Full Length Article

Genetic Association of Seed Yield with Component Traits in *Glycine max* under Different Water Regimes

Min Wang[1], Wanming Yang[2], Aiqin Yue[1], Jinzhong Zhao[1], ChunYan Gao[1], YongPo Zhang[1] and Weijun Du[1*]

[1]*College of Agronomy, Shanxi Agricultural University, Taigu Shanxi 030801, China*
[2]*College of Biological Science and Technology, Jinzhong University, Yuci Shanxi 030600, China*
[*]*For correspondence: wangmin3502@126.com*

Abstract

Selecting soybean lines that can maintain high yields during drought is important to enhance the breeding of drought-tolerance strains of soybean. In this study, 200 BC_1F_4 lines and two parental lines were grown in 2011 and 2012 at Shanxi Agricultural University in China. Yield and its component characters were measured and analyzed under different water treatments. The results revealed that yield and its component characters value in drought stressed environments were lower than in non-stressed environments. Fifteen QTLs involved in nine traits were detected in the linkage groups G1-A1, G5-C1, G6-C21, G10-D2, G11-E, G14-G and G22-N. Large-effect loci were detected on near satt514 in the G10-D2 linkage group, Satt606 in the G11-E linkage group and Satt640 in the G6-C21 linkage group as in previous reports. The loci near satt514 in the G10-D2 linkage group were associated with majority of yield related traits under different water conditions. They are qPH-DS-D2-1, qPDN-DS-D2-1, qPNP-NS-D2-2, qPNP-DS-D2-1, qSP-NS-D2-1, qSP-DS-D2-1 and qSWP-DS-D2-1, respectively, in which the phenotypic contribution of qPDN-DS-D2-1, qPNP-DS-D2-1, qSP-DS-D2-1 and qSWP-DS-D2-1was more than 10.00%. Most loci associated with yield related traits are sensitive to water regimes. The additive and additive epistatic interaction effects (*aa* effects) was observed for controlling podding number of stem under drought stressed conditions and nine QTLs controlled yield related traits had additive and environment interaction effects (*ae* effects). Conditional QTL SWP-DS-D2-1 for SWP can be detected only by performing the phenotypic values of SWP conditioned on PDN, PNP or SP, indicating the expression of the QTL SWP-DS-D2-1 related to seed weight per plant was closely associated with variation in PDN, PNP and SP, which was consistent with the high correlation of DTI and yield related traits under DS. The results from this study facilitates the understanding of the genetic mechanism of the complex interactions among soybean major-effect drought-yield QTLs and molecular breeding for the improvement of soybean adaptability to drought in specific and/or broad regions. © 2018 Friends Science Publishers

Keywords: Soybean; BIL population; Seed weight per plant; Drought stressed conditions; Quantitative trait loci (QTLs)

Introduction

Drought is an increasingly important factor affecting crop productivity globally. Both arid and semi-arid areas worldwide have been increasing yearly, which together are estimated to represent 36% and 43% of land and arable land surface area, respectively. The arid and semi-arid areas in China accounts for over half of the size, affected the most of the annual crop production. Although improving tillage cultivation techniques (i.e., implementing drought-tolerance tilling methods of reduced and no-till farming, plastic film mulching and irrigation development) to eliminate the threat of drought may alleviate some symptoms, they do not fundamentally solve the problem. Considering that it is difficult to increase the total area for planting crops, that fertilizer usage has nearly reached a limit. So increasing crop yield under drought stress by improving tillage cultivation techniques is not feasible, genetic improving drought tolerance is preferred.

Drought tolerance in plants is a complex quantitative trait, which is dependent on a variety of related genes. Quantitative trait locus (QTL) mapping is an efficient way to elucidate the genetic composition of complex quantitative traits. Knowledge about drought tolerant traits using molecular markers in differently mapping populations have provided extensive data concerning QTLs, including their abundance, mechanisms of inheritance, complex interactions and role in drought tolerance. Genetic studies of molecular marker on the effect of drought in soybeans have been performed by assessing several traits such as those related to water use efficiency (Mian *et al*., 1996, 1998; Specht *et al*., 2001), root characters (Liu *et al*., 2005), relative germination rate (Li *et al*., 2009), leaf pubescence density, water status traits (Du *et al*., 2009a,b), and water retention curve (WRC), as well as additional drought-tolerance traits (Li *et al*., 2011). The selection of above

QTLs hinges on the value of phenotypic variation explained and by their consistency across various genetic backgrounds.

Yield is an important characteristic of plants used as food crops, and it is important to study how it is affected by the environment and genetic background. There is still not a clear selection criterion in drought tolerance breeding; additive and environment interaction effects (*ae* effects) exist revealing that selection for particular adaptation might offer more straight forward methods of genetically improving drought tolerance (Specht *et al.*, 1986; Carter, 1989). The ultimate objective of these studies has been to reveal the genetic basis of yield in different environments and develop a series of cultivars characterized by high yield and strong drought resistance. Since drought resistance is a complicated quantitative character affected by both genetic and non-genetic factors, the identification of the yield QTLs across different water regimes and QTLs related to drought tolerance traits has been conducted. Du *et al.* (2009c) identified QTLs related to yield per plant maintained in different water regimes and determined the drought susceptibility index in a field and greenhouse. While some studies exist, the main QTLs underlying yield related traits across various water environments remain unidentified. Therefore, the objective of this study was to map QTLs and lay a foundation for soybean drought tolerance breeding.

Materials and Methods

Plant Material

A backcross inbred lines(BIL) population described by Wang *et al.* (2012) was used for this study. The population consisted of 200 BC_1F_4 lines was used to test the ability to confer drought tolerance to the entire soybean genome. The recipient SNWS0048 was an accession of the common wild soybean from Shanxi Province, China, and was characterized by strong drought tolerance, while the donor JD73 was an improved variety, and was characterized by superior agronomic traits and drought-sensitivity.

