

**QUANTITATIVE TRAIT LOCI FOR YIELD AND MORPHOLOGICAL
TRAITS IN MAIZE UNDER DROUGHT STRESS**

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Drought is one of the most important factors contributing to crop yield loss. In order to develop maize varieties with drought tolerance, it is necessary to explore the genetic basis. Mapping quantitative trait loci (QTL) that control the yield and associate agronomic traits is one way of understanding drought genetics. QTLs associated with grain yield (GY), leaf width (LW3, LW4) plant height (PH), ear height (EH), leaf number (NL), tassel branch number (TBN) and tassel length (TL) were studied with composite interval mapping. A total of 43 QTLs were detected, distributed on all chromosomes, except chromosome 9. Phenotypic variability determined for the identified QTLs for all the traits was in the range from

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20.99 to 87.24%. Mapping analysis identified genomic regions associated with two traits in a manner that was consistent with phenotypic correlation among traits, supporting either pleiotropy or tight linkage among QTLs.

Key words: drought, grain yield, maize, morphological traits, QTLs.

INTRODUCTION

Global mean temperatures are increasing and the climate is becoming erratic, with more severe drought in some areas and more and stronger storms (IPCC, 2007). In this context, the future challenges of crop production will be related to higher temperatures and less rainfall (SIVAKUMAR *et al.*, 2005).

Maize is the third most important crop for food, feed, forage and fuel production after rice and wheat (PALIWAL *et al.*, 2000). Progress in increasing yield and its stability under water limited conditions through a direct selection has been hampered by the low heritability of yield, particularly under drought, and by its large 'genotype \times environment' interaction (BLUM, 1988; CECCARELLI *et al.*, 1996). Morpho-physiological and other so-called secondary traits (anthesis-silking interval-ASI, leaf rolling, leaf erectness, canopy temperature etc.) correlated with yield and displaying increased genetic variability in drought conditions, have been commonly identified and selected for in maize breeding programs (CAMPOS *et al.*, 2004).

Drought often delays developmental stages: plant height and leaf growth are reduced and tassel architecture traits are affected. Consequently, yields are affected since plant needs to reach a sufficient stature to have adequate photosynthate (SARI-GORLA *et al.*, 1999).

Traditional breeding programs that depend on phenotype selection are time consuming and non efficient but applying molecular marker techniques can improve the efficiency of breeding drought tolerant crops (TUBEROSA *et al.*, 2002; ANDELKOVIĆ and THOMPSON, 2006; QUARRIE *et al.*, 2006; MARKOVIĆ *et al.*, 2008; GUO *et al.*, 2008; KAMOSHITA *et al.*, 2008; ANDELKOVIĆ and IGNJATOVIĆ-MIČIĆ, 2011). Extensive genetic dissections of drought tolerance traits have been carried out in maize over the last two decades, yielding numerous QTL (quantitative trait loci) involved in determination of morphological traits and regulatory pathways (BEAVIS, 1994; VELDBOOM and LEE, 1996a, 1996b; SARI-GORLA *et al.* 1999; GUO *et al.*, 2008; MESSMER *et al.*, 2009). Besides identification of QTLs, it is also important to analyze cause-effect relationships among traits (LEBRETON *et al.*, 1995).

DTP (drought tolerant population) originally developed by CIMMYT is being used for more than ten years as a source of drought tolerance at Maize Research Institute. In the present paper, one of the inbred lines from this population was used with the aim to identify the QTLs associated with yield and morphological traits under drought conditions. Herein, the number, genomic positions and gene effects of the identified QTLs are presented and discussed. Results of this study were also compared with QTLs involved in expression of the analyzed traits in different maize genotypes previously identified by other authors.

MATERIALS AND METHODS

Plant materials and field trials

Inbred lines, DTP79 (drought tolerant) and B73 (drought susceptible) were crossed to make F₂ mapping population. Field data were obtained from trials of 116 F₃ families, produced by selfing F₂ plants.

Filed trials were carried out in Maize Research Institute „Zemun Polje“, in 2007 according to a randomized complete block design, with three replications. Plots consisted of single rows with a total of 20 plants per row after thinning.

