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QTL mapping of soybean resistance to whitefly (*Bemisia Tabaci* Gennadius) under multi-environment conditions

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Abstract

Whitefly (*Bemisia tabaci* Gennadius) is an agricultural pest that widely occurs and severely harms soybeans around the world. Preventing and controlling whitefly infestation is difficult. In addition, identification of resistance to whitefly is difficult and time-consuming. Marker assisted selection (MAS) has been considered as a most effective way to breed whitefly-resistant soybean varieties. This study investigates the quantitative trait loci (QTL) of whitefly resistance in soybean in multi-year and multi-site trials to provide useful information for soybean breeding. The JRB1F_2 population (Huapidou × Qihuang26), consisting of 170 plants, was used to construct a genetic linkage map with simple sequence repeat markers to identify the QTLs associated with whitefly resistance. Eight QTLs, directly associated with whitefly resistance, were identified in the JRB1$F_{2:3}$ population derived from the JRB1F_2 population in Jinan and Guanxian in 2008 to 2010, using both of the composite interval mappings of Win QTL Cartographer Version 2.5. Six QTLs were detected in Jinan, in which the maximal accounts for 37.3% on chromosome 17 between sat_326 and sat_172, whereas the minimal accounts for 9.2% on chromosome 5 between satt236 and sat_271. Two QTLs were detected in Guanxian, accounting for 36.9% and 16.1% on chromosomes 1 and 2, respectively. These identified QTLs would be beneficial for MAS of whitefly resistant soybean varieties.

Keywords: Soybean; Whitefly (*Bemisia tabaci* Gennadius); Simple sequence repeats; Quantitative trait loci; Multi-environment.
Abbreviations: QTL- quantitative trait loci; MWPL- the mean of whitefly nymphs per leaflet; SSR- simple sequence repeats; LOD- logarithm of odds; MAS- marker assisted selection.

Introduction

Soybean (*Glycine max*) is one of the most important crop plants because of its seed protein and oil content, as well as its capacity to fix atmospheric nitrogen through symbiosis with soil-borne microorganisms. Soybean is important as a predominant plant source of both animal feed protein and cooking oil (Schmutz et al., 2010). Whitefly (*Bemisia tabaci* Gennadius) is an agricultural pest that widely occurs and severely harms soybeans around the world. Preventing and controlling whitefly infestation is difficult. Planting of resistant cultivars is the most effective, economical and environmentally friendly strategy to manage whitefly.

Whitefly needs temperature higher than 26°C and 60% relative humidity for optimum development (Butler et al., 1983). A female adult lays approximately 160 eggs in a generation, with 11 to 12 generations in a year. Whiteflies reduce crop yield by direct plant consumption and is also a vector for numerous plant viruses (Mann et al., 2008; Sidhu et al., 2009). Whitefly nymphs and adults feed in the phloem and obtain sap that contains various sugars (Hendrix et al., 1992). The injury caused by whiteflies to soybeans is attributed to whitefly nymphs and adults that suck sap from the leaves, thereby secreting abundant honeydew. This honeydew contains metabolized sugars and forms a suitable medium for the development of a dark sooty mold that inhibits light penetration and reduces photosynthesis. Whitefly infestation is usually heaviest during the pod-filling period, causing severe yield reductions. Chemical control of whitefly is expensive because insecticides lose their effects rapidly (Ullah et al., 2006). Chemical control of whitefly is also difficult because of the development of pesticide-resistant whitefly strains. The development of pesticide resistant strains is extremely fast because of the short generation time (egg to adult in as little as 12 days during summer) of whitefly, which can develop into billions/ha (Horowitz and Ishaaya, 1996). Soybean plants cannot grow normally due to whitefly damage, forcing the fruit to ripen earlier than the normal maturity (Touhidul and Shunxiang, 2009). Arioglu et al. (1989) reported a significant decrease in seed yield due to whitefly damage in a Mediterranean environment.

Therefore, breeding whitefly-resistant soybean cultivars is one of the most important factors to consider increasing or maintaining seed yield in whitefly infested soybean planting areas. Identification of whitefly resistance genotypes is difficult and time-consuming; thus, marker assisted selection (MAS) is the most effective way to breed whitefly-resistant soybean varieties.

