

Identification of QTL for ear row number and two-ranked versus many-ranked ear in maize across four environments

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Abstract Ear row number (ERN) is not only a key trait involved in maize (*Zea mays* L.) evolution but also an important component directly related to grain yield. In this report, 325 recombinant inbred lines (RILs, F_{6,7}) derived from a cross between B73 with 16 rows and SICAU1212 with four rows (two-ranked with two rows per rank) were utilized to detect quantitative trait loci (QTL) associated with ERN and two-ranked versus many-ranked ears (TR). Compared to modern maize that formed approximately 8–20 rows, SICAU1212 with four rows was the extreme case. A total of 12 and 8 QTLs were associated with ERN and TR across four environments through single-environment mapping, respectively. Each QTL responsible for ERN explained 2.33–21.28 % of the phenotypic variation. And the TR variation contributed by individual TR QTL ranged

from 2.09 to 12.99 %. Notably, only three QTLs, *qERN2-1* (bin 2.02), *qERN8-1* (bin 8.02) and *qERN8-2* (bin 8.04), were consistently detected in each environment and by joint analysis among all environments, which simultaneously influenced ERN and TR. One of the three QTLs, *qERN8-1* was also identified as interacting with environment. In addition, nine pairs of significant epistatic interactions (two for ERN and seven for TR) were detected among all QTLs. The epistasis between *qTR2-1* and *qTR8-1* was consistent in most environments. This present study may provide the understanding of the genetic basis of ERN and TR and a foundation for further fine-mapping of these common QTLs.

Keywords Maize · Ear row number · Two-ranked ear · Many-ranked ear · QTL

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Introduction

The growing population exerts great pressure on the achievement of further improvement in grain yield. Compared with other crops, maize (*Zea mays* L.) presents better ideal plant type in terms of the structure of the photosynthetic reaction and it plays a crucial role in securing the world's food supply. Therefore, the inheritance of grain yield of maize has been the focus of many studies by agricultural scientists and plant breeders (Collard and Mackill 2008). As a complex quantitative

trait, however, maize grain yield is influenced by many genetic and environmental factors due to its relatively low heritability (Beavis et al. 1994; Yan et al. 2006). As an important yield determinant, the ear row number (ERN) exhibited significantly positive correlation with the grain yield (Li et al. 2009; Lu et al. 2011; Sreckov et al. 2011). Meanwhile, the inheritance of ERN presented a significant additive effect and was less influenced by situational factors (Dofing et al. 1991; Leng 1963; Petrovic 1998). Thus, maize grain yield could be dissected into its several related components, and its genetic basis could be preliminarily explained by the effects of QTLs that control its components such as ERN.

Previously, maize \times teosinte populations including F_2 (Doebley 1992; Doebley and Stec 1991, 1993; Doebley et al. 1990; Edwards et al. 1987; Stuber et al. 1987), BC_1 (Briggs et al. 2007), TC_1 (Lauter and Doebley 2002) and nearly isogenic recombinant inbred lines (NIRILs) (Lemmon and Doebley 2014) were used for the detection of loci, which controlled the changes in ERN during early domestication. Among these studies, the most consistent result was that a certain region on the short segment of chromosome 2 of maize had a large effect on ERN. In addition, a continuous distribution of two-ranked versus many-ranked ears (TR) value was observed in segregating populations derived from maize to teosinte hybrids. TR was considered to be one of the key morphological traits that distinguish maize and teosinte ears (Doebley 2004). Langham (1940) firstly reported *tr1* gene controlling TR, which had a large effect on the TR (Doebley and Stec 1991). Nevertheless, several inconsistent results have been pointed out, namely regions of chromosomes 3, 5 and 6 also had strong effects on this trait (Rogers 1950; Szabó and Burr 1996). These results suggest that the accurate location of QTL for TR could be influenced by different measurements of TR, the lack of the limited number of linkage markers and the utilization of teosintes with different genetic background.

For decades, with the rapid development of molecular genetic marker technology and quantitative genetics, diverse maize populations have been used to detect QTLs for ERN, which contribute to maize diversification, such as F_2 (Yu et al. 2014), $F_{2:3}$ (Cai et al. 2014; Choe and Rocheford 2012; Karen Sabadin et al. 2008; Lu et al. 2011; Veldboom and Lee 1994; Yan et al. 2006), $F_{2:4}$ (Beavis et al. 1994), BC_1S_1

(Upadyayula et al. 2006), BC_2F_2 (Li et al. 2007, 2011), $BC_3F_{2:3}$, $BC_5F_{2:3}$ (Tian et al. 2014), IF_2 (Tang et al. 2010), CSSLs (Li et al. 2014a) and RILs (Austin and Lee 1996; Guo et al. 2008; Liu et al. 2010). To date, few consistent QTL having large effects on ERN have been detected across diverse populations or environments. One QTL explaining 41 % of ERN variation was mapped on chromosome 2 near marker *umc78* in a $F_{2:3}$ lines, which was derived from a single cross between Mo17 and H99 (Veldboom and Lee 1994). More recently, a total of 36 QTLs associated with ERN and 261 significant SNPs were observed by joint linkage and genome-wide association studies (GWAS) in a nest association mapping (NAM) population, consisting of 5000 RILs from 25 families that represented the global diversity of maize (Brown et al. 2011). While numerous QTLs controlling ERN have been identified on the whole genome of maize, only three or four genes have been determined through the use of maize mutants. The use of *mutator* (*Mu*) transposon insertions in the maize gene has suggested that the activity of *zfl2* may influence the ERN (Bombliès and Doebley 2006; Bombliès et al. 2003). A leucine-rich repeat receptor-like protein denoted *fea2* could increase the inflorescence meristems size (Taguchi-Shiobara et al. 2001) and enhance ERN of ~ 3 rows (Bommert et al. 2013). Maize *SBP-box* transcription factors genes *ub2* and *ub3* affected the ERN by regulating the rate of lateral primordia initiation (Chuck et al. 2014). The molecular mechanism underlying ERN variation has only been preliminarily determined, although its genetic basis has been well understood.

In this study, a RIL segregation population derived from B73 \times SICAU1212 was made to identify consistent QTL responsible for ERN and TR across different environments, detect the epistatic interaction for these traits and attempt to investigate the correlation between ERN and TR. This study could provide interesting information about the genetics underlying these traits.

