

RESEARCH ARTICLE



Comparative mapping of quantitative trait loci for tassel-related traits of maize in F_{2:3} and RIL populations

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Abstract. Tassel architecture is an important trait in maize breeding and hybrid seed production. In this study, we investigated total tassel length (TTL) and tassel branch number (TBN) in 266 F_{2:3} families across six environments and in 301 recombinant inbred lines (RILs) across three environments, where all the plants were derived from a cross between 08-641 and Ye478. We compared the genetic architecture of the two traits across two generations through combined analysis. In total, 27 quantitative trait loci (QTLs) (15 in F_{2:3}; 16 in RIL), two QTL × environment interactions (both in F_{2:3}), 11 pairs of epistatic interactions (seven in F_{2:3}; four in RIL) and four stable QTLs in both the F_{2:3} and RILs were detected. The RIL population had higher detection power than the F_{2:3} population. Nevertheless, QTL × environment interactions and epistatic interactions could be more easily detected in the F_{2:3} population than in the RILs. Overall, the QTL mapping results in the F_{2:3} and RILs were greatly influenced by genetic generations and environments. Finally, fine mapping for a novel and major QTL, *qTTL-2-3* (bin 2.07), which accounted for over 8.49% of the phenotypic variation across different environments and generations, could be useful in marker-assisted breeding.

Keywords. maize; tassel; comparative quantitative trait loci mapping; generation.

Introduction

Maize is a thermophilic, short-day crop that is widely planted in China, and it represents the largest cultivated area and yield in the country (United Nations Food and Agriculture Organization, FAO, <http://www.fao.org/>; State Statistics Bureau, <http://www.stats.gov.cn/>). The tassel in maize is important for single-cross hybrid seeds (Upadyayula *et al.* 2006). As tassel size becomes smaller there is an associated decrease in grain yield (Lambert and Johnson 1977; Geraldi *et al.* 1985; Fischer *et al.* 1987). Due to the competition between the tassel primordia and the ear primordia for nutrients, detasselled maize plants growing at high plant densities have much less barrenness

and higher grain yields compared to nondetasselled plants (Leonard and Kiesselbach 1932; Grogan 1956; Duvick 1958; Schwanke 1965; Mock and Schuetz 1974). Tassel branch number, tassel size and tassel weight decrease consistently in hybrids and recurrent selected populations (Duvick 1997; Duvick and Cassman 1999; Duvick *et al.* 2004; Brekke *et al.* 2011; Edwards 2011). A moderate tassel size can be useful in improving canopy structure and light penetration (Sofi 2007). The maize ideotype that would be produced when the plants are grown in an optimum production environment would be characterized by small tassel size (Mock and Pearce 1975). Previous quantitative genetic studies demonstrated that tassel branch number was quantitatively inherited with high

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heritability, and additive, dominance and epistatic gene action all influenced its inheritance (Mock and Schuetz 1974; Schuetz and Mock 1978). A model for the control of meristem identity and determinacy in the architecture of maize inflorescences has been suggested by Kaplinsky and Freeling (2003). The underlying organization and development in the mature tassel and ear are remarkably similar until the flowers are initiated (Kaplinsky and Freeling 2003; Upadyayula et al. 2006), and many genes have been identified as being involved in the development of the tassel and ear (McSteen and Hake 2001; Taguchi-Shiobara et al. 2001; Vollbrecht et al. 2005). Eveland et al. (2014) uncovered discrete developmental modules for RA1-mediated regulation and integration with KN1-based meristem maintenance pathways.

Tassel-related traits are complex, however, and few QTLs have been colocalized with known genes that control the inflorescences. Berke and Rocheford (1999) demonstrated that six, three and seven QTLs were significantly associated with tassel branch angle, branches per tassel and tassel weight, respectively. Mickelson et al. (2002) reported six QTLs for tassel branch number using IBM populations, and these mapped close to the *umc53a* marker on chromosome 2. Upadyayula et al. (2006) also observed five QTLs for tassel branch number and four QTLs for tassel weight in a set of B73 S₁ families (Illinois Low Protein B73), thereby providing initial information that would permit new gene discovery for the control of inflorescence architecture. Brown et al. (2011) compared the genetic architecture of male and female maize inflorescence traits in the maize nested association mapping (NAM) population, and they identified some pleiotropic inflorescence loci that have large effects. Brewbaker (2015) evaluated the diversity and genetics of tassel branch number (TBN) in maize using diallels, generation mean analyses (GMAs), near isogenic lines (NILs), and recombinant inbred lines (RILs), and concluded that reducing tassel size might not lead to higher grain yields in tropical hybrids. A number of QTLs have thus been identified that alter tassel length and tassel branch number.

It is a common approach to search for consistent and stable QTLs across different populations (Brown et al. 2011; Ku et al. 2012; Li et al. 2015), generations (Austin and Lee 1996; Li et al. 2007, 2008, 2011), and environments (Li et al. 2003; Lan et al. 2005; Semagn et al. 2013). Many published meta-QTLs have been integrated into a joint map through meta-analysis (Chardon et al. 2004; Semagn et al. 2013; Wang et al. 2013). Previous studies comparing F_{2:3} populations and RIL populations derived from the same parents in maize have evaluated flowering-related traits (Li et al. 2007) and grain yield and its components (Austin and Lee 1996; Li et al. 2011). Studying populations across different generations has some advantages, and investigating QTLs across different generations can be informative. Nevertheless, few QTL comapping studies have been reported for tassel traits across generations.

In this study, total tassel length (TTL) and tassel branch number (TBN) were investigated in 266 F_{2:3} families and 301 recombinant inbred lines (RILs) derived from a cross between 08-641 (foundation parent from southeast China, PB) and Ye478 (foundation parent from China, PA). We detected QTLs via joint analysis across all environments (JAAE). The first objective of our study was to detect QTLs that have a large effect and can be observed in different environments and across two generations. The second objective was to find identical and novel QTLs that could be useful for further research on QTL cloning, candidate gene identification and marker-assisted breeding for tassel-related traits. Since there is a close developmental relationship between male and female maize inflorescences, this will allow us to have a better understanding of the genetic architecture of maize tassels.