A total of 109 soybean cultivars were screened against whitefly between 1976 and 1986. Forty two cultivars exhibited high resistance, in which 25 cultivars were resistant, 16 cultivars moderately resistant, 14 cultivars susceptible and 12 cultivars highly susceptible (Arioglu, 1987). Lambert et al. (1997) evaluated 14 soybean genotypes in maturity groups VII–VIII for resistance to *Bemisia argentifolii* in 1993 and

Table 1. Difference between two parents and variations among the JRB1F_2 in the mean of whitefly nymphs per leaflet.

Environment	Parent		JRB1F_2 population		
	Huapidou	Qihuang26	Average	Range	CV (%)
E108	1.27±0.18	8.37±0.55	3.64±0.15	0.30－10.90	53.49
E109	1.33±0.30	8.67±0.30	3.65±0.13	0.48－9.50	44.10
E110	2.08±0.28	7.68±0.40	3.36±0.15	0.07－14.82	57.63
E209	1.33±0.31	8.23±0.57	3.54±0.17	0.20－14.33	60.79
E210	0.04±0.01	7.50±0.47	3.75±0.17	0.04－12.48	59.23

E108, E109, E110, at the Experimental Field of Shandong Academy of Agricultural Sciences, Jinan, China for 2008 to 2010; E209, E210, at Base Seed Production Farm in Guanxian, Shandong Province, China for 2009 and 2010; CV, coefficient of variation.

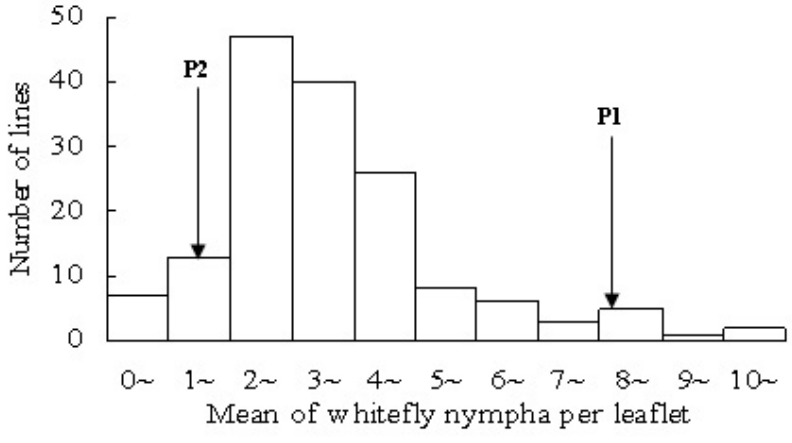

Fig 1. Frequency distribution of MWPL in JRB1F_2 population at Jinan in 2008

1994. They observed significant difference in the mean whitefly density among the 14 soybean genotypes. Xu et al. (2005) screened 223 cultivars and obtained 6 cultivars with high whitefly resistance. Recently, Perez-Sacketta et al. (2011) identified the quantitative trait loci (QTL) for whitefly resistance in soybeans in Northwest Mexico. They used two F_2 segregating populations for whitefly resistance development. They showed that whitefly resistance is a polygenic trait controlled by QTL on different chromosomes.

The significant QTLs detected were located on chromosomes 12, 18 and 19. However, little work has been done to identify QTL in multi-year and multi-site trails for whitefly resistance in soybean. Therefore, this study investigates the QTL of whitefly resistance in soybean in multi-year and multi-site trails, which would provide information for MAS of whitefly-resistant soybean varieties.

Results

Trait performance

The male parent, Qihuang26, had significantly higher the mean of whitefly nymphs per leaflet (MWPL) than that of the female parent, Huapidou, in a multi-environment (Table 1). The MWPL of JRB1F_2 was lower than that of the mid-parent in a multi-environment. MWPL values in the JRB1F_2 population showed a continuous variation and distorted distribution (Figs. 1–5).