Materials and methods

Plant materials and field experiments

A population of 325 $F_{6:7}$ RIL families was derived from a cross between inbred B73 and SICAU1212 (Fig. 1). SICAU1212 (two-ranked with two rows per rank) was derived from four-rowed waxy maize,

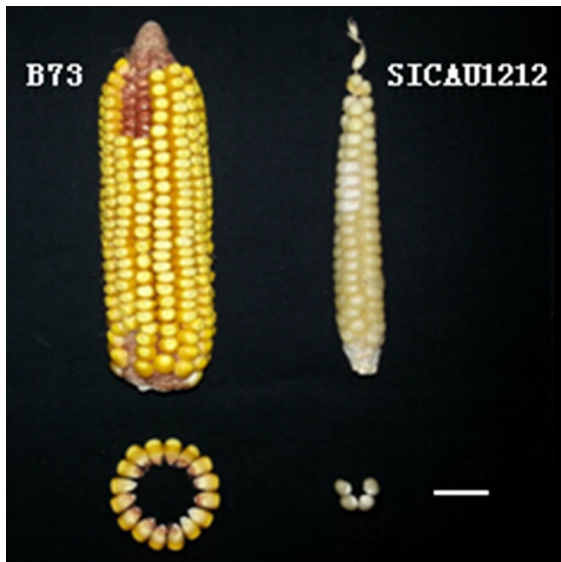


Fig. 1 Mature ear phenotypes illustration of B73 (*left*) and SICAU1212 plants (*right*), normal B73 ear (female inflorescence) with approximately 16 regular rows, a non-waxy and yellow kernel (endosperm) and a red cob (pericarp). The SICAU1212 plant often produces approximately four female inflorescences with approximately four rows, a waxy and white kernels and a white cob. In addition, the ear of SICAU1212 exhibits a barren patch devoid of kernels in the adaxial side of the ear. Scale bar 2 cm. (Color figure online)

silunuo, which was planted in Xishuangbanna, Yunnan Province of China, and subsequently self-pollinated for seven generations. Notably, *silunuo* with many primordial traits was considered as the progenitor of Chinese waxy corn (Tian et al. 2009).

The 325 RIL families used the single-seed descent and both parents were planted in a completely random design with two replications in three experimental stations located in Yunnan, Sichuan and Neimenggu Provinces of China, during 2012, 2013 and 2014, respectively. The abbreviations 12YN, 13YN, 14SC and 14NMG represented the following environments: Yunnan in 2012, Yunnan in 2013, Sichuan in 2014 and Neimenggu in 2014, respectively. Each RIL was grown in a single-row. Each row (approximately 14 plants) was 3.5 m in length with a space of 0.75 m between rows. Standard cultivation management practices and a density of 52,500 plants per ha were performed in each environment. After maturity, the ERN value in the middle point of ear was measured in individual ears (Taguchi-Shiobara et al. 2001). The ear of B73 exhibited many ranks of paired spikelets,

whereas that of SICAU1212 had two ranks of paired spikelets. Some RIL ears showed an intermediate phenotype (Fig. 2). The value of the TR (%) was calculated from the following formula:

$$\text{TR (\%)} = \text{FEL}/\text{EL} \times 100 \%$$

here, *FEL* is the length of ear with four rows, and *EL* is the whole ear length. The average ERN and TR value of ten plants from the middle of each row was utilized as the preliminary data in the analyses.

Phenotypic data analysis

Both the analyses of variance (ANOVA) and the Pearson phenotypic correlation coefficient between ERN and TR in each environment were performed using the SPSS19.0 software (<http://www.spss.com>). The variance components including genotype, environment, replication and interaction between genotype and environment of each trait were estimated by mixed model program. The broad-sense heritability (H^2) for each trait was estimated: $H^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{ge}^2 + \sigma_e^2 / m)$, where σ_g^2 is the genetic variance, σ_{ge}^2 is the interaction of the genotype with the environment, σ_e^2 is the error variance, r is the number of replications, and n is the number of environments (Hallauer and Miranda 1988). As described by Knapp et al. (1985), the 90 % confidence intervals (CI) for H^2 were calculated.

Genetic linkage maps

Genomic DNA was extracted and purified using the modified CTAB procedure from the fresh leaf tissue of the parental lines and 325 RIL families' plants (Saghai-Marouf et al. 1984). A total of 910 SSR probes chosen from the maize genome database (<http://www.maizegdb.org/>) were used for screening the parental lines. Of which, 107 SSR markers were finally employed to genotype the 325 RIL families. Meanwhile, 334 insertion/deletion polymorphism (Indel) markers developed by our laboratory were used to cover more of the bins within the maize genome. One hundred sixty-six of the Indel markers were added to the identification of genotype of the entire RIL families (Supplementary Fig. S1; Table S1). The 325 RIL families were eventually genotyped by 273 markers consisting of 107 SSRs markers and 166 Indels. All PCR products were electrophoresed on 6 % denaturing polyacrylamide gels and stained with approximately 0.33 % silver nitrate (Santos



Fig. 2 Ears exhibit the two-ranked versus many-ranked (TR). From *left to right*, the numbers 4/6, 4/8, 4/10, 4/12, 4/14 indicate that the TR value are 65.5, 52.8, 42.0, 44.2, 50.0, 37.5 and

48.3 %, respectively; The transition points are indicated by *arrows*. (Color figure online)

et al. 1993). The linkage map was developed using Mapmaker/EXP (version 3.0b) with a linkage group at a minimal logarithm of odds (LOD) threshold of 3.00 and a maximum distance between two loci of 50 cM (Lincoln 1992). The result showed that the total length of the molecular linkage map was 1395.4 cM across the maize genome with average intervals between adjacent markers of 5.11 cM. The genomic analysis revealed that the RIL was approximately 96.05 % homozygous and 50.24 % of B73-allele. In the genetic linkage map, the orders of most molecular markers were consistent with those of their physical position. However, two exceptions were observed in this study: the Indel marker chr7-10777 was located at bin 3.07 rather than at bin 7.01 and chr4-84108 was located in bin 9.04 rather than in bin 4.05.