Materials and methods

Plant material

The two mapping populations consisted of 266 F_{2:3} families and 301 RILs derived from a 08-641 × Ye478 cross, the two foundation parents representing the southwest maize zone and the Yellow and Huai River maize zone, respectively (Hou et al. 2015). These two elite lines have given rise to many important hybrids and inbred descendant lines that play an important role in the Chinese germplasm of maize (Qiao et al. 2009; <http://www.most.gov.cn/>). The formation of the 08-641 × Ye478 mapping population has been described by Hou et al. (2015).

Field experiments

The 266 F_{2:3} families along with the two parent lines and their F₁ were tested in 2012 and 2013 in six environments: at the Duoying farm of the Maize Research Institute of Sichuan Agricultural University, Ya'an, Sichuan (EY, 30°N, 103°E); at the Xishuangbanna maize breeding base of the Maize Research Institute of Sichuan Agricultural University, Jinghong, Yunnan Province (EJ, 22°N, 100.5°E); and at the Maize Research Institute of Guangxi, Nanning, Guangxi Zhuang Autonomous Region (EN, 22.5°N, 108.2°E). Two replicates were evaluated in each environment for a total of six trials, under a complete randomized block design of one-row plots at each location. The rows were 3-m long and spaced 0.76 m apart, with a total of 14 plants per row (58,000 plants/ha). Field management was in accordance with local practices (Hou et al. 2015). The 301 RILs and the two parent lines were evaluated in three environments in 2014 and 2015: three at the Xishuangbanna maize breeding base of the Maize Research Institute of Sichuan Agricultural University, Jinghong, Yunnan Province (EJ, 22°N, 100.5°E) in

March 2014, 2015, and April 2015, with two replications. The cultivation methods were the same as were used for the $F_{2:3}$ plants.

Phenotypic measurements and analysis

Methods for the collection of trait data were in accordance with Upadhyayula *et al.* (2006). The measurements taken were TTL, the length (cm) of the tassel measured from the nonbranching node below the lowermost primary branch to the tip of a central spike, and TBN, the number of primary branches. The normal distributions, the combined analyses of variance, and the Pearson's phenotypic correlations were calculated using the statistical software package SPSS 17.0 (<http://www.spss.com>), using a mixed model with effects for family lines, and with replications fixed and the environment effect random. Broad-sense heritabilities (H^2) for the $F_{2:3}$ families and RILs were computed on an entry mean basis as described by Hallauer and Miranda (1988):

$$H^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{ge}^2/n + \sigma^2/nb).$$

where σ_g^2 represents the genetic variance, σ_{ge}^2 represents the genotype \times environment interaction variance, σ^2 represents the error variance, 'b' represents the number of replications, and 'n' is the number of environments. The 90% confidence intervals on H^2 were determined according to Knapp *et al.* (1985).

Molecular linkage map construction and QTL mapping

Following the modified CTAB protocol of Chen and Ronald (1999), DNA was isolated from seven-day-old seedling leaves of the 301 RILs and the parents grown in shade. The oligonucleotide pool assay (OPA) consisted of 3072 well-distributed, high-quality SNPs from all 10 maize chromosomes that were selected from 56,110 SNPs in 513 maize inbred lines developed by the National Maize Improvement Center of China using Illumina GoldenGate technology. The protocol for genotyping SNPs using an Illumina BeadStation 500 G (Illumina, San Diego, CA) was described by Fan *et al.* (2006). Marker data from the RILs were screened for heterozygous data points (< 20%), missing data points (< 20%), segregation distortion (in accordance with the expected Mendelian segregation ratio of 1:1), and similarity between markers or individuals. SNPs with a high number of heterozygous values, missing values, or segregation distortion were deleted. A total of 683 SNPs selected for their uniform distribution throughout all 10 maize chromosomes were used to construct the linkage map with a total genetic length of 1786.1 cM and an average interval distance of 2.61 cM. Composite interval mapping (CIM) was used to map QTLs and estimate their eVects for each trait (Zeng 1993, 1994).

The genetic map was developed using MapDisto 1.7.5 (<http://mapdisto.free.fr/DL/>) at a LOD threshold of 3.0 (Mathias 2012). The Kosambi mapping function was used for converting recombination frequencies to genetic distances (Kosambi 1943). Analyses of QTL locations, origins of positive alleles, effects of the QTLs on each trait for each environment, and a joint analysis across all environments were performed using QTLNetwork software ver. 2.1 (Yang *et al.* 2008) with mixed-model-based composite interval mapping (MCIM) (Wang *et al.* 1999; Yang *et al.* 2007). The threshold for declaring the presence of a significant QTL was defined by 1000 permutations at a significance level of $P = 0.05$. A QTL was considered to be stable when the QTL \times environment interaction was not significant (Peng *et al.* 2011). Drawings of the combined linkage maps produced by JoinMap 4.0 (<https://www.kyazma.nl/index.php/mc.JoinMap/>) were generated with MapChart (Voorrips 2002). Gene action was judged according to the criteria of Stuber *et al.* (1987), and was considered to be an A or an OD if it only had an additive or dominant effect. The level-of-significance results of epistatic interactions between QTLs were corrected using sequential Bonferroni correction analyses (Rice 1989). A total of 471 SNPs were used to genotype the 266 $F_{2:3}$ families as described by Hou *et al.* (2015); other details of the procedure also followed Liu *et al.* (2016a).