Field Experiments

Drought phenotyping experiments were carried out in the experimental field of Shanxi Agricultural University, Taigu, China, in 2011 and 2012. Drought stress (DS) and non-stress (NS) conditions were applied in separate experiments during each trial year, for a total of four environments utilized for the QTL analysis. Daily maximum and minimum temperature and rainfall were collected during the growing season in Taigu, Shanxi Province, China. The mean daily maximum and minimum temperature was about 27.0°C and 15.4°C during the growing season in 2011 and the mean daily maximum and minimum temperature was about 27.7°C and 15.7°C in 2012, respectively. A split block design on two factors was used, including water and materials. Each plot was 2 m in length by 0.5 m wide, with spacing of 25 cm and 50 cm rowing spacing. Drought stress plots had rainfall with a total of 421 mm during the growing season of the year 2011 and a total of 376 mm during the growing season of the year 2012. Control plots were irrigated twice: once during the transition from vegetative to reproductive growth and second during the flowering and podding period with 650 mm of water applied in two years respectively. Field management including fertilization and pest disease control, followed standard agricultural practice. Five representative individuals of each plot were harvested at maturity.

Trait Measurements

Seed yield and eight component traits were investigated. Plant height (PH) was measured from the cotyledonary node to tip-shoot Branch number (BN) indicates the number of branches from the main stem. Podding height (PHT) was measured from the position of the cotyledonary node to the position of the first pod in the main shoot. Pitch number of main stem (PN) was the amount of pitch in the main stem. Podding number of the main stem (PDN) indicated the number of plump pods that grow from the main shoot. Podding number per plant (PNP) referred to the number of plump pods. Seeds per plant (SP) indicated the numbers of plump seeds. Seed weight per plant (SWP) was the average weight of seeds the harvested individuals.

Phenotypic Data Analysis

Phenotypic data for the population was treated using descriptive statistic programs in Excel 2003 software and analysis of variance with DPS software. The drought tolerance index was determined to be equal to the measured value in water stress divided by the measured value in the control.

Simple Sequence Repeat (SSR) Marker Analysis and Genetic Linkage Map Construction

A genetic linkage map was constructed using SSR markers in the BIL population. Total genomic DNA was isolated using the modified CTAB extraction method (Kabelka *et al.*, 2006). PCR was adopted, and the amplification products were separated using methods described by Wang *et al.* (2003).

Linkage analyses were performed using Mapmaker/EXP 3.0b software (Lincoln and Lander, 1993). A linkage map of 122 SSR markers distributed among 24 chromosomes covering 1655.4 cM with an average distance of 13.6 cM between markers (Wang *et al.*, 2012). QTLs associated traits were identified by composite interval mapping (CIM) using QTL Network 2.0 software (Yang *et al.*, 2007, 2008). The QTLs were detected according to the mixed linear model, with the significance determined by values, where $P < 0.005$ (Zhu, 1997).

Results

Phenotypic Variation of Yield Related Traits

The values of yield related traits in population under different moisture treatments in 2011 and 2012 were shown in Table 1 and 2, respectively. All traits were decreased in different degree under drought stress, which were no difference between two years. For example, the mean of SWP in BIL population under DS treatment was declined from 43.62 to 22.13 g in 2011 and 32.10 to 20.30 g in 2012. This suggested that DS level was a reasonable level adequate for this study. PH, BN, PN, PDN and SP were higher for SNWS0048 than for JD73. Meanwhile, PHT was lower for SNWS0048 than for JD73. These suggested that the parents had difference in the genes involved these traits. The coefficient of variation (CV) of the BIL plants in PNP, SP and SWP were higher in DS than in NS in both years. It indicated that these traits were sensitive to DS. The CV in PN and PDN were lower in DS than in NS in both years, and the CV in other traits had different performance in different years. For all traits, the means of the lines were between the two parents. Values of lines were beyond the scope of two parents. The distribution of phenotypic data according to the values of skewness and kurtosis was basically in normal and used for further location of QTL.

Correlation Analysis between Drought Tolerance Index (DTI) and Yield Related Traits

Correlation among yield-related traits and drought tolerance index in different water conditions were shown in Tables 3 and 4. Correlation analysis between SWP and other yield related traits in NS and DS conditions showed that there was a significant or highly significant correlation between SWP and other yield related traits in the NS conditions, and in the DS conditions there was a highly significant correlation between SWP and other yield related traits except BN. Correlation analysis between DTI and yield related traits showed that in NS conditions the negative relation between DTI and PH (r = -0.192) were highly significant, and the positive relation between DTI and PNP (r=0.163) were significant. In DS conditions, DTI was highly significantly positive correlated with BN, PDN, PNP, SP and SWP. Correlation indexes between DTI and SWP with 0.5557 was the highest. It indicated that the more in BN, PDN, PNP, SP, the heavier in SWP, the higher level of drought tolerance. These results were consistent with previous studies (Xu and Zhang, 1989; Liu, 1991).

Mapping of Yield Related Traits

Mixed model approaches and interval mapping were used to detect putative QTLs for yield related traits under water stress (Table 5). Fifteen QTLs involed in nine traits were detected on linkage group G1-A1, G5-C1, G6-C21, G10-D2, G11-E, G14-G, G22-N. In these QTLs, six QTLs only had

significant in *a* effects, indicating that these QTLs might have the same expression patterns in different environments. Nine QTLs had additive effects (*a* effects) and *ae* effects, showing that these QTLs might lead to the yield related traits changes in special environment.

QTLs for Plant Height

One QTL detected for plant height under non-stressed conditions showed significant *a* effects and *ae* effects. This QTL marked by Satt237 -Sat_ 241 on G22-N. It detected accounted for 17.1261 plant height increase, with corresponding contribution of 6.55%, and detected accounted for 9.8529 plant height decreased under different year, with corresponding contribution of 2.69%. Another QTL detected for plant height under drought stressed conditions had significant in *a* effects and *ae* effects. It marked by Satt543-Satt514 on G10-D2, increased the plant height by 5.2540, with corresponding contribution of 6.79%, and decreased the plant height by 2.4243 in different year, with corresponding contribution of 1.78%.