Very severe air drought occurred in April, July and August in 2007. Nineteen days in July were with extremely high temperatures (35-45°C) - one of the hottest July ever in Serbia. Maximum temperature of 44.6 °C, recorded on 24th of July in Belgrade, was the highest temperature ever measured. Rainfall conditions were also far from optimal for maize with very low precipitation in April (3.8mm) and July (17.5mm).

Traits were measured on ten randomly chosen plants from all three replicas, and mean value for each family was calculated. Grain yield (GY) was expressed in grams per plant. Leaf width was measured on the third and fourth leaves from the top of plants (LW3 and LW4, respectively). The *leaf width* was determined at the mid portion that had the maximum *width*. Shortly after flowering, plant height (PH) was measured from the soil line to the tip of the tassel and ear height (EH) was measured from the soil line to the upper ear node. At seedling stage, the third leaf of the chosen plants was designated as marker for evaluating leaf number (LN). Tassel length (TL) was measured from the non branching node present below the lowermost primary branch to the tip of central spike. Number of tassel branches (TBN) was recorded, too.

Molecular analysis

One hundred fifty plants of F₂ population were used for linkage map construction using MAPMAKER (LANDER *et al.*, 1987) with Haldane function (HALDANE, 1919). The population was genotyped with 192 restriction fragment length polymorphism (RFLP), 33 simple-sequence repeats (SSR), and nine amplified fragment length polymorphism (AFLP) markers. The map was made with a total of 234 markers, the most informative 200 markers were used for QTL analysis.

Statistical analysis

Phenotypic correlations between the analyzed traits using row data were calculated with Pearson correlation coefficient. Microsoft Office Excel 2003 was used for data analysis.

QTL analysis was performed using WinQTL cartographer, 2.5 version software (<http://statgen.ncsu.edu>). For QTL identification with WinQTL cartographer composite interval mapping (CIM) methods (ZENG, 1993, 1994) were used. A putative QTL was declared significant when the LOD score was >2.0. The maximum LOD score along the interval was taken as the position of the QTL (the QTL peak), and the confidence interval of each QTL is the 'one-LOD support

interval', which is determined by finding the region on both sides of a QTL peak that corresponds to a decrease of 1 LOD score. QTL additive effects were calculated according to SANGUINETI *et al.* (1999).

Average levels of dominance of each QTL and across all QTLs were calculated as the l_d/l_a ratio. Gene action was determined on the basis of the average level of dominance by using the criteria of STUBER *et al.* (1987): additive (A)=0 to 0.20; partial dominance (PD)=0.21 to 0.80; dominance (D)=0.81 to 1.20; and overdominance (OD)>1.20.

RESULTS

Phenotypic relationships among the traits

Phenotypic correlation coefficients were estimated to determine the association of different traits, with the emphasis on correlations with grain yield per plant. Correlation matrix determined using Pearson coefficient is presented in Table 1.

Grain yield was positively correlated with LW4, PH, LN ($P<0.001$) and TL ($P<0.05$) and negatively with TBN ($P<0.001$). Significant positive correlation was identified between LW3 and LW4 ($P<0.001$). LW3 was negatively correlated with EH and TBN ($P<0.05$). LW4 showed significant positive correlation with LN ($P<0.05$) and negative correlation with TBN ($P<0.05$). PH was strongly positively correlated with EH, LN and TL ($P<0.001$). LN was also positively correlated with TL ($P<0.05$) and negatively correlated with TBN ($P<0.01$). EH showed positive correlation with TBN ($P<0.05$).

Table 1 Phenotypic Pearson correlations among different traits: grain yield (GY), leaf width (LW3, LW4), plant height (PH), ear height (EH), leaf number (LN), tassel branch number (TBN), tassel length (TL)

	GY	LW3	LW4	PH	EH	LN	TBN	TL
GY	1							
LW3	0.19	1						
LW4	0.39***	0.83***	1					
PH	0.37***	-0.19	0.01	1				
EH	0.08	-0.22*	-0.08	0.63***	1			
LN	0.63***	0.14	0.27*	0.35***	0.04	1		
TBN	-0.35***	-0.23*	-0.27*	0.12	0.22*	-0.24**	1	
TL	0.23*	0.03	0.12	0.35***	0.17	0.22*	-0.11	1

Significant * 0.218 at $P<0.05$, ** 0.280 at $P<0.01$, *** 0.328 at $P<0.001$

QTL analysis

Comparative QTL analysis (CIM, $LOD > 2.0$) revealed a total number of detected significant QTLs for each trait, their chromosome positions, LR ($LOD = LR/2Ln10$) values, additive and dominant effects and percentage of phenotypic variation explained by the QTL (Table 2a and Table 2b). Locations of identified QTLs are shown in maize genetic map (Figure 1).

