## RESEARCH

# QTL mapping for plant height and fruit branch number based on RIL population of upland cotton

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## Abstract

**Background:** Plant height (PH) and fruit branch number (FBN) are important traits for improving yield and mechanical harvesting of cotton. In order to identify genes of PH and FBN in cotton germplasms to develop superior cultivars, quantitative trait loci (QTLs) for these traits were detected based on the phenotypic evaluation data in nine environments across four locations and 4 years and a previously reported genetic linkage map of an recombinant inbred line (RIL) population of upland cotton.

**Results:** In total, 53 QTLs of PH and FBN, were identified on 21 chromosomes of the cotton genome except chromosomes c02, c09-c11, and c22. For PH, 27 QTLs explaining 3.81%–8.54% proportions of phenotypic variance were identified on 18 chromosomes except c02, c08-c12, c15, and c22. For FBN, 26 QTLs explaining 3.23%–11.00% proportions of phenotypic variance were identified on 16 chromosomes except c02-c03, c06, c09-c11, c17, c22-c23, and c25. Eight QTLs were simultaneously identified in at least two environments. Three QTL clusters containing seven QTLs were identified on three chromosomes (c01, c18 and c21). Eleven QTLs were the same as previously reported ones, while the rest were newly identified.

**Conclusions:** The QTLs and QTL clusters identified in the current study will be helpful to further understand the genetic mechanism of PH and FBN development of cotton and will enhance the development of excellent cultivars for mechanical managements in cotton production.

Keywords: Upland cotton, RIL population, Agronomic traits, QTL, Plant height, Fruiting branch number

## Introduction

Agronomic traits, especially plant morphological attributes such as PH, FBN, height of the node of first fruiting branch, and angle between stem and fruiting branch, play a decisive role in the architectural construction of crops, which impact agricultural practices, including reasonable increases in planting density and mechanical managements of crops (Mei et al. 2016; Shang et al. 2016). Among them, PH and FBN are important plant morphological attributes, which have a certain impact on the formation of yield (Ge et al. 2012; Hussain et al.

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2000; Li et al. 2010; Tang et al. 2009). In rice, a point mutation in OsSPL14 perturbs OsmiR156-directed regulation of OsSPL14, generating an ideal plant with a reduced tiller number, increased lodging resistance and enhanced grain yield (Jiao et al. 2010; Miura et al. 2010). In maize, a valuable PH gene ZmRPH1 was demonstrated to be useful in molecular breeding to improve PH and lodging resistant traits (Li et al. 2019).

Cotton is an important cash crop and a major source of natural fiber for the textile industry (Paterson et al. 2012). Upland cotton (*Gossypium hirsutum* L.) is planted worldwide because of its high yield and good fiber quality (Chen et al. 2007; Huang et al. 2017). PH is an important component of ideal plant architecture and plays an important role in cotton breeding (Jiao et al. 2010; Ma et al. 2019b;







Miura et al. 2010; Wang et al. 2018). Studies demonstrated that PH and FBN had important effects on cotton yield and mechanical harvesting (Su et al. 2018; Ma et al. 2019b), but it is still necessary for researchers to understand the genetic basis of PH and FBN and how they impact plant architecture (Qi et al. 2017; Shang et al. 2016; Song and Zhang 2009; Wang et al. 2006; Zhang et al. 2006). Therefore, further study on these agronomic traits will be of great significance for cotton plant-type breeding and the application and distribution of mechanical harvesting technologies in cotton production.