QTLs for Podding Height

Two QTLs controlling podding height under non-stressed conditions had significant *a* effects, which located on chromosomes C1-1 and G-2, were named as qPHT-NS-C1-1 and qPHT-NS-G-2, respectively. One QTL of qPHT-NS-C1-1 in marked by Sat_ 337-Satt476, increased the podding height by 0. 8923 come from SNWS0048, with corresponding contribution of 3.36%. Another QTL of qPHT- NS-G-2 marked by Sat_223-Satt594, reduced the podding height by 0.7477, come from JD73, with corresponding contribution of 3.40%. An effect of qPHT-NS-C1-1 was the inverse of *an* effect of qPHT-NS-G-2, while contribution of these two QTLs were essentially equal. One QTL detected to be responsible for podding height under drought stressed conditions had significant a effects, which located on chromosome G22-N, decreased the podding height by 1.0148 come from JD73, with corresponding contribution of 7.76%.

QTLs for Branching Number

One QTL affecting branch number under non-stressed conditions were significant *a* effects, which marked by Satt217-Satt352 on G14-G, decreased the branching number come from JD73, with corresponding contribution of 1. 24%. No QTL was found to affect significantly branching number under drought stressed conditions.

QTLs for Pitch Number of Stem

One QTL detected for pitch number of stem under non-stressed conditions had significant *a* effects and *ae* effects. It marked by Satt606-Satt045 on G11-E linkage group, increased the pitch number of stem come from SNWS0048,

Table 1: The performances of correlated yield traits in BIL population and parents in 2011

Trait	Treatment	BIL population					Parents	
		Mean±SD	Range	CV (%)	Skewness	Kurtosis	SNWS0048	Jinda73
Plant height(PH)	NS	110.18±21.77	62.22-163.60	19.76	0.01	-0.06	332.68	107.84
/cm	DS	96.88±14.89	44.65-134.75	15.37	0.07	-0.34	227.33	81.60
Podding height(PHT)	NS	9.10±3.33	4.25-19.60	36.59	0.48	-0.69	3.86	13.20
/cm	DS	7.93±3.07	2.25-17.12	38.71	1.02	1.08	3.50	8.60
Branching number(BN)	NS	8.39±3.19	2.80-25.60	38.02	0.69	3.28	20.70	10.32
	DS	6.78±1.69	1.20-12.20	24.93	0.18	0.07	13.28	6.40
Pitch number of stem (PN)	NS	26.96±3.89	17.23-36.20	14.43	-0.29	-0.42	30.21	27.65
	DS	24.31±2.91	16.60-31.02	11.97	-0.37	-0.42	27.70	24.20
Podding number of stem (PDN)	NS	40.13±15.08	10.20-86.88	37.58	0.23	-0.17	70.72	50.21
	DS	37.46±12.45	6.60-82.05	33.24	0.28	0.27	44.50	38.20
Podding number per plant (PNP)	NS	166.41±29.81	42.60-212.05	25.61	0.37	-0.10	306.30	110.20
	DS	101.99±33.93	22.50-198.81	33.27	0.20	-0.24	258.32	84.60
Seeds per plant (SP)	NS	399.66±80.35	97.33-539.60	26.81	0.47	0.08	605.67	225.00
	DS	242.43±83.58	51.00-494.21	34.48	0.28	-0.02	498.24	156.32
Seed weight per plant (SWP)/g	NS	43.62±9.82	12.66-59.51	29.21	0.36	-0.40	36.40	40.24
	DS	22.13±8.62	4.86-55.98	38.95	0.58	0.98	20.56	22.67

Table 2: The performances of correlated yield traits in BIL population and parents in 2012

Trait	Treatment	BIL population					Parents	
		Mean±SD	Range	CV (%)	Skewness	Kurtosis	SNWS0048	Jinda73
PH/cm	NS	133.96±20.81	55.67-167.68	15.53	1.41	1.35	355.00	110.00
	DS	91.95±19.14	44.23-135.42	20.81	0.12	-0.51	236.20	82.98
PHT/cm	NS	8.49±2.26	0-43.20	43.79	1.13	1.38	3.90	10.60
	DS	5.16±3.26	2.60-22.67	38.39	0.78	1.35	3.55	6.32
BN	NS	8.49±2.13	1.25-14.50	28.27	1.47	2.43	15.40	8.40
	DS	6.19±2.43	0-8.25	39.25	0.06	-0.53	10.32	5.34
PN	NS	29.66±5.98	12.25-42.36	20.16	-0.35	-0.30	30.60	28.20
	DS	25.72±3.90	14.03-38.20	15.16	-0.32	0.03	27.22	24.80
PDN	NS	51.29±20.48	2.23-139.08	39.92	0.48	0.81	100.25	45.51
	DS	37.29±12.92	9.85-72.84	34.65	0.23	-0.37	73.70	35.20
PNP	NS	147.71±27.45	13.67-381.25	28.09	1.60	0.99	245.80	103.20
	DS	93.54±28.08	15.08-212.26	30.02	0.33	-0.29	177.20	84.30
SP	NS	337.18±56.15	37.25-846.05	23.67	1.39	1.08	530.20	205.20
	DS	220.49±63.84	35.67-510.50	28.95	0.36	-0.23	383.00	143.32
SWP/g	NS	32.10±4.25	1.78-71.53	15.68	0.79	0.34	20.25	34.88
	DS	20.30±3.26	2.00-54.26	16.06	0.68	0.21	15.44	20.39

Table 3: Correlation among yield-related traits and drought tolerance index in non-stressed condition

	PH	PHT	BN	PN	PDN	PNP	SP	SWP
PHT	0.248**							
BN	0.054	-0.067						
PN	0.443**	0.365**	0.024					
PDN	0.197**	0.085	-0.206**	0.564**				
PNP	0.269**	0.168*	0.326**	0.126	-0.003			
SP	0.218**	0.143*	0.194**	0.075	-0.047	0.949**		
SWP	0.290**	0.226**	0.221**	0.242**	0.144*	0.807**	0.824**	
DTI	-0.192**	0.121	-0.010	-0.132	-0.056	0.163*	0.060	0.009