QTL identification

The identification of QTL for each trait in single environment was performed by the QTL IciMapping software version 3.0 (Li et al. 2008). The additive and dominant effects (ICIM-ADD) mapping method in ICIM was employed to identify QTL through stepwise regression with 1000 permutations and a walk speed of 2 cM. The CI of the QTL were estimated: $CI = 163/N \times R^2$. Here, N is the population size, and R^2 is the value of the phenotypic variation contributed by the QTL (Darvasi and Soller 1997; Qi et al. 2011). If the LOD confidence

interval of two QTLs overlapped, the corresponding QTLs were assumed to be the same one in this study. Additionally, the joint QTL, the epistatic QTL in a single environment and QTL environment interaction based on the multi-environment phenotypic values were identified by the QTL Network software version 2.0 with mixed liner model based on composite interval mapping approach (MCIM) (Yang et al. 2007). Testing window, walk speed and filtration window of genome scan were set at 10, 2 and 10 cM, respectively. The LOD threshold scores for significant QTL were obtained with a permutation test of 1000 cycles (Churchill and Doerge 1994). The letter ‘J’ was labeled into the middle of this QTL name while one QTL was only detected in joint analysis with MCIM but not in single environment through ICIM-ADD program. In the present report, if QTLs for different traits were detected within the same marker interval or their confidence intervals overlapped, the corresponding loci were assumed to be the one common QTL or QTL with pleiotropic effects.

Results

Phenotypic analysis

Compared with the ERN of B73 (16.31–17.80 rows), that of SICAU1212 presented lower value (four rows). In contrast with the ERN value of SICAU1212, its TR

value (92.8–100.0 %) was always higher than that of B73 (0.0 %). In addition, B73 and SICAU1212 exhibited highly significant differences in ERN and TR, regardless of the environment (Table 1). Among the RIL families, the distributions of the numbers of ERN were approximately normal, and there were wide variations in four environments (Fig. 3), which was noteworthy that the ERN values basically presented obvious unidirectional transgressive segregation in each environment, indicating polygenic quantitative genetic control. A negative exponential distribution of TR was found in each environment (Fig. 3), seemed to indicate a potential for several major genes or oligogene influencing this phenotype (Zhou et al. 2014). The genotypic variance components (σ_g^2) were highly significant for ERN and TR based on the ANOVA analysis, indicating the existences of significant genetic variability in RILs (Table 2). The variance of the genotype \times environment interactions (σ_{ge}^2), the environmental variance and the variance of replications (environment) were highly significant. The broad-sense heritabilities (H^2) of ERN and TR were estimated to be 89.46 and 92.92 %, respectively. The relatively high heritability indicated that genetic factors controlled much of the phenotypic variance. The analyses of Pearson correlation coefficient showed that the ERN significantly correlated with each other ($r = 0.781\text{--}0.931$) measured in different environments, as well as TR ($r = 0.847\text{--}0.928$) (Table 3). Notably, highly negative phenotypic correlations between ERN and TR were observed in four environments ($r = -0.596$ to -0.799), suggesting that

there was a potential for simultaneous improvements in ERN and TR.

Identification of QTLs for ERN and TR

A total of 12 QTLs located on chromosomes 1, 2, 4, 5, 8 and 10 were associated with ERN through single-environment mapping (Table 4; Fig. 4). Each QTL accounted for 2.33–21.28 % of phenotypic variation with *qERN8-1* contributing the highest percentage in any environment. The total phenotypic variation explained by all identified QTLs ranged from 40.03 to 48.30 %. Five of the 12 QTLs were detected across three environments, and the other seven QTLs were location-specific QTLs. Notably, three of the five QTLs, *qERN2-1*, *qERN8-1* and *qERN8-2*, were consistently identified in each environment, and the ERN variation explained by them ranged from 24.92 % for 13YN to 37.36 % for 12YN. In addition, the positive alleles of all the 12 QTLs indicated that B73 had a positive effect on increasing the ERN.

Eight putative QTLs for TR were observed in the present study and located on chromosome 1, 2, 3, 4, 6 and 8. The phenotypic variation explained by individual QTL ranged from 2.09 (*qTR4-1*) to 12.99 % (*qTR8-1*). Together, those detected QTLs explained 23.57–33.78 % of TR variation across different environments. Among them, five QTLs were repeatedly identified in multiple environments, and the rest QTLs were environment-specific. The negative additive effect of all QTLs indicated that alleles came from

Table 1 Phenotypic performance of the two traits for two parents and in the RIL population

Trait	Environment	Parent		Population				
		B73 \pm SE ^a	SICAU1212 \pm SE	Range	Average \pm SE	CV (%)	Skewness	Kurtosis
ERN	12YN	16.31 \pm 0.29	4.00 \pm 0.00**	4.00–15.83	9.80 \pm 0.13	0.24	–0.28	–0.72
	13YN	17.18 \pm 0.27	4.00 \pm 0.00**	6.00–15.89	10.66 \pm 0.11	0.18	–0.11	–0.86
	14SC	16.80 \pm 0.53	4.00 \pm 0.00**	4.33–17.33	10.54 \pm 0.13	0.23	–0.18	–0.27
	14NMG	17.80 \pm 0.47	4.00 \pm 0.00**	4.33–19.17	11.08 \pm 0.16	0.26	–0.13	–0.28
TR (%)	12YN	0.0 \pm 0.0 %	100.0 \pm 0.0 %**	0.0–100.0 %	15.1 \pm 1.2 %	1.43	1.51	1.88
	13YN	0.0 \pm 0.0 %	92.8 \pm 3.7 %**	0.0–90.0 %	11.8 \pm 0.9 %	1.46	1.66	2.78
	14SC	0.0 \pm 0.0 %	100.0 \pm 0.0 %**	0.0–79.8 %	10.9 \pm 0.9 %	1.58	1.70	2.26
	14NMG	0.0 \pm 0.0 %	100.0 \pm 0.0 %**	0.0–77.5 %	13.0 \pm 1.1 %	1.46	1.50	1.48

The abbreviations 12YN, 13YN, 14SC and 14NMG represent the following environments: Yunnan in 2012, Yunnan in 2013, Sichuan in 2014 and Neimenggu in 2014, respectively

^a The numbers are the mean values with standard errors (SE)