The genetic linkage maps have been used to detect quantitative trait locus (QTL) for cotton fiber quality, yield and various agronomic traits, which is of great significance for both marker-assisted selection as well as functional studies of candidate genes (Ma et al. 2019a; Zhang et al. 2016). However, the disadvantages of previous genetic maps, such as low marker density, asymmetric distribution of mapped markers, and unavailability of reference genomes for upland cotton, hindered the above-mentioned applications of the QTL detection results (Deschamps et al. 2012; Jamshed et al. 2016; Yang et al. 2015). Due to the rapid development of highthroughput sequencing technologies, the reduction of sequencing cost, and the establishment of the reference genome of upland cotton (TM-1), a number of highdensity genetic maps have been constructed by single nucleotide polymorphism (SNP) markers including genotyping by sequencing (GBS) (Diouf et al. 2018; Qi et al. 2017), restriction-site associated DNA sequencing (RAD-Seq) (Hegarty et al. 2013; Kundu et al. 2015; Wang et al. 2017), specific locus-amplified fragment sequencing (SLAF-seq) (Ali et al. 2018; Zhang et al. 2016), CottonSNP63K array (Hulse-Kemp et al. 2015; Li et al. 2016; Li et al. 2018a; Zhang et al. 2016), and CottonSNP80K array (Cai et al. 2017; Tan et al. 2018; Liu et al. 2018; Zou et al. 2018). These high-density genetic maps significantly improved QTL detection accuracy (Ma et al. 2019a; Su et al. 2018; Jia et al. 2016).

This study was based on a previously constructed high-density genetic map through chip-SNP genotyping (cottonSNP80K array) (Cai et al., 2017; Liu et al., 2018). The field phenotypes of PH and FBN were evaluated and analyzed across multiple environments, and their QTLs were detected. Our results will be helpful to further understand the genetic mechanism of these important agronomic traits and lay a promising foundation for developing excellent cultivars to meet the challenges of mechanical harvesting technologies in the future.

#### Materials and methods

#### Experimental materials and field management

A segregation population consisting of 231  $F_{6:8}$  RIL individuals was developed from an intra-specific cross of *G*.

*hirsutum* between two homozygous cultivars Lumianyan28 (LMY28) and Xinluzao24 (XLZ24). The attributes of the two parental lines and the development procedures of the population were previously described (Liu et al. 2018). Briefly, the cross was made in an experimental farm at the Institute of Cotton Research of Chinese Academy of Agricultural Sciences in Anyang in 2008. Then, the RIL population was developed via multiple cycles of selfing, and a random single plant selection was made the F<sub>6</sub> generation to form F<sub>6:8</sub> seeds. F<sub>6:8</sub> and beyond generations were regarded as RILs. From 2013 to 2016, phenotypes of the target traits of the RILs were evaluated in three different locations throughout China with a randomized complete block design in two biological replications in each environment.

#### Phenotyping

The phenotypes of PH and FBN were evaluated throughout a four-year-three-location experiment arrangement, composed from a total of six environments (Table 1). PH was usually evaluated from the cotyledonary node to the apex of the stem. In the experiment locations of this study, removing the stem apex was a normal practice in cotton production for plant architectural control. According to local practices, the stem apex was pinched off manually (in Anyang and Quzhou) or with chemicals (in Kuerle) in July, and PH was evaluated in September before harvest. PH was measured immediately from the soil surface to the pinching point of the plant. FBN was the number of effective branches on which mature bolls set. These phenotype data across multiple environments were collected and analyzed with SPSS21.0 software. The heritability of PH and FBN across environments was evaluated by QTLIciMapping software (version 4.1) (Meng et al. 2015; Ma et al. 2019a).

#### QTL mapping

QTLs for the target traits were identified with Windows QTL Cartographer 2.5 software (Wang et al. 2007) with composite interval mapping (CIM) algorithms. The threshold of logarithm of odds (LOD) for a significant QTL declaration was calculated by a 1 000 permutations test and a walking speed of 1.0 cM. QTLs for the same trait identified in different environments were regarded as the same QTL when their confidence intervals were fully or partially overlapped. The QTL identified at least in two environments was declared as a stable one. Nomenclature of QTL was designated following Sun's description (Sun et al. 2012). MapChart 2.2 (Voorrips 2002) was used to graphically present the QTLs on the genetic map.

Year	Environments	Abbreviation used	Replications	Layout (row length (m) $\times$ row spacing (m) $\times$ plant spacing (m))
2013	Anyang	13ay	2	5 × 0.8 × 0.25
	Quzhou	13qz	2	5 × 0.8 × 0.25
2014	Anyang	14ay	2	5 × 0.8 × 0.25
	Kuerle	14kel	2	3 × (0.66+0.10) × 0.12
2015	Anyang	15ay	2	5 × 0.8 × 0.25
2016	Anyang	16ay	2	5 × 0.8 × 0.25

Table 1 Details of seven environments used to evaluate 231  $F_{6:8}$  RIL individuals and their parents

#### The candidate gene annotation

The genes contained in the physical interval of stable QTLs underwent Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) analyses using BMKCloud (www.biocloud.net). The transcriptome sequencing data of root, stem, and leaf of TM-1 (Zhang et al. 2015) were referenced to reveal the expression pattern of candidate genes. The expression heatmap was drawn by TBtools software (Chen et al. 2018).