Table 4: Correlation among yield-related traits and drought tolerance index in drought-stressed condition

	PH	PHT	BN	PN	PDN	PNP	SP	SWP
PHT	0.271**							
BN	0.415**	-0.229**						
PN	0.622**	0.480**	0.059					
PDN	0.293**	0.165*	-0.158*	0.626**				
PNP	0.508**	-0.121	0.604**	0.269**	0.299**			
SP	0.511**	-0.091	0.577**	0.260**	0.277**	0.976**		
SWP	0.577**	-0.027	0.548**	0.387**	0.376**	0.913**	0.900**	
DTI	-0.092	-0.068	0.252**	-0.067	0.234**	0.297**	0.556**	0.346**

with corresponding contribution of 15.30% and detected accounted for 0.8849 pitch number of stem decreased under different year, with corresponding contribution of 2.07%. No QTL was found to affect significantly pitch number of stem under drought stressed conditions.

QTLs for Podding Number of Stem

One QTL mapped for podding number of stem under non-stressed conditions were significant *a* effects, which located within the interval Satt640-Satt281 on G6-C21 linkage group, increased the podding number of stem come from SNWS0048, with corresponding contribution of 15.53%. Two QTLs and one pair of QTLs controlling podding number of stem under drought stressed conditions were significant in *a* and additive × additive epistatic (*aa*) effect. The two QTLs on chromosomes G1-A1 and G10-D2 were named as qPDN-DS-A1-1 and qPDN-DS-D2-1, respectively. One QTL of qPDN-DS-D2-1 increased the podding number of stem, with corresponding contribution of 15.93%, and detected accounted for 2.8934 podding number of stem decreased under different year, with corresponding phenotypic variation rate of 4.86%. Another QTL of qPDN-DS-A1-1 also decreased the podding number of stem, with corresponding contribution of 4.70%. For the pair of QTLs qPDN- DS-A1-1 and qPDN-DS-D2-1, the *aa* effect in parental type increased the podding number of stem by 2.0196, with corresponding contribution of 1.39% (Table 6).

QTLs for Podding Number Per Plant

One QTL detected for podding number per plant under non-stressed conditions had significant *a* effects and *ae* effects. It located within Satt514-Satt311 on G10-D2, increased podding number per plant come from SNWS0048, with corresponding contribution of 1.65%, and detected accounted for 7.3469 podding number per plant decreased under different year, with corresponding contribution of 3.18%. One QTL detected for podding number per plant under drought stressed conditions had significant *a* effects and *ae* effects. It located within Satt543-Satt514 on G10-D2 linkage group, increased podding number per plant come from SNWS0048, with corresponding contribution of 18.87%, and detected accounted for 5.7828 podding number per plant decreased under different year, with corresponding contribution of 2.17%. These two QTLs controlling podding number per plant were distributed in the neighbouring position in the same linkage group.

QTLs for Seeds Per Plant

One QTL mapped for seeds per plant under two water conditions, bordered by the marker Satt543-Satt514 on G10-D2 linkage group, increased seeds per plant come from SNWS0048. Under non-stressed conditions it had non-

addictive effects and took part in *ae* effects, with corresponding contribution of 3.33%. Under drought stressed conditions it had significant *a* effects and *ae* effects, with corresponding contribution of 12.79 and 2.63% respectively.

QTLs for Seed Weight Per Plant

One QTL detected for seed weight per plant under drought stressed conditions had significant *a* effects and *ae* effects. It located within Satt543-Satt514 on G10-D2 linkage group, increased seed weight per plant come from SNWS0048, with corresponding contribution of 30.49%, and detected accounted for 1.5258 seed weight per plant decreased under different year, with corresponding contribution of 2.21%. It indicated that *an* effect plays a main role in the performance of seed weight per plant. No QTL was found to affect significantly seed weight per plant under non-stressed conditions.

QTL SWP-DS-D2-1 for seed weight per plant was detected with different effects conditioned on each of the 4 yield related traits (PH, PHT, BN, PN) compared with the unconditional QTL (Table 7). The unconditional QTLs SWP-DS-D2-1 controlling SWP failed to be detected when SWP was conditioned on PDN, PNP or SP, indicating that the expression of this QTL was completely contributed by the variation in PDN, PNP and SP. But this QTL was detected again with similar effect when given PH, it thus was considered to be independent of PH. Similarly, this QTL was independent of PH, but was partially contributed by PHT, BN and PN since the conditional and the unconditional effects of the QTL were different.

In total, large-effect loci were detected on near satt514 in the G10-D2 linkage group, Satt606 in the G11-E linkage group and Satt640 in the G6-C21 linkage group as in previous reports. The majority of QTLs affecting yield related traits under different water conditions were detected near satt514 on G10-D2 linkage group. They are qPH-DS-D2-1, qPDN-DS-D2-1, qPNP-NS-D2-2, qPNP-DS-D2-1, qSP-NS-D2-1, qSP-DS-D2-1 and qSWP-DS-D2-1, respectively, in which the phenotypic contribution of qPDN-DS-D2-1, qPNP-DS-D2-1, qSP-DS-D2-1 and qSWP-DS-D2-1was more than 10%. The genes controlling different traits were closely linked or the same gene had phenomenon of pleiotropism. The expression of the consistency major QTLs are beneficial to strengthen the resistance of soybean to drought stress. These QTL enriched region may exist some key genes controlling yield traits in soybean under DS, which is worth of further research.

Discussion

The identification of QTLs about yield related traits in soybean has been several reported. But the drought environmental effect on the genetic variation of soybean yield related traits had not been well documented.