Polymorphic markers and genetic linkage map

Among the 600 simple sequence repeats (SSR) primers, 93 (16%) polymorphisms were detected between Huapidou and Qihuang26. A genetic map that consist of 83 SSR markers on 16 chromosomes was constructed, which was 1714.4 cM long, with an average distance of 20.7 cM between adjacent markers (Fig. 6). Using the χ^2-test for the goodness of fit, the expected allelic frequency was 1:1 (Huapidou allele: Qihuang26 allele). All 93 microsatellite loci were tested for segregation distortion. Although 47.3% of the tested markers exhibited distortion segregation in the JRB1F_2 population (P<0.05), their order and distribution on 20 chromosomes still coincided with the observation of Cregan et al. (1999) and Song et al. (2004). The total allele frequency for the JRB1F_2 population was 0.465 and 0.535 for Huapidou and Qihuang26, respectively, fitting the 1:1 expected allelic frequency.

Thirty-five unlinked markers were arranged according to the sequence of markers on the soybean physical map. Satt184 was upstream of satt436 on chromosome 1. Satt157 was upstream of satt579, whereas satt271 and sat_183 were downstream of satt041 on chromosome 2. Sat_084 and sct_195 were upstream of satt660 on chromosome 3. Sct_191 was downstream of satt646 on chromosome 4. Satt211 was located between satt236 and sat_271, whereas sat_368 was upstream of satt619 on chromosome 5. Satt323 and sat_148 were downstream of satt540 on chromosome 7. Satt177 was upstream of satt119 on chromosome 8. Satt196 was downstream of satt326 on chromosome 9. Satt173 was located between satt479 and satt241, whereas satt358 was upstream of satt259 on chromosome 10. Satt444 was downstream of satt638 on chromosome 11. Satt425 was upstream of satt072, whereas satt656 was downstream of satt490 on chromosome 13. Satt411 was upstream of satt598 on chromosome 15. Satt244 and sat_165 were downstream of satt654 on chromosome 16.

Table 2. QTLs identified for the mean of whitefly nymphs per leaflet using the WinQTLCart method in multi-year and multi-site trails

QTL	Environment	Marker interval[a]	Distance(cM)[b]	LOD value	Additive effect[c]	Variance explained(%)
qRWF-1	E209	satt071-satt147	3.6	2.76	+0.69	36.9
qRWF-2	E210	satt604-satt041	6.3	3.15	+0.37	16.1
qRWF-3	E108	sat_304-satt022	13.1	2.52	+0.22	11.1
qRWF-3	E110	sat_304-satt022	1.1	2.54	+0.14	12.6
qRWF-5-1	E109	satt619-satt545	1.0	3.77	+0.37	23.6
qRWF-5-2	E109	satt236-sat_271	3.0	2.74	-0.17	9.2
qRWF-16	E109	satt654-sct_065	2.0	3.00	+0.20	12.4
qRWF-17-1	E110	satt674-sat_326	5.2	2.51	+0.16	16.0
qRWF-17-2	E108	sat_326-sat_172	11.7	3.09	+0.10	37.3

[a]Bold letters indicate the nearest marker; [b] Distance from the nearest marker to putative QTL; [c] '+' and '–' mean that positive alleles come from Huapidou and Qihuang26, respectively. E108, E109, E110, at the Experimental Field of Shandong Academy of Agricultural Sciences, Jinan, China for 2008 to 2010; E209, E210, at Base Seed Production Farm in Guanxian, Shandong Province, China for 2009 and 2010

