Genetic control and phenotypic characterization of panicle architecture and grain yield-related traits in foxtail millet (Setaria italica)

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Received: 21 January 2021 / Accepted: 27 May 2021 / Published online: 3 June 2021
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Key message Multi-environment QTL mapping identified 23 stable loci and 34 co-located QTL clusters for panicle architecture and grain yield-related traits, which provide a genetic basis for foxtail millet yield improvement.

Abstract Panicle architecture and grain weight, both of which are influenced by genetic and environmental factors, have significant effects on grain yield potential. Here, we used a recombinant inbred line (RIL) population of 333 lines of foxtail millet, which were grown in 13 trials with varying environmental conditions, to identify quantitative trait loci (QTL) controlling nine agronomic traits related to panicle architecture and grain yield. We found that panicle weight, grain weight per panicle, panicle length, panicle diameter, and panicle exsertion length varied across different geographical locations. QTL mapping revealed 159 QTL for nine traits. Of the 159 QTL, 34 were identified in 2 to 12 environments, suggesting that the genetic control of panicle architecture in foxtail millet is sensitive to photoperiod and/or other environmental factors. Eighty-eight QTL controlling different traits formed 34 co-located QTL clusters, including the triple QTL cluster qPD9.2/qPL9.5/qPEL9.3, which was detected 23 times in 13 environments. Several candidate genes, including Seita.2G388700, Seita.3G136000, Seita.4G185300, Seita.5G241500, Seita.5G243100, Seita.9G281300, and Seita.9G342700, were identified in the genomic intervals of multi-environmental QTL or co-located QTL clusters. Using available phenotypic and genotype data, we conducted haplotype analysis for Seita.2G002300 and Seita.9G064000, which showed high correlations with panicle weight and panicle exsertion length, respectively. These results not only provided a basis for further fine mapping, functional studies and marker-assisted selection of traits related to panicle architecture in foxtail millet, but also provide information for comparative genomics analyses of cereal crops.

Communicated by Emma Mace.

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Introduction

Foxtail millet (Setaria italica) is one of the most important cereal crops that domesticated in China about 10,000 years ago (Hu et al. 2018; Lu et al. 2009). The mature panicle of foxtail millet contains many primary branches that are attached to the main axis (often referred to as the rachis), several secondary branches on the primary branches, tertiary branches on the secondary branches, and each of the tertiary branches bears numbers of spikelets (grains). A major goal of foxtail millet breeding is to improve the grain yield per unit growing area by cultivating varieties with large panicles, long branches, a high grain number, and enlarged grains. Despite a significant progress has been made in foxtail millet grain production during 40 years of scientific breeding in China (Diao et al. 2014), the molecular and genetic mechanisms underlying foxtail millet grain yield, especially panicle architecture, remain unclear.

Most of foxtail millet cultivars have only one tiller, which bears one panicle (Doust 2007). Traits related to panicle architecture, such as panicle length (PL), panicle diameter (PD), primary branch number (PBN), primary branch length (PBL), and grain number per panicle (GNP), mainly determine the grain yield per plant. Panicle architecture is mainly determined by the fate of the meristem, and by the timing of the meristem phase shift from the branch meristem to the spikelet meristem (Kyozuka et al. 2014). Studies on rice and maize have shown that many genes involved in CLAVATA-WUS signaling pathway, such as FLORAL ORGAN NUMBER 1 (FON1) (Suzaki et al. 2004), FON4 (Chu et al. 2006), OsWUS, ZmWUS, ZmWUS2 (Nardmann and Werr 2007), and thick tassel dwarf 1 (TD1) (Bommert et al. 2005), and many MADS-box transcription factors, including OsMADS34 (Gao et al. 2010), OsMADS14, OsMADS15, and OsMADS18 (Kobayashi et al. 2012), affect panicle architecture by regulating meristem size and specification of meristem identity. Additionally, the MADS-box transcription factors can also regulate inflorescence branching by repressing the expression of REDUCED CULM NUMBER 4 (RCN4), a homolog of TERMINAL FLOWER 1 (TFL1)/CENTORADIALIS in rice (Liu et al. 2013). Overexpression of TFL1 homologs (RCN1 and RCN2) in rice (Nakagawa et al. 2002) and CENTORADIALIS 1 (ZCN1) to ZCN6 in maize (Danielevskaya et al. 2010) delay the changes from branch shoot to floral meristem and lead to a highly branched inflorescence. Gain of function mutations in DENSE AND ERECT PANICLE1 (DEP1) enhances meristematic activity, resulting in shortening of the inflorescence internode, and increased number of grains per panicle (Huang et al. 2009a). In addition, mutants of DEP2 and DEP3 also exhibit a characteristic erect panicle phenotype and increased panicle length and grain size (Qiao et al. 2011; Zhu et al. 2010). Phytohormones, including auxin, cytokinin, and gibberellin, play essential roles in regulating inflorescence meristem identity, initiation, and enlargement. Loss-of-function mutations in genes that participate in local auxin biosynthesis, signaling and transport significantly affect panicle architecture development (Komatsu et al. 2001, 2003; Phillips et al. 2011). Grain number 1a (Gn1a) encodes a cytokinin oxidase/dehydrogenase (OsCKX2) that degrades cytokinin, loss-of-function mutations in Gn1a accumulate higher levels of cytokinin in inflorescence meristems, resulting in a larger number of branches and spikelets (Ashikari et al. 2005). By contrast, the dysfunction mutant of LONELY GUY (LOG), which encodes an enzyme catalyzing the conversion of inactive cytokinin nucleotides to the active free-base forms, displays a small inflorescence with a decreased number of branches and spikelets (Kurakawa et al. 2007). Class 1 KNOTTED 1–like homeobox (KNOX) genes, such as rice homeobox 1 (OSH1) (Tsuda et al. 2011), maize knotted 1 (KN1) (Vollbrecht et al. 2000), and Arabidopsis SHOOT MERISTEMLESS (STM) (Long et al. 1996), play a central role in promoting shoot apical meristem identity by decreasing the levels of GA and increasing the amount of cytokinin. Due to a KNOX-mediated transcriptional feedback loop, overexpression of Grain Number per Panicle1 (GNP1), which encodes rice GA20ox1 that degrades active GAs, increases grain number and yield by increasing cytokinin activity in rice panicle meristems (Wu et al. 2016).