Table 5: The QTL locations and estimated additive effects associated with yield related traits

Traits	QTL	MLG	Marker interval	Location/cM	*a* effects	h^2(*a*) /%	*ae*1 effects	h^2(*ae*) /%
PH- NS	qPH- NS -N-4	G22-N	Satt237-Sat_241	70.6	17.1261***	6.55	-9.8529*	2.69
PH- DS	qPH-DS-D2-1	G10-D2	Satt543-Satt514	6.0	5.2540***	6.79	-2.4243	1.78
PHT- NS	qPHT- NS -C1-1	G5-C1	Sat_337-Satt476	11.0	0.8923***	3.36		
	qPHT- NS -G-2	G14-G	Sat_223-Satt594	21.6	-0.7477***	3.40		
PHT- DS	qPHT-DS-N-1	G22-N	Satt530-Satt584	0.0	-1.0148***	7.76		
BN- NS	qBN- NS -G-5	G14-G	Satt217-Satt352	64.2	-0.8709*	1.24		
PN- NS	qPN- NS -E-2	G11-E	Satt606-Satt045	53.5	2.7476***	15.30	-0.8849*	2.07
PDN- NS	qPDN- NS -C21-1	G6-C21	Satt640-Satt281	0.0	8.4854***	15.53		
PDN- DS	qPDN-DS-A1-1	G1-A1	Satt276-Satt454	0.0	-3.2682***	4.70		
	qPDN-DS-D2-1	G10-D2	Satt543-Satt514	7.0	6.0123***	15.93	-2.8934***	4.86
PNP- NS	qPNP- NS -D2-2	G10-D2	Satt514-Satt311	11.2	5.5687**	1.65	-7.3469**	3.18
PNP- DS	qPNP-DS-D2-1	G10-D2	Satt543-Satt514	7.0	18.1859***	18.87	-5.7828*	2.17
SP- NS	qSP- NS -D2-1	G10-D2	Satt543-Satt514	11.0			-18.8626**	3.33
SP- DS	qSP-DS-D2-1	G10-D2	Satt543-Satt514	6.0	36.9556***	12.79	-15.8302*	2.63
SWP- DS	qSWP-DS-D2-1	G10-D2	Satt543-Satt514	10.0	5.7292***	30.49	-1.5258**	2.21

Table 6: The QTL locations and estimated epistasis *aa* effects associated with correlative yield traits

Traits	QTL	Marker interval	Location/cM	*aa* effects	h^2(*aa*)/%
PDN- DS	qPDN-DS-A1-1	Satt276-Satt454	0.0	2.0196**	1.39
	qPDN-DS-D2-1	Satt543-Satt514	7.0		

Table 7: The QTL estimated additive effects associated with seeds weight per plant in conditions

QTL		Additive	Conditional additive			
		SWP-DS	SWP-DS|PH-DS	SWP-DS|PHT-DS	SWP-DS|BN-DS	SWP-DS|PN-DS
SWP-DS-D2-1	*a*	5.7292***	3.9927***	5.7205***	4.3687***	3.2086***
	*ae*1	-1.5258**	-1.0502*	-1.5484**	-	-1.1625*

In our previous study, a recombinant inbred population with 184 F$_{2:7:11}$ lines were selected to analyze the effects of water-stress on yield and leaf water status traits (Du *et al.*, 2009a) or drought susceptibility index((Du *et al.*, 2009b). These studies mapped several QTL associated with yield and drought-related traits. The results enhanced the understanding of the water-stress effects on yield related traits at the phenotypic and genetic level. However, it was speculated that the variation of yield related traits mostly resulted from the *aa* effect and *ae* effects. The effects of loci related to environmental and genetic interaction of yield related traits across water stress conditions were not reported. In this study, environmental and genetic interaction of yield related traits was observed, indicating that water regimes conditions played an essential role in determining soybean yield related traits in addition to the genetic effects. Yield and its component characters in drought stressed environments lower than in non-stressed environments indicating very high stress levels. Such high water stress treatments in this study provided a good opportunity for clearly identify lines with drought-resistance. We have also evaluated the effects of yield-related loci across different water stress conditions. The result showed effects of genetic loci on soybean yield related traits are dependent on different water regimes conditions. Some loci were detected in only DS or NS environment; others were in two water environments. The number of loci and their associated effects varied across different water-stress conditions. Among fifteen QTLs detected in this study, six of them harbored significant *a* effects, while eight of

them had *a* effects and *ae* effects. The results from this study facilitates the understanding of the genetic mechanism of the complex interactions among soybean major-effect drought-yield QTLs and molecular breeding for the improvement of soybean adaptability to drought in specific and/or broad regions.

We also identified a consistence of several yield QTLs. Under natural growing conditions, some researchers mentioned some relatively stable yield QTLs across locations and (or) environments and (or) populations. identified a yield QTL by satt281 on C2. Guzman *et al.* (2007) mapping a yield QTL by satt640. In our study, a QTL controlling for PDN under non-stressed conditions located within the interval Satt640-Satt281. Kazi *et al.* (2010) reported a QTL controlling seed yield marked by satt543 and satt514. QTLs for yield related traits including PH, PDN, PNP, SP and SWP under drought stressed conditions and SP under non-stressed conditions in this paper was also detected on chromosome G10-D2 within the interval satt543-satt514. This QTL coincided with the same interval of a QTL involving cqSCN SDS, Scleroand Phytoph, reported by Arahana *et al.* (2001), Kazi *et al.* (2008, 2010) and Nguyen *et al.* (2012). This seems to indicate that this QTL tended to have pleiotropism, and seems to serve on a major gene. Vieira *et al.* (2006) and Alcivar *et al.* (2007) reported a QTL controlling for pod number marked by Satt476 and QTLs for seed weight and internode length marked by Satt594. We also identified a QTL for PHT under non-stressed conditions nearby satt476 and satt594. Du *et al.* (2009a) detected a QTL for yield under water stress in the greenhouse marked by