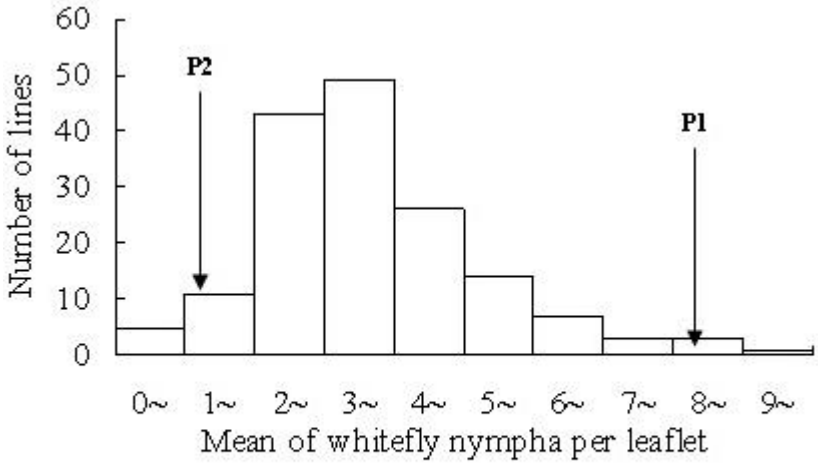

Fig 2. Frequency distribution of MWPL in JRB1F_2 population at Jinan in 2009

Satt311 was located between satt461 and satt574, satt672 was located between satt186 and satt031, sctt008 was upstream of satt397 on chromosome 17. Sat_191 was upstream of satt156 on chromosome 19 (Fig. 6). In addition, ten markers were located on chromosomes 6, 12, 14, 18 and 20 of this unlinked experiment.

QTL for MWPL detected using WinQTLCartographer method

According to the genome-wide type I and error of 5%, the logarithm of odds (LOD) threshold value for MWPL were 2.49, 2.69 and 2.47 in the E108, E109 and E110 environment, 2.67 and 2.91 in the E209 and E210 environment, respectively. Eight QTLs, namely, qRWF-1, qRWF-2, qRWF-3, qRWF-5-1, qRWF-5-2, qRWF-16, qRWF-17-1 and qRWF-17-2, were detected on chromosomes 1, 2, 3, 5, 5, 16, 17 and 17, respectively. These QTLs accounted for the phenotypic variances from 9.2% to 37.3%. One QTL, qRWF-3, was detected in both environments, accounting for 11.1% in the E108 environment and 12.6% in the E110 environment of the phenotypic variances, respectively. The alleles from Qihuang26 increased the MWPL at qRWF-5-2, whereas the alleles from Huapidou decreased the MWPL at qRWF-1, qRWF-2, qRWF-3, qRWF-5-1, qRWF-16, qRWF-17-1 and qRWF-17-2. No significant genotype and environment interaction were observed in these QTLs (Table 2).

Discussion

The present situation of the insect-resistance of crops

Improving the insect-resistance of crops is an important study in genetic breeding. Studying the genetic rule and molecule mechanism of insect-resistance is necessary to gain insights of theories to increase breeding efficiency. The resistance of soybean to whitefly is an important contribution to the study of insect-resistance; however, this topic is less studied.

The study situation of QTL genetic map

We obtained 93 SSR markers (out of 600 primers) that showed polymorphisms between soybean cultivars Huapidou and Qihuang26 and constructed a genetic linkage map based on the resistance/susceptibility of soybean to whitefly, derived from the JRB1F_2 population. Huapidou had high resistance, whereas Qihuang26 was highly susceptible to whitefly. Compared with other genetic linkage maps based on soybean intra-subspecies population, the current genetic linkage map has the following

two advantages. First, more informative sites were contained in the map; whitefly resistance showed an obvious advantage. Second, the SSR markers in this map were facilitated for subsequent research. However, 35 markers were unlinked on the map when MAPMAKER/EXP VER3.0 was implemented. We tried to insert the 35 markers on our genetic linkage map according to the sequence of markers on the physical map of soybean using two-point testcross and the Kosambi function conversion method. Unexpectedly, the distance of two adjacent markers was more than 50 cM, although the recombination rate was less than 50%. Three SSR markers with both whitefly-resistant association and with other trait association were observed (Cregan et al., 1999; Song et al., 2004). Satt022 was associated with leaf length, oil and plant height. Satt147 was associated with *Sclerotinia Sclerotiotum* (Lib.) de Bary seed weight. Satt545 was associated with *S. sclerotiotum* (Lib.) de Bary plant height, node numbers and leaf width.