A total of five GY QTLs were identified. One QTL was identified per chromosomes 2, 7 and 10, while two QTLs were identified on chromosome 5. The percentage of variation explained by these QTLs ranged from 0.1 to 15.86%. DTP79 line contributed towards the increase of the trait values for QTLs identified on two chromosomes. For the other three identified QTLs, alleles increasing GY were contributed by B73 (Table 2b). Two of five identified QTLs displayed dominance effect (overdominance), another two very large dominance effect and only one QTL for GY showed additive gene action.

A total of 12 QTLs affecting leaf width (nine for LW3, and three for LW4) were identified. Phenotypic variance explained by these QTLs ranged from 0.9 to 14.5% for LW3 and from 1.4 to 34% for LW4. Alleles from B73 were increasing the trait values for LW3 QTLs detected on four chromosomes, while DTP79 contributed beneficial alleles for the QTL detected on three chromosomes (Table 2b). For all QTLs identified for LW4, DTP79 contributed towards the increase of the trait value. Two of the nine QTLs identified for LW3 showed overdominance, six QTLs partial dominance, and only one additive effect. All three QTLs identified for LW4 showed dominant gene action - two of them displayed overdominance and one partial dominance.

Fifteen QTLs were identified for PH and EH. Eight QTLs for PH were detected on chromosomes 1, 2, 3 (two QTLs), 4, 5 (two QTLs), and 6. Individual QTL accounted for 0.6 – 8.07% of the phenotypic variation. For four of the eight QTLs identified for PH, alleles were contributed by DTP79, and for another four QTLs by B73 (Table 2b). One QTL displayed additive effect and seven QTLs displayed dominance (three of them showed overdominance, two dominance and two partial dominance).

Seven QTLs were detected for EH (six QTLs on chromosome 2 and one on chromosome 6). Phenotypic variance explained by these QTL ranged from 0.1 to 16.96%. For three QTLs DTP79 alleles contributed to the increase of trait values, and for the four QTLs by B73. Only one of the seven identified QTLs, located on chromosome 2 showed additive effect, six QTLs displayed dominant effect (one QTL showed partial dominance, one QTL dominance and four showed overdominance).

Only one QTL for LN was detected on chromosome 6. The QTL accounted for 35.48% of the phenotypic variation. DTP79 alleles contributed towards the increase of the trait. Detected QTL displayed additive effect.

Table 2a Intervals containing QTL with a LOD score of >2.0 (abbreviations as per Table 1)

Trait	Number of QTLs	Ch.	Interval (markers)	left fl. mar.	LR ¹	R (%) ²
GY	5	2	umc49a-csu109	18	9.79	0.1
		5	rgc488-rz508	7	13.76	4.51
		5	csu26-php10017	18	10.12	5.31
		7	csu11-bnlg434	3	11.05	3.46
		10	M49/2C-sb134b	14	10.65	15.86
						Σ=29.24
LW3	9	1	bcd1072-umc161	23	12.08	13.13
		2	umc53-bnlg1327	3	11.54	12.6
		4	umc123-umc31	1	9.27	12.8
		4	psr128b-bnl8.45	8	9.17	8.76
		5	sb736-rgc746	3	11.78	11.7
		6	umc132-cdo202	17	10.94	11.8
		7	csu129-cdo412	2	12.61	14.5
		7	cdo412-asg49	5	14.67	0.9
		7	bnlg434-bnl14.07	8	9.32	1.1
						Σ=87.29
LW4	3	2	bnlg108-csu481	12	9.26	1.4
		5	sb736-csu108	3	25.81	34
		6	bnlg1043-csu70	3	13.11	3.7
						Σ=39.10
PH	8	1	bnlg1014-M52/1b	2	11.00	8.07
		2	umc33-sb134a	1	14.47	0.6
		3	cdo344-psr156	13	9.31	5.69
		3	rgc122-csu36b	16	10.81	1.89
		4	cdo497-bnl8.45	10	9.4	7.34
		5	sb854-csu566	13	13.85	12.35
		5	csu26-php10017	17	14.47	5.09
		6	bnlg1043-bnlg426	1	10.54	9.58
						Σ=50.61
EH	7	2	bnlg1327-umc61	3	15.3	0.1
		2	umc61-umc34	5	0.15	0.3
		2	csu45-umc5	9	11.11	3.11
		2	bnlg108-bcd855	12	15.51	1.02
		2	csu481-npi409	14	11.01	0.09
		2	bnlg1520-csu166	18	11.84	10.55
		6	psr129b-M54/1C'	8	14.52	16.96
						Σ=32.05
LN	1	10	csu103b-umc130	6	12.28	35.48
						Σ=35.48
TBN	8	1	tub1-bnlg1014	1	19.06	18.88
		1	blt01.97-umc67	7	13.72	4.34
		2	umc53-bnlg1327	1	37.45	5.24
		3	csu16-MACE01E07	3	10.11	5.12
		3	umc60a-rgc122	14	21.86	19.22
		5	cdo89a-rgc746	1	19.24	11.81
		6	bnlg1043-rz143b	1	10.21	5.02
8	csu31b-umc30	7	20.99	21.55		
						Σ=91.18
TL	2	2	M54'2'Ca-bnlg108	11	16.67	20.89
		3	psr156-bnlg1257	15	16.91	0.1
						Σ=20.99

