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ORIGINAL ARTICLE

QTL Detection for Internode Component Index in Wheat Using a RIL Mapping Population

Ran Qin[1] · Tianhang Ma[1] · Mingsu Cao[1] · Xijian Liu[1] · Xiaohan Zhou[1] · Guimei Hu[1] · Wen Zhong[2] · Xiaohui Sun[3] · Jingguo Xiao[1] · Jiajin Dong[1] · Wenchao Kong[1] · Chunhua Zhao[1] · Yongzhen Wu[1] · Han Sun[1] · Jun Ji[4] · Fa Cui[1]

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Abstract

Plant height (PH) is one of the most important traits related to plant architecture in wheat. Together, the lengths of individual internodes determine plant height and have a great influence on lodging resistance. To specify the genetic basis of wheat internode characteristics, we identified quantitative trait loci (QTLs) for each internode component index (ICI) and plant height component index (PHCI) using a recombinant inbred line (RIL) mapping population derived from 'Kenong 9204' ('KN9204') × 'Jing 411' ('J411'). Up to 57 putative additive QTLs for the four ICIs and PHCI were detected, which together covered 20 of the 21 wheat chromosomes, with the exception of chromosome 1B. Among them, eight QTLs were major, stable QTLs with a logarithm-of-odds (LOD) score of ≥ 3.0 and a phenotypic variance explained (PVE) of ≥ 7.0%. In the epistatic analysis, only one pair of epistatic QTLs was identified for the first internode component index (FIITCI) and three pairs of epistatic QTLs for the third internode component index (TITCI). A total of 20 of the 57 detected QTLs (35.1%) were co-localized QTLs for PH, spike length, and internode lengths, indicating that those traits have their own individual genetic basis in most cases. Moreover, 12 QTL clusters for PHCI/ICIs and yield-related traits were identified, indicating that plant architecture plays a potential role in the formation of yield in wheat. The plant architecture with gradually bottom-up shortened internode lengths tends to be high-yielding potential, especially for the uppermost internode. This study may provide useful information for understanding the genetic basis of plant height components, thus accelerating the genetic improvement of plant ideotypes designed to increase yield.

Keywords Wheat · Plant architecture · Internode component index · Plant height component index · QTL · Yield

Introduction

Wheat (*Triticum aestivum* L.) is one of the world's most important food crops, providing approximately 20% of the food energy for global human consumption (Xia et al. 2017). Plant height (PH) is a complex trait that has great influence on yield potential as well as on yield stability in wheat (Peng et al. 1999; Sourdille et al. 2000; Hedden 2003; Würschum et al. 2014). The introduction of *Rht* semi-dwarfing genes into wheat cultivars resulted in huge wheat yield increases, creating a new situation called the "Green Revolution" from the 1970s (Hedden 2003). The stem of a wheat plant consists of nodes and internodes. Internode lengths and internode component indices (ICIs) together determine the final PH and then affect plant architecture (Cui et al. 2011, 2012; Zhang et al. 2018a, b). ICI, a derivative trait of PH, is the ratio of internode length to the sum of the corresponding internode length and the next lower internode length (Cui et al. 2012). Wheats possessing ideotype especially with short basal internode length not only have characteristics of lodging resistance, but also have considerable yield potential (Pinthus and Levy 1983; Cui et al. 2011, 2012).

With the advances in wheat genomics and genetics, increasing numbers of QTLs for PH have been reported in

Ran Qin and Tianhang Ma contributed equally to this work.

Key Message
QTLs for each internode component index (ICI) and plant height component index (PHCI) were identified using a recombinant inbred line (RIL) mapping population. The QTL clusters for PHCI/ICI and plant height and plant height components together with yield-related traits were simultaneously analyzed in the present study.

✉ Fa Cui
sdaucf@126.com

✉ Jun Ji
jijun@sjziam.ac.cn

Extended author information available on the last page of the article

wheat (Law et al. 1978; Cui et al. 2011; Liu et al. 2011; Li et al. 2013; Zhang et al. 2017; Chai et al. 2019). By now, more than 25 genes that control PH and related traits have been reported in wheat (Evans 1998; Worland et al. 1998; Tian et al.2017; Würschum et al. 2017). Previous studies indicated that different QTLs for final PH might be induced by variation of different PH components (PHCs) (Kato et al. 1999; Cui et al. 2011; Maria and Herman 2016; Zhang et al. 2017), including spike length and internode lengths. However, most previous QTL studies have focused on the impact on final PH without considering its component traits (Qiao et al. 2007; Singh et al. 2016; Zhang et al. 2018a, b; Ma et al. 2019; Xue et al. 2019). There have been few studies on QTL localization for ICIs and PHCI (Cui et al. 2012; Li et al. 2013; Ren et al. 2014; Zhang et al. 2017).

The objectives of the present study were (1) to detect QTLs with additive effects for ICIs and PHCI in multiple environments, (2) to characterize the genetic relationships between PH and PHC, and (3) to reveal the genetic relationships among ICIs, PHCI, and yield-related traits.

Materials and Methods

Experimental Populations and Trait Evaluation

A recombinant inbred line population (RIL) containing 187 lines (denoted as KJ-RILs) derived from the $F_{8:9}$ generation of the cross 'Kenong 9204' ('KN9204') × 'Jing 411' ('J411') was used in this study. The KJ-RILs, together with the two parents, were planted in Yantai (37°53′N, 121°37′E, altitude 4 m) in Shandong Province, eastern China in four environments (2 years × 2 nitrogen treatments), namely high-nitrogen (HN) and low-nitrogen (LN) treatments over 2 years, i.e., 2016–2017 with HN, 2016–2017 with LN, 2017–2018 with HN, and 2017–2018 with LN, respectively (Zhao et al. 2019a, b), which were defined as E1, E2, E3, and E4, respectively. In the HN plot, 300 kg ha^{-1} of diammonium phosphate and 225 kg ha^{-1} of urea were applied to the seedbed before sowing, and 150 kg ha^{-1} of urea was applied as a top dressing at the elongation stage each year. In the LN plots, no nitrogen fertilizer was applied during the planting season. A randomized block design with two replications was used in each of the four environments, and each row was planted with 40 seeds by hand in two plots with a row spacing of 0.25 m and a length of 2 m. All of the locally recommended agronomic practices were followed in each of the trials except for the nitrogen fertilization treatment described above.

Five representative plants in the middle of each row were selected to measure plant height (PH) and the internode lengths from the first to the fifth internode counted from the top, i.e., the first internode length (FIRITL), the second internode length (SECITL), the third internode length (THITL), the fourth internode length (FOITL), and the fifth internode length (FIFITL).

The internode component indices (ICIs) from the first internode (top internode) to the fourth internode were referred to as the first internode component index (FIITCI), the second internode component index (SITCI), the third internode component index (TITCI), and the fourth internode component index (FOITCI). The plant height component index (PHCI) and the internode component indices (ICIs) were calculated as follows (Cui et al. 2012):

$$\mathrm{PHCI} = (\mathrm{FIRITL} + \mathrm{SECITL})/\ \mathrm{PH}$$
$$\mathrm{FIITCI} = \mathrm{FIRITL}/\ (\mathrm{FIRITL} + \mathrm{SECITL})$$
$$\mathrm{SITCI} = \mathrm{SECITL}/\ (\mathrm{SECITL} + \mathrm{THITL})$$
$$\mathrm{TITCI} = \mathrm{THITL}/\ (\mathrm{THITL} + \mathrm{FOITL})$$
$$\mathrm{FOITCI} = \mathrm{FOITL}/\ (\mathrm{FOITL} + \mathrm{FIFITL})$$

The yield-related traits (YRTs) were thousand-kernel weight (TKW), kernel number per spike (KNPS), yield per plant (YPP), and spike number per plant (SNPP) were determined as described by Cui et al. (2014, 2016) and Fan et al. (2019).