Most research on genes related to panicle architecture has been conducted using maize and rice. In contrast, only a few genes related to panicle architecture have been cloned from Seteria mutants and molecularly characterized in detail. By screening for visible inflorescence mutant phenotypes via an N-nitroso-N-methylurea (NMU) mutagenesis of Setaria viridis, Huang et al. (2017) identified two sparse panicle mutants, spp1 and spp3. Both were found to have disruptive mutations in the SvAUX1 (AUXIN1) gene. Further study revealed that loss-of-function mutations in SvAUX1 and ZmAUX1 disrupt the inflorescence branch development in S. viridis and maize, leading to sparse panicle phenotypes. In previous studies, we isolated two mutants with abnormal panicle architecture from the EMS mutant library constructed in our laboratory. One is the loose-panicle mutant, in which a single G-to-A transition in the fifth intron of the WRKY transcription factor gene results in three disorganized splicing events in mutant plants, leading to a lax primary branching pattern and aberrant branch morphology (Xiang et al. 2017). The other is simads34, in which an alternative splicing event introduces an early termination codon in Simads34. This results in increased panicle width, primary branch length, and number of primary branches, but
decreased panicle length and grain weight in simads34 compared with wild-type plants (Hussin et al. 2021).

Forward genetic studies have identified many quantitative trait loci (QTL) associated with panicle architecture or grain yield from various bi-parental populations. Doust et al. (2005) conducted QTL analyses on the basis of differences in the inflorescence between foxtail millet and green foxtail. They detected 14 replicated QTL for PL and primary branch density, spikelet number, and bristle number. Using an F2 population derived from different foxtail millet cultivars, Fang et al. (2016) identified 12 QTL for PL, PD, panicle weight per panicle (PW), grain weight per panicle (GWP), and 1000-grain weight (TGW). Wang et al. (2017) identified 11 major QTL for eight agronomic traits, including five QTL for PL, PD, and PW. Wang et al. (2019) mapped 57 QTL for 11 agronomic traits, including 31 QTL for PD, PBL, PW, grain weight, and TGW. By analyzing different recombinant inbred line (RIL) populations, Liu et al. (2020) detected 47 QTL for straw weight, PW, GWP and TGW; and Zhang et al. (2017) detected 32 QTL for PW, PL, PD, CN, TGW, and panicle exertion length (PEL). Using a natural population, Jia et al. (2013) phenotyped 916 varieties under five different environments and identified 512 loci associated with 47 agronomic traits, including 39 loci for PW, PL, PD, PBL, and TGW. Jaiswal et al. (2019) performed a genome-wide association study (GWAS) on 10 agronomic traits using 142 foxtail millet accessions, and identified 17 and 10 loci for grain yield and TGW, respectively. However, neither of those QTL have been cloned, nor have any of the candidate genes located in the QTL intervals been isolated. This has hindered the understanding of the mechanisms underlying foxtail millet panicle architecture and grain size development.

In the present study, an RIL population was developed from derivatives of the cross between the foxtail millet cultivars Ai 88 and Liaogu 1. Panicle architecture varied greatly between the two parents and within the RIL population. A large-scale and multi-environment analysis using the RIL population was carried out. An ultra-high density genetic map was constructed to explore the genetic control of panicle architecture and yield-related agronomic traits in 13 environments. The QTL mapping identified 159 QTL, whose genetic intervals contain many candidate genes involved in panicle development. The favorable QTL alleles from either parent will be of great value to optimize panicle architecture and increase the grain yield of foxtail millet.

Materials and methods

Plant materials

A foxtail millet RIL population comprising of 333 lines was used in this study. This RIL population was generated from a cross between a backbone line Ai88 and an elite variety Liaogu1 as described by He et al. (2021). From 2015 to 2018, the RIL population was grown at seven geographical locations during the growing season (Fig. 1 and Table S1). Nanbin Farm (NB, 109.19°E/18.37°N, Hainan Province) represents a short-day photoperiod location where the daily sunshine was <12 h during the plant growing season. Six locations in Northern-China, including Zhengzhou (ZZ, 113.64°E/34.75°N, Henan Province), Changzhi (CZ, 113.13°E/36.20°N, Shanxi Province), Taiyuan (TY, 112.55°E/37.88°N, Shanxi Province), Shunyi (SY, 116.66°E/40.13°N, Beijing), Chaoyang (CY, 120.46°E/41.58°N, Liaoning Province), and Gongzhuling (GZL, 124.83°E/43.51°N, Jilin Province), represent long-day photoperiod locations. From Southern China (lower latitude) to Northern China (higher latitude), the geographical order of seven locations is as follows: NB, ZZ, CZ, TY, SY, CY, and GZL (Fig. 1a). Plants were grown in 3 m × 0.9 m plots in three lines using standard agronomic practices (e.g., irrigation, weeding, and pest control). Five individuals in the middle of each row were harvested individually to score the traits.

Phenotype evaluation

When panicles and grains were fully mature, PL was measured for the main panicle, and PD was measured at the thickest location on the main panicle. The PEL was measured from the uppermost node to the panicle base. Harvested panicles were air-dried and stored at room temperature for 1 month, then primary branches were removed from the panicle and grains were removed from the branches for measurements. The PBL was measured using a ruler. The PW, GWP, and TGW were evaluated using a Mettler-Toledo analytical balance (model XP204S/M, Mettler-Toledo, Greisensee, Switzerland). The PBN per panicle and grain number per primary branch (GNB) were counted manually. Both PL and PEL were measured in all 13 environments; PD, PW, and GWP were evaluated in 12, 11, and 10 environments, respectively; PBN and TGW were measured in two environments; and PBL and GNB were measured in one environment (Fig. 1). All traits were measured with three to five replicates.