¹ likelihood ratio test statistic, ² phenotypic variance explained by each QTL

Table 2b Effects and types of individual gene action of QTLs for analyzed traits (abbreviations as per Table 1)

Trait	Chromosome	a ¹	d ²	Direction ³	ldl/ al	Type ⁴
GY	2	-1.8	14.3	DTP79	7.79	OD
	5	-11.38	10.31	DTP79	0.91	D
	5	11.3	8.81	B73	0.78	PD
	7	10.48	13.84	B73	1.32	OD
	10	21.99	3.22	B73	0.15	A
				Σ=0.55	PD	
LW3	1	0.38	0.01	B73	0.03	A
	2	0.35	-0.13	B73	0.37	PD
	4	0.36	-0.24	B73	0.67	PD
	4	0.31	-0.12	B73	0.39	PD
	5	-0.38	0.1	DTP79	0.26	PD
	6	-0.36	0.22	DTP79	0.61	PD
	7	0.41	-0.31	B73	0.75	PD
	7	0.16	-0.35	B73	2.19	OD
				Σ=0.54	PD	
LW4	2	-0.12	0.35	DTP79	2.92	OD
	5	-0.60	0.18	DTP79	0.3	PD
	6	-0.34	0.44	DTP79	1.29	OD
				Σ=0.49	PD	
PH	1	-6.88	8.52	DTP79	1.24	OD
	2	1.81	-9.54	B73	5.27	OD
	3	6.45	1.65	B73	0.26	PD
	3	-3.41	10.69	DTP79	3.13	OD
	4	-7.09	0.63	DTP79	0.09	A
	5	-8.86	9.04	DTP79	1.02	D
	5	5.39	4.41	B73	0.87	D
				Σ=0.82	D	
EH	2	0.29	-7.70	B73	27.24	OD
	2	-1.26	-3.58	DTP79	2.84	OD
	2	-4.79	0.23	DTP79	0.05	A
	2	2.01	-8.45	B73	4.2	OD
	2	6.62	-6.65	B73	1.00	D
	2	-5.4	1.21	DTP79	4.46	OD
	6	7.94	-5.16	B73	0.65	PD
				Σ=1.99	OD	
LN	10	-2.08	0.39	DTP79	0.19	A
				Σ=0.19	A	
TBN	1	1.87	-0.44	B73	0.24	PD
	1	-0.94	-0.17	DTP79	0.18	A
	2	-0.89	-1.73	DTP79	1.94	OD
	3	1.14	-0.06	B73	0.05	A
	3	1.93	-0.45	B73	0.23	PD
	5	1.47	-0.13	B73	0.09	A
	6	1.00	0.08	B73	0.08	A
				Σ=0.37	PD	
TL	2	-3.18	-0.63	DTP79	0.20	A
	3	0.21	2.86	B73	13.62	OD
				Σ=5.54	OD	

¹additive effect, ²dominant effect, ³parental line that increases the value of the trait, ⁴type of gene action
 OD-overdominance, D-dominance, PD-partialdominance, A-additive