Data Analysis and QTL Mapping

Basic descriptive statistical analysis was performed on the experimental data, using EXCEL 2016 and SPSS 24.0 (Chicago, IL, USA). A high-density wheat genetic map with 119,566 loci spanning 4424.4 cM has been published by Cui et al. (2017). We used the Basic Local Alignment Search Tool (BLAST) (ftp://ftp.ncbi.nlm.nih.gov/blast/executables/release/) to align the single-nucleotide polymorphism (SNP) probes to the KN9204 genome assembly (unpublished data) to locate the physical positions of these SNPs. The physical positions of the SNPs of KN9204 rather than their genetic locations were used for QTL mapping analysis in this study. The best linear unbiased estimate (BLUE) values of each of the 187 KJ-RILs were calculated by the QGAStation 2.0 based on the phenotypic data from the four environments. The data from each of the four environments, as well as the BLUE data, were used for QTL analysis in the current study. QTL detection was conducted using inclusive composite interval mapping by QTL IciMapping 4.1 software (https://isbreeding.caas.cn/rj/index.htm), based on stepwise regression of simultaneous consideration of all marker information (http://www.isbreeding.net/). For QTLs with additive effects, the walking speed chosen for all QTLs was 0.01 Mb, and the *P* value inclusion threshold was 0.001. The threshold of log-of-odds (LOD) scores was evaluated using 1000 permutations with a type I error of 0.05. For QTLs with epistatic effects, the walking speed chosen for all QTLs was 5.0 Mb, and the *P* value inclusion threshold was 0.001. The

LOD scores were set at no less than 5. Only the datasets of the BLUE values for PHCI and ICIs were used for epistatic QTL detection.

Quantitative Trait Loci Nomenclature

The name of each QTL was designated as follows: the first letter 'Q' meant 'QTL'; the letters between 'Q' and '-' (dash) represented the abbreviation of the corresponding trait; the letter 'KJ' stood for the mapping population of KJ-RILs; the letters and numbers following the second dash represent the wheat chromosomes where the corresponding QTL was located; and the last number referred to the sequence number that the QTL was detected in the same wheat chromosome, from the short arm to the long arm. When two or more QTLs associated with the same trait with overlapping confidence intervals were detected in different environments, they were considered to be congruent QTLs.

Results

Phenotypic Performance for Internode Component Indices in the KJ-RIL Population

For the four environments, all the ICIs along with PHCI in the 187 KJ-RILs showed continuous variation with the absolute values of skewness and kurtosis being less than 1.0 in most cases, with the traits approximating to a normal distribution, indicating that they were typical quantitative traits and suitable for QTL analysis (Fig. 1; Table 1). The correlation coefficients of ICIs and PHCI among the four environments were significant ($P \leq 0.01$) (Table 2). The broad heritability scores for the five traits ranged from 75.25 (FIITCI) to 19.86% (TITCI). These results indicated that genetic factors played important roles in determining the phenotypic variation of ICIs and PHCI in the 187 KJ-RILs.

Correlation Analysis Between Plant Height/Internode Component Index and Individual Internode Lengths in the KJ-RIL Population

Correlation analysis results showed that PH was significantly negatively correlated with TITCI and FOITCI under both LN and HN conditions as well as with SITCI and PHCI under HN conditions (Table 3). On the other hand, PH was significantly positively correlated with FIITCI under both LN and HN conditions. FIRITL was significantly positively correlated with PHCI and FIITCI under both LN and HN conditions as well as with SITCI, but with the latter under only LN conditions. FIRITL was significantly negatively correlated with TITCI and FOITCI under both LN and HN conditions. SECITL and SITCI were significantly positively correlated with each other under both LN and HN conditions. Furthermore, SECITL was significantly negatively correlated with FIITCI and TITCI, although only under HN conditions. THITL was significantly negatively correlated with PHCI, FIITCI, SEITCI, TITCI, and FOITCI simultaneously under both LN and HN conditions, except for FIITCI and TITCI, which were significantly correlated with THITL only under HN conditions. FOITL was significantly negatively correlated with PHCI, SITCI, TITCI, and FOITCI under both LN and HN conditions, and FIFITL was significantly negatively correlated with PHCI, SITCI, TITCI, and FOITCI under both LN and HN conditions. In addition, FIFITL was significantly positively correlated with FIITCI under LN conditions.

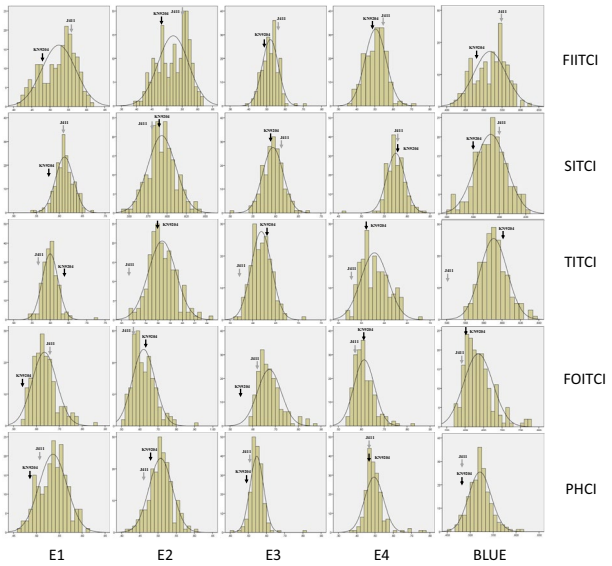


Fig. 1 Phenotypic distribution of wheat internode and plant height component indices in KJ-RILs under different environments. Parent value of KN9204 and J411 are shown by black and gray arrows, respectively. FIITCI, the first internode component index; SITCI, the second internode component index; TITCI, the third internode component index; FOITCI, the fourth internode component index; PHCI, the plant height component index

Correlation Analysis Between Plant Height/Internode Component Index and Yield-Related Traits in the KJ-RIL Population

The correlation coefficients between yield-related traits and both PHCI and ICIs in the KJ-RIL population are shown in Table 4. TKW was significantly positively correlated with PHCI under LN conditions but was significantly negatively correlated with TITCI under LN conditions as well as with FOITCI under both LN and HN conditions. SNPP was significantly negatively correlated with PHCI only under HN conditions as well as with FIITCI under both LN and HN conditions. KNPS and TITCI were significantly positively

Table 1 Phenotypic performance for internode and plant height component indices in the KJ-RIL population among four environments