Statistical analysis of panicle phenotypic variations

Analyses of all the phenotypic variations in the RIL population, including calculations of the mean value, standard deviation, skewness, kurtosis, as well as the broad-sense heritability (h2) and correlation analysis, were performed using R packages. Analysis of variance (ANOVA) was carried out to test the statistical significance of differences in traits of RILs among various environments. Variance
components of genotype ($V_G$), genotype and location interaction ($V_{G\times L}$), genotype and year interaction variance ($V_{G\times Y}$), and residual variance ($V_r$) were estimated using a mixed linear model using the R package lme4. Broad-sense heritability was calculated using the following formula:

$$h^2 = \frac{V_G}{V_G + \frac{V_{G\times L}}{n_L} + \frac{V_{G\times Y}}{n_Y}}$$

where $n_L$ and $n_Y$ are the number of location and year, respectively.

QTL mapping, QTL comparison and candidate gene identification

The high-density genetic map constructed by He et al. (2021) was used in this study. The R/qtl package was used to perform QTL mapping using the CIM model with a scanning window size of 5 cM. The loci with LOD (logarithm of odds ratio) over 2.5 were considered as QTL and the confidence intervals were estimated using the 1.5 LOD-drop method (He et al. 2021). By running 1,000 permutation tests for each trait, high-confidence QTL (those with LOD over the significance thresholds, $p < 0.05$) were identified. Meanwhile, QTL across different environments for the same trait
were considered to be the same when the supporting intervals overlapped and the additive effects originated from the same parental line. Overlapping of genomic regions for QTL controlling different traits was indicative of co-located QTL clusters. QTL and environment interaction study followed the methods described by Li et al. (2015). First, the loci with LOD over 4.7 (the average threshold (LOD ≥ 4.7) of all traits by 1,000 permutation test without environment interaction) was considered as a QTL for Q × E interaction. Many QTL exceeded the threshold (LOD ≥ 4.7) for some traits such as PL, PEL, and PD. Therefore, to reduce the false positive rate, we considered the top 20 QTL for traits with more than 20 QTL with LOD ≥ 4.7.

The QTL nomenclature followed the rules described by Mccouch et al. (1997), and QTL on the same chromosome were listed in alphabetical order. The QTL with a positive or negative additive effect for a specific trait indicate that the increase in the phenotypic value of the trait is contributed by the alleles from Liaogu1 or Ai88, respectively. For QTL comparison, if the physical coordinates of a reported QTL were within a 0.5-Mb interval of a QTL detected in this study, they were considered to be the same QTL.

Based on amino acid similarity, candidate genes located in QTL intervals showing homology to genes related to panicle architecture in rice were identified. Amino acid similarity was further confirmed using tools at Phytozome (https://phytozome.jgi.doe.gov/portal.html). Candidate genes with nucleotide variations in the untranslated region (UTR) or coding sequence between the two parental lines were subjected to haplotype analysis. Protein domain enrichment analysis was performed using STRING software (https://string-db.org/cgi/organisms).

Haplotype analysis of candidate genes

We collected the available data for phenotypes related to panicle architecture for 900 accessions in our previous study (Jia et al. 2013). The genotype data for those accessions were obtained by high-depth resequencing (unpublished). The haplotype analysis was performed using in-house python and R scripts.

Results

Phenotypic variation and broad-sense heritability

In this study, all nine traits exhibited diverse phenotypic variations and obvious transgressive segregations in the RIL population (Figure S1 and Table S1). All phenotypes in the RIL population showed normal distributions, suggesting that these traits related to panicle architecture were controlled by QTL. The performances of PW, GWP, PL, and PD were influenced by the geographical location (Fig. 1b–e and Table S1). The phenotypic variations in the RIL population were quite stable across years at a given location, except for PD and PEL in 2017_CY and 2018_CY. The average phenotypic values for PW, GWP, PL, and PD in the RIL population increased dramatically from the lower latitude locations to the higher latitude locations. For example, the RIL population grown in 2018_GZL (26.31 cm) had the largest mean value of PL, followed by 2016_GZL (24.91 cm), 2016_CZ (23.61 cm), 2017_CY (22.91 cm), 2018_CY (22.44 cm), 2017_CZ (21.91 cm), 2017_TY (21.01 cm), 2018_SY (20.17 cm), 2018_ZZ (18.05 cm), 2017_ZZ (17.44 cm), 2015_NB (17.31 cm), 2016_NB (16.26 cm), and 2017_NB (14.19 cm) (Fig. 1d and Table S1). Similar to PL, the traits PW, GWP, and PD showed phenotypic variations that were highly correlated with latitude (or photoperiod) (Fig. 1b, c, e), while the variation in PEL was not correlated with latitude (Fig. 1f).

In this study, most of the traits related to panicle architecture displayed significant variations in different environments. Therefore, we evaluated the broad-sense heritability ($h^2$) of PW, GWP, PL, PD, and PEL on the basis of RIL phenotypic data in six to seven locations across 3 to 4 years (Table 1). The PL trait exhibited the highest heritability ($h^2$ = 0.93), while GWP showed the lowest heritability.

Table 1: Genotype × environment interactions and heritability of panicle morphology and grain yield-related traits

| Trait | Location number | Year | Variance components | Genotype × Location | Genotype × Year | Genotype | Location | Year | Residual | broad-sense heritability |
|-------|-----------------|------|---------------------|---------------------|----------------|----------|----------|------|----------|------------------------|
| PW    | 7               | 3    | 0                   | 0                   | 0              | 1.59     | 138.7    | 38.82| 49.28    | 0.40                   |
| GWP   | 6               | 3    | 0                   | 0                   | 0              | 1.01     | 79.63    | 18.68| 35.78    | 0.34                   |
| PL    | 7               | 4    | 0.32                | 0                   | 0              | 2.34     | 12.11    | 1.16 | 3.88     | 0.93                   |
| PD    | 7               | 4    | 0                   | 0                   | 0              | 4.52     | 13.55    | 3.89 | 15.21    | 0.90                   |
| PEL   | 7               | 4    | 0                   | 0                   | 0              | 2.82     | 36.88    | 12.41| 13.51    | 0.85                   |