** Difference between two parents is highly significant at the $P < 0.01$ level, as determined by a *t* test

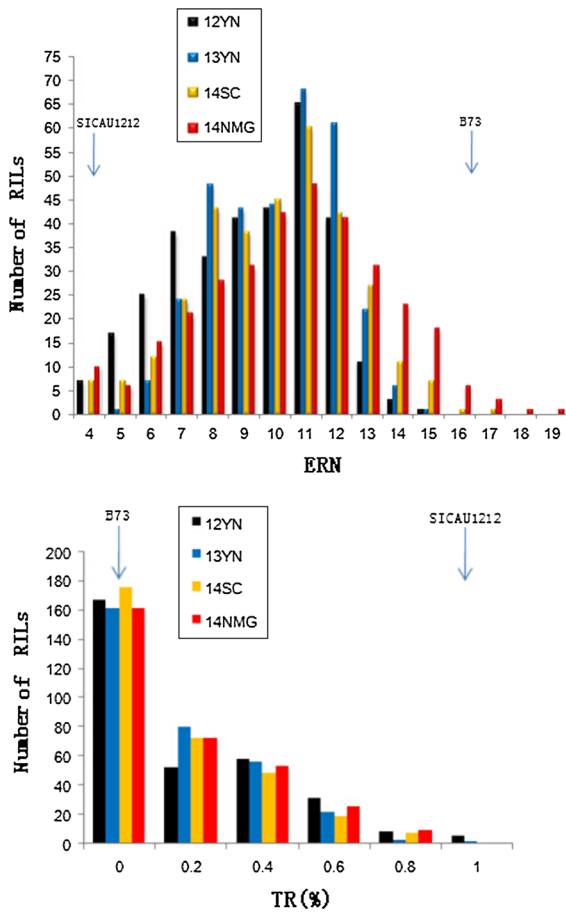


Fig. 3 Distributions of the two traits value in RIL derived from B73-SICAU1212hybrids among four environments. The trait values for B73 and SICAU1212 were indicated by arrows. 12YN, 13YN, 14SC and 14NMG represented Yunnan in 2012, Yunnan in 2013, Sichuan in 2014 and Neimenggu in 2014, respectively. (Color figure online)

SICAU1212 except one location-specific QTL, *qTR3-1*. Interestingly, two of the five QTLs (*qTR8-1* and *qTR8-2*) basically had stronger effects on TR,

Table 3 Pearson correlation (*r*) coefficient between the ERN and TR across four environments

Trait	Environment	TR	12YN	13YN	14SC
ERN	13YN		0.831**		
	14SC		0.839**	0.784**	
	14NMG		0.842**	0.781**	0.931**
TR	13YN		0.898**		
	14SC		0.847**	0.900**	
	14NMG		0.878**	0.910**	0.928**
ERN	12YN	-0.799**			
	13YN	-0.596**			
	14SC	-0.716**			
	14NMG	-0.722**			

The abbreviations 12YN, 13YN, 14SC, and 14NMG represent Yunnan in 2012, Yunnan in 2013, Sichuan in 2014 and Neimenggu in 2014, respectively

** Highly significant difference at the $P < 0.01$ level

regardless of the environment. Remarkably, one QTL, *qTR2-1* mapped in the same marker interval chr2-zf12–chr2-13000, was associated with the TR across all environments explaining 4.27–4.92 % of the phenotypic variation. It was noteworthy that these three QTLs and two location-specific QTLs (*qTR1-2* and *qTR4-1*) were detected in the same map position with QTLs for the ERN. In a word, five common QTLs, located within chr1-90229–chr1-100909, chr2-zf12–chr2-13000, chr4-203129–chr4-213371, chr8-18426–chr8-19676 and chr8-103366–chr8-111393, may simultaneously control ERN and TR.

The joint QTL and QTL environment interaction

Thirteen and ten significant QTLs were mapped for ERN and TR by joint analysis, respectively (Supplementary Table S2). Ten of the 13 and four of the ten

Table 2 Analysis of variance (ANOVA) for ERN and TR of the RILs in four environments

Trait	Variation	<i>F</i>	<i>H</i> ²	90 % Confidence interval
ERN	Environment	41.252**	89.46	87.72–90.95
	Replication (Environment)	5.711**		
	Genotype	18.811**		
	Genotype × Environment	2.730**		
TR	Environment	7.281*	92.92	91.75–93.92
	Replication (Environment)	8.450**		
	Genotype	30.570**		
	Genotype × Environment	2.397**		

*H*² indicates the Broad-sense heritability
 *, ** Significant differences at $P < 0.05$ and $P < 0.01$ level, respectively

Table 4 QTLs detected for the ERN and TR across multiple-environments

Trait	Environment	QTL	Chromosome	Position (cM)	Left marker	Right marker	LOD	Est A ^a	PVE (%) ^b	
ERN	12YN	<i>q12yERN1-2</i>	1	86.0	chr1-90229	chr1-100909	3.88	0.37	2.41	
		<i>q12yERN2-1</i>	2	40.0	chr2-13401	bnlg125	12.23	0.66	7.96	
		<i>q12yERN4-3</i>	4	122.0	chr4-CLV1	chr4-227109	8.83	0.59	6.20	
		<i>q12yERN5-1</i>	5	74.0	chr5-168871	umc1687	3.48	0.36	2.33	
		<i>q12yERN8-1</i>	8	30.0	chr8-18426	chr8-19676	27.02	1.08	21.28	
		<i>q12yERN8-2</i>	8	54.0	chr8-103366	chr8-111393	12.81	0.67	8.12	
	13YN	<i>q13yERN2-1</i>	2	36.0	chr2-11948	chr2-zfl2	8.49	0.50	6.92	
		<i>q13yERN2-2</i>	2	70.0	umc1448	bnlg1018	3.23	0.31	2.61	
		<i>q13yERN4-3</i>	4	122.0	chr4-CLV1	chr4-227109	12.14	0.62	10.41	
		<i>q13yERN5-1</i>	5	66.0	chr5-139354	chr5-160457	3.05	0.31	2.57	
		<i>q13yERN8-1</i>	8	30.0	chr8-18426	chr8-19676	14.41	0.67	12.34	
		<i>q13yERN8-2</i>	8	52.0	chr8-97475	chr8-103366	7.28	0.46	5.66	
	14SC	<i>q14sERN2-1</i>	2	34.0	chr2-11541	chr2-11948	9.84	0.63	6.86	
		<i>q14sERN2-4</i>	2	120.0	bnlg1721	bnlg1520	3.23	0.49	4.12	
		<i>q14sERN4-1</i>	4	10.0	umc2148	phi213984	3.10	0.42	2.95	
		<i>q14sERN4-2</i>	4	114.0	chr4-213371	chr4-223017	9.32	0.64	7.00	
		<i>q14sERN5-1</i>	5	76.0	chr5-168871	umc1687	5.07	0.50	4.22	
		<i>q14sERN8-1</i>	8	30.0	chr8-18426	chr8-19676	18.46	0.98	16.39	
	14NMG	<i>q14nERN2-1</i>	2	36.0	chr2-11948	chr2-zfl2	6.64	0.64	4.84	
		<i>q14nERN2-3</i>	2	88.0	umc1080	chr2-180662	4.04	0.51	2.99	
		<i>q14nERN4-3</i>	4	122.0	chr4-CLV1	chr4-227109	11.36	0.86	8.66	
		<i>q14nERN8-1</i>	8	24.0	chr8-16745	chr8-17389	16.77	1.06	13.39	
		<i>q14nERN8-2</i>	8	54.0	chr8-103366	chr8-111393	10.23	0.79	7.29	
		<i>q14nERN10-1</i>	10	26.0	chr10-77445	umc1336	3.88	0.49	2.86	
	TR	12YN	<i>q12yTR1-2</i>	1	85.0	chr1-90229	chr1-100909	4.37	-0.04	3.74
			<i>q12yTR2-1</i>	2	37.0	chr2-zfl2	chr2-13000	5.02	-0.05	4.27
			<i>q12yTR4-2</i>	4	113.0	chr4-203129	chr4-213371	2.56	-0.03	2.09
			<i>q12yTR8-1</i>	8	24.0	chr8-16745	chr8-17389	14.29	-0.08	12.99
<i>q12yTR8-2</i>			8	55.0	chr8-103366	chr8-111393	12.73	-0.07	10.69	
<i>q13yTR1-1</i>			1	67.0	chr-P1	chr1-51322	3.45	-0.03	3.64	
13YN		<i>q13yTR2-1</i>	2	37.0	chr2-zfl2	chr2-13000	4.93	-0.04	4.92	
		<i>q13yTR3-1</i>	3	20.0	umc2258	umc1495	3.17	0.03	3.23	
		<i>q13yTR8-1</i>	8	29.0	chr8-18426	chr8-19676	11.79	-0.05	7.01	
		<i>q13yTR8-2</i>	8	58.0	chr8-120059	umc1309	7.31	-0.04	4.77	
		<i>q14sTR2-1</i>	2	37.0	chr2-zfl2	chr2-13000	4.78	-0.04	4.77	
		<i>q14sTR6-1</i>	6	64.0	chr6-120914	umc2055	2.51	-0.03	2.81	
14SC		<i>q14sTR8-1</i>	8	24.0	chr8-16745	chr8-17389	8.00	-0.05	8.46	
		<i>q14sTR8-2</i>	8	55.0	chr8-103366	chr8-111393	11.74	-0.06	11.70	
		14NMG	<i>q14nTR1-1</i>	1	65.0	chr1-P1	chr1-51322	2.66	-0.03	2.57
			<i>q14nTR2-1</i>	2	37.0	chr2-zfl2	chr2-13000	4.76	-0.04	4.56