Traits	Environment[a]	KJ-RILs							
		Min	Max	Mean	Std	Variance	Skewness	Kurtosis	Heritability (%)
FIITCI	E1	0.41	0.61	0.52	0.05	0.0021	−0.41	−0.76	75.25
	E2	0.40	0.61	0.52	0.05	0.0025	−0.30	−0.97	
	E3	0.39	0.70	0.52	0.04	0.0020	0.16	1.05	
	E4	0.37	0.71	0.50	0.06	0.0033	0.15	0.25	
	BLUE	0.42	0.62	0.52	0.04	0.0020	−0.25	−0.74	
SITCI	E1	0.54	0.67	0.61	0.02	0.0004	−0.21	0.93	21.84
	E2	0.54	0.64	0.59	0.02	0.0003	0.09	−0.07	
	E3	0.51	0.67	0.59	0.02	0.0005	−0.10	0.94	
	E4	0.46	0.64	0.58	0.02	0.0004	−0.63	0.27	
	BLUE	0.56	0.62	0.59	0.01	0.0001	−0.12	0.02	
TITCI	E1	0.55	0.72	0.60	0.02	0.0005	0.89	0.99	19.86
	E2	0.51	0.65	0.57	0.02	0.0005	0.47	0.62	
	E3	0.57	0.71	0.62	0.02	0.0005	0.35	0.65	
	E4	0.52	0.68	0.58	0.03	0.0009	0.44	−0.45	
	BLUE	0.56	0.63	0.59	0.01	0.0002	0.45	0.14	
FOITCI	E1	0.53	0.87	0.63	0.05	0.0029	0.94	1.45	44.83
	E2	0.51	0.91	0.62	0.06	0.0038	0.99	1.75	
	E3	0.59	0.87	0.67	0.05	0.0027	1.20	1.90	
	E4	0.54	0.83	0.61	0.04	0.0020	1.35	2.83	
	BLUE	0.57	0.78	0.64	0.04	0.0015	1.18	1.83	
PHCI	E1	0.46	0.61	0.54	0.03	0.0009	−0.10	−0.42	28.99
	E2	0.42	0.60	0.51	0.03	0.0010	0.01	0.25	
	E3	0.42	0.81	0.55	0.04	0.0014	1.79	3.36	
	E4	0.38	0.77	0.50	0.05	0.0027	2.08	8.08	
	BLUE	0.45	0.61	0.52	0.02	0.0006	0.49	1.26	

PHCI the plant height component index, *FIITCI* the first internode component index, *SITCI* the second internode component index, *TITCI* the third internode component index, *FOITCI* the fourth internode component index

[a]The BLUE values based on the four environments were also used for phenotypic performance analysis

correlated with each other only under HN conditions. YPP was significantly negatively correlated with PHCI, TITCI, and FOITCI simultaneously under HN conditions. The above findings indicated that PHCI and ICIs might affect yield potential to some extent, especially under HN conditions, and that common genetic factors underlying PHCI, ICIs and yield-related traits might exist.

Table 2 Phenotypic correlation coefficients among environments for internode and plant height component indices

Environments	PHCI	FIITCI	SITCI	TITCI	FOITCI
E1&E2	0.59**	0.85**	0.38**	0.41**	0.58**
E1&E3	0.56**	0.80**	0.50**	0.28**	0.19*
E1&E4	0.35**	0.69**	0.43**	0.31**	0.55**
E2&E3	0.53**	0.82**	0.40**	0.30**	0.19*
E2&E4	0.42**	0.75**	0.28**	0.49**	0.58**
E3&E4	0.26**	0.72**	0.18**	0.42**	0.35**

PHCI the plant height component index, *FIITCI* the first internode component index, *SITCI* the second internode component index, *TITCI* the third internode component index, *FOITCI* the fourth internode component index

*Correlation is significant at $P \leq 0.05$ level; **Correlation is significant at $P \leq 0.01$ level

Putative Additive QTLs for Internode and Plant Height Component Indices

Up to 57 putative additive QTLs for the four ICIs and PHCI were detected in the KJ-RIL population. Together, they covered all of the 21 wheat chromosomes with the exception of 1B (Table 5). Of these, 21, 14, and 22 QTLs were mapped to the A, B, and D subgenomes, respectively. There were 10, 17, 6, 11, and 13 QTLs detected for FIITCI, SITCI, TITCI, FOITCI, and PHCI, respectively, which individually explained 1.16–57.40% of the phenotypic variance with LOD scores ranging from 2.02 to 51.05 (Fig. 2).

A total of ten putative, additive QTLs for FIITCI were identified in the four environments and the BLUE analysis

Table 3 Phenotypic correlation coefficients between plant height/internode length and their component indices in the KJ-RIL population

Environments (LN/HN)	PHCI	FIITCI	SITCI	TITCI	FOITCI
PH	0.22**/−0.16*	0.41**/0.21**	0.07/−0.16*	−0.30**/−0.69**	−0.42**/−0.39**
FIRITL	0.65**/0.54**	0.81**/081**	0.20**/0.030	−0.23**/−0.31**	−0.37**/−0.28**
SECITL	0.26**/−0.10	−0.12/−0.27**	0.39**/0.17*	−0.06/−0.50**	−0.07/0.02
THITL	−0.16*/−0.33**	−0.12/−0.23**	−0.31**/−0.31**	−0.06/−0.58**	−0.32**/−0.15*
FOITL	−0.19**/−0.30**	0.02/0.04	−0.25**/−0.10**	−0.59**/−0.62**	−0.45**/−0.38**
FIFITL	−0.25**/−0.45**	0.21**/−0.09	−0.35**/−0.39**	−0.52**/−0.71**	−0.88**/−0.71**

For each entry, the left cells show correlation coefficients at a low-nitrogen (LN) level, and the right cells depicted correlation coefficients at a high-nitrogen (HN) level

PHCI the plant height component index, *FIITCI* the first internode component index, *SITCI* the second internode component index, *TITCI* the third internode component index, *FOITCI* the fourth internode component index, *PH* plant height, *SL* spike length, *FIRITL* the first internode length, *SECITL* the second internode length, *THITL* the third internode length, *FOITL* the fourth internode length, *FIFITL* the fifth internode length

*Indicates significant at $P \leq 0.05$ level; **Indicates significant at $P \leq 0.01$ level

(Fig. 2; Table 5). Individually, they explained 1.16–57.40% of the phenotypic variance (Table 5). Of these, *QFiitci-KJ-1D.1*, *QFiitci-KJ-4A.1*, *QFiitci-KJ-6A.1*, *QFiitci-KJ-6B.1*, and *QFiitci-KJ-7A.1* were repeatedly detected in at least two datasets including the BLUE analysis. Among them, *QFiitci-KJ-6B.1* was a major, stable QTL with high LOD scores of 4.77 to 51.05 and high phenotypic variance explained (PVE) values of 6.09 to 57.40%; the allele of *QFiitci-KJ-6B.1* which caused increases in FIITCI was from parent 'J411'. In addition, both *QFiitci-KJ-4D.2* and *QFiitci-KJ-4D.3* were major QTLs with LOD scores ≥ 3.0 and PVEs ≥ 7.0%, although *QFiitci-KJ-4D.3* was an environment-specific QTL, detected in only one environment. There were eight and two QTL alleles donated by the parents 'J411' and 'KN9204', respectively, which increased FIITCI.

For SITCI, 17 QTLs were identified across the four environments (Fig. 2), which individually explained 3.50–29.00% of the phenotypic variance (Table 5). *QSitci-KJ-3A.1* could be detected in multiple environments of E1, E3, E4, and the BLUE analysis. QTLs *QSitci-KJ-3A.2* and *QSitci-KJ-4B.1* had high LOD scores of 5.85 and 18.20, respectively, with high PVEs of 15.06% and 29.00%, respectively, although they were both identified in only one environment. In addition, *QSitci-KJ-1A.1*, *QSitci-KJ-1A.2*, *QSitci-KJ-4B.2*, *QSitci-KJ-4D.2*, *QSitci-KJ-4D.2*, and *QSitci-KJ-6D.1* also displayed environment-dependent expression, with LOD scores ≥ 3.0 and PVEs ≥ 7.0%, which were defined as environment-dependent, major QTLs for SITCI. Alleles of eleven and six QTLs, which caused increasing SITCI, were contributed by 'J411' and 'KN9204', respectively.