satt_223 on G. We mapped a QTL for PHT under non-stressed conditions by satt_223. Kim *et al.* (2010) and Li *et al.* (2008) detected a seed weight QTL marked by Satt530. We also identified a QTL for PHT under drought stressed conditions nearby it. Sun *et al.* (2006) reported a plant height QTL marked by Satt045. We also mapped a QTL for PN under non-stressed conditions nearby it. Some QTLs for yield component traits including pod number, seed weight per plant and plant height marker by Satt276 were reported by Sun *et al.* (2006), Chen *et al.* (2007) and Zhang *et al.* (2010). We mapped a QTL for PDN under drought stressed conditions in the vicinity of it. Han *et al.* (2012) reported a seed weight QTL by Satt454. We also identified a QTL for PDN under drought stressed conditions within the interval Satt276-satt454. Some QTLs mapped the regions in this study in line with the regions controlling drought resistant related traits in previous studies. Abdel-Haleem *et al.* (2012) reported a canopy wilt QTL marked by Satt276. Carpentieri-Pipolo *et al.* (2012) reported a drought tolerance QTL marked by Satt454. We mapped a QTL for PDN under drought stressed conditions within the interval Satt276-satt454.

Some other QTLs located the regions in accord with the regions controlling other traits in previous studies. Some were associated with resistances. For example, QTLs marked by Satt237 were detected for salt tolerance (Ha *et al.*, 2013). QTLs by Satt311 were detected for Al tolerance (Korir *et al.*, 2011) and lodging (Reinprecht *et al.*, 2006). Some were associated with chemical constituents of seeds. For example, the locus of Satt237 was detected to control seed phytate (Scaboo *et al.*, 2003; Gao *et al.*, 2008) and seed glycitein (Kassem *et al.*, 2004); the locus of Sat_337 was found to control Seed isoflavone, seed daidzein and seed genistein (Gutierrez-Gonzalez *et al.*, 2010); the locus of Satt530 was detected to control seed oil (Qi *et al.*, 2011); the locus of Satt045 was detected to control seed N (Panthee *et al.*, 2004), seed palmitic and seed oil (Wang *et al.*, 2012). The locus of Satt276 was detected to control seed glycitein (Yoshikawa *et al.*, 2010) and seed daidzein (Kassem *et al.*, 2004).

Yield components are important indirect traits for improving seed yield. Oz *et al.* (2009) think that the number of pods per plant and the number of seeds per pod could be used as a selection criterion in breeding. El-Zeadani *et al.* (2014) think that number of plants per unit area and number of seeds per plant were important features to determine yield potential. Zhu (1995) proposed a conditional analysis approach to dissect the complex relationship and to reveal the net contribution of one trait to another. If the effects change because of conditional mapping 2 close-vicinity QTLs for two traits may be identified as a pleiotropic QTL. Conversely, if the effects of unconditional and conditional QTLs coincide they are more likely to gene linkage for QTLs. In this study, QTL SWP-DS-D2-1 might be pleiotropic, because it involves SWP-DS and 4 yield related traits (PH-DS, PHT-DS, BN-DS and PN-DS)

simultaneously. Meanwhile, it also might be closely linked QTLs in PDN-DS, PNP-DS and SP-DS. Overlapping QTLs for several properties that possibly share a common morpho-physiological basis, or that are reasonably associated on a cause-effect basis, should reduce the false positive rate in the regions where QTLs overlap (Tuberosa *et al.*, 2002). Thus, this QTL was more validity for marker-assisted breeding in the further.

Conclusion

In this study, the yield- related traits under drought stressed environments were different degree decreased. Large-effect loci were detected on near satt514 in the G10-D2 linkage group, Satt606 in the G11-E linkage group and Satt640 in the G6-C21 linkage group as in previous reports. Near satt514 on G10-D2 linkage group, a series of QTLs affecting yield related traits under different water conditions were detected. These QTLs will provide a foundation for further fine mapping and marker-assisted selection under drought stress. Effects of genetic loci on soybean yield related traits were dependent on different water regimes conditions. The *aa* epistatic and *ae* interactions effects were observed for the yield related traits. The QTL SWP-DS-D2-1 for seed weight per plant was considered to be dependent of PDN, PNP and SP; it was partially contributed by PHT, BN and PN; and it unassociated with the variation in PH. These indicated that selection for PDN, PNP and SP is needed in high-yielding line development. This study identified some new loci of *a*, *aa* and *ae* effects for yield related traits, and conditional QTLs for SWP when SWP was conditioned on PDN, PNP or SP in every ambient condition, and refined chromosomal regions of known loci associated with yield related traits in soybean.

Acknowledgments

References

Abdel-Haleem, H., T.E. Carter, L.C. Purcell, C.A. King, L.L. Ries, P. Chen, W. Schapaugh, T.R. Sinclair and H.R. Boerma, 2012. Mapping of quantitative trait loci for canopy-wilting trait in soybean (*Glycine max L. Merr*). *Theor. Appl. Genet.*, 125: 837–846

Alcivar, A., J. Jacobson, J. Rainho, K. Meksem, D.A. Lighfoot and M.A. Kassem, 2007. Genetic analysis of soybean plant height, hypocotyl and internode lengths. *J. Agric. Food Environ. Sci.*, 1: 1–20

Arahana, V.S., G.L. Graef, J.E. Specht, J.R. Steadman and K.M. Eskridge, 2001. Identification of QTLs for resistance to sclerotinia sclerotiorum in Soybean. *Crop Sci.*, 41: 180–188

Carpentieri-Pipolo, V., A.E. Pipolo, H. Abdel-Haleem, H.R. Boerma and T.R. Sinclair, 2012. Identification of QTLs associated with limited leaf hydraulic conductance in soybean. *Euphytica*, 186: 679–686

Carter, Jr. T.E., 1989. Breeding for drought tolerance—where do we stand. *In*: *Proc. World Soybean Research Conf.*, pp: 1001–1008. Pascale, J. (ed.). IV, Buenos Aires. 5–9 March. Asociacion Argentina de la Soja, Buenos Aires, Argentina