Table 4 continued

Trait	Environment	QTL	Chromosome	Position (cM)	Left marker	Right marker	LOD	Est A ^a	PVE (%) ^b
		<i>q14nTR6-1</i>	6	64.0	chr6-120914	umc2055	2.64	−0.03	2.79
		<i>q14nTR8-1</i>	8	29.0	chr8-18426	chr8-19676	11.16	−0.07	11.96
		<i>q14nTR8-2</i>	8	55.0	chr8-103366	chr8-111393	10.50	−0.06	9.87

The abbreviations 12YN, 13YN, 14SC and 14NMG represent Yunnan in 2012, Yunnan in 2013, Sichuan in 2014 and Neimenggu in 2014, respectively

^a A, additive effect of the QTL for ERN: positive values indicate that the alleles from B73 increased the trait score; on the contrary, additive effect of the QTL for TR: negative values indicate that the alleles from SICAU1212 increased the trait score

^b PVE, percent of the phenotypic variations explained by each QTL

QTLs were consistent with those of ERN and TR through single environment mapping, respectively. Each significant ERN QTL with additive effect explained from 0.01 to 0.27 of phenotypic variance. For TR, the phenotypic variance contributed by individual QTL with additive effect varied between 0.001 and 0.24. The total phenotypic variances of ERN and TR explained by respective QTLs were the same (0.87). Only one QTL, *qERN8-1*, was involved in significant QTL × environment interaction and represented additive by environment interaction effect in this study. And 0.71 % of the heritability was accounted for by this QTL.

Epistatic interaction among identified QTLs

A total of nine pairs of significant epistatic interactions (two for ERN and seven for TR) were detected with additive by additive interaction among all the four environments (Table 5). These involved 12 QTLs dispersed on chromosomes 1, 2, 3 and 8. Eight of 9 epistatic interactions existed within significant QTLs detected by joint analysis, while the rest occurred between a significant QTL and a non-significant QTL located on chromosome 2. The epistatic interaction between *qTR3-1* and *qTR-J8-(3)* detected in 13YN explained the largest heritability of the additive by additive epistatic interaction and had the decreasing effect on TR. One epistatic interaction between *qTR2-1* and *qTR8-1* was repeatedly identified in all environments with the exception of 12YN, indicating that this epistasis consistently affected the genetic basis of TR. In addition, two genomic regions simultaneously influencing ERN and TR within chr2-zf2–chr2-13000 and chr8-16745–chr8-18426, were identified as involved in five and four epistasis, respectively.

Although several epistasis were detected for the two traits, their effects were all less lower than those of the corresponding QTLs, indicating that the main effect of significant QTL may have stronger effect on ERN and TR.

Discussion

The domestication process from teosinte to maize may be influenced by three major mutations. The first mutation was that the glumes of teosinte kernels changed from hardened to softening, which could increase the accessibility of kernels for harvest (or liberation); the second was that the pedicellate spikelets did not abort early in development; and the third was that the value of ERN varied from four to more (Iltis 2000). The occurrence of two-ranked specimens supported the above mentioned hypothesis (Benz 2001). After domestication, wild four-rowed maize with two ranks was the extreme case, whereas modern maize forms approximately 8–20 rows with many ranks. A four-rowed maize material *P4* derived from an eight-rowed variety was made to analysis the inheritance of the ERN in maize (Daniel 1963). Interestingly, SICAU1212 exhibited two ranks with two rows per rank (Fig. 1), and its progenitor, *silunuo*, had many primordial traits similar to teosinte (two ranks with one rows per rank) (Zeng et al. 1981). Some studies showed that the alleles that increase the ERN originated equally from both parents (Li et al. 2007, 2011; Upadyayula et al. 2006; Veldboom and Lee 1994), on the contrary, any decreasing effects of QTLs on the ERN were attributed to the parent (SICAU1212) with the lower ERN in this study, which agrees with the findings obtained from