Six putative, additive QTLs for TITCI were identified in the four environments, which individually accounted for 4.62–31.81% of the phenotypic variance, with LOD scores from 2.65 to 26.93 (Fig. 2; Table 5). *QTitci-KJ-4B.1* was a major, stable QTL with LOD scores of 6.62–26.93 and PVEs of 6.14–31.81%, which was

Table 4 Phenotypic correlation coefficients between plant height/internode component index and yield-related traits in the KJ-RIL population

Environments (LN/HN)	PHCI	FIITCI	SITCI	TITCI	FOITCI
TKW	0.18*/−0.07	0.11/0.02	0.09/0.03	−0.17*/−0.42	−0.28**/−0.17*
SNPP	−0.05/−0.28**	−0.16*/−0.21*	0.11/0.04	−0.01/0.01	0.07/−0.07
KNPS	−0.07/0.02	0.02/0.08	−0.14/-0.04	0.08/0.22**	0.10/−0.06
YPP	0.03/−0.19**	−0.01/0.02	0.01/−0.09	−0.05/−0.27**	−0.09/−0.24**

For each entry, the left cells show correlation coefficients at a low-nitrogen (LN) level, and the right cells depicted correlation coefficients at a high-nitrogen (HN) level

PHCI the plant height component index, *FIITCI* the first internode component index, *SITCI* the second internode component index, *TITCI* the third internode component index, *FOITCI* the fourth internode component index, *TKW* thousand-kernel weight, *KNPS* kernel number per spike, *YPP* yield per plant, *SNPS* spike number per spike.

*Indicates significant at $P \leq 0.05$ level; **Indicates significant at $P \leq 0.01$ level

Table 5 Putative additive QTLs for internode component indices in KJ-RIL population

Trait	QTL[a]	Environments	Position (Mb)[b]	Flanking markers	LOD score[c]	Add[d]	PVE (%)[e]
FIITCI	*QFiitci-KJ-1D.1*	E1/E3/BLUE	35.13/42.13/46.13	*AX-109933798 – AX-109984820*	6.76/4.13/5.08	−0.010/−0.009/−0.008	4.95/3.84/3.06
	QFiitci-KJ-4A.1	E2/E3	569.91/570.91	*AX-94881516 – AX-110526171*	2.30/3.59	−0.007/−0.008	1.70/3.40
	QFiitci-KJ-4A.2	E1/BLUE	656.91/620.91	*AX-110906980 – AX-111711476*	3.02/2.08	−0.007/−0.005	2.14/1.16
	QFiitci-KJ-4D.1	E1	251.53	*AX-111461162 – AX-111405194*	3.62	−0.007	2.54
	QFiitci-KJ-4D.2	E2/BLUE	398.53/366.53	*AX-109082249 – AX-110289945*	6.91/3.54	−0.006/−0.007	12.77/2.09
	QFiitci-KJ-4D.3	E2	402.53	*AX-109305626 – AX-109001644*	6.04	0.005	9.75
	QFiitci-KJ-6A.1	E2/E4	27.01/22.01	*AX-108954713 – AX-108992536*	2.10/2.22	−0.007/−0.014	1.8/5.99
	QFiitci-KJ-6B.1	E1/E2/E4/BLUE	598.77/616.77/591.77/616.76	*AX-110459394 – AX-109400480*	4.77/5.08/7.01/51.05	−0.004/−0.004/−0.004	6.09/7.11/7.90/57.40
	QFiitci-KJ-7A.1	E1/E3	658.95/664.95	*AX-110979428 – AX-109874881*	3.23/3.47	−0.007/−0.008	2.26/3.26
	QFiitci-KJ-7B.1	E1/E3	670.06/638.06	*AX-110023909 – AX-109053174*	4.69/4.14	0.009/0.009	3.56/3.88
SITCI	***QSitci-KJ-1A.1***	E3	136.13	*AX-110565910 – AX-110396556*	4.89	0.002	12.59
	QSitci-KJ-1A.2	E3	320.13	*AX-109479036 – AX-109507922*	4.03	−0.002	9.19
	QSitci-KJ-2D.1	E3	52.75	*AX-94461511 – AX-109879970*	2.62	0.004	3.50
	QSitci-KJ-3A.1	E1/E3/E4/BLUE	54.76/58.76/54.76/54.76	*AX-110446594 – AX-111661409*	4.35/4.75/4.56/7.28	−0.006/−0.007/−0.006/−0.005	7.74/9.44/8.78/12.20
	QSitci-KJ-3A.2	E2	571.76	*AX-111523636 – AX-94485283*	5.85	−0.007	15.06
	QSitci-KJ-4B.1	E3	30.70	*AX-109298160 – AX-109284839*	18.20	−0.012	29.00
	QSitci-KJ-4B.2	E4	208.71	*AX-109378163 – AX-109036402*	8.58	0.008	17.36
	QSitci-KJ-4B.3	E3	597.70	*AX-108786567 – AX-111609222*	3.65	0.005	4.80
	QSitci-KJ-4D.1	E1	342.53	*AX-111419619 – AX-94566944*	5.26	−0.006	9.53
	QSitci-KJ-4D.2	E3	473.53	*AX-111047156 – AX-111567243*	9.36	−0.008	13.30
	QSitci-KJ-5A.1	E1/E2/BLUE	570.67/549.67/559.67	*AX-110510491 – AX-109494596*	3.59/3.42/2.92	−0.005/−0.005/−0.003	6.39/6.26/4.64
	QSitci-KJ-5B.1	E2	549.32	*AX-110138658 – AX-110524034*	2.84	−0.004	3.78
	QSitci-KJ-5D.1	E2	260.62	*AX-109418073 – AX-109119487*	3.18	−0.005	6.12
	QSitci-KJ-6B.1	E4	698.76	*AX-109498878 – AX-109424039*	2.56	0.004	4.56
	QSitci-KJ-6D.1	E1	2.44	*AX-111167730 – AX-111211808*	4.23	0.006	7.52
	QSitci-KJ-7A.1	E2	544.95	*AX-109628791 – AX-110434148*	2.51	−0.004	4.61
	QSitci-KJ-7D.1	E1	463.79	*AX-109307518 – AX-109685044*	2.77	−0.004	4.84
TITCI	*QTitci-KJ-2B.1*	E3	787.06	*AX-94732752 – AX-109838927*	3.08	−0.005	5.25
	QTitci-KJ-3A.1	E2/E4/BLUE	55.76/54.76/58.76	*AX-110446594 – AX-111661409*	4.06/6.86/12.77	−0.007/−0.007/−0.007	8.41/6.21/12.74
	QTitci-KJ-3B.1	E2	12.17	*AX-111608694 – AX-94483555*	2.65	0.005	4.62
	QTitci-KJ-4B.1	E2/E3/E4/BLUE	30.70/25.70/35.70/35.70	*AX-109471924 – AX-108914451*	10.19/6.62/26.93/24.79	0.011/0.008/0.017/0.009	21.02/6.14/31.81/21.41
	QTitci-KJ-6A.1	E1	98.01	*AX-109270777 – AX-109912270*	3.60	−0.006	7.55
	QTitci-KJ-7D.1	E1	109.79	*AX-109303860 – AX-108838578*	2.86	0.005	6.06
FOITCI	*QFoitci-KJ-2D.1*	E3	24.75	*AX-110315690 – AX-109842248*	3.28	−0.012	5.42

Table 5 (continued)