### Result

#### Evaluation of phenotype performances

We observed that all of the traits showed continuous variations and that a transgressive segregation phenomenon was detected. The values of skewness and kurtosis of all traits in six environments showed that they fit normal distributions (Table 2). The heritabilities of PH and FBN were 0.76 and 0.52, respectively. We also identified significant  $G \times E$  influences for both PH and FBN (Additional file 1: Table S1).

#### QTL mapping the target traits

A total of 53 QTLs for the target traits were identified on 21 chromosomes except c02, c09-c11, and c22, using the composite interval mapping method. These QTLs could explain 3.23%–11.00% of the observed phenotypic variances (PVs) (Additional file 2: Table S2). Among them, eight QTLs were simultaneously identified in at least two environments on c03-c04, c14, c17-c19, and c25, which were regarded as stable ones which could explain 3.29%–8.54% of the total observed PVs (Fig. 1; Table 3).

#### Plant height

Twenty-seven QTLs for PH were detected, which could explain 3.81%–8.54% of the observed PVs and were distributed on 18 chromosomes except c02, c08-c12, c15, and c22. Six stable QTLs could be simultaneously detected in at least two environments, with an overall explanation of 3.89%–8.54% of the observed PVs, which were identified on c03, c04, c17, c19, and c25. That is, qPH-c03–1, qPH-c04–1, qPH-c04–3, qPH-c17–1, qPH-c19–1, and qPH-c25–1 could explain 4.53%–4.98%, 3.97%–4.11%, 5.43%–6.84%, 3.89%–5.82%, 7.17%–8.54%, and 5.77%–7.11% of the observed PV, respectively.

#### Fruiting branch number

Twenty-six QTLs for FBN were detected on 16 chromosomes, except c02-c03, c06, c09-c11, c17, c22-c23, and c25, which could explain 3.23%–11.00% of the observed PV. Two stable QTLs on c14 and c18 were simultaneously detected in at least two environments, with an overall explanation of 3.29%–8.49% of the observed PV. That is, qFBN-c14–1 and qFBN-c18–2 could explain

**Table 2** The descriptive statistical analysis of the parents and the recombinant inbred lines ( $F_{6:8}$ ) population