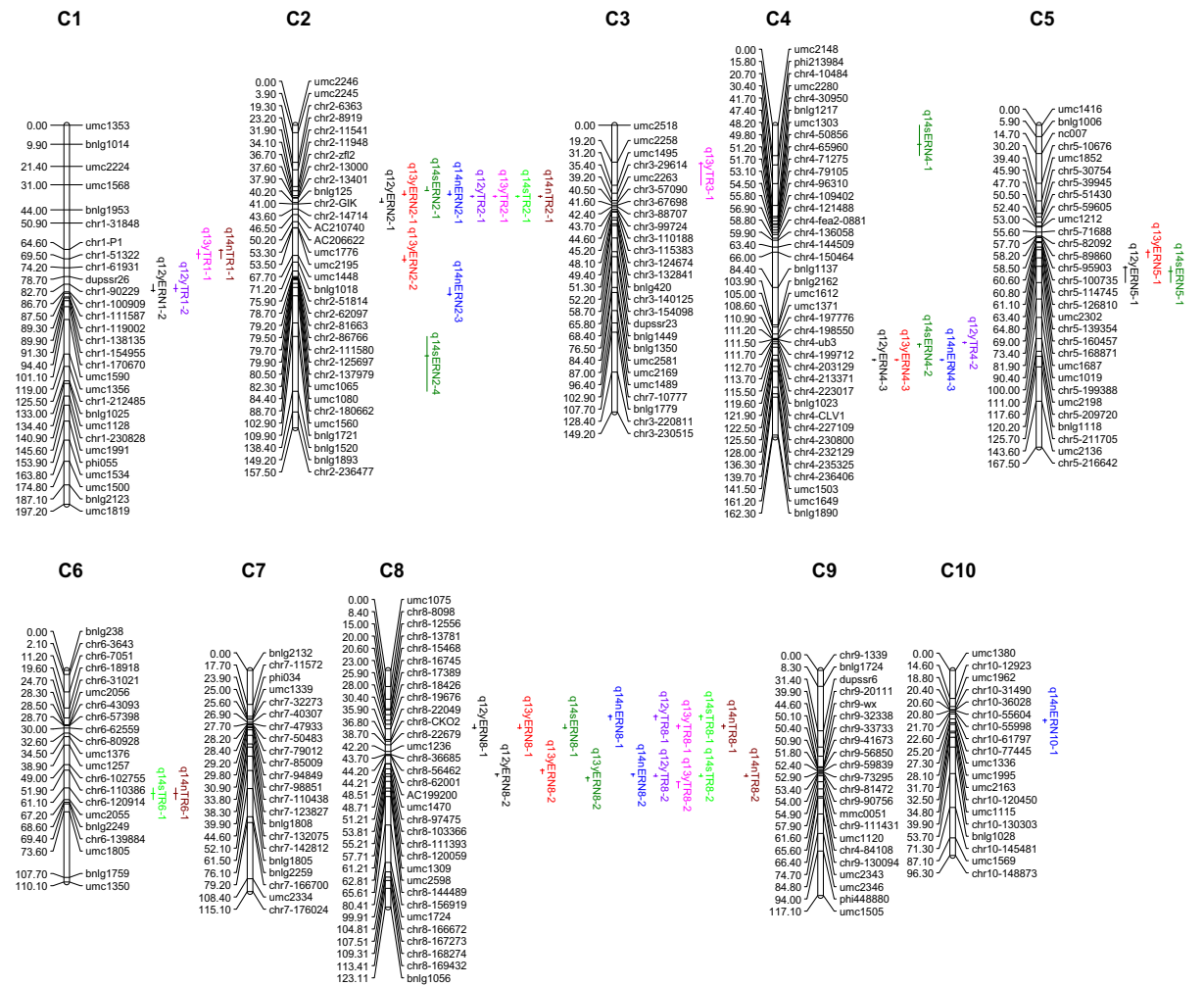


Fig. 4 Molecular linkage map of RIL and locations of QTL for ERN and TR across multiple environments. The letter ‘C’ means chromosome. The QTLs for each trait in each environment are differentiated by lines with different colors. The traits attached environments represent the QTLs detected in Yunnan

maize × teosinte segregating populations (Briggs et al. 2007; Doebley and Stec 1991, 1993) and those from a part of maize × maize segregations (Cai et al. 2014; Tian et al. 2014; Yu et al. 2014). One possible reason elucidating the above phenomenon is that there is not more variation on ERN within modern maize germplasms, namely due to limited variation in the ERN. The missing genetic variation from 4 to more rows could not be determined, although MT-6 with an ERN of six was crossed with B73 to produce different populations (Cai et al. 2014). Thus, SICAU1212 × B73 population made to detect the

in 2012, Yunnan in 2013, Sichuan in 2014, Neimenggu in 2014, respectively. The linkage map was produced by the Mapchart 2.2 software (<http://www.wageningenur.nl/en/show/Mapchart.htm>). (Color figure online)

QTL for ERN and TR could increase the phenotypic difference between the parents, further gain some genetic basis underlying ERN during maize subsequent improvement and provide some effective information about the TR inheritance in maize.

Genetic architectures of ERN and TR

Segregations between maize and teosinte were made to identify ERN QTL associated with domestication, while diverse maize populations were suitable for detection of QTL affecting diversification. The first

Table 5 QTL with epistatic effects identified in different environments

Trait	Environment	QTL_i	Interval_i	QTL_j	Interval_j	AA ^b	H ² (aa) ^c
ERN	13YN	<i>non-chr2</i> ^a	umc1590-umc1356	<i>qERN2-1</i>	chr2-GIK-chr2-14714	0.216 [*]	0.0086
	13YN	<i>qERN8-1</i>	chr8-18426-chr8-19676	<i>qERN8-2</i>	chr8-111393-chr8-120059	-0.223 ^{**}	0.0090
TR	12YN	<i>qTR1-2</i>	chr1-90229-chr1-100909	<i>qTR8-2</i>	chr8-120059-umc1309	0.029 ^{**}	0.0195
	12YN	<i>qTR2-1</i>	chr2-13401-bnlg125	<i>qTR-J8-(2)</i>	chr8-22679-umc1236	0.039 ^{**}	0.0325
	13YN	<i>qTR1-1</i>	chr1-P1-chr1-51322	<i>qTR-J8-(3)</i>	chr8-144489-chr8-156919	0.025 ^{**}	0.0135
	13YN	<i>qTR2-1</i>	chr2-13401-bnlg125	<i>qTR8-1</i>	chr8-15468-chr8-16745	0.023 ^{**}	0.0243
	13YN	<i>qTR3-1</i>	bnlg1449-bnlg1350	<i>qTR-J8-(3)</i>	chr8-144489-chr8-156919	-0.042 ^{**}	0.0456
	14SC	<i>qTR2-1</i>	chr2-13401-bnlg125	<i>qTR8-1</i>	chr8-15468-chr8-16745	0.028 ^{**}	0.0232
	14NMG	<i>qTR2-1</i>	chr2-13401-bnlg125	<i>qTR8-1</i>	chr8-15468-chr8-16745	0.0275 ^{**}	0.0190