Results

Comparative analysis of performance, variance, and correlation in $F_{2:3}$ and RIL populations across multiple environments

The performance for tassel length and tassel branch number of 08-641 and Ye478 plants showed significant differences (figure 1; table 1). The 08-641 plants had a lower TBN but a longer TTL than Ye478 plants. Transgressive segregations were observed for two traits. This suggests that large differences exist in both populations. In general, RIL population showed larger TTL and TBN than $F_{2:3}$ population, and TTL and TBN were both normally distributed in the $F_{2:3}$ populations and in the RIL population as the absolute values of skewness and kurtosis were less than 1. The results of the combined analyses of variance demonstrated that the genetic variances within the $F_{2:3}$ population and the RIL population, the variances of the environments, and the variances of the genotype \times environment interactions were all significant or highly significant (table 2). Broad-sense heritabilities (H_B^2) for TTL and TBN in two generations across joint multiple environments were high, ranging from 84.3 to 93.4. The results also suggested that the RIL population had higher H_B^2 values for TBN but lower H_B^2 values for TTL than the $F_{2:3}$ population. According to the results of the joint data across the three environments in the RIL population, TBN was

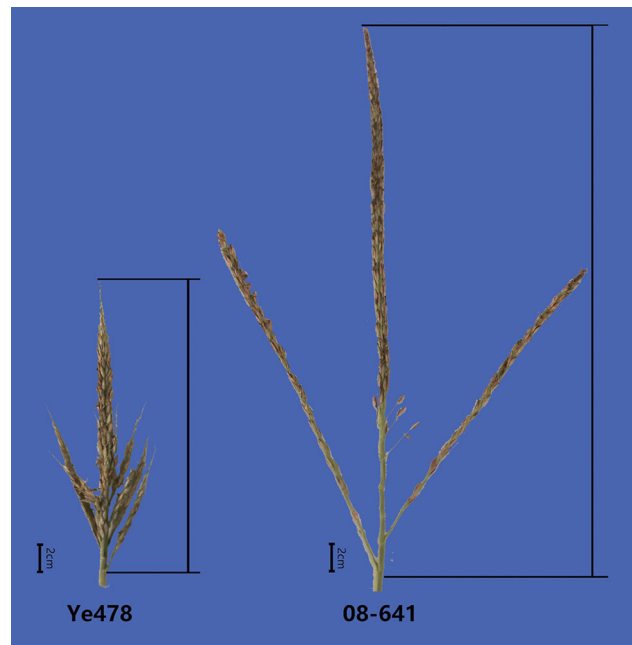


Figure 1. Tassel of Ye478 and 08-641. Scale bar = 2 cm.

positively correlated with TTL (correlation coefficient = 0.77, $P < 0.01$; data not shown). This suggests that they both belong to a complex trait.

QTL analysis and comparisons across the $F_{2:3}$ population and the RIL population

In our study, 27 QTLs were detected for the tassel-related traits across two generations via joint across-all-environments analysis (JAAE): six TTL QTLs in $F_{2:3}$, eight TTL QTLs in RIL, nine TBN QTLs in $F_{2:3}$ and eight TBN QTLs in RIL, which were located in all 10 chromosomes (figure 2; table 3). Notably, the total phenotypic variance explained by all QTLs identified for the two traits ranged from 28.44% (TTL $F_{2:3}$) to 54.84% (TBN in RIL).

For TTL, each QTL explained from 0.89% to 12.31% of the phenotypic variation with $qTTL2-2$ accounting for the highest per cent. Two QTL located in bin 1.09/1.11 and bin 2.07 accounted for 10.79 and 12.31% of R^2 , respectively. Remarkably, most of QTLs (11/13) had negative additive effects, indicating that alleles from the 08-641 parent contributed to an increasing TTL. And all QTLs in RIL and 2 QTLs in $F_{2:3}$ generation were additive, while four QTLs with partial dominance or dominance were identified in $F_{2:3}$.

For TBN, 13 putative QTLs were observed, which were mapped on all chromosomes except chromosomes 5, 8 and 10. Each QTL for TBN accounted between 0.78 and 16.08% of the phenotypic variance with three QTLs in RIL contributed over 10% of the phenotypic variance. Remarkably, one TTL QTL and four TBN QTLs were detected in

Table 1. Phenotypic performance for total tassel length and tassel branch number of the parents, $F_{2:3}$ population across six environments and RIL population across three environments.

Trait	Population type	08-641 (cm)	Ye478 (cm)	Mean (cm)	Minimum (cm)	Maximum (cm)	CV (%)	Skewness	Kurtosis
Total tassel length	$F_{2:3}$	37.8	24.8	34.9	20.1	48.5	9.01	− 0.31	1.01
TTL	RIL	38.3	23.2	31.2	16.1	47.6	15.26	0.03	0.03
Tassel branch number	$F_{2:3}$	4.8	7.9	8.7	1.7	20.2	34.27	0.32	− 0.26
TBN	RIL	4.4	8.3	7.2	0	17.8	42.39	0.43	0.039

CV, coefficient of variation.

Table 2. Combined analysis of variances for total tassel length and tassel branch number in the $F_{2:3}$ families under six environments and in the RIL population under three environments.

Sources	$F_{2:3}$		RIL	
	TTL	TBN	TTL	TBN
Families	56.5**	37.3**	42.93**	24.15**
Environment	1367**	2750**	413.45**	182.49**
Families × environment	6.67**	3.89*	6.76**	1.6*
Error	4.58	3.47	4.15	1.25
H^2 (%)	88.2	89.6	84.3	93.4
90% CI on H^2	86.1–89.9	87.7–91.1	81.4–86.6	92.1–94.4

H^2 , broad-sense heritability; CI, confidence intervals of H^2 between 5 and 95% significance levels. *, **Significance at 0.05 and 0.01 levels, respectively.