Environment	Parents			RIL Population								
	XLZ24	LMY28	Range	Minimum	Maximum	Range	Mean	Standarddeviation	Variance	Skewness	Kurtosis	
13ay	98.70	103.50	-4.80	80.40	117.85	37.45	99.73	7.40	0.07	-0.01	-0.25	
13qz	102.40	99.05	3.35	78.55	111.45	32.90	94.37	6.52	0.07	0.15	-0.25	
14ay	104.05	94.84	9.21	67.90	110.25	42.35	89.30	9.30	0.10	-0.15	-0.54	
14kel	64.14	63.29	0.86	49.14	78.86	29.72	64.11	5.93	0.09	-0.14	-0.36	
15ay	99.45	90.15	9.30	75.80	114.95	39.15	93.00	6.88	0.07	0.22	0.13	
16ay	84.94	75.38	9.56	74.81	111.89	37.08	91.31	7.51	0.08	0.04	-0.07	
13ay	13.05	13.55	-0.50	10.40	14.95	4.55	12.87	0.85	0.07	-0.30	0.04	
13qz	13.85	13.45	0.40	9.90	13.65	3.75	11.79	0.86	0.07	-0.21	-0.58	
14ay	12.55	11.50	1.05	5.25	13.15	7.90	10.32	1.72	0.17	-0.92	0.42	
14kel	7.79	7.43	0.36	5.43	9.50	4.07	7.68	0.82	0.11	-0.15	-0.56	
15ay	14.25	13.45	0.80	11.22	15.25	4.03	13.21	0.82	0.06	-0.14	-0.35	
16ay	11.44	12.75	-1.31	8.92	15.24	6.32	12.34	1.17	0.09	-0.61	0.75	
	Environment 13ay 13qz 14ay 14kel 15ay 16ay 13qz 14ay 14kel 15ay 14ay 14kel 15ay 16ay	Parents   Parents   XLZ24   13ay 98.70   13qz 102.40   14ay 104.05   14kel 64.14   15ay 99.45   16ay 84.94   13ay 13.05   13qz 13.85   14ay 12.55   14kel 7.79   15ay 14.25   16ay 14.25	Parents   XLZ24 LMY28   13ay 98.70 103.50   13qz 102.40 99.05   14ay 104.05 94.84   14kel 64.14 63.29   15ay 99.45 90.15   16ay 84.94 75.38   13ay 13.05 13.55   13qz 13.85 13.45   14ay 12.55 11.50   14ay 7.79 7.43   15ay 14.25 13.45	Parents   XLZ24 LMY28 Range   13ay 98.70 103.50 -4.80   13qz 102.40 99.05 3.35   14ay 104.05 94.84 92.1   14kel 64.14 63.29 0.86   15ay 99.45 90.15 9.30   16ay 84.94 75.38 9.56   13ay 13.05 13.55 -0.50   13qz 13.85 13.45 0.40   14ay 12.55 11.50 1.05   14ay 12.55 11.50 0.36   14ay 12.55 13.45 0.36   14ay 12.55 13.45 0.36   14ay 12.55 13.45 0.36   14ay 12.55 13.45 0.36   15ay 14.25 13.45 0.80   15ay 14.25 13.45 0.80	Parents Range Minimum   XLZ24 LMY28 Range Minimum   13ay 98.70 103.50 -4.80 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6.23%-8.49% and 3.29%-5.25% of the observed PV, respectively.

#### **QTL clusters**

The QTL cluster was defined as a DNA region that harbored at least two QTLs for different traits (Jamshed et al. 2016; Palanga et al. 2017; Said et al. 2013). In the current study, when confidence intervals of QTLs for different traits fully or partially overlapped, we defined these QTLs to form a QTL cluster. Three QTL clusters were formed from 7 out of 53 QTLs for PH and FBN, and the marker intervals of these clusters were less than 20 cM on the genetic map (Said et al. 2013). They were identified on three chromosomes, namely c01, c18, and c21 (Additional file 3: Table S3). The cluster on c21, clu-c21–1, harbored three QTLs, namely, qFBN-c21–3(-), qPH-c21–1(-), and qFBN-c21–4(+), explained 4.64%–7.18% of the observed PV. The cluster on c01, clu-c01–1, harbored two QTLs, namely, qPH-c01–1(+) and qFBN-c01–1(+), explained 5.56%–6.82% of the

Table 3 The stable QTLs for agronomic traits identified by the composite intervalmapping (CIM) in multiple environments

Trait	QTL	Environment	Position /cM	Marker Interval	LOD	Additive	R <sup>2</sup> /%	Physical interval /Mb	Genes number	Reported previously
PH	qPH-c03-1	16ay	49.21	TM6645-TM6845	2.51	2.35	4.53	15.21-77.91	503	Said et al. 2013
		13qz	50.71		2.65	1.49	4.98			
	qPH-c04–1	15ay	4.01	TM9846-TM9831	2.17	-1.67	3.97	60.53-60.81	26	
		16ay	4.01		2.26	-1.74	4.11			
	qPH-c04–3	13qz	32.91	TM9589-TM9576	3.4	2.13	6.84	52.11-54.03	46	
		13ay	36.31		2.79	1.75	5.43			
	qPH-c17-1	13ay	0.11	TM53503-TM53577	3.03	-1.99	5.82	2.47-3.73	88	Zhang et al. 2019a
		14kel	4.61		2	-1.38	3.89			
	qPH-c19–1	15ay	17.21	DPL0022-CGR5590	3.74	1.85	7.17	3.87-5.71	218	Su et al. 2018
		16ay	20.21		4.89	2.27	8.54			
		14kel	20.91		4.4	1.96	8.24			
	qPH-c25-1	14kel	6.81	TM58955-TM58998	3.09	1.44	5.77	1.27-1.70	44	
		16ay	7.51		3.79	2.02	7.11			
FBN	qFBN-c14–1	14kel	56.61	TM52927-TM52567	2.43	0.25	6.23	56-60.31	156	
		14ay	61.61		3.16	0.73	8.49			
	qFBN-c18–2	13qz	34.71	TM80422-TM80570	1.7	0.18	3.29	7.79–15.74	281	
		14ay	38.41		2.17	0.41	4.32			
		15ay	38.41		2.65	0.2	5.25			