*Variance components*
QTL were not detected in the non-Q × E interaction study (Table S4). Forty-three major effect Q × E interactions showed that more than 67% (89) of the top 20 QTL intervals shared by two, three, four, and five QTL for different traits, respectively (Table S3 and Figure S2). The Q × E interactions were highly positively correlated between PD and PW and between PL and GWP in all environments tested (p < 0.01). The traits PW and GWP were evaluated in 11 and 10 environments, respectively, and PW was highly positively correlated with GWP in all environments tested (p < 0.001). We analyzed the correlations of PEL and PW, PEL, and GWP in 11 and 10 environments, respectively, and found that PEL was positively correlated with PW and GWP in 2016_NB, 2017_ZZ, 2018_ZZ, and 2016_GZL, and PEL was negatively correlated with PW in 2017_CY (p < 0.05). We measured the TGW and GNB in 2017_TY, and found that TGW was positively correlated with PL, PD, PW, and GWP (p < 0.05); and GNB was positively correlated with PD, PW, and GWP (p < 0.05). The PBN was positively correlated with PL in 2017_CY and 2018_CY (p < 0.01), and positively correlated with PW and GWP in 2017_CY (p < 0.001). The PBL was positively correlated with PL, PD, PW, and GWP in 2018_CY (p < 0.05), but negatively correlated with PEL in 2018_CY (p < 0.05). No significant correlations were detected for other traits related to panicle architecture in this study. Overall, PL, PD, TGW, GNB, PBN, and PBL were positively correlated with PW and GWP; and PEL was negatively correlated with PD in most environments investigated.

**Correlation analysis**

We investigated the relationships between pairs of traits related to panicle architecture in each of the 13 environments (Figure S1). The traits PL, PD, and PEL were evaluated in all 13 environments, except for PD in 2016_CZ. The trait PL was positively correlated with PD and PEL in seven and nine environments (p < 0.05), respectively. We detected positive correlations between PD and PW and between PL and GWP in all environments tested (p < 0.01). The traits PW and GWP were evaluated in 11 and 10 environments, respectively, and PW was highly positively correlated with GWP in all environments tested (p < 0.001). We analyzed the correlations of PEL and PW, PEL, and GWP in 11 and 10 environments, respectively, and found that PEL was positively correlated with PW and GWP in 2016_NB, 2017_ZZ, 2018_ZZ, and 2016_GZL, and PEL was negatively correlated with PW in 2017_CY (p < 0.05). We measured the TGW and GNB in 2017_TY, and found that TGW was positively correlated with PL, PD, PW, and GWP (p < 0.05); and GNB was positively correlated with PD, PW, and GWP (p < 0.05). The PBN was positively correlated with PL in 2017_CY and 2018_CY (p < 0.01), and positively correlated with PW and GWP in 2017_CY (p < 0.001). The PBL was positively correlated with PL, PD, PW, and GWP in 2018_CY (p < 0.05), but negatively correlated with PEL in 2018_CY (p < 0.05).

**QTL mapping**

In total, 239 loci, including 73 high-confidence loci, formed 159 QTL for nine traits that were detected under 13 environments across 4 years (Table S2). The LOD values of these QTL ranged from 2.51 to 22.36, and explained 0.29% to 25.55% of the phenotypic variation. Out of the 159 QTL, 34 were identified in two to 12 environments (Table S2). We also compared the genomic intervals of QTL controlling different traits, and found 17, 14, one, and two genomic intervals shared by two, three, four, and five QTL for different traits, respectively (Table S3 and Figure S2). The Q × E analysis showed that more than 67% (89) of the top 20 QTL detected in interaction studies overlapped with non-Q × E interaction QTL (Table S4). Forty-three major effect Q × E QTL were not detected in the non-Q × E interaction study for PW, GWP, PD, GNB (Table S4).

**Panicle weight**

Twenty-four QTL related to PW were detected in 11 environments across 3 years, explaining 0.58% to 8.69% of the phenotypic variation (Table S2). Of these, qPW2.6, qPW3.1, qPW4.2, qPW6.2, and qPW7.2 were detected in two environments. The additive effects of qPW3.1 and qPW7.2 were from Liaogu1, while the favorable alleles qPW2.6, qPW4.2, and qPW6.2 originated from Ai88. The other 19 QTL for PW were only identified in a single environment. The additive effects of 13 QTL were from Liaogu1, while the others came from Ai88.

**Grain weight per panicle**

Sixteen QTL for GWP were detected across nine environments, and explained 2.70%–7.58% of the phenotypic variation. One of them, qGWP4.1, was identified in two environments. The favorable allele was from Ai88. The remaining 15 QTL were only identified in a single environment. The additive effects of seven QTL were derived from Liaogu1.

**Panicle length**

Thirty-five QTL mapped on all chromosomes were found to be related to PL in 13 environments, accounting for 0.29%–25.55% of the phenotypic variation. Of them, qPL7.2 and qPL9.5 were identified across 12 and seven environments, respectively, and the additive effect of these two QTL was contributed by Liaogu1. qPL9.5 accounted for 14.95%–25.55% of the phenotypic variation. qPL5.2 was identified in three environments, and the favorable allele originated from Liaogu1. qPL2.6, qPL3.1, qPL3.8, qPL4.3, qPL5.1, qPL7.3, qPL9.2, and qPL9.3 were detected in two environments, all of the additive effects for PL were derived from Liaogu1, except for qPL3.8 and qPL5.1, which were derived from Ai88. The other 24 QTL for PL were identified in a single environment. The additive effects of 12 of them were from Liaogu1 and the others were from Ai88.