The abbreviations 12YN, 13YN, 14SC and 14NMG represent Yunnan in 2012, Yunnan in 2013, Sichuan in 2014 and Neimenggu in 2014, respectively

^a *non-chr2*, was not a significant QTL on chromosome 2, but associated with epistatic interaction

^b AA, the estimated additive by additive epistatic interaction effect

^c H²(aa), the heritability of additive by additive epistatic interaction effect

^{*}, ^{**} Significant differences at $P < 0.05$ and $P < 0.01$ level, respectively

consistent QTL in this study, *qERN2-1*, was also located on bin 2.02. Multiple studies have shown that this region on the short arm of chromosome 2 had a large effect on ERN (Cai et al. 2014; Doebley and Stec 1991, 1993; Karen Sabadin et al. 2008), indicating a potential QTL region near *qERN2-1* may play a novel role in both maize domestication and later improvement processes. Both the second and third consistent QTLs (*qERN8-1* at bin 8.02 and *qERN8-2* at bin 8.04) were located on chromosome 8. The former QTL was differentiated from the latter one by having larger effect on ERN. Previous reports of QTL for ERN identified in the two genomic regions in other maize populations were rather sparse. Briggs et al. (2007) reported that a chromosomal region near *qERN8-1* influenced ERN in a large BC₁ population derived from maize and teosinte. One minor QTL near *qERN8-2* explaining 6 % of ERN variation has been identified (Doebley 1992; Doebley et al. 1990). These implied that *qERN8-1* and *qERN8-2* may be domestication-related QTLs those control the initial switch from four to more rows of kernel.

In addition to the three consistent QTLs, other two QTLs (*qERN4-3* at bin 4.08 and *qERN5-1* at bin 5.04) identified in only three environments also influenced the genetic architecture of ERN. An interesting case is the QTL detected on bin 4.08, which has been repeatedly reported to significantly affect ERN (Austin and Lee 1996; Li et al. 2014a; Veldboom

and Lee 1994, 1996; Yan et al. 2006) and also contained QTLs for other agronomic traits, such as grain yield (Lu et al. 2006), tassel branch number (Chuck et al. 2014), ear diameter (Li et al. 2011), kernel number per row (Lu et al. 2011), kernel weight, width and thickness (Liu et al. 2014). Therefore, bin 4.08 is noteworthy for genetic improvement of morphological traits in maize. Similarly, region near *qERN5-1* was also frequently reported to be involved in the QTL for ERN in diverse populations (Li et al. 2007, 2009; Szabó and Burr 1996; Tian et al. 2014). By 259 highly homozygous NIRILs, one QTL accounting for 53.4 % of ERN variation was mapped to approximately 168 Mb (physical position) on chromosome 5 (Lemmon and Doebley 2014). Collectively, there are high probabilities that genes underlying ERN variation change exist in the five regions. High-density SNP arrays and DNA re-sequencing have supplied more comprehensive information of the genotypes of plants and animals. GWAS aims to detect variants at candidate loci or genes for traits. Notably, eight of the 12 QTLs for ERN detected in single environment in our study had the coincident marker intervals with those of GWAS (physical distance of two <10 Mb) (Brown et al. 2011). It seems that the location of QTL for ERN in this study had a high reliability.

Recently, K10HEX206 with four rows also derived from *silunuo* has been employed to dissect the genetic

improvement of ERN (Jiao et al. 2014). Of the 12 QTLs identified by them in 210 $F_{2,3}$ families genotyped by 173 molecular markers, only six QTLs exhibited coincidence with those of the present study, possibly due to the different genetic background, population size and marker densities. On the one hand, RIL raised the recombinant frequency between linked loci and presented the stronger power for the identification of QTL compared with the F_2 population (Cowen 1988). On the other hand, the lack of a moderate segregation population size affected the consistency of QTL detection (Melchinger et al. 1998) and estimates of the allelic richness similarly (Kalinowski 2004, 2005).

As noted earlier, TR was considered to be one key trait distinguishing maize and teosinte (Doebley 2004). In an overview of QTL distribution in the previous reports (Doebley and Stec 1991; Doebley et al. 1990; Langham 1940; Mangelsdorf 1947; Rogers 1950; Szabó and Burr 1996), QTL for TR were located on all chromosomes with the exception of chromosome 7. In this study, QTLs involved in inheritance of TR were identified on all chromosomes except for chromosomes 7, 9 and 10 based on the results of single environment mapping and joint analysis. A QTL region (or *tr1* gene) with the strongest on the segment of 2S has been detected for this trait (Doebley and Stec 1991), which was consistent with our finding that a region near marker chr2-zfl2 showed stable association with TR. However, our results revealed that the QTL with strongest effect on TR was located on chromosome 8 not 2, which also disagreed with those of previous studies (Doebley 1992; Doebley and Stec 1993).

Several explanations may be advanced to account for the discrepancies between the above researches. The first concerned the different measurement of TR prior to the analysis of its inheritance. Some researchers performed similar Mendelian analyses, with exploring its inheritance by fitting quantitative variants into discrete categories and omitting the mixed ranks (two-ranked on the top whereas many-ranked on the basal). However, mixed phenotype occurred not only in natural maize-teosinte hybrids but also in ears of a high-altitude Toluca teosinte (Orr et al. 2002). We also have attempted to make two- (the TR value $\geq 25\%$) versus many-ranked (the TR value $< 25\%$) ears approach an approximately 1:3 ratio. The result showed that four QTLs (*qTR1-1*,