observed PV. The cluster on c18, clu-c18–1, harbored two QTLs, namely qFBN-c18–2(+) and qPH-c18–1(+), explained 3.29%–6.64% of the observed PV. All of the QTLs in clu-c18–1 showed positive additive effects, in which FBN-c18–2 was a stable QTL identified across three environments.

#### The gene annotation

In total, 925 and 437 genes in the physical interval of the QTLs for PH and FBN were identified and annotated by Gene Ontology (GO) and Kyoto Encyclopedia and Genomes (KEGG) analysis, respectively. In GO term analysis, the genes of both PH and FBN were mainly assorted into three categories of cellular component, molecular function, and biological process. The genes in the cellular component were further enriched in subcategories of cell part, cell, and organelle. The genes in molecular function were enriched in catalytic activity and binding, and the genes in the biological process were enriched in metabolic process, cellular process, and single-organism process (Fig. 2). When the P-value < 0.05 was used to define the significance of functional enrichment (Additional file 4: Table S4), for PH, a total of 106 genes were enriched in molecular function, in which 22 were found to act with sequence-specific DNA binding transcription factor activities and 11 to have sequence-specific DNA binding functions. Thirteen genes were enriched in cellular components, in which three were found to function in the "proteasome complex" and "proton-transporting ATP synthase complex and catalytic core F(1)". One hundred forty-five genes were enriched in biological processes, in which 33 genes were found to act in "regulation of transcription, DNAtemplated" processes and 10 genes in "lipid metabolic processes". For FBN, a total of 59 genes were enriched in molecular function, in which 12 and 10 genes were found to act in "nucleic acid binding" and "binding" activities, respectively. Five genes were enriched in cellular components, and 98 genes in biological processes (Additional file 4: Table S4). KEGG pathway analysis revealed

that, when a significance level of *P*-value < 0.05 was used to define the effectiveness of functional enrichment for PH, most possible pathways were "Carbon metabolism" (enriched 16 genes), "Oxidative phosphorylation" (enriched 12 genes), "Glycerolipid metabolism" (enriched 7 genes), and "Glycerophospholipid metabolism" (enriched 7 genes). For FBN, most possible pathways were "Spliceosome" (enriched 6 genes), "Pentose and glucuronate interconversions" (enriched 5 genes), and "Glycerolipid metabolism" (enriched 4 genes) (Additional file 5: Table S5).

#### Discussion

#### The significance of QTL mapping for agronomic traits

With the continuous reducing of total cotton planting acreages due to the shortage of labor force and the increase of labor cost in production, the full mechanization of cotton production becomes inevitable in the future development in China (Lu et al. 2018). Mechanical managements in the whole growth procedure of cotton in China have not been fully applied in practical productions, probably due to the following reasons. First, there are relatively few excellent cotton varieties suitable for mechanization because mechanical harvesting has certain strict requirements on plant architecture, such as at least a 20-cm node-height of the first fruiting branch above the ground and a plant height of 100-120 cm (Gao et al. 2016). Second, cotton is planted in small acreage of scales. The lack of large batches of planting scales is mainly due to the planting of various alternative crops, including corn and soybean, which have advantages of high degree of mechanization, short growth period, and easy management (Lei et al. 2014). Third, to some extent, mechanical picking partially reduces fiber qualities. Studies indicated that mechanical harvesting might result in a loss of 1-2 mm fiber length and an increasing of impurity rate (Mao et al. 2016; Shi and Zhou 2014). Therefore, it would be of great importance to breed improved cotton varieties suitable for



mechanized operations through molecular markerassisted selections for these important agronomic traits.