For tassel architecture traits (TBN, TL) ten QTLs were identified. Eight QTLs for TBN were identified on chromosomes 1 (two QTLs), 2, 3 (two QTLs), 5, 6 and 8. Total phenotypic variance explained by these eight QTLs ranged from 4.34% to 21.55%. For two QTLs alleles were contributed by DTP79, and for seven QTLs by B73 (Table 2). Four QTLs displayed additive and four dominant gene effect (three QTLs partial dominance and one QTL overdominance). Only two QTLs were identified for TL on chromosomes 2 and 3. Phenotypic variance ranged from 0.1 to 20.89%. DTP79 contributed beneficial alleles for the QTL on chromosome 2 and B73 contributed alleles for the QTL on chromosome 3. Both QTLs displayed dominance (overdominance).

QTL overlapping between yield and morphological traits

Coincident QTLs for GY and morphological traits were found on three chromosomes (2, 5 and 7). A QTL for GY overlapped with QTL for LW4 on chromosome 2, and three QTLs for LW3 overlapped with a QTL for GY on chromosome 7. Coinciding QTLs for GY and EH were found chromosome 2, and also for GY and PH on chromosome 5. Some of the traits (LW4 and PH) that had coinciding QTL with GY, also showed significant phenotypic correlation.

QTL overlapping between different morphological traits

QTLs for LW3 and TBN overlapped with QTLs for PH in one region and with QTL for EH in another region of chromosome 2. Coinciding QTLs were found for LW4 and EH, while QTL for TL only partially overlapped with a QTL for LW4 on chromosome 2.

QTL for TBN partially overlapped with QTL for PH in one, and with a QTL for TL in another region of chromosome 3. The second of the two QTLs for PH detected on chromosome 3 partially overlapped with already mentioned QTL for TL.

Coincident QTLs for PH and LW3 were found on chromosome 4. QTL coincidence between TBN, LW3 and LW4 was identified on chromosome 5. A chromosome region harbouring coinciding QTLs affecting LW4, PH and TBN was found on chromosome 6.

For some pairs of these traits phenotypic correlations were significant, too.

DISCUSSION

The use of molecular markers has provided construction of plant genetic maps, insights into the genomic location and gene action of individual QTL and the potential to enhance the efficiency of trait selection in plant breeding.

In this study, QTL analysis between grain yield and morphological traits was performed. For all the analysed traits, a total of 43 QTLs was identified. QTLs were detected on all maize chromosomes except the chromosome 9. More than half of total QTLs detected for all the traits (61, 4%) displayed dominant effect. Out of 43 QTLs 32% exhibited partial dominance, 9% dominance, 36% overdominance and 23% exhibited additive effects.

The PH and EH traits have additive gene action or partial dominance for QTLs affecting these traits. Their gene action depends on the genotypes and experimental conditions applied (SIBOV *et al.*, 2003). In this study, gene action for PH and EH is not in agreement with previous studies. These traits displayed dominant and overdominant gene action. This result is due mainly to QTLs which had dominance effects several times greater than the corresponding additive effects and may reflect the effect of several QTLs in one genomic region, a situation that could result in overestimation of overdominance.

Individual QTLs explained great phenotypic variation with a range from 25% to 35% in many studies (RAGOT *et al.*, 1995; AJMONE-MARSON *et al.*, 1995; VELDBOOM and LEE, 1994; BEAVIS, 1994; JIANG *et al.*, 1999). In our study, several QTLs for different investigated traits explained approximate phenotypic variation (34% for LW4, 35,48% for LN, 21,55 % for TBN and 20.89% for TL). For each trait at least one QTL explaining phenotypic variance greater than 10% was identified. Also, for three analysed traits (LW3, PH and TBN) ratio of the phenotypic variation explained by all the QTLs was greater than 50%. The remaining variation, not explained by the QTLs detected in this population can be due to: 1) the QTLs in regions not mapped in the genome; 2) QTLs with small effect not detected; 3) epistatic effect between QTLs.