**Panicle diameter**

Twenty-seven QTL for PD located on all chromosomes except chromosomes 4 and 7 were detected in 12 environments across 4 years, and accounted for 0.72%–16.34% of the phenotypic variation. Among them, qPD3.1, qPD6.4, and qPD9.2 were identified across five, three and 10 environments, respectively. The additive effects of qPD3.1 and qPD9.2 were derived from Liaogu1 and the favorable allele qPD6.4 was from Ai88. qPD9.2 explained 4.33%–16.34% of the phenotypic variation across 10 environments. qPD2.4, qPD3.4, and qPD5.3 were detected in two environments, the remaining 21 QTL were identified in a single environment.
Panicle exsertion length

Thirty-five QTL mapped on all chromosomes were found to be related to PEL in 13 environments, and explained 1.84%–11.59% of the phenotypic variation. Among them, \(q_{PEL1.5}, q_{PEL1.7}, q_{PEL5.5}, q_{PEL9.3}, \) and \(q_{PEL9.5}\) were identified in six, three, five, six, and eight environments, respectively, and all additive effects originated from Liaogu1. \(q_{PEL1.5}, q_{PEL1.7}, q_{PEL5.5}, q_{PEL9.3}, \) and \(q_{PEL9.5}\) were identified in six, three, five, six, and eight environments, respectively, and all additive effects originated from Liaogu1. \(q_{PEL3.1}, q_{PEL5.7}, q_{PEL6.1}, q_{PEL6.2}, \) and \(q_{PEL9.1}\) were detected in two environments. The additive effects of \(q_{PEL3.1}\) and \(q_{PEL9.1}\) were derived from Liaogu1, while \(q_{PEL5.7}, q_{PEL6.1}, q_{PEL6.2}\) were from Ai88. The remaining 25 QTL were identified in a single environment.

Panicle primary branch length, primary branch number, grain number per branch, and 1000-grain weight

Four QTL for PBL mapped on chromosomes 2, 3, and 4 were detected in 2018_CY, and explained 2.88%–5.49% of the phenotypic variation. The additive effects of \(q_{PBL3.1}\) and \(q_{PBL3.2}\) originated from Liaogu1, while \(q_{PBL2}\) and \(q_{PBL4}\) were from Ai88.

Seven QTL for PBN were identified in 2017_TY, and accounted for 0.44%–8.86% of the phenotypic variation. Of them, favorable alleles for increasing PBN (\(q_{PBN2.2}, q_{PBN5}, q_{PBN9.1}, q_{PBN9.2}, q_{PBN9.3}\) were derived from Liaogu1, while \(q_{PBN2.1}\) and \(q_{PBN6}\) were from Ai88. \(q_{PBN2.2}\) was detected in 2017_TY and 2018_GZL, and explained 3.20% and 3.49% of the total phenotypic variation, respectively.