Trait	QTL[a]	Environments	Position (Mb)[b]	Flanking markers	LOD score[c]	Add[d]	PVE (%)[e]
	QFoitci-KJ-2D.2	E2	404.75	*AX-109120561 – AX-110425009*	3.38	0.015	5.94
	QFoitci-KJ-2D.3	E1/E2	636.75/630.75	*AX-110700052 – AX-109949983*	2.10/2.23	−0.012/−0.013	5.12/4.66
	QFoitci-KJ-3A.1	E1/E2	455.76/492.76	*AX-110455859 – AX-111020709*	6.24/3.46	−0.017/−0.015	10.58/6.14
	QFoitci-KJ-3A.2	E3	586.76	*AX-109434477 – AX-111127766*	4.86	−0.014	7.29
	QFoitci-KJ-3D.1	E3	417.08	*AX-109383426 – AX-108891293*	5.91	−0.016	8.92
	QFoitci-KJ-5A.1	E1/E4	581.67/577.67	*AX-109323231 – AX-111799065*	2.69/2.17	−0.012/−0.010	4.62/4.98
	QFoitci-KJ-6A.1	E3	438.01	*AX-109063873 – AX-110590550*	3.14	0.012	4.59
	QFoitci-KJ-6A.2	E1/E2	553.01	*AX-110117565 – AX-110110944*	3.00/3.24	0.012/0.015	4.93/5.67
	QFoitci-KJ-6B.1	E2/E4	536.77/533.77	*AX-111125950 – AX-89438665*	4.08/8.43	0.017/0.019	11.71/17.74
	QFoitci-KJ-6B.2	E2	543.77	*AX-110046357 – AX-109033120*	18.44	−0.031	38.76
PHCI	*QPhci-KJ-2A.1*	E2	636.93	*AX-109984287 – AX-111584914*	2.74	−0.005	2.65
	QPhci-KJ-2D.1	E2	32.75	*AX-111696354 – AX-110668803*	4.48	−0.007	4.41
	QPhci-KJ-2D.2	E2	484.75	*AX-110561316 – AX-111157026*	5.13	0.007	5.08
	QPhci-KJ-3A.1	E1/E3/BLUE	54.76/58.76/54.76	*AX-110446594 – AX-111661409*	2.67/2.02/4.91	−0.007/−0.010/−0.007	5.16/6.81/6.62
	QPhci-KJ-3A.2	E2/E4	570.76/575.76	*AX-111523636 – AX-94485283*	5.49/2.62	−0.009/−0.013	7.56/5.97
	QPhciKJ-3A.3	E1/E2	693.76/692.76	*AX-94401889 – AX-109312388*	2.60/6.75	0.007/0.009	4.86/7.12
	QPhci-KJ-3D.1	E2/E3	368.08/368.08	*AX-111589572 – AX-109900541*	4.88/4.71	−0.007/−0.012	4.84/9.83
	QPhci-KJ-3D.2	E2	553.08	*AX-109270593 – AX-111912848*	2.75	0.005	2.65
	QPhci-KJ-4B.1	E4	25.70	*AX-109471924 – AX-108879111*	3.01	0.014	6.83
	QPhci-KJ-5D.1	E2	259.62	*AX-109418073 – AX-109119487*	26.49	−0.019	34.85
	QPhci-KJ-5D.2	E2	286.62	*AX-110186027 – AX-111504657*	15.92	0.014	18.26
	QPhci-KJ-5D.3	E3	494.62	*AX-109671031 – AX-111212888*	2.77	0.009	5.89
	QPhci-KJ-6B.1	E2	624.77	*AX-111665314 – AX-111640010*	15.88	−0.014	18.13

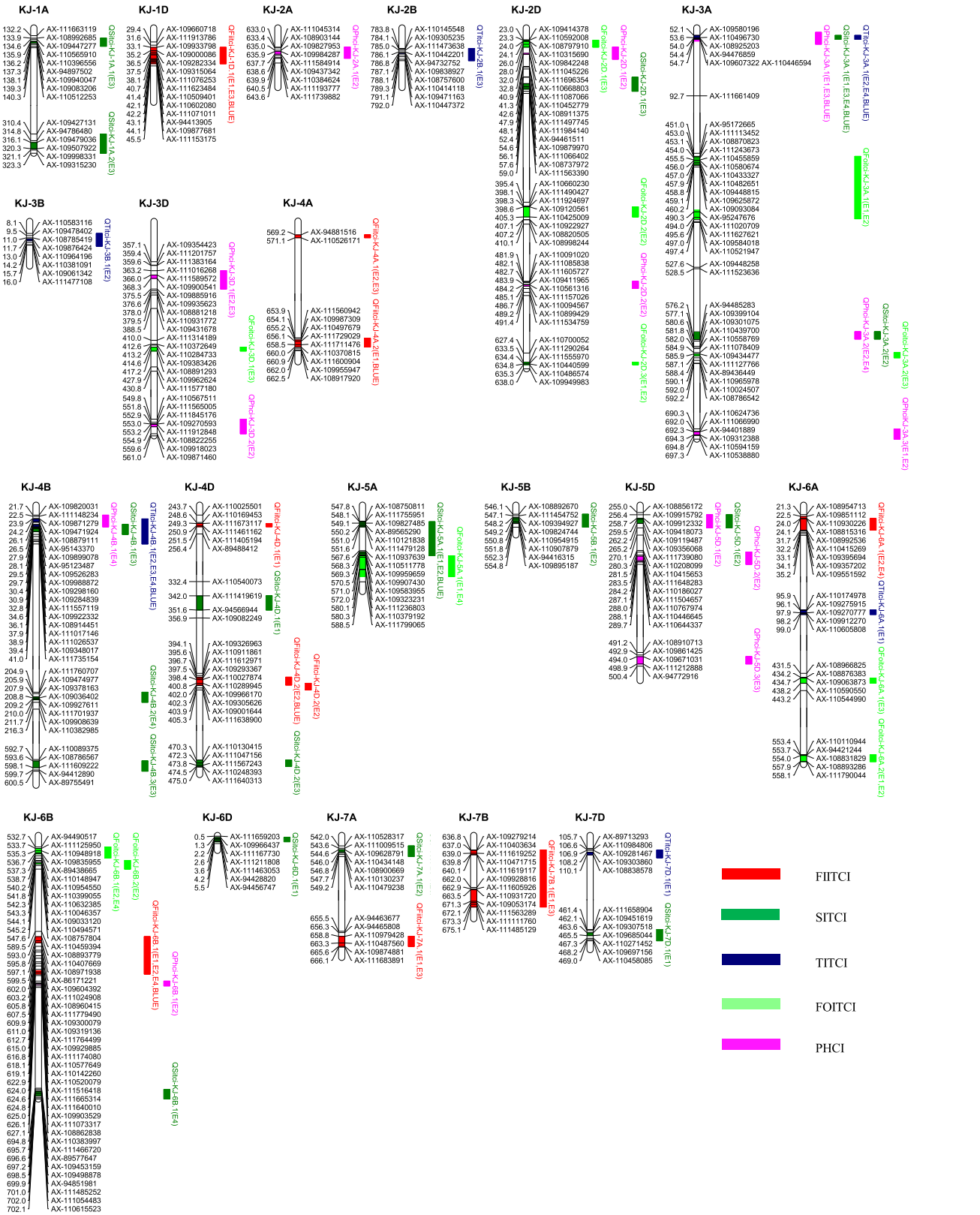
[a]A putative major QTL was marked in bold typeface and was characterized by a mean LOD score ≥ 3.0 and a mean PVE ≥ 7.0% (the average over environments), and a putative stable QTL was underlined, indicating that the QTL was detected in at least two of the four environments (E1, E2, E3, E4). A major and stable QTL was with both characteristics of major QTL and stable QTL

[b]The physical positions of markers on 'KN9204' genome

[c]The LOD scores ≥ 2.0 of detected QTLs

[d]The positive values indicate that the alleles from 'KN9204' could increase the phenotype values, while the negative values indicate that the alleles from 'J411' could increase the phenotype values