qTR2-1, *qTR8-1* and *qTR8-2*) had significant associations with the inheritance of TR during four environments (Supplementary table S3), indicating that the inheritance of TR was always controlled by polygenic model, whichever phenotypic measurement was performed, which agreed with Iltis' views (1983), namely the inheritance of the morphological differences between maize and teosinte was polygenic. Additionally, the lack of the limited number of linkage markers influenced the power of QTL identification. Most investigators used few morphological markers per chromosome, resulting in a part of genomic region may not be adequately covered. The probability of getting false positive would also rise while a relatively larger number of markers genotyped a small number of individuals (Szabó and Burr 1996). These possibilities were minimized as the interval between any two markers in one chromosome was approximately 10 Mb in the present report. Thirdly, genetic background (SICAU1212) used to study the inheritance of TR in this study was quite different from those of the previous researches (teosinte used). As mentioned earlier, the progenitor of SICAU1212, *silunuo*, exhibited many primordial traits similar to teosinte (Zeng et al. 1981), and it might be derived from normal maize under special ecological environments (Tian et al. 2009), but two key issues are (1) SICAU1212 is not really a teosinte; (2) whether the molecular mechanism underlying the TR was the same under different genetic backgrounds? Thus, we used SICAU1212 as a parent so that we could detect the TR loci or genes involved in maize improvement rather than those associated with maize domestication. In conclusion, QTL region on chromosome 2 seems to mainly contribute to TR during domestication, whereas QTL region on chromosome 8 seems to be mainly responsible for lateral improvement steps.

Epistasis between QTL

Epistasis, or interactions between genes may play important roles in understanding the genetic basis of complex quantitative traits (Phillips 2008). In this study, the total phenotypic variation explained by all significant QTLs was always less than the broad-sense heritability, regardless of the trait and environment, indicating that the missing proportion of phenotypic variation may be partly explained by epistasis (Carlberg and Haley 2004). For ERN, two pairs of

significant epistatic interactions have been detected in our report, mostly among significant QTLs, indicating that the inheritance of ERN was controlled by few major genes plus several minor genes and epistatic effects. Similar results were previously observed (Li et al. 2009; Yan et al. 2006). Notably, one stable epistasis involved in region near *qERN2-1* has been found in different environments (Cai et al. 2014). More recently, Sa et al. (2015) showed that genetic interactions involved in regions near *qERN8-1* or *qERN8-2* were associated with ear height, stem thickness or grain yield. Additionally, one pair of epistatic interaction involved in region near *qERN8-2* controlling kernel length was reported by Zhang et al. (2014). Therefore, the three QTL regions may be considered as epistatic regulators, which act on the development of maize.

Although dozens of QTLs controlling TR have been detected in diverse maize-teosinte hybrids, no epistasis for this trait has been reported. One stable epistatic interaction (*qTR2-1/qTR8-1*) was identified in our study. It was noteworthy that *qTR2-1* has *tr1* gene as flanking marker. Similar to a strong epistatic effect between *teosinte branched1 (tb1)* and one QTL on chromosome arm 3L occurred, other epistasis for other key traits controlling the evolution of maize could exist. These epistatic interactions may indirectly affect the developmental processes (Doebley 2004). Thus, the cryptic region near *qTR8-1* or *qERN8-1* may arouse more experts' interest.

Mutant genes and the formation of the ERN and TR

The ERN is considered one of the key traits selected by humans during maize domestication and an obviously unique characteristic of maize ear development. If one QTL region related with certain trait contained or was adjacent to a known mutant gene, which was the only candidate gene affecting the development of this trait, the mutant gene may be regarded as a logical candidate gene (Robertson 1985; Upadyayula et al. 2006).

In the present study, one stable QTL (*qERN8-1*) near 18 Mb (based on the AGI's B73 RefGen_v2 sequence) simultaneously influenced the ERN and TR. Two mutant genes (*vt2* and *bif1*) mapped to approximately 17 and 22 Mb on chromosome 8, respectively, are possible candidate genes in this region. The

vt2 mutant ear typically had barren patches on one or both sides of the ear (Phillips et al. 2011) and this phenotype was similar to that of SICAU1212 (Fig. 1). The mutant gene *bif1* played a role in auxin transport and may make ear exhibit an intermediate (two/more-ranked) ear (phyllotaxy), similar to the characteristic of TR (Barazesh and McSteen 2008). Another QTL (*qERN2-1*) on chromosome 2S responsible for both ERN and TR has *zfl2* gene as flanking marker. The *zfl2* gene was not only contributed to changes in ERN during maize domestication but also associated with further improvement of ERN during the diversification stage (Bomblies and Doebley 2006; Bomblies et al. 2003; Doebley 2004). Maize *SBP-box* transcription factor gene, *ub3*, which affected the rate of cell differentiation to the lateral domains of meristems and directly influenced yield (Chuck et al. 2014), was located approximately 199 Mb on chromosome 4 near the QTL *qERN4-3*. One environment-specific QTL for ERN, *qERN4-1*, located approximately 4 Mb on chromosome 4 contain *sos1* gene. *Sos1* caused a reduction in the number of tassel branch and ERN (Doebley et al. 1995). *Ramosal enhancer locus2 (rel2)* was co-localized with another location-specific QTL (*qERN10-1*). *Rel2* physically interacted with *ramosa1*, resulting in the determinacy of spikelet-pair meristems (Gallavotti et al. 2010). Many of the mutant genes affecting ear development have not yet been mapped across B73 × SICAU1212 segregation. One reason for this lack may be that these genes do not control the ERN diversity between B73 and SICAU1212. Further studies are needed to determine whether these candidate genes are the causal genetic variants for these QTLs.

Common QTL

The ultimate objective of mapping the QTL for certain trait is to dissect the molecular and genetic basis of its variation. Meanwhile, the identification and confirmation of QTL that simultaneously influences several agronomic traits (common QTL or QTL with pleiotropic effect) could offer greater opportunities for plant breeding. For example, gene controlling grain chalkiness in rice, *Ckalk5* (Li et al. 2014b), was located within the region simultaneously associated with grain width and length–width ratio in an earlier report (Tan et al. 2000); *GS3* in rice, which was regarded as a major QTL for grain length, weight,

width and thickness (Fan et al. 2006), could vary grain size by modifying four putative domains (Mao et al. 2010); in maize, one QTL on chromosome 10 that had pleiotropic effect on kernel number per row (KN), ERN and ear diameter in high and low phosphorus treatments has been fine mapping for KN (Li et al. 2010; Zhang et al. 2013).

Three common QTLs detected in this report simultaneously controlled ERN and TR due to the utilization of SICAU1212 with four rows. Although SICAU1212 may not be an appropriate breeding base, this research could well aid in understanding the genetic basis of these traits and provide a foundation for further fine-mapping of these common QTLs.

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Conflict of interest All of the authors declare that they have no conflict of interest.

Ethical standards The experiments comply with the current laws of the country in which they were performed.

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