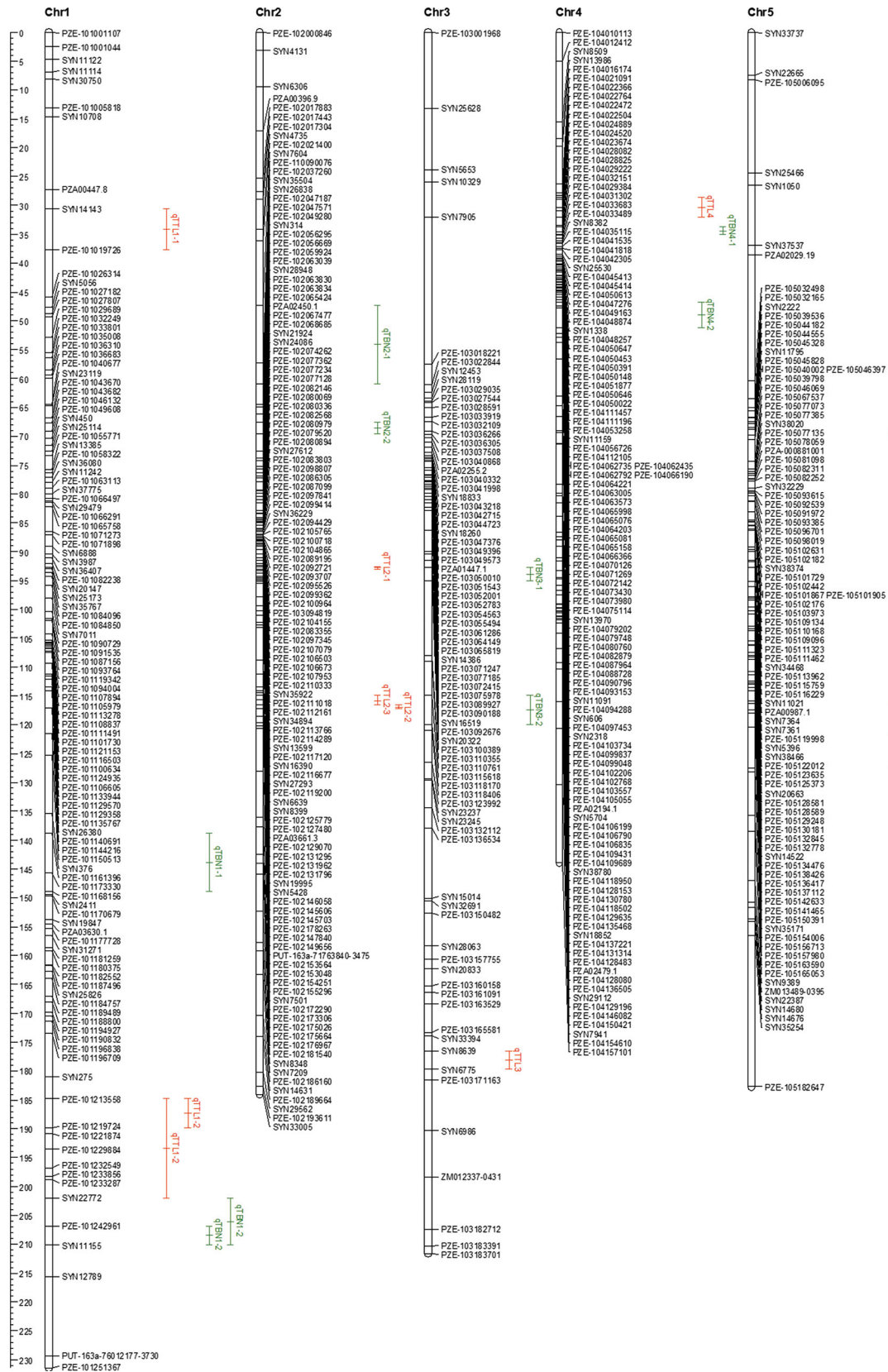


Figure 2 (contd)