Whiteflies distribution, harm and resistance mechanisms

Whiteflies are complex cryptic species distributed across Africa, southern Europe, the Middle East, the Indian Subcontinent, Asia, Australia, the Pacific and the Americas (Dinsdale et al., 2010). A number of the species that commercially cause a complex damage to important plant species either through direct feeding (Oliveira et al., 2001) or the transmission of more than 120 plant viruses primarily belonging to the genus *Begomovirus* (family Geminiviridae) (Hogenhout et al., 2008). Whitefly resistance is an important genetically controlled trait and is directly related to the genetic structure and phenologic characteristics of the cultivars (Perez et al., 2009). A study provides the most comprehensive sequence resource available for whitefly study and demonstrates that the Illumina sequencing allows *de novo* transcriptome assembly and gene expression analysis in a species lacking genome information (Wang et al., 2010).

There are findings that provide important information about tobacco whitefly chlorpyrifos resistance mechanisms and guidance to combat resistance and optimize use patterns of chlorpyrifos and other organophosphate and carbamate insecticides (Zhang et al., 2012).

Compared the insect-resistance of crops

Compared with previous studies on QTL controlling MWPL, whitefly resistance is a polygenic trait controlled by QTL on different chromosomes. The significant detected QTLs were located on chromosomes 12, 18 and 19 (Perez-Sacketta et al., 2011). This study showed the distribution of MWPL QTLs on chromosomes 1, 2, 3, 5, 16 and 17, which may be attributed to the different QTLs result in the interactions between genotype and environment, different types of insects, or different materials. The QTL of other insect-resistant strains were located in the soybean. QTL have also been detected from corn borer (Boerma et al., 2005; Walker et al., 2004; Zhu et al., 2006) and cotton worm [*Prodenia litura* (L.) Fabricius] (Komatsu et al., 2005; Wang et al., 2004; Liu et al., 2005), a gene of soybean aphid (Li et al., 2007). The major effective QTL of corn borer antibiosis and selection of resistance (Rector et al., 2000), the major effective QTL of cotton worm (Komatsu et al., 2005) and gene of resistant aphid (Li et al., 2007) were located on satt463 in chromosome 7. The QTLs of corn borer resistance were detected at four different populations in chromosome 12 (Terry et al., 2000). The greater effective QTLs of corn borer were located at three different populations on

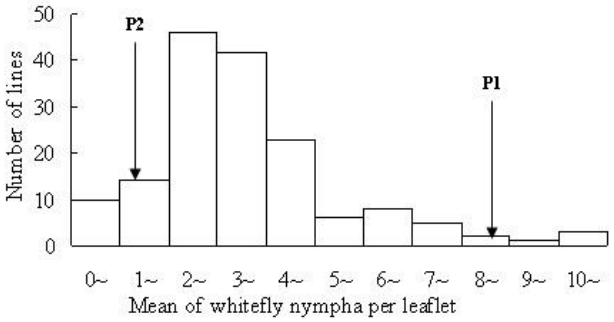

Fig 3. Frequency distribution of MWPL in JRB1F$_2$ population at Gunanxian in 2009

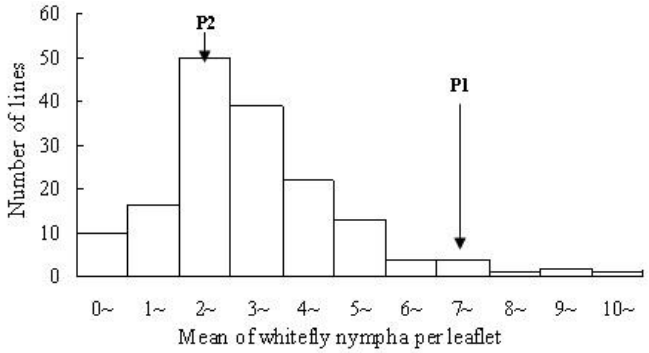

Fig 4. Frequency distribution of MWPL in JRB1F$_2$ population at Jinan in 2010

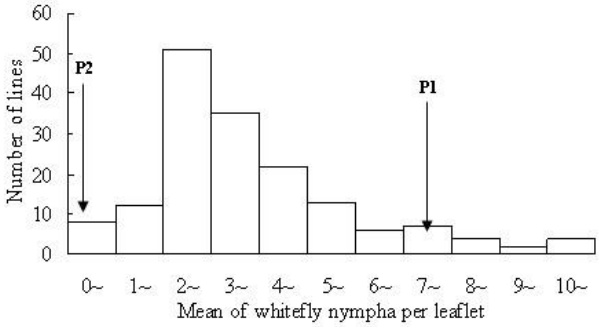

Fig 5. Frequency distribution of MWPL in JRB1F$_2$ population at Guanxian in 2010