Chen, Q.S., Z.C. Zhang, C.Y. Liu, D.W. Xin, H.M. Qiu, D.P. Shan, C.Y. Shan and G.H. Hu, 2007. QTL analysis of major agronomic traits in soybean. *Agric. Sci. Chin.*, 6: 399–405

Du, W.J., D.Y. Yu and S.X. Fu, 2009a. Analysis of QTLs for the trichome densityon the upper and downer surface of leaf blade in soybean [*Glycine max (L.)Merr.*]. *Sci. Agric. Sin.*, 8: 529–537

Du, W.J., S.X. Fu and D.Y. Yu, 2009b. Genetic analysis for the leaf pubescence density and water status traits in soybean [*Glycine max (L.)Merr.*]. *Plant Breed.*, 128: 259–265

Du, W., M. Wang, S. Fu and D. Yu, 2009c. Mapping QTLs for seed yield and drought susceptibility index in soybean (*Glycine max L.*) across different environments. *J. Genet. Genom.*, 36: 721–731

El-Zeadani, H., A.B. Puteh, M.M.A. Mondal, A. Selamat, Z.A. Ahmad and M.M. Shalgam, 2014. Seed growth rate, seed filling period and yield responses of soybean (*Glycine max*) to plant densities at specific reproductive growth stages. *Int. J. Agric. Biol.*, 16: 923–928

Gao, Y., R.M. Biyashev, M.A. Maroof, N.M. Glover, D.M. Tucker and G.R. Buss, 2008. Validation of low-phytate QTLs and evaluation of seedling emergence of low-phytate soybeans. *Crop Sci.*, 48: 1355–1364

Gutierrez-Gonzalez, J.J., X. Wu, J.D. Gillman, J.D. Lee, R. Zhong, O. Yu, G. Shannon, M. Ellersieck, H.T. Nguyen and D.A. Sleper, 2010. Intricate environment-modulated genetic networks control isoflavone accumulation in soybean seeds. *BMC Plant Biol.*, 10: 105–120

Guzman, P.S., B.W. Diers, D.J. Neece, S.K.S. Martin, A.R. LeRoy, C.R. Grau, T.J. Hughes and R.L. Nelson, 2007. QTL associated with yield in three backcross-derived populations of soybean. *Crop Sci.*, 47: 111–122

Ha, B.K., T.D. Vuong, V. Velusamy, H.T. Nguyen, J.G. Shannon and J.D. Lee, 2013. Genetic mapping of quantitative trait loci conditioning salt tolerance in wild soybean (*Glycine soja*) PI 483463. *Euphytica*, 193: 79–88

Han, Y., D. Li, D. Zhu, H. Li, X. Li, W. Teng and W. Li, 2012. QTL analysis of soybean seed weight across multi-genetic backgrounds and environments. *Theor. Appl. Genet.*, 125: 671–683

Kabelka, E.A., S.R. Carlson and B.W. Diers, 2006. *Glycine soja* PI468916 SCN resistance loci associated effects on soybean yield and other agronomic traits. *Crop Sci.*, 46: 622–629

Kassem, M.A., K. Meksem, M.J. Iqbal, V.N. Njiti, W.J. Banz, T.A. Winters, A. Wood and D.A. Lightfoot, 2004. Definition of soybean genomic regions that control seed phytoestrogen amounts. *J. Biomed. Biotechnol.*, 1: 52–60

Kazi, S., J. Shultz, J. Afzal, R. Hashmi, M. Jasim, J. Bond, P.R. Arelli and D.A. Lightfoot, 2010. Iso-lines and inbred-lines confirmed loci that underlie resistance from cultivar 'Hartwig' to three soybean cyst nematode populations. *Theor. Appl. Genet.*, 120: 633–644

Kazi, S., J. Shultz, J. Afzal, J. Johnson, V.N. Njiti and D.A. Lightfoot, 2008. Separate loci underlie resistance to root infection and leaf scorch during soybean sudden death syndrome. *Theor. Appl. Genet.*, 116: 967–977

Kim, H.K., Y.C. Kim, S.T. Kim, B.G. Son, Y.W. Choi, J.S. Kang, Y.H. Park, Y.S. Cho and I.S. Choi, 2010. Analysis of quantitative trait loci (QTLs) for seed size and fatty acid composition using recombinant inbred lines in soybean. *J. Life Sci.*, 20: 1186–1192

Korir, P.C., B. Qi, Y. Wang, T. Zhao, D. Yu, S. Chen and J. Gai, 2011. A study on relative importance of additive, epistasis and unmapped QTL for Aluminum tolerance at seedling stage in soybean. *Plant Breed.*, 130: 551–562

Li, C.D., H.W. Jiang, C.Y. Liu, P.C. Qiu, W.B. Zhang, W.F. Li, Y.L. Gao, Q.S. Chen and G.H. Hu, 2009. Genotype and QTL analysis of drought tolerance loci for directional population in soybean. *Chin. J. Oil Crop Sci.*, 31: 285–292

Li, C.D., X.F. Miao, H.W. Jiang, T. Guo, Z.X. Wang, X.H. Wu, W. Zheng, C.Y. Liu, P.C. Qiu, W.B. Zhang and Y.N. Luan, 2011. QTL identification of WRC to soybean in drought tolerance selection population. *Chin. Agric. Sci. Bull.*, 27: 152–155

Li, W., D.H. Zheng, K. Van and S.H. Lee, 2008. QTL Mapping for major agronomic traits across two years in soybean (*Glycine max* L. Merr.). *J. Crop Sci. Biotechnol.*, 11: 171–190

Lincoln, S.E. and S.L. Lander, 1993. *Mapmaker/exp 3.0 and Map-Maker/QTL 1.1*. Whitehead Inst. Med. Res. Tech. Report. White head Inst., Cambridge, UK

Liu, X.Y., 1991. *Culture Technique in Soybean*. Shanxi higher education joint press, Taiyuan China

Liu, Y., J.Y. Gai, H.N. Lu, Y.J. Wang and S.Y. Chen, 2005. Identification of drought tolerant germplasm and inheritance and QTL mapping of related root traits in soybean [*Glycine max (L.) Merr.*]. *Acta. Genet. Sin.*, 32: 855–863