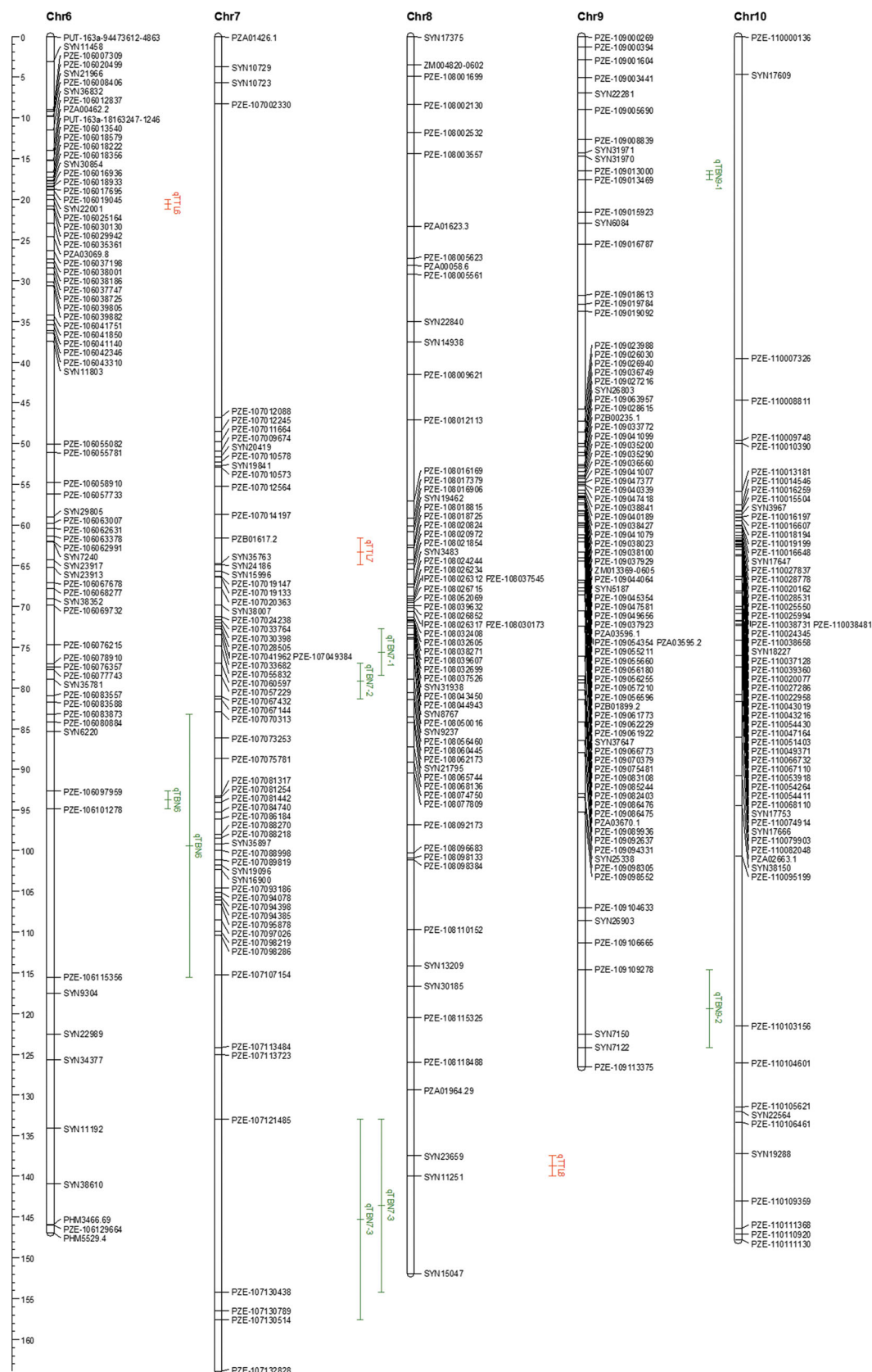


Figure 2. Distribution of identified QTL for total tassel length and tassel branch number on combined genetic linkage maps of F_{2:3} and RIL population. Letter 'Chr' represents chromosome. QTL confidence intervals were indicated by vertical lines. QTLs with confidence interval overlap will be nominated as the same.

Table 3. QTL for tassel related traits of F_{2:3} population and RIL population through JAAE.

Trait	Population type	QTL	Binlocus ^a	Flanking marker	Peak position (cM)	Range (cM) ^b	A ^c	D ^d	Gene action ^e	R ² (%) ^f	Subtotal R ² (%) ^g	F (0.05) ^h
TTL	F _{2:3}	<i>qTTL1-2</i>	1.09/1.10	PZE-101213558/PZE-101219724	276.1	273.1–278.8	–1.2175**	0.0112	A	10.79	28.44	3.16
		<i>qTTL2-3</i>	2.07/2.09	PZE-102149656/PZE-102178263	182.3	181.3–183.3	–1.342**	0.0429	A	8.96		
		<i>qTTL4</i>	4.04	PZE-104022472/PZE-104023674	20.2	19.5–23.2	–0.2018*	0.8471**	PD	1.79		
		<i>qTTL5-1</i>	5.03	PZE-105039798/PZE-105040002	3.8	0.0–11.9	–0.308**	0.3009*	PD	1.15		
		<i>qTTL7</i>	7.02	PZB01617.2/SYN24186	77.4	67.4–83.6	–0.7247**	0.5232**	PD	4.65		
		<i>qTTL10</i>	10.02/10.03	PZE-110010390/SYN3967	42.9	40.4–46.9	–0.1413	0.2808*	D	1.1		
		<i>qTTL1-1</i>	1.01	SYN14143/PZE-101019726	5.3	2.3–8.3	–1.0069**		A	7.14	45.4	6.76
		<i>qTTL1-2</i>	1.09/1.11	PZE-101213558/SYN22772	205.9	198.9–212.9	–0.6631**		A	4.64		
		<i>qTTL2-1</i>	2.05	PZE-102113766/PZE-102114289	101.6	100.6–101.8	–0.7065**		A	6.44		
		<i>qTTL2-2</i>	2.07	PUT-163A-71763840-3475/PZE-102149656	138.9	136.9–140.3	–0.8354**		A	12.31		
TBN	F _{2:3}	<i>qTTL3</i>	3.09	SYN8639/SYN6775	188.4	186.4–189.1	–0.9237**		A	8.25		
		<i>qTTL5-2</i>	5.06	PZE-105141465/PZE-105156713	158	152.0–158.8	0.5548**		A	0.89		
		<i>qTTL6</i>	6.01	PZE-106025164/PZE-106029942	23.8	22.8–24.0	–0.4939**		A	3.77		
		<i>qTTL8</i>	8.08	SYN23659/SYN11251	163.7	162.7–163.9	0.6247**		A	1.96		
		<i>qTBN1-1</i>	1.07	PZE-101161396/PZE-101168156	214.6	210.2–217.6	–0.5318**	0.2723**	PD	1.76	41.18	3.19
		<i>qTBN1-2</i>	1.11	PZE-101242961/SYN11155	304.6	301.6–308.1	–0.7802**	–0.3623**	PD	8.56		
		<i>qTBN2-2</i>	2.03	PZE-102047571/PZE-102049280	69.9	68.4–71.8	0.9272**	0.4539**	PD	7.4		
		<i>qTBN3-1</i>	3.05	PZE-103100389/SYN20322	150.8	148.2–150.8	–0.3031**	–0.0601	A	0.78		

Table 3 (contd)