#### Comparison with previous QTLs

Plenty of genetic maps have been constructed, based on which QTLs of target traits were identified in upland cotton. Compared with QTLs identified for fiber quality and vield traits, OTLs for agronomic traits are comparatively less reported (Li et al. 2014; Song and Zhang 2009; Wang et al. 2006; Zhang et al. 2006). Therefore, it is necessary to map QTLs for agronomic traits using highdensity genetic maps. In the current study, QTL mapping for agronomic traits is based on a high-density genetic map that covers a total genetic distance of 2 477.99 cM, composing 4 729 SNP markers and 122 SSR markers. Comparing the results of this study with previous common QTLs summarized with meta-analysis (Said et al. 2013), and QTLs identified in recent years (Jia et al. 2016; Su et al. 2018; Zhang et al. 2019a; Zhang et al. 2019b; Ma et al. 2019a), QTLs on c04 for PH and those on c01, c07, c12, c20-c21, c24, and c26 for FBN were all newly identified ones. As the existence of significant G × E interactions, QTLs identified in every environment moved around. Windows QTL Cartographer 2.5 is unable to evaluate the G x E influences. In order to increase QTL mapping accuracy, phenotypic data across multiple environments were evaluated and used to identify the QTL in our study. The stable QTLs that could be detected across multiple environments were probably more reliable, while the environment-specific QTLs revealed the interaction between the G x E influences.

QTL-wise comparisons were also conducted with the physical position of the markers harbored in the QTL confidence intervals. When a QTL for a correspondent trait shared a fully or partially overlapped physical fragment with a previously identified one, it was regarded as a repetitive identification of a common QTL. We found that 9 of the 27 QTLs for PH might be common ones (Additional file 2: Table S2), of which qPH-c03-1, qPHc17–1, and qPH-c19–1 were stable in the current study. The rest were probably newly discovered QTLs. Two of the 26 QTLs for FBN may be common ones, while the rest were probably newly discovered QTLs. In previous studies, when SSR markers were applied to construct the linkage maps, the QTLs in different studies were usually compared through common markers in their confidence intervals. When the SSR markers were aligned back to the reference genome, their positions in the physical map were very often not unique, possibly misleading the mapping results. However, in current studies, when SNPs were applied to map the QTL, although it was not easy to compare common markers, it was convenient to identify the physical position of the QTL. In recent studies (Su et al. 2018; Zhang et al. 2019a), the physical positions of stable QTLs for PH and FBN traits were clearly shown. When comparing these studies with our current study, the QTLs of qPH-c17–1 and qPH-c19–1 were probably previously identified by Zhang et al. (2019a) and Su et al. (2018), respectively. This alternative comparison of common QTL might provide a promising choice of comparing the QTLs which were identified in different studies.