Mian, M.A.R., D.A. Ashley and H.R. Boerma, 1998. An additional QTL for water use efficiency in soybean. *Crop Sci.*, 38: 390–393

Mian, M.A.R., M.A. Bailey, D.A. Ashley, R. Wells, T.E. Carter, W.A. Parrott and H.R. Boerma, 1996. Molecular markers associated with water use efficiency and leaf ash in soybean. *Crop Sci.*, 36: 1252–1257

Nguyen, V.T., T.D. Vuong, T. VanToai, J.D. Lee, X. Wu, M.A. Mian, A.E. Dorrance, J.G. Shannon and H.T. Nguyen, 2012. Mapping of quantitative trait loci associated with resistance to Phytophthora sojae and flooding tolerance in soybean. *Crop Sci.*, 52: 2481–2493

Oz, M., A. Karasu, A.T. Goksoy and Z.M. Turan, 2009. Interrelationships of agronomical characteristics in soybean (*Glycine max*) grown in different environments. *Int. J. Agric. Biol.*, 11: 85–88

Panthee, D.R., V.R. Pantalone, C.E. Sams, A.M. Saxton, D.R. West and W.E. Rayford, 2004. Genomic regions governing soybean seed nitrogen accumulation. *J. Amer. Oil Chem. Soc.*, 81: 77–81

Qi, Z.M., Q. Wu, X. Han, Y.N. Sun, X.Y. Du, C.Y. Liu, H.W. Jiang, G.H. Hu and Q.S. Chen, 2011. Soybean oil content QTL mapping and integrating with meta-analysis method for mining genes. *Euphytica*, 179: 499–514

Reinprecht, Y., V.W. Poysa, K. Yu, I. Rajcan, G.R. Ablett and K.P. Pauls, 2006. Seed and agronomic QTL in low linolenic acid, lipoxygenase-free soybean (*Glycine max (L.) Merrill*) germplasm. *Genome*, 49: 1510–1527

Scaboo, A.M., V.R. Pantalone, D.R. Walker, H.R. Boerma, D.R. West, F.R. Walker and C.E. Sams, 2003. Confirmation of molecular markers and agronomic traits associated with seed phytate content in two soybean RIL populations. *Crop Sci.*, 49: 426-432

Specht, J.E., K. Chase, M. Macrander, G.L. Graef, J. Chung, J.P. Markwell, M. Germann, J.H. Orf and K.G. Lark, 2001. Soybean response to water: A QTL analysis of drought tolerance. *Crop Sci.*, 41: 493–509

Specht, J.E., J.H. Williams and C.J. Weidenbenner, 1986. Differential responses of soybean genotypes subjected to a seasonal soil water gradient. *Crop Sci.*, 26: 922–934

Sun, D., W. Li, Z. Zhang, Q. Chen, H. Ning, L. Qiu and G. Sun, 2006. Quantitative trait loci analysis for the developmental behavior of Soybean (*Glycine max L. Merr.*). *Theor. Appl. Genet.*, 112: 665–673

Tuberosa, R., M.C. Sanguineti, P. Landi, M.M. Giuliani, S. Salvi and S. Conti, 2002. Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two regimes. *Plant. Mol. Biol.*, 48: 697–712

Vieira, A.J.D., D.A.D. Oliveira, T.C.B. Soares, I. Schuster, N.D. Piovesan, C.A. Martinez, E.G.D. Barros and M.A. Moreira, 2006. Use of the QTL approach to the study of soybean trait relationships in two populations of recombinant inbred lines at the F_7 and F_8 generations. *Braz. J. Plant. Physiol.*, 18: 281–290

Wang, D., J. Shi, S.R. Carlson, P.B. Cregan, R.W. Ward and B.W. Diers, 2003. A low-cost, high-throughput polyacrlylamide gel electrophoresis system for genotyping with microsatellite DNA markers. *Crop Sci.*, 43: 1828–1832

Wang, M., W.M. Yang and W.J. Du, 2012. Construction of a molecular marker linkage map and its use for quantitative trait locus (QTLs) underlying drought tolerance at germination stage in soybean. *Afr. J. Biotechnol.*, 11: 12830–12838

Wang, X., G.L. Jiang, M. Green, R.A. Scott, D.L. Hyten and P.B. Cregan, 2012. Quantitative trait locus analysis of saturated fatty acids in a population of recombinant inbred lines of soybean. *Mol. Breed.*, 30: 1163–1179

Xu, Z.R. and X.Z. Zhang, 1989. *Soybean Physiology and Physiological Breeding*. Heilongjiang Science and Technology Press, Harbin, China

Yang, J., C. Hu, H. Hu, R. Yu, Z. Xia, X. Ye and J. Zhu, 2008. QTL Network: mapping and visualizing genetic architecture of complex traits in experimental populations. *Bioinformatics*, 24: 721–723

Yang, J., J. Zhu and R.W. Williams, 2007. Mapping the genetic architecture of complex traits in experimental populations. *Bioinformatics*, 23: 1527–1536

Yoshikawa, T., Y. Okumoto, D. Ogata, T. Sayama, M. Teraishi, M. Terai, T. Toda, K. Yamada, K. Yagasaki, N. Yamada and T. Tsukiyama, 2010. Transgressive segregation of isoflavone contents under the control of four QTLs in a cross between distantly related soybean varieties. *Breed. Sci.*, 60: 243–254

Zhang, D., H. Cheng, H. Wang, H. Zhang, C. Liu and D. Yu, 2010. Identification of genomic regions determining flower and pod numbers development in soybean (*Glycine max L*). *J. Genet. Genomics*, 37: 545–556

Zhu, J., 1995. Analysis of conditional genetic effects and variance components in developmental genetics. *Genetics*, 141: 1633–1639

Zhu, J., 1997. *Analysis Approaches for Genetic Models*. Chinese Agricultural Press, Beijing, China