Trait	Population type	QTL	Binlocus ^a	Flanking marker	Peak position (cM)	Range (cM) ^b	A ^c	D ^d	Gene action ^e	R ² (%) ^f	Subtotal R ² (%) ^g	F (0.05) ^h
		<i>qTBN4-2</i>	4.05/4.06	PZE-104073430/SYN13970	79.2	76.2–82.1	0.8851**	0.1875*	PD	6.42		
		<i>qTBN6</i>	6.05	PZE-106097959/PZE-106101278	139.8	138.7–141.8	0.6325**	–0.0846	A	5.32		
		<i>qTBN7-2</i>	7.02/7.03	PZE-107060597/PZE-107067144	100.6	98.9–104.6	0.7078**	0.1691	A	2.86		
		<i>qTBN7-3</i>	7.06	PZE-107121485/PZE-107130514	169	163.1–174.0	0.5063**	0.1474	A	6.63		
		<i>qTBN9-1</i>	9.02	PZE-109013000/PZE-109013469	22.9	19.8–28.7	0.3628**	0.091	A	1.45		
RIL		<i>qTBN1-2</i>	1.11	SYN22772/SYN11155	221.7	217.7–224.5	–0.7185**		A	2.38	52.84	6.69
		<i>qTBN2-1</i>	2.02/2.03	SYN7604/PZE-102037260	25.1	21.1–28.6	0.9808**		A	13.69		
		<i>qTBN3-2</i>	3.06	PZE-103115618/PZE-103118170	123.5	122.5–126.5	–0.5207**		A	2.14		
		<i>qTBN4-1</i>	4.05	PZE-104029222/PZE-104029384	38.8	37.8–39.5	0.4807**		A	2.55		
		<i>qTBN6</i>	6.05-6.07	PZE-106083873/PZE-106115356	127.2	117.2–127.5	0.3627**		A	2.26		
		<i>qTBN7-1</i>	7.02	PZE-107049384/PZE-107057229	65.7	62.7–66.0	0.7588**		A	10.56		
		<i>qTBN7-3</i>	7.06	PZE-107121485/PZE-107130438	140.9	137.9–144.9	0.9555**		A	16.08		
		<i>qTBN9-2</i>	9.07/9.08	PZE-109109278/SYN7122	160.8	157.8–161.8	0.5717**		A	3.18		

^aThe specific genetic region included the peak position of QTL (<http://www.maizegdb.org/>).^bThe confidence interval of QTL position.^cThe additive effect of the QTL; positive values indicate that the alleles for increasing trait value are contributed by Ye478; negative values indicate that the allele for increasing trait value are contributed by another parent 08-641.^dThe dominant effect of the QTL.^eA, D, PD, and OD represent additive, dominance, partial dominance, over-dominance effect, respectively.^fPercentage of phenotypic variance explained by a single QTL.^gTotal percentage of phenotypic variance explained by all the mapped QTL for each trait.^hThe *F*-statistic ($P < 0.05$) value were conducted by QTLNetwork with 1000 random permutation.

*, **Significance at 0.05 and 0.01 levels, respectively.

both two generations. One stable QTL *qTBN7-3* accounting for 16.08% of R^2 mapped in the marker interval *PZE-107121485/PZE-107130514* was detected via two generations, indicating that this QTL may be involved in tassel development.

QTL × environment interaction (QEI) and epistatic interaction analyses

Only two QTLs for tassel-related traits detected in the F_{2:3} population showed a significant ($P < 0.05$) additive × environment interaction with minor effects through joint analysis (table 4), and none of the QTLs detected in the RIL population had a significant dominant × environment interaction in this study, indicating that the effects of the additive × environment interaction merely observed in the F_{2:3} populations were minor. Meanwhile 11 pairs of QTLs with exhibited significant ($P < 0.05$) epistatic effects: seven in F_{2:3} and four in RIL (table 5). Among the results, 11, 4 and 5 pairs of loci were observed with additive × additive epistatic, additive × dominant epistatic and dominant × additive epistatic effects accounting 0.08% to 1.32% variance. No QTLs with significant ($P < 0.05$) interaction effects between epistasis and the environment in our study were detected for the two tassel-related traits, indicating tassel in maize mainly influenced by QTLs per se. Additionally, additive × additive epistatic effects could be detected across two generations, while additive × dominant epistatic effects, dominant × additive epistatic effects, and dominant × dominant epistatic effects could only be detected in the F_{2:3} population. No similar interactions could be detected across two generations in our study.

Discussion

Comparison of QTLs detected in the F_{2:3} and RIL generations via JAAE

Previous studies that included QTL consistency and meta-analysis across generations (RIL, F_{2:3}, and BC₂F₂) derived from the same cross showed that the power for detecting QTLs was influenced by many factors, including generations (Austin and Lee 1996; Li *et al.* 2007, 2011), environments (Li *et al.* 2003; Lan *et al.* 2005; Semagn *et al.* 2013), genetic backgrounds (Brown *et al.* 2011; Ku *et al.* 2012; Li *et al.* 2015), additional recombination and homozygosity (Knapp and Bridges 1990; Austin and Lee 1996), sampling variation (Li *et al.* 2007, 2008), genetic heterogeneity of the phenotype (Beavis *et al.* 1991), backcrosses (Moreno-Gonzalez 1993; Li *et al.* 2007), and germplasm and traits (Mihaljevic *et al.* 2004; Blanc *et al.* 2006). Over the trials reported about generations, Austin and Lee (1996) reported that 16 QTLs for grain yield components were detected with F_{2:3} and F_{6:7} lines in the same regions with the same parental effects. Notably, Li

Table 4. QEI influencing tassel related traits of F_{2:3} population under six environments.

Trait	QTL	Interval	AENN2012 ^a	AENN2013 ^a	AEYA2012 ^a	AEYA2013 ^a	AEJH2012 ^a	AEJH2013 ^a	H ² (ae)%
TTL	<i>qTTL5-1</i>	<i>PZE-105039798/PZE-105040002</i>							1.08
TBN	<i>qTBN1-2</i>	<i>PZE-101242961/SYN11155</i>			−0.4004*	−0.4061*		0.3565*	0.67

^aAE is the additive by designated environment interaction effect.

H² (ae) is the contribution rate of additive by environment interaction.

*Significance at 0.05 levels.

Table 5. Epistatic effect of QTL for tassel related traits identified in F_{2:3} population under six environments and RIL population under three environments.

