. Xingfeng Li designed the experiment and prepared the manuscript. All authors reviewed and approved the manuscript.

Ethical standards The manuscript has not been submitted to other journals for simultaneous consideration. The submitted article is original and has not been published elsewhere in any form or language. This study was not be split up into several parts to increase the number of submissions and submitted to various journals or one journal over time. Results are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation (including image-based manipulation). No data, text, or theories by others are presented as if they were the author’s own. Authors have permission for the use of software questionnaires surveys and scales. References articles are cited appropriate and relevant literature in support of the claims made. Authors avoid untrue statements about an entity or descriptions of their behavior or actions that could potentially be seen as personal attacks or allegations about that person. Research has no threat to public health or national security. The author group, the Corresponding Author, and the order of authors are all correct. *Authors respect all of the above guide-
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