Mutli-environment QTL and QTL clusters for multiple traits

Out of the 159 QTL, 34 were detected in two to 12 environments (Fig. 2 and Table S2). Twenty-three QTL for PW, GWP, PL, PD, PEL, and TGW were identified in two environments. Three QTL, \(q_{PL5.2}, q_{PD6.4}, q_{PEL1.7}\) were identified in three environments. \(q_{PD3.1}\) and \(q_{PEL5.5}\) were identified in five environments. \(q_{PEL1.5}\) and \(q_{PEL9.3}\) were detected in six environments. \(q_{PL9.5}, q_{PEL9.5}, q_{PD9.2}\) and
There were 14 triple co-located QTL: qPL7.2/qPEL7.2/qTGW2.1, double co-located QTL: qPD2.1/qPW2.1/qGWP2.3, qPL3.2/qPEL3.2/qPL3.4/qPD3.7, qPW3.1/qGWP3.3, qPEL4.2/qPL4.3, qGWP4.2/qTGW4.2, qPEL5.2/qPBN5, qPL6.2/qPBN6, qPL7.2/qPEL7.2, qPW7.2/qGWP7.1, qTGW7/qGWP7.2, qPL8/qPEL8, qPEL9.1/qPBN9.1, and qGWP9.1/qPBN9.2. There were 14 triple co-located QTL: qPL1.2/qGWP1.2/qPEL1.7, qPL2.2/qPBN2.1/qPD2.1, qPW2.5/qGWP2.2/qPD2.3, qPW2.6/qGWP2.3/qTGW2.3, qPL3.1/qPEL3.1/qPD3.1, qPL3.3/qPD3.5/qPEL3.3, qPW4.2/qGWP4.1/qPL4.3, qPW5/qPL5.3/qPD5.2, qPW6.1/qGWP6.1/qPEL6.1, qPW8/qGWP8/qTGW8, qPW9.1/qPL9.2/qPEL9.2, qPD9.2/qPL9.6/qGWP9.2/dqPD9.3, and qPW9.2/qGWP9.2/qPD9.3. There was one quadruple co-located QTL: qPL9.2/qGWP9.2/qPEL9.2/qGWP9.3. The amino acid sequence similarities of *Seita.4G281800, Seita.9G281300, and Seita.9G409600* to *FON1 (LOC_0s06g50340.1)* were 72.2%, 64.7%, and 58.5%, respectively. Five genes (*Seita.1G328500, Seita.4G077200, Seita.2G002300, Seita.2G383000, and Seita.9G342700*) located at qPD2.1, qPW2.6, qTGW2.3, qPL4.2, and qPD9.2/qPL9.5/qPEL9.3, respectively, putatively encode MADS-box transcription factors. These transcription factors may regulate panicle architecture by specifying meristem identity. *Seita.6G051500* located at qPD6.2 was found to be homologous to the *ABERRANT SPIKELET AND PANICLE 1 (ASPI)*, which is involved in the regulation of meristem fate (Yoshida et al. 2012). *Seita.4G185300* located at qGWP4.1/qPL4.3/qPW4.2 showed homology to *ABERRANT PANICLE ORGANIZATION 1 (APO1)*, which temporally regulates meristem identity. Loss-of-function mutants of *APO1* display a precocious conversion of inflorescence meristems to spikelet meristems and have reduced numbers of primary branches and spikelets (Ikeda et al. 2005). *Seita.9G222400* located at qPBN9.2 showed homology to *TAWAWA1 (TAW1)* in rice (Yoshida et al. 2013); *TAW1* regulates panicle architecture by suppressing meristem phase transition. *Seita.2G219800, Seita.6G171500, and Seita.9G369300* located at qPD2.2/qTGW2.3, qPD6.5, and qPD9.3/qPEL9.4, respectively, were identified as being homologous to rice *DENSE AND ERECT PANICLE 1 (DEP1)* (Huang et al. 2009a), *Seita.9G388700* showed similarity to *OsDEP2* (Zhu et al. 2010), suggesting that it may regulate panicle erectness, panicle length and grain size in foxtail millet. *Seita.7G126900* located at qPPL7.2 and *Seita.5G243100* located at qPW5/qPL5.3/qPD5.2 were predicted to encode proteins involved in auxin biosynthesis (Abu-Zaitoon 2014; Suzuki et al. 2009; Zhang and Yuan 2014). *Seita.4G101300, Seita.1G314700, Seita.5G241500, and Seita.3G136000* located at qPL4.2, qPL1.2, qPW5/qPL5.3/qPD5.2, and qPW3.1/qGWP3.1/qPD3.2/qPBL3.2, respectively, were predicted to encode putative auxin efflux carrier components, which may regulate PW, PL, PD, and PBL via auxin signaling pathways (Xu et al. 2005). *Seita.5G140300* located at qPBN5/qPEL5.2 was identified as being homologous to the *GRAIN NUMBER 1A/Cytokinin oxidase 2 (Gln1a/OsCKX2)* gene of rice, which is located at a major QTL contributing to grain number improvement (Ashikari et al. 2005). *Seita.9G064000* located at qPEL9.1 was predicted to encode the zinc finger transcription factor *DROUGHT AND SALT TOLERANCE (DST)*, whose homolog directly regulates OsCKX2 expression in the rice reproductive meristem (Huang et al. 2009b; Li et al. 2013). *Seita.9G004400* located at qPBN9.1 showed homology to *Grain Number per Panicle 1 (GPN1)*, which encodes a gibberellin 20 oxidase 1 (GA20ox1) involved in the GA degradation pathway (Wu et al. 2016).
| QTL       | Candidate gene | Rice ortholog | Gene ID          | Name       | Annotation                                                                 | Reference          |
|-----------|----------------|---------------|------------------|------------|-----------------------------------------------------------------------------|--------------------|
| qPL1.2    | Seita.1G317400 | LOC_Os02g50960.1 | PIN1B            |            | Auxin efflux carrier component OsMADS22—MADS-box family gene with MIKCc type-box | Xu et al. (2005)   |
|           | Seita.1G328500 | LOC_Os02g52340.1 | OsMADS22        |            |                                                                             | Liu et al. (2013)  |
| qPW2.1    | Seita.2G002300 | LOC_Os07g01820.3 | OsMADS15        |            | Phosphatidylethanolamine-binding protein (PEBP) like domain protein         | Kobayashi et al. (2012) |
| qPD2.2/qTGW2.2 | Seita.2G219800 | LOC_Os09g26999.1 | DEP1            |            |                                                                             | Huang et al. (2009a) |
| qPW2.6/qTGW2.3 | Seita.2G383000 | LOC_Os07g41370.1 | OsMADS18        |            |                                                                             | Kobayashi et al. (2012) |
| qGWP2.3/qPW2.6/qTGW2.3 | Seita.2G388700 | LOC_Os07g42410.1 | DEP2            |            | Hypothetical conserved gene that regulate of panicle erectness, panicle length and grain size | Zhu et al. (2010)   |
| qPW3.1/qGWP3.1/qPD3.2/ qPBL3.2 | Seita.3G136000 | LOC_Os05g50140.1 | PIN3B          |            | Similar to PIN1-like auxin efflux carrier protein                            | Xu et al. (2005)   |
| qGWP3.2/qPD3.3 | Seita.3G189300 | LOC_Os05g42130.1 | GRAS transcription factor domain containing protein that similar to MONOCULM 1 | | | |
| qPL4.2    | Seita.4G077200 | LOC_Os02g52340.1 | OsMADS22        |            |                                                                             | Liu et al. (2013)  |
|           | Seita.4G101300 | LOC_Os06g12610.1 | PIN1A           |            | Similar to PIN1-like auxin efflux carrier protein                            | Xu et al. (2005)   |
| qGWP4.1/qPL4.3 /qPW4.2 | Seita.4G185300 | LOC_Os06g45460.1 | APO1            |            | F-box protein, Inflorescence form, Lodging resistance and grain yield       | Ikeda et al. (2005) |
| qGWP4.2   | Seita.4G281800 | LOC_Os06g50340.1 | FON1            |            | Receptor protein kinase CLAVATA1 precursor                                   | Suzaki et al. (2004) |
| qPBN5/qPEL5.2 | Seita.5G140300 | LOC_Os01g10110.1 | Gln1            |            | Cytokinin oxidase/dehydrogenase                                             | Ashikari et al. (2005) |
| qPWS/qPL5.3/qPD5.2 | Seita.5G241500 | LOC_Os01g45550.2 | PIN3A           |            | Auxin efflux carrier component                                              | Xu et al. (2005)   |
|           | Seita.5G243100 | LOC_Os01g45760.1 | YUC1            |            | Flavin monoxygenase-like enzyme                                              | Abu-Zaitoon 2014   |
| qPD6.2    | Seita.6G051500 | LOC_Os08g06480.1 | ASP1            |            | Transcriptional co-repressor, lissencephaly type-1-like homology             | Yoshida et al. (2012) |
| qPD6.5    | Seita.6G171500 | LOC_Os09g26999.1 | DEP1            |            | Phosphatidylethanolamine-binding protein (PEBP) like domain protein         | Huang et al. (2009a) |
| qPL7.2    | Seita.7G126900 | LOC_Os04g38950.1 | TDD1            |            | Similar to anthranilate synthase beta chain                                 | Sazuka et al. (2009) |
| qPBN9.1   | Seita.9G004400 | LOC_Os03g63970.1 | GNP1            |            | Gibberellin 20 oxidase 1                                                    | Wu et al. (2016)   |
| qPEL9.1   | Seita.9G064000 | LOC_Os03g57240.1 | DST              |            | C2H2 zinc finger transcription factor                                         | Li et al. (2013)   |
| qPBN9.2   | Seita.9G222400 | LOC_Os10g33780.1 | TAWA1           |            | DUF640 domain containing protein                                            | Yoshida et al. (2013) |
| qPW9.1/qPL9.2/qPEL9.2 | Seita.9G281300 | LOC_Os06g50340.1 | FON1            |            | Receptor protein kinase CLAVATA1 precursor                                   | Suzaki et al. (2004) |
Table 2 (continued)