Trait	Population type	QTL _i	QTL _j	AA ^a	H ² (aa) (%) ^b	H ² (aae) (%) ^c	AD ^a	H ² (ad) (%) ^b	H ² (ade) (%) ^c	DA ^a	H ² (da) (%) ^b	H ² (dae) (%) ^c	DD ^a	H ² (dd) (%) ^b	H ² (dde) (%) ^c
TTL	F _{2:3}	<i>qTTL1-2</i>	<i>qTTL10</i>	-0.6663**	1.32	0.12	0.3017	0.07	0.33	-0.0115	0	0.26	-0.2913	0.09	0.23
		<i>qTTL2-3</i>	<i>qTTL5-1</i>	0.3749**	0.38	0.12	0.3248	0.05	0.34	-0.3677*	0.08	0.12	-0.8731**	0.64	0.07
		<i>qTTL2-3</i>	<i>qTTL7</i>	-0.7392**	0.95	0.08	1.2319**	1.11	0.04	0.481**	0.39	0.17	0.4993*	0.2	0.13
		<i>qTTL4</i>	<i>qTTL7</i>	0.2913**	0.89	0.4	0.7173**	0.33	0.12	0.2654	0.18	0.12	-0.1258	0	0.34
TBN	F _{2:3}	<i>qTBN1-1</i>	<i>qTBN7-2</i>	-0.4188**	0.61	0.01	0.4144**	0.16	0.12	-0.3339*	0.15	0.05	-0.5515**	0.21	0.12
		<i>qTBN3-1</i>	<i>qTBN9</i>	-0.1262	0.28	0.02	0.046	0.03	0.27	0.5488**	0.34	0.14	0.5921**	0.25	0.05
		<i>qTBN7-2</i>	<i>qTBN7-3</i>	-0.5764**	0.88	0.22	0.5014**	0.4	0.1	0.3423**	0.27	0.51	-0.4303*	0.09	0.05
		<i>qTBN1-2</i>	<i>qTBN4-1</i>	-0.271**	0.72	0.03									
RIL	RIL	<i>qTBN1-2</i>	<i>qTBN7-3</i>	-0.3373**	0.87	0.03									
		<i>qTBN4-1</i>	<i>qTBN7-1</i>	0.1877*	0.14	0.12									
		<i>qTBN7-1</i>	<i>qTBN7-3</i>	-0.3572**	0.92	0.02									

^aAA, AD, DA and DD were additive × additive, additive × dominant, dominant × dominant effect interactions, respectively.^bH²(aa), H²(ad), H²(da) and H²(dd) % were contribution rate of additive × additive effect interaction, additive × dominant effect interaction, dominant × additive effect interaction and dominant × dominant effect interactions, respectively.^cH²(aae), H²(ade), H²(dae) and H²(dde) % were contribution rate of additive × additive by environment interaction, additive × dominant by environment interaction, dominant × additive by environment interaction and dominant × dominant by environment interaction, respectively.

*, **Significance at 0.05 and 0.01 levels, respectively.

et al. (2007, 2008) demonstrated that six QTLs for grain yield components and nine QTLs for agronomical characters were located in the same/near chromosome intervals across both the BC₂S₁ and F_{2:3} generations. Two stable QTLs for TTL were identified on chromosomes 5 (between phi109188-umc1221) and 8 (between umc1360-bnlg1863) across both the BC₂S₁ and F_{2:3} generations therein. And Li *et al.* (2011) found that no common QTL for grain yield components across three generations (RIL, F_{2:3} and BC₂F₂) were located in the same marker intervals. In our study, 11 QTLs and 12 QTLs were F_{2:3} population-specific and RIL population-specific, respectively (table 3). Of the detected QTLs, only four were detected across both generations via JAAE. Four major QTLs were detected in RIL, whereas only one QTL in the F_{2:3} generation. The total phenotypic variances explained 45.4% (TTL) and 54.84% (TBN) in RIL is greater than 28.44% (TTL) and 41.18% (TBN) in F_{2:3}. The results of the joint analysis indicate RIL populations have a higher power for detecting QTLs than the F_{2:3} progeny. Meanwhile, the QTLs with partial dominant and over-dominant were only detected in the F_{2:3} but not in the RIL generation. This is similar to other studies (Li *et al.* 2011). Besides, QEI and epistasis between QTLs may have small effects on the improvement of tassel-related traits (1.32% of the phenotypic variance, the highest per cent) and no similar interactions could be detected across two generations in our study, which is similar to other studies (Li *et al.* 2011; Hou *et al.* 2015; Yang *et al.* 2016). QTL consistency across generations in our study was less than in previous studies (Austin and Lee 1996; Li *et al.* 2007), possibly for a number of reasons. There were many differences in our study, including genetic background, marker numbers that were higher than in previous studies (471 and 683 SNP markers in the F_{2:3} and RIL generations, respectively) (Austin and Lee 1996; Li *et al.* 2007, 2011), environment (six in F_{2:3} vs three in RIL), population size (266 F_{2:3} vs 301 RIL), and analysis method and traits (only two traits). However, the main reason may be accounted for by the additional recombination experienced during the production of the RILs (Austin and Lee 1996). Generally speaking, it is a good idea to combine the results of the F_{2:3} and RIL generations.

QTL detection of tassel-related traits, and QTL pleiotropy

Recently, much attention has been paid to the genetic basis of canopy-architecture-related traits (Hou *et al.* 2015), flowering-related traits (Buckler *et al.* 2009), maize kernel composition (Cook *et al.* 2012; Yang *et al.* 2016), and tassel-related traits (Upadhyayula *et al.* 2006; Brown *et al.* 2011). Some maize inflorescence genes including *ramosa1* (*ra1*) (Vollbrecht *et al.* 2005), *ramosa2* (*ra2*) (Bortiri *et al.* 2006) and *ramosa3* (*ra3*) (Satoh-Nagasawa *et al.* 2006) have been cloned. Many studies have found that several QTLs/genes associated with tassel-related traits show tight