#### Candidate gene functioning analysis

Some genes which may play an important role in the growth and development of PH and FBN were identified by functional annotation of homologous genes in Arabidopsis based on GO and KEGG analysis and Arabidopsis annotation information (Additional file 5: Table S5). In stable QTLs of the current study, 723 of 925 genes for PH and 335 of 437 genes for FBN had annotation information (Additional file 6: Table S6). In previous studies, Gh\_D03G0922 (MADS-box family gene; AT5G60910) and Gh\_D01G1471 (GhPIN3; AT1G70940) were, respectively, annotated as AGAMOUSlike 8 and Auxin efflux carrier family protein in Arabidopsis and were verified to be responsible for PH in cotton (Su et al. 2018; Ma et al. 2019a). OsPIN2 and ZmPIN1a, which were also the PIN gene family members, were verified to have an effect on PH of rice and maize (Chen et al. 2012; Li et al. 2018b). However, in the current study, the gene in qPH-c03-1, Gh\_A03G0634 (AT5G60910), was also annotated as AGAMOUS-like 8 in Arabidopsis, and Gh\_ A03G1052 (AT1G23080), Gh\_A03G1053 (AT1G70940), Gh\_A03G1054 (AT5G57090), and Gh\_A03G1069 (AT1G71090) were annotated as Auxin efflux carrier family proteins in Arabidopsis (Additional file 5: Table S5). An expression heat-map revealed that Gh\_A03G1069 and Gh\_ A04G1054 had a specific expression in stem in TM-1 (Zhang et al. 2015) (Fig. 3). Therefore, these genes could also have a certain role in plant height determination in cotton. Evidence indicated that gibberellin caused a reduction in plant height (Monna et al. 2002; Sakamoto et al. 2004; Braun et al. 2019; Annunziata. 2018). In this study, Gh\_A03G0973 (AT4G21200) in qPH-c03-1 and Gh\_D03G0239 (AT2G14900) in qPH-c17-1, were respectively annotated as gibberellin 2-oxidase 8 and Gibberellin-regulated family protein genes, which could be involved in gibberellin biosynthesis. Gh\_A04G1054 (AT4G34710) in qPH-c04-1 was annotated as an arginine decarboxylase 2 gene, which could be involved in Polyamines biosynthesis (Watson et al. 1998). Gh\_D03G0284 (AT4G37760) in qPH-c17-1 was annotated as a squalene epoxidase 3 (SQE3) gene, which may be involved in sterol biosynthesis (Laranjeira et al. 2015). Gh\_ D13G0612 (AT5G23190) and Gh\_D13G0806 (AT2G23180) in qFBN-c18-2 were annotated as cytochrome P450 genes, which may be involved in brassinosteroid (BR) biosynthesis (Wu et al. 2016). Gh\_D13G0732 (AT1G68640) in qFBN-



c18–2 was annotated as bZIP transcription factor family protein, which may be involved in multiple biological processes in plants (Hu et al. 2016; Lozano-Sotomayor et al. 2016; Yan et al. 2019). In general, these candidate genes for PH and FBN could play an important role in cell elongation, and tissue and organ differentiation and formation in plant development, but their specific functions need to be further verified. The results of this study will not only contribute to promote an understanding of the genetic mechanism of PH and FBN formation of cotton, but also enhance the practical application for plant-type breeding through MAS.

## Conclusions

In this study, QTLs for PH and FBN were detected, based on the phenotypic evaluations of an intraspecific RIL population of upland cotton across six environments in three locations from 2013 to 2016 and the previously reported (Liu et al. 2018) genetic linkage map of that population. A total of 27 QTLs for PH and 26 QTLs for FBN were identified, in which six for PH and two for FBN were stable QTLs, and seven QTLs formed three QTL clusters. The possible candidate genes behind the QTLs were also identified and annotated. The results could be of great importance to further understand the genetic mechanism of plant type determination of cotton and for pragmatic applications in future breeding programs for cultivar development to meet the challenges of mechanization in cotton production.

#### Supplementary information

Supplementary information accompanies this paper at https://doi.org/10. 1186/s42397-020-0046-x. Additional file 1: Table S1. The ANOVA analysis and heritability analysis of PH and FBN traits.

Additional file 2: Table S2. The QTLs for agronomic traits identified in multiple environments.

Additional file 3: Table S3. Distribution of the QTL clusters.

Additional file 4: Table S4. The genes in stable QTL for PH and FBN used for GO analysis.

Additional file 5: Table S5. The genes in stable QTLs for PH and FBN used for KEGG analysis.

Additional file 6: Table S6. The genes annotation information in stable QTLs for PH and FBN.

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#### Authors' contributions

Gong WK, Yuan YL initiated the research; Gong WK and Liu RX designed the experiments; Liu RX, Xiao XH, Zhang Z, Gong JW, Li JW, Liu AY, Shang HH, Shi YZ, Ge Q, Iqbal MS, Lu QW, and Chen QJ conducted the phenotypic evaluations and collected the data from the field; Liu RX, Gong WK and Yuan YL performed the analysis; Liu RX drafted the manuscript; Yuan YL and Gong WK finalized the manuscript. All authors contributed in the interpretation of results and approved the final manuscript.

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#### Availability of data and materials

The data and materials for supporting the results of this article are included within the article and its supplementary material files.

## Ethics approval and consent to participate

Not applicable.

#### Consent for publication

Not applicable.

#### Competing interests

The authors declare that they have no competing interests.

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