| QTL         | Candidate gene | Rice ortholog     | Gene ID          | Name          | Annotation                                                                 | Reference        |
|-------------|----------------|-------------------|------------------|---------------|----------------------------------------------------------------------------|------------------|
| qPD9.2/qPL9.5/qPEL9.3 | Seita.9G342700 LOC_Os10g39130.1 | LOC_Os10g39130.1 | OsMADS56       | Phosphatidylethanolamine-binding protein (PEBP) like domain protein | Liu et al. (2013) |
| qPD9.3/qPEL9.4 | Seita.9G693000 LOC_Os09g26999.1 | DEP1 | Phosphatidylethanolamine-binding protein (PEBP) like domain protein | Huang et al. (2009a) |
| qPW9.3       | Seita.9G4096000 LOC_Os06g50340.1 | FON1 | Receptor protein kinase CLAVATA1 precursor | Suzaki et al. (2004) |

Haplotype analysis of candidate genes

Analyses of sequencing coverage and previously collected phenotypic data identified two candidate genes (Seita.2G002300 and Seita.9G064000) with sufficient phenotypic data for haplotype analysis (Fig. 3). For Seita.2G002300, there were 11 haplotypes in 603 accessions (Fig. 3a). H5 had the lowest panicle weight, and the PW of H5 was significantly different from those of H1, H2, H3, H6, and H7 (Fig. 3b). Most of the variations in H5 were located in the 5' untranslated region (UTR), suggesting that 5'UTR of Seita.2G002300 might play an important role in panicle weight regulation. There were 12 haplotypes of the candidate gene of qPEL9.1 (Seita.9G064000) in 318 accessions. The PEL of H1 was significantly lower than those of H2 and H3, indicating that Seita.9G064000 was a potential candidate gene controlling the PEL of foxtail millet (Fig. 3c, d).

Discussion

Foxtail millet has many excellent characteristics as a model system for C₄ plants, because of its small diploid genome, short growth duration, self-fertility, fertile seed setting, small morphological stature, and easy management in the laboratory (Doust et al. 2009). In the present study, we investigated the phenotypic variations in a RIL population of...
foxtail millet grown in 13 environments and analyzed the broad-sense heritability of traits related to panicle architecture and grain yield. We found that PW, GWP, PL, and PD increased with increasing latitude (Fig. 1). The daylength increases from southern China to northern China, suggesting that longer daylength contributes to panicle development and enhances the grain yield of foxtail millet. Zhang et al. (2017) observed similar phenomena, in that the mean values of PW, PL, PBN, and GNB were higher for plants grown under a long-day photoperiod (Zhangjiakou, Hebei province) than for those grown under short-day photoperiod (Sanya, Hainan province). Because panicle development is strongly affected by environmental factors such as photoperiod, we evaluated the broad-sense heritability of PL, PD, PW, GWP, and PEL. We found that the heritability of PL ($h^2 = 0.93$) and PD ($h^2 = 0.89$) was higher than that of PW ($h^2 = 0.40$) and GWP ($h^2 = 0.34$) (Table 1). This result is consistent with those of other studies reporting higher heritability of PL and PD (>70%) than TGW, PW, and GWP (39.8%–59%), regardless of different environments (Diao and Jia 2017). Additionally, correlations among nine traits related to panicle architecture and yield were analyzed in 13 environments. We found that PL, PD, TGW, GNB, PBN, and PBL were positively correlated with PL and GWP in most environments investigated. Thus, improvement of TGW, GNB, PNB, and PBL, especially PL and PD with high heritability ($h^2 > 89$%), is a promising strategy to increase the grain yield of foxtail millet.

Comparison of the QTL identified in this study with previous studies

Based on the physical coordinates of the QTL confidence intervals, we compared the genomic regions of the QTL identified in this study with those detected in other bi-parental and natural populations. Eleven QTL overlapped with QTL previously detected in other studies. One QTL was 0.5 Mb away from a previously identified QTL (Table S2). The genomic regions of $qPW2.6$, $qPD8.2$, and $qPEL5.6$ overlapped with those of $qPW2$, $qPD8.2$, and $qNL5$ identified in a $F_2$ population of foxtail millet comprising 543 lines derived from a cross between Aininghuang and Jingu 21 (Wang et al. 2019). Eight QTL ($qPW6.1$, $qPL4.2$, $qPL4.3$, $qPL5.2$, $qPD2.2$, $qPD5.3$, $qPBN2.1$, and $qPEL9.5$) overlapped with, or were close to, the genomic regions of $apw6$, $apl4.1$, $apl4.2$, $apl5.1$, $apd2$, $apd5$, $qcn2.1$, and $qnl9$ that were isolated from a foxtail millet population of 439 RILs (Zhang et al. 2017). $qGWP3.3$, a QTL for GWP identified in the present study, overlapped with the position of $qGWP3.3$ that was detected in a RIL population derived from a cross between Longgu7 and Yugu1 (Liu et al. 2020). The physical position of $qPD5.3$, a QTL for PD, overlapped with that of $qMPD5.2$ for PD detected in a Yugu1 × Longgu7 $F_2$ population (Fang et al. 2016). The genomic regions of six QTL were the same as those of six QTL identified in a previous study from a natural population of 916 accessions (Jia et al. 2013). The genomic intervals of $qPL1.2$, $qPL2.6$, and $qPL7.2$ covered the physical positions of three QTL for PL; (Chr1: 37,343,439 and 37,378,964), (chr2: 22,845,341), and (chr7: 21,691,982), respectively. The genomic interval of $qPL9.5$ covered the genomic regions of two QTL for PL. (Chr9: 38,568,427 and 39,540,370), $qPD6.3$ and $qPD6.4$ were close to the QTL (chr6: 8,035,171) and (chr6: 22,571,518) for PD detected previously (Jia et al. 2013).