linkage and/or pleiotropic effects on canopy-architecture-related traits and yield-grain-related traits (Austin and Lee 1996; Brown *et al.* 2011; Li *et al.* 2011). Generally, the correlated traits shared regions associated with QTLs (Austin and Lee 1996; Li *et al.* 2007, 2011). The correlation among central spike length, central spike spikelet pair density and total spikelets on central spike, was supported with both the QTL detected for the tassel-related traits (in bins 5.04 and 9.02, Upadyayula *et al.* 2006) being in common. Tassel length was positively correlated with plant height, ear height, and leaf area (Li *et al.* 2008). Additionally, previous studies demonstrated that the underlying genetic control of maize tassel and ear development was similar (Upadyayula *et al.* 2006; Zhuang *et al.* 2007; Brown *et al.* 2011). *Ramosa1* and *ramosa2* mutants were also found to have phenotypic effect on the tassel and ear. Meanwhile, Upadyayula *et al.* (2006) reported that four of 25 QTLs for tassel and ear traits shared the regions in bin 3.07, bin 5.04 and bin 7.02. Brown *et al.* (2011) also suggested that pleiotropic loci control the elongation of the ear and tassel, consistent with their common developmental origin. Common chromosome regions at Bin 4-650 affecting TBN and ear length and Bin 5-588 associated with TBN and kernel number per row (KNR) have also been shown to have similar pleiotropic effects (Chen *et al.* 2014).

In this study, one stable TTL QTL and three stable TBN QTLs were detected via two generations. The results are in well accordance with those via SEA (see table 1 in electronic supplementary material at <http://www.ias.ac.in/jgenet/>). The *qTBN4-2* in bin 4.05 was located in the same region as one common QTL for TBN and central spike length detected by Upadyayula *et al.* (2006). The RIL-specific *qTTL2-2* with major effect in bin 2.07 was collocated in same regions near to large-effect SNP (*PZE-102149923*) affecting TBN and spike length detected in the maize nested association (Brown *et al.* 2011). We also identified stable QTLs for TTL and TBN in bins 1.09–1.11 and 7.02. The *qTBN1-2* and *qTTL1-2* in bin 1.09–1.11 were comapped to *teosinte branched1 (tb1)* (Doebley *et al.* 1997) affecting the formation of female inflorescences, *Dwarf8 (D8)* (Peng *et al.* 1999) influencing the tassel length and plant height, *knotted1 (kn1)* (Vollbrecht *et al.* 1991), and indeterminate spikelet1 (*ids1*) determining spikelet meristem fates (Chuck *et al.* 1998). They were also collocated to a QTL cluster controlling the width of the first leaf above the primary ear at its widest point and the length from ligula to tip of the first leaf above the primary ear in $F_{2:3}$ (Hou *et al.* 2015). Additionally, *ramosa3 (ra3)* (Satoh-Nagasawa *et al.* 2006) and branched silkless1 (*bd1*) (Chuck 2002) collocated with *qTBN7-3* identified in both five single environments and two generations in bin 7.06, influence the tassel differentiation and tassel branch number. *Ramosa1 (ra1)* (Vollbrecht *et al.* 2005) comapped with *qTTL7*, *qTBN7-1* and *qTBN7-2* in bin 7.02, influence kernel rows and tassel branch. Upadyayula *et al.* (2006) also reported the bin 7.02 regions have also been found to show pleiotropic

effects on tassel and ear traits. Thus, the tassel-related traits are strongly associated with other traits, especially canopy-architecture-related traits and yield-grain-related traits. Nevertheless, some genes cloned including have not been detected in this study and some QTLs have not identified in other studies, which may indicate big difference in background.

Origin analysis of favourable QTL in breeding

Previous studies (Yamasaki *et al.* 2005; Jiao *et al.* 2012; Liu *et al.* 2016b) suggested that the foundation parents were formed primarily through the accumulation of rare alleles during breeding, and major-effect genes had already undergone the most stringent selection during crop improvement, and many different identity-by-descent (IBD) segments and genes were included in the formation of foundation parent lines, and complex regulatory networks exist among them (Wu *et al.* 2016). As for the origin of favour alleles in this study, the alleles coming from 08-641 contributed to an increasing TTL and a part of the TBN, while the alleles from Ye478 mainly contributed to an increasing TBN of identified QTLs. The tassel inflorescence in maize tends to be smaller in modern breeding to reduce competition with the female inflorescence (Grogan 1956; Duvick *et al.* 2004), i.e. favour alleles for decreasing TTL and TBN are mainly derived from the foundation parents YE478 and another line 08-641, respectively. Favourable alleles from 478 were located in bin 1.09–1.10 and 2.07 decreasing tassel length, whereas bin 7.02 and 7.06 from 08-641 have been shown to decreasing TBN. It is confirmed that foundation parents or elite maize line may accumulate different specific favourable alleles (Liu *et al.* 2016b). Generally, elite characteristics in germplasm could be recovered through 1–2 backcrosses with elite germplasm as the recurrent parents (Dofing *et al.* 1991; Ziegler and Ashman 1994; Li *et al.* 2002, 2008). Thus, one elite line especially for its tassel-related traits could be improved more specifically.

Considering multiple affecting factors synthetically, a new QTL, *qTTL-2-3* (*PZE-102145703/PZE-102146058*; Only six genes were found in this region; based on the AGI's B73 RefGen_v2 sequence, <http://www.maizegdb.org>; table 1 in electronic supplementary material) located in bin 2.07 with accounting for over 8.49% of the phenotypic variation through different environments and generations, was identified in 2014JH as closed linked to a predicted gene GRMZM2G178182 (*ZmHHLH23*) similar to *AtHHLH137* (Cao *et al.* 2006). And ERF11 directly represses RGA-induced *AtHHLH137* expression (a DELLA target genes), and promotes internode elongation by activating gibberellin biosynthesis and signaling (Zhou *et al.* 2016). In addition, we reported in our former study that *qTTL-2-3* in bin 2.07 was located in a

crucial genomic region containing genes affecting plant height and tassel length (Liu *et al.* 2016b). Fine mapping of *qTTL-2-3* for TTL could be helpful in marker-assisted breeding.

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