Blocks of common loci for some traits were revealed. Regions of some of the identified QTLs completely or partially overlapped. Genomic regions for GY QTLs overlapped with QTLs for LW, PH and EH and their additive effects were in the expected directions. Also, phenotypic correlations between GY and some of these morphological traits (LW4, PH) were significant. This phenomenon has also been observed in other studies (LEBRETON *et al.*, 1995; SIMKO *et al.*, 1997; SANGUINETI *et al.*, 1999; THUMMA *et al.*, 2001). According to AASTVEIT and AASTVEIT, (1993) and SANGUINETI *et al.*, (1999) there are three primary causes of correlation among traits: pleiotropy, linkage and environmental effects. Mapping analysis identified genomic regions associated with two traits in a manner that was consistent with phenotypic correlation among traits, supporting either pleiotropy or tight linkage among QTLs. New methods of analysis should be used to increase the power of the resolution of QTL mapping, for testing pleiotropy versus linkage.

An important consideration in detection of QTLs is if the location of a QTL detected in one population can be observed in other populations (LEE, 1995). Matching of the results for QTLs mapped in different studies is difficult due to: the differences in methodology, size and the type of the mapped populations, lack of common marker loci and different tested environments (LEE, 1995). In spite of that, comparing QTLs identified in this study with previously identified QTLs in different studies, revealed common regions for some of them. The same QTLs for yield were identified on bin 2.09 (BEAVIS, 1994) and on chromosome 5 (AGRAMA and MOUSSA, 1996). QTL for this trait on chromosome 7 was detected in the region between bins 7.02 - 7.03 in our study, while various authors detected QTLs for yield in between 7.04 - 7.05 bins (BEAVIS, 1994; AUSTIN and LEE, 1996; RIBAUT *et al.*, 1997; MELCHINGER *et al.*, 1998; STUBER *et al.*, 1987), Positions of QTLs for PH in this

study were the same as the positions for the QTLs detected on chromosome 2 (SARI-GORLA *et al.*, 1999), on chromosome 3 (AUSTIN and LEE, 1996), on chromosome 4 (TUBEROSA *et al.*, 2002; BEAVIS, 1994; VELDBOOM and LEE, 1996a; GUO *et al.* 2008; AJMONE-MARSON *et al.*, 1995) and on chromosome 5 (JI-HUA *et al.*, 2007). QTL positions identified for EH on chromosomes 2 and 6 were also found in other studies (BEAVIS, 1994; VELDBOOM and LEE, 1996a, AGRAMA and MOUSSA, 1996). The QTLs we have detected for TBN on chromosomes 1, 2 and 3 are in the same region as QTLs identified for the same trait in MICKELSON *et al.*, (2002).

The mapped QTL could be used in marker-assisted selection (MAS) to design more efficient breeding programmes, but the identification of QTLs is only the first step of a longer process.

CONCLUSION

After identification of a (major) QTL, the next step is to identify the most suitable candidate sequence and to validate its role. The identification of candidate genes and the elucidation of their role can be greatly facilitated by combining QTL analysis with different sources of information and technological platforms. Recent progress in high-throughput profiling of the transcriptome, proteome and metabolome enables the investigation of the concerted expression of thousands of genes and measure the level of their products. In this context, identified QTLs in our work, especially those also detected in other experiments and further research will help in elucidating genetic basis of drought tolerance and enable more effective breeding for drought tolerant maize hybrids.

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IDENTIFIKACIJA LOKUSA ZA KVANTITATIVNA SVOJSTVA KOD KUKURUZA U USLOVIMA SUŠE: PRINOS I MORFOLOŠKA SVOJSTVA

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I z v o d

Suša je jedan od najznačajnijih faktora koji utiče na smanjenje prinosa. Mapiranje lokusa za kvantitativna svojstva (QTL) koja kontrolišu prinos i vezane agronomske osobine daju uvid u genetičku osnovu odgovora biljke na stres suše i omogućavaju stvaranje tolerantnih genotipova. Lokusi za kvantitativna svojstva vezani za prinos, širinu lista, visinu biljke, visinu biljke do klipa, broj listova, broj grana metlice i dužinu metlice identifikovani su primenom *composite interval mapping* metode. Detektovano je ukupno 43 QTL-a, na svim izuzev na 9 hromozomu. Fenotipska varijabilnost za ova svojstva bila je u opsegu od 20.99 to 87.24%. Identifikovani su genomski regioni vezani za dva ili više svojstva, i istovremeno je kod njih detektovana visoka fenotipska korelacija, što ukazuje na postojanje plejotropnih ili epistatičkih interakcija između QTL-ova.

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