Candidate genes located at QTL related to panicle architecture or grain yield

The inflorescence of foxtail millet, like all panicoid grasses, is a compound raceme called a panicle. The inflorescence meristem is composed of a rachis, primary branches, secondary branch meristems, and tertiary branches with a number of spikelet meristems, which develop into two-flowered spikelets. Many genes involved in specifying inflorescence meristem identity have been cloned. In rice, $ASP1$ encodes a TOPLESS-related transcriptional co-repressor that is involved in the regulation of meristem fate. A recessive $aps1$ mutant displays a disorganized branching pattern and aberrant spikelet morphology (Yoshida et al. 2012). $APO1$ temporally regulates meristem identity in rice. The inflorescence meristem of $apo1$ is converted into a spikelet meristem, and produces a small number of primary branch meristems, resulting in small panicles (Ikeda et al. 2005). $OsMADS14$, $OsMADS15$, and $OsMADS18$ are APETALA1 (AP1)/FRUITFULL (FUL)-like genes involved in inducing the transition from the shoot apical meristem to the inflorescence meristem in rice. Triple knock-down plants in the $pap2$ mutant show inhibited transition of the meristem to the inflorescence meristem (Kobayashi et al. 2012). In this study, we identified four candidate genes homologous to $ASP1$, $APO1$, $OsMADS15$, and $OsMADS18$ of rice, in the genomic regions of $qPD6.2$, $qGWP4.11$, $qPL4.3$, $qPW4.2$, $qPW2.1$, and $qPW2.6$. $qTGW2.3$, respectively. These genes may play essential roles in regulating PW, GWP, TGW, and PL in foxtail millet. Moreover, delays in spikelet meristem specification lead to iterations of branching, resulting in larger panicles that could potentially produce more grain. In the dominant gain-of-function mutant $tawawa1-D$, the activity of the inflorescence meristem is extended and spikelet specification is delayed, resulting in prolonged branch formation and increased numbers of spikelets. In contrast, a reduction in $TAWA1$ expression by RNAi results in a similar but stronger small inflorescence phenotype in which both primary and secondary branches are reduced (Yoshida et al. 2013). We identified a gene ($Setia.9G222400$) homologous to rice $TAWA1$ located at $qPBN9.2$, a QTL.
related to PBN, suggesting that this gene may play a role in the formation of primary branch number in foxtail millet. OsMADS22 and OsMADS56 are homologs of Arabidopsis SVP and SOC1, respectively, and regulate inflorescence branching by repressing the expression of RCN genes in rice (Liu et al. 2013). The gene SiMADS56 (Seita.9G342700) was identified at the genomic region of qPL9.6/qPD9.2/qPEL9.3, which was detected 23 times in 13 environments for three traits. Thus, SiMADS56 may play an essential role in regulating branching in foxtail millet, independently of the environment.

**Phytohormones might play important roles in foxtail millet panicle architecture and grain yield**

Auxin plays a key role in determining axillary meristem initiation and outgrowth. Two of the candidate genes detected in this study, Seita.5G243100 and Seita.7G126900, showed homology to the auxin biosynthesis genes YUC1 and TDD1 in rice. Seita.1G317400, Seita.3G136000, Seita.4G101300, and Seita.5G241500 were predicted to encode auxin efflux carrier proteins involved in auxin transport. Cytokinin and GAs play antagonistic roles in regulating reproductive meristem activity. Increased cytokinin activity leads to higher grain number, whereas GAs negatively affect meristem activity. In the genomic regions of qPBN9/qPEL5.2, we identified a gene (Seita.5G140300) showing homology to the rice gene Gn1a, which encodes a cytokinin oxidase/dehydrogenase (OsCKX2) that degrades cytokinin (Ashikari et al. 2005). Intriguingly, we also detected a rice DST homolog (Seita.9G064000) located at qPEL9.1. In rice, DST enhances grain production through controlling Gn1a/OsCKX2 expression. Seita.9G004400, located at the genomic region of qPBN9.1, showed homology to rice GNPI, which encodes a GA20ox1 protein. KNOX proteins function as modulators, and balance cytokinin and GA activity in the meristem. Increased expression of the GA catabolism genes GA20ox in NIL-GNPIQ decreases GA accumulation, resulting in increased cytokinin activity, which consequently improves grain number and yield (Wu et al. 2016).

**Conclusion**

In summary, we analyzed the phenotypic variations in nine traits related to panicle architecture in one to 13 environments, and found that phenotypic variations in the RIL population varied across different geographical locations. The QTL mapping revealed 239 loci, including 73 high-confidence loci, forming 159 QTL for nine traits. Of these, 34 QTL were identified in two to 12 environments, and 34 were pleiotropic QTL related to two to five traits. We anticipate that further analyses of these QTL will provide a foundation for further genetic improvement of the yield of foxtail millet.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00122-021-03875-2.

**Acknowledgements** We thank Dr. Jin Gao helped in data analysis. This work was supported by National Key R&D Program of China (grant nos. 2019YFD1000700, and 2019YFD1000701), China Agricultural Research System (CARS06-13.5), National Natural Science Foundation of China (31871630), China Postdoctoral Science Foundation (2018M641553), the Agricultural Science and Technology Innovation Program of CAAS (ICS2020YJ08BX-2), and the Agricultural Science and Technology Innovation Program of the Chinese Academy of Agricultural Sciences.

**Author Contributions statement** HZ and QH did data analysis and drafted the manuscript. XD and HZ designed the experiment, developed the RIL population, and revised the manuscript. JL helped in the data analysis and discussion. ST, JY, WZ, HL, YJ, GJ, AZ, YL, EG, MG, SL, JL, NQ, CZ, CM, HZ, GC, WZ, HW, ZQ, SL, RC, LX, SW, and JL collected the phenotype. All authors have read and approved the final manuscript.

**Funding** This work was supported by National Key R&D Program of China (grant nos. 2019YFD1000700, and 2019YFD1000701), China Agricultural Research System (CARS06-13.5), National Natural Science Foundation of China (31871630), China Postdoctoral Science Foundation (2018M641553), the Agricultural Science and Technology Innovation Program of CAAS (ICS2020YJ08BX-2), and the Agricultural Science and Technology Innovation Program of the Chinese Academy of Agricultural Sciences.

**Declarations**

**Conflict of interest** The authors declare no conflict of interest.

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