[e]The phenotypic variance explained (PVE) by one QTL


KJ-1A
KJ-1D
KJ-2A
KJ-2B
KJ-2D
KJ-3A
KJ-3B
KJ-3D
KJ-4A
KJ-4B
KJ-4D
KJ-5A
KJ-5B
KJ-5D
KJ-6A
KJ-6B
KJ-6D
KJ-7A
KJ-7B
KJ-7D
FIITCI
SITCI
TITCI
FOITCI
PHCI

◂**Fig. 2** Location of QTLs for internode and plant height component indices identified in four different environments based on a population of 187 KJ-RILs derived from a cross between 'KN9204' and 'J411'. The chromosome number is marked at the top of each chromosome. The positions of markers are listed on the left of the bars, and the names of markers and QTLs are listed on the right of the corresponding chromosomes. The colored segments on the chromosome indicate the confidence interval of the corresponding QTL, and the segment of red, green, black, fluorescent green, and pink colors represent the traits for the first internode component index (FIITCI), the second internode component index (SITCI), the third internode component index (TITCI), the fourth internode component index (FOITCI), the plant height component index (PHCI), respectively. The environments where the corresponding QTLs detected are shown in parenthesis

consistently identified in three different environments as well as under BLUE analysis. In addition, *QTitci-KJ-3A.1* was another stable, major QTL that was detected repeatedly in two of the four environments as well by BLUE analysis. In total, there were three and three QTL alleles increasing TITCI from parents 'KN9204' and 'J411', respectively.

Eleven putative, additive QTLs for FOITCI were detected across the four environments (Fig. 2). These QTLs individually explained 4.59–38.76% of the phenotypic variance with LOD scores ranging from 2.10 to 18.44 (Table 5). Five QTLs, namely *QFoitci-KJ-2D.3*, *QFoitci-KJ-3A.1*, *QFoitci-KJ-5A.1*, *QFoitci-KJ-6A.2*, and *QFoitci-KJ-6B.1*, could be identified in two environments. Of these, *QFoitci-KJ-6B.1* was a major, stable QTL with LOD score of 4.08–8.43 and PVE of 11.71–17.74%; *QFoitci-KJ-6B.2* was approximately 10 Mb away from *QFoitci-KJ-6B.1*, and it had a LOD score of 18.44 and a PVE of 38.76% in environment E2; 'KN9204' and 'J411' contributed positive alleles of *QFoitci-KJ-6B.1* and *QFoitci-KJ-6B.2*, respectively, that increased FOITCI. Four and seven QTL alleles increasing FOITCI were derived from 'KN9204' and 'J411', respectively.

For PHCI, 13 putative, additive QTLs were identified across all the tested environments and the BLUE analysis (Fig. 2; Table 5), which individually explained 2.65–34.85% of the phenotypic variance, with LOD scores ranging from 2.02 to 26.49. Six and seven QTL alleles which increased PHCI were derived from 'KN9204' and 'J411', respectively. At least four QTLs (*QPhci-KJ-3A.1*, *QPhci-KJ-3A.2*, *QPhciKJ-3A.3*, and *QPhci-KJ-3D.1*) were reproducibly detected in two different environments. Of these, only *QPhci-KJ-3D.1* was a major QTL with a PVE of 4.84 to 9.83. In addition, *QPhci-KJ-5D.1*, *QPhci-KJ-5D.2*, and *QPhci-KJ-6B.1* were major QTLs that could be identified in only one environment; however, they had relatively high LOD scores of 26.49, 15.92, and 15.88, respectively, and contributed 34.85%, 18.26%, and 18.13% of the phenotypic variance, respectively.

Epistatic QTL Analysis for Internode and Plant Height Component Indices

For FIITCI, only one pair of epistatic QTLs was detected (Table 6; Fig. 3). This interactive effect referred to the chromosomal regions of 20.13 Mb on chromosome 1A and 589.67 Mb on chromosome 4D. No significant additive effects existed from these two loci. These two loci came from parent 'KN9204' and could reduce FIITCI, and their interaction could explain 8.87% of the FIITCI phenotypic variation.

For TITCI, three pairs of epistatic QTLs were detected (Table 6; Fig. 3). The first interaction effects referred to the chromosomal regions of 792.17 Mb on chromosome 3B and 480.70 Mb on chromosome 4B. No significant additive effects existed in these two loci. The two loci genotypes being the same as those in 'KN9204' could reduce TITCI, and this interactive effects could explain 9.46% of the TITCI phenotypic variation. The second interaction referred to the chromosomal regions of 289.67 Mb on chromosome 4D and 659.67 Mb on chromosome 4D. No significant additive

Table 6 Epistatic QTLs for internode and plant height component indices in KJ-RIL population

Trait	Chr	Position (Mb)	Flanking marker	Chr	Position (Mb)	Flanking marker	LOD score	PVE (%)	AA[a]
FIITCI	1A	20.13	AX-111703433 – AX-111512097	4D	589.67	AX-110008535 – AX-110127489	5.86	8.87	−0.008
TITCI	3B	792.17	AX-108755014 – AX-89377431	4B	480.70	AX-109493306 – AX-110127489	5.50	9.46	−0.005
TITCI	4D	289.67	AX-94627936 – AX-109846736	4D	659.67	AX-111658400 – AX-111114294	5.15	16.27	0.006
TITCI	3B	812.17	AX-108727006 – AX-111008767	5D	372.88	AX-109401717 – AX-110031634	7.10	7.00	0.004

FIITCI, the first internode component index, *TITCI* the third internode component index

[a]AA indicates the additive × additive (AA) effect. The positive values mean the two QTLs are the same as those in parent 'KN9204' (or 'J411') taking the positive effect, while the two QTL recombinants take the negative effect. The negative values represent the opposite

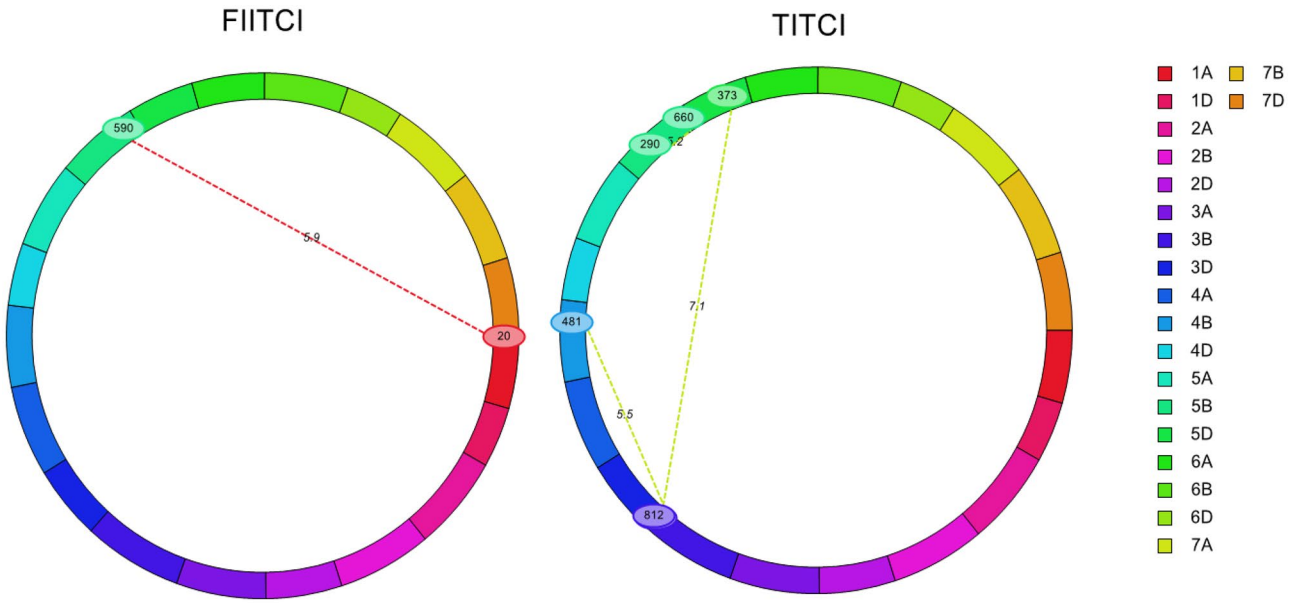


Fig. 3 Epistatic QTL analysis for the first internode component index (FIITCI) and the third internode component index (TITCI). The values on the line represent the phenotypic variance explained by the two interacting QTLs, and the values in the ellipse represent the physical position (Mb) on the 'KN9204' genome

effects existed in these two loci. The two loci genotypes being the same as those in 'KN9204' could increase TITCI, and their interactive effect could explain 16.27% of the TITCI phenotypic variation. For the third pair of epistatic QTLs, the two chromosomal regions involved were 812.17 Mb on chromosome 3B and 372.88 Mb on chromosome 5D, and no significant additive effects were detected in these two loci. The two loci genotypes being the same as those in 'KN9204' could increase TITCI, and this interactive effect could explain 7.00% of the phenotypic variation of TITCI.

No epistatic QTLs were detected for SITCI, FOITCI, or PHCI, indicating that single, additive effects play key roles in the phenotypic variation of these traits in the 187 KJ-RILs.

Discussion

Independent Genetic Basis Underlying Plant Height, Plant Height Components, and Their Component Indices Exist in Most Cases

The introduction of *Rht* genes reducing PH without altering the yield components has resulted in yield increases in wheat and other cereals (Carrillo et al. 1985; Hedden 2003). Thereafter, numerous studies focused on characterizing the genetic basis of PH and identifying novel *Rht* genes (Law et al. 1978; Wu et al. 2010; Cui et al. 2011; Liu et al. 2011; Li et al. 2013; He et al. 2016; Zhang et al. 2017; Chai et al. 2019). Previous studies have proved that PH and PHC might share their individual genetic basis in most cases (Carrillo et al. 1985; Cui et al. 2012; Ren et al. 2014; Zhang et al. 2017; Li et al. 2020). To date, no report regarding the genetic relationships between PH, PHC, PHCI, and ICIs at the QTL level has been published.

Traits with stronger genetic correlations tend to share more common QTL regions than those with weaker genetic correlations. In the present study, PH and internode lengths showed moderate or even weak correlations with PHCI and ICIs in most cases, implying that limited co-located QTLs or QTL clusters could be identified (Table 3). We performed QTL analysis for PH, spike length, internode length, and their component indices based on a high-density physical map (data not shown). The results revealed that 20 QTLs (35.1%) for ICIs and/or PHCI were co-localized with QTLs for PH, SL, and internode length, which comprised ten QTL clusters (Fig. 2; Table S1), indicating that ICIs and PHCI had influences on PH and its components in some cases. Approximately 64.9% of the QTLs for ICIs and PHCI have no association with either PH or individual internode lengths. This finding was consistent with their moderate or even weak phenotypic correlations in Table 3, indicating that ICIs and PHCI exhibited their specific genetic basis independent of PH and internode lengths in most cases. Therefore, it is essential to perform QTL analysis for ICIs and PHCI in order to better understand the genetic basis of plant architecture and thus to improve plant architecture in molecular breeding programs designed to improve yield.

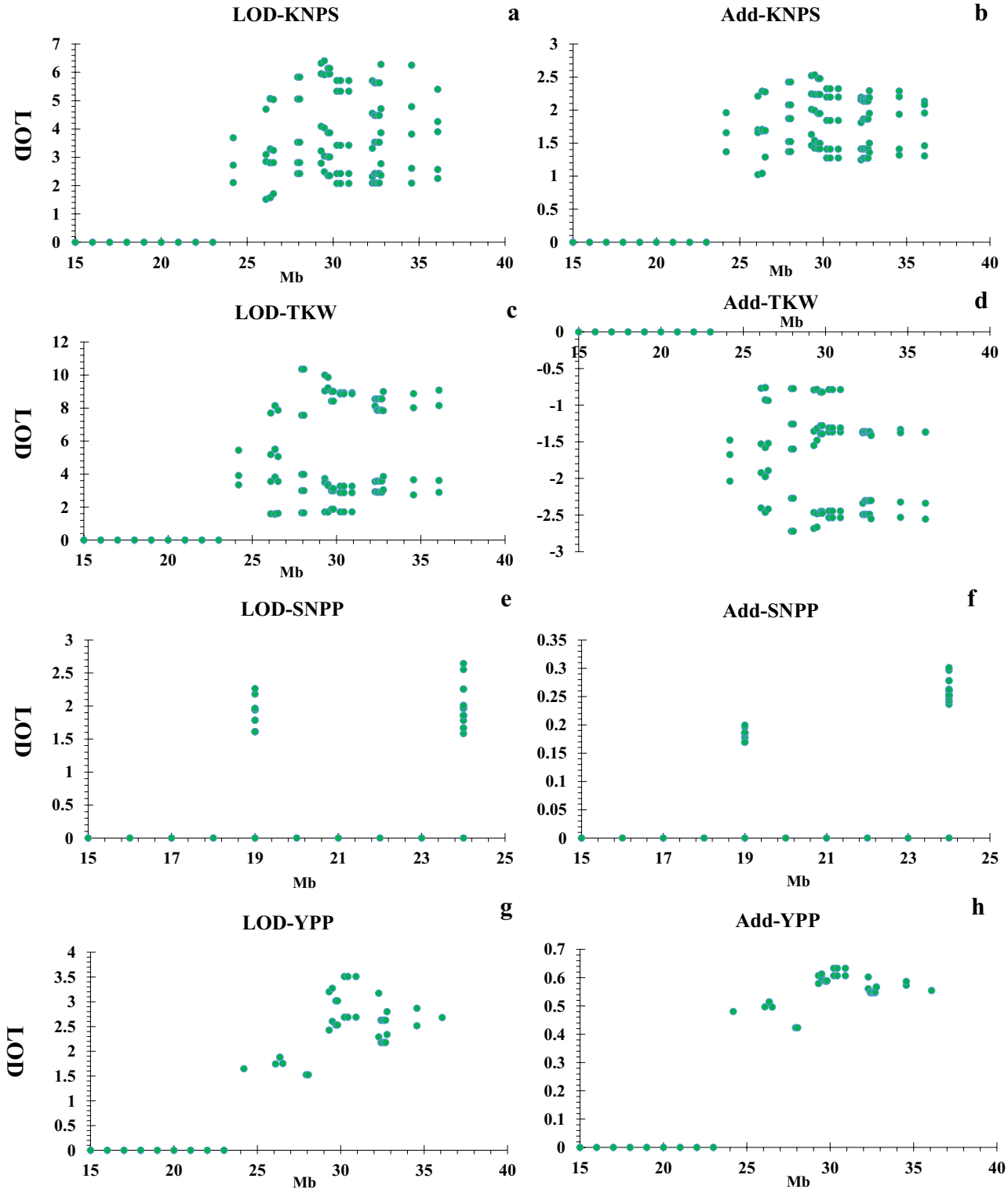


Fig. 4 Single-marker QTL analysis for TKW, KNPS, SNPP, and YPP on chromosome 4B (KN4B:15–36 Mb) based on phenotypic values in eight environments in Cui et al. (2016, 2017). The left-hand figures show the LOD scores of the corresponding traits in eight different environments; the right-hand figures show the additive effect values of the corresponding traits in eight different environments. Of the eight scatter diagrams, **a** and **b**, **c** and **d**, **e** and **f**, and **g** and **h** indicate the QTL LOD profiles and additive effects for kernel number per spike (KNPS), thousand-kernel weight (TKW), spike number per plant (SNPP), and yield per plant (YPP), respectively

Plant Height Component Indices and Internode Component Indices Affect Yield Formation in Some Cases

In general, PH has considerable effects on both yield potential and yield stability, especially in terms of environmental adaptation (Zhang et al. 2021). Gao et al. (2020) showed that PH was strongly, negatively correlated with grain yield under irrigation conditions, whereas a significant positive correlation was detected under no-irrigation condition. Zhang et al. (2021) demonstrated that four QTLs for PH were strongly associated with yield-related traits by using seven pairs of near-isogenic wheat lines. *Rht* gene that had no adverse effects on yield potential was of great value in high-yielding molecular breeding programs (Tian et al. 2021). As mentioned above, ICIs and PHCI shared their individual genetic basis in most cases. No study regarding genetic association analysis among ICI, PHCI, and yield-related traits had previously been published.

In this study, moderate or even weak correlations were observed among PHCI, ICI, and yield-related traits at the phenotypic level (Table 4). This finding implied that PHCI and ICIs might affect yield potential in some cases, especially under HN conditions. It is worth mentioning that more significant negative associations were observed between yield-related traits and PHCI/ICIs, especially for TITCI and FOITCI, albeit with moderate or low correlation coefficients (Table 4). This finding implied that the plant architecture with gradually bottom-up shortened internodes tended to have high-yielding potential, especially for the uppermost internode.

QTLs for yield-related traits have been documented in Cui et al. (2016, 2017). Among the 57 QTLs for PHCI and four ICIs, 19 QTLs (32.8%) were co-located with those for yield-related traits, which represented 12 QTL clusters (Table S2). Taking the fourth cluster of yield (CY4) as an example, *QPhci-KJ-3A.1*, *QSitci-KJ-3A.1*, and *QTitci-KJ-3A.1* were co-localized with two QTLs for yield-related traits (namely YPP, KNPS) on chromosome 3A. The favorable alleles from 'KN9204' increased KNPS and YPP, while reducing PHCI, SITCI, and TITCI. For CY8, *QPhci-KJ-4B.1*, *QSitci-KJ-4B.1*, and *QTitci-KJ-4B.1* were co-localized with QTLs for TKW, KNPS, and YPP (Table S2). The alleles from 'KN9204' increased PHCI, TITCI, KNPS, and YPP but reduced SITCI and TKW. Single-marker QTL analysis for TKW, KNPS, SNPP, and YPP in CY8 was performed based on phenotypic values across eight environments by Cui et al. (2016, 2017), with the aim of characterizing the genetic effects of PHC, SITCI, and TICI on yield-related traits in detail. The results confirmed that alleles from 'KN9204' increased PHCI, TITCI, KNPS, and YPP but reduced SITCI and TKW in multiple environments (Fig. 4). Moreover, significant signals for SNPP were identified, with alleles from 'KN9204' increasing SNPP (Fig. 4). These significant correlations and QTL co-localizations among PHCI, ICIs, and yield-related traits provide new genetic evidence supporting the hypothesis that PHCI and ICIs have influences on yield-related traits in wheat in some cases.

Stable QTLs for Plant Height/Internode Component Indices Are of Value to Further Explore Candidate Genes

Closely linked markers are essential tools for molecular breeding in wheat (Landjeva et al. 2007; William et al. 2007). In general, a stable QTL is less affected by the environment, and the corresponding linked markers are of great value in molecular breeding programs. In the present study, we defined a relative stable QTL that was confirmed in at least two of the four environments. A total of 21 of the 57 QTLs (36.8%) for PHCI and the four ICIs could be repeatedly identified in no less than two of the four environments as well as the BLUE analysis.

Of the 21 environment-reproducible QTLs, the effects of *QSitci-KJ-3A.1*, *QTitci-KJ-4B.1*, and *QFiitci-KJ-6B.1* could be determined in three of the four environments as well as the BLUE analysis. In the region of *QSitci-KJ-3A.1*, there were 44 candidate genes distributed (Fig. S1). As the primary interval is still relatively large, it is difficult to predict which one is the most likely candidate gene behind *QSitci-KJ-3A.1*. In addition, it was approximately 0.06–4.1 Mb away from the SNP markers of *AX-109607322* and *AX-110446594* (Fig. 2). Moreover, *AX-94476859*, *AX-108925203*, *AX-110496730*, and *AX-109580196* were closely linked with *QSitci-KJ-3A.1*. Therefore, *QSitci-KJ-3A.1* could be efficiently used in molecular breeding programs. PCR-based markers need to be developed based on probes specific for the sequences of these SNP markers in the future. *QTitci-KJ-4B.1* overlapped with *Rht-B1* and co-located with a major, stable QTL for PH (Fig. 2; Table S1 and S2). Therefore, we predict that *Rht-B1* might be the candidate gene of *QTitci-KJ-4B.1*, which showed pleiotropic effects on PH, PHC, PHCI, and ICIs. *QFiitci-KJ-6B.1* were mapped to a more concentrated region with the peak values of LODs at 591.77, 598.77, 616.77, and 616.76 Mb in E1, E2, E4, and the BLUE analysis, respectively. In view of its stability, higher LODs, and PVEs, fine-mapping analysis of this QTL should be performed to furtherly determine its precise physical position, albeit the high-density map of this chromosomal region.

Conclusion

Up to 57 putative additive QTLs were detected for PHCI and the four ICIs. Three major and stable QTLs of *QSitci-KJ-3A.1*, *QTitci-KJ-4B.1*, and *QFiitci-KJ-6B.1* are of value to further explore the candidate genes behind. PH, PHC, PHCI, and ICI

appear to have their own individual genetic basis at the QTL level in most cases. Moreover, we first specify the genetic correlations among ICIs, PHCI, and yield-related traits and found that PHCI and ICIs might have an influence on yield formation.

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Author Contribution Cui F, Ji J, and Qin R designed the research; Ji J and Cui F developed the KJ-RIL population; Ma TH, Cao MS, Liu XJ, Zhou XH, Hu GM, Zhong W, and Sun XH conducted phenotyping of the KJ-RIL population; Cui F and Ji J conducted genotyping of the KJ-RIL population; Qin R, Ma TH, Xiao JG, Dong JJ, Kong WC, Zhao CH, Wu YZ, and Sun H analyzed the data; Qin R, Ma TH, and Cui F wrote and revised the paper; all authors read and approved the final manuscript.

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Declarations

Competing Interests The authors declare no competing interests.

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Authors and Affiliations

Ran Qin[1] · Tianhang Ma[1] · Mingsu Cao[1] · Xijian Liu[1] · Xiaohan Zhou[1] · Guimei Hu[1] · Wen Zhong[2] · Xiaohui Sun[3] · Jingguo Xiao[1] · Jiajin Dong[1] · Wenchao Kong[1] · Chunhua Zhao[1] · Yongzhen Wu[1] · Han Sun[1] · Jun Ji[4] · Fa Cui[1]

[1] Key Laboratory of Molecular Module-Based Breeding of High Yield and Abiotic Resistant Plants in Universities of Shandong, School of Agriculture, Ludong University, Yantai 264025, Shandong, China

[2] Shandong Seed Administration Station, Jinan 250100, Shandong, China

[3] Yantai Academy of Agricultural Sciences, Yantai 264025, Shandong, China

[4] Center for Agricultural Resources Research, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Shijiazhuang 050022, Hebei, China