chromosome 15 (Terry et al., 2000; Boerma et al., 2005). Thus, the QTL of corn borer were detected in chromosomes 7, 12 and 15. In addition, the QTLs of corn borer were located at two populations in chromosomes 6, 13 and 16, at a population in chromosomes 5, 14, 1, 2, 17 and 18. This study identified the QTLs similar to those of previous studies on different chromosomes, which would be beneficial for MAS of whitefly resistant varieties. The whitefly resistance of soybean has the complexity of inheritance and needs the identification and analysis of multi-year, multi-site trails and multi-population. The analysis of QTL in a segregating population can identify the markers linked to QTL, which can be used in MAS to decrease soybean whitefly damage, with the ultimate aim of increasing soybean yield.

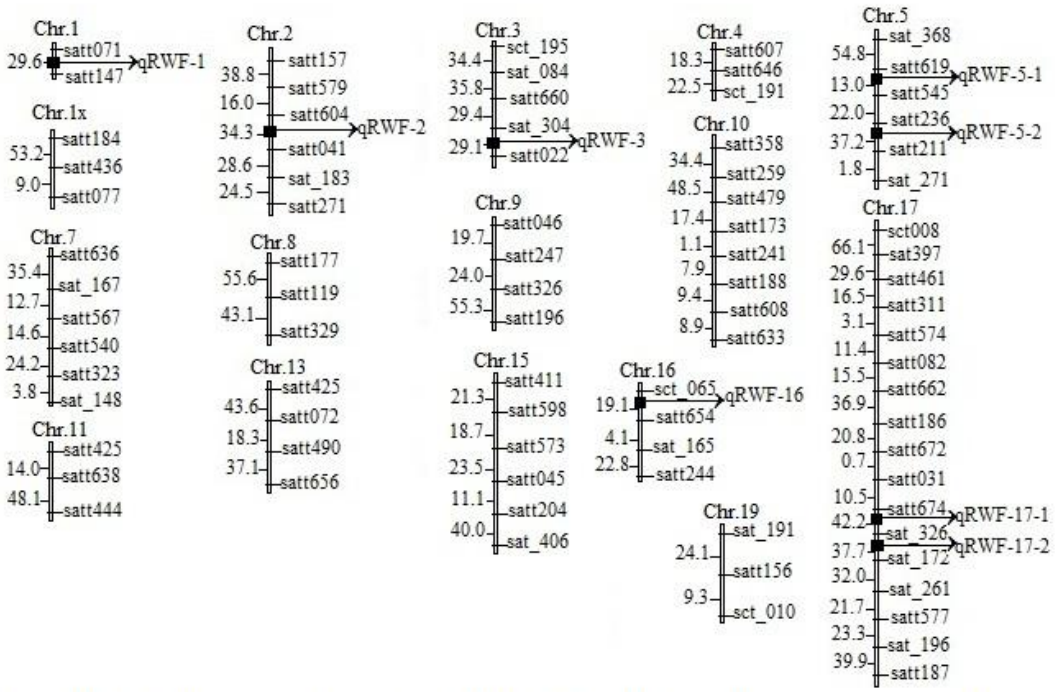

Fig.6 SSR lingkage map based on JRB1F$_2$ derived from the soybean cross Huapidou/ Qihuang26 and chromosomal locations of QTLs for the mean of whitefly nymphs per leaflet

Moreover, the QTL analysis for the soybean resistance to whitefly can also lead to the prediction of candidate genes that determine whitefly development in the detected QTL regions.

Materials and methods

Experimental population and phenotypic measurement

Huapidou, the high whitefly-resistant soybean landrace and Qihuang26, the high whitefly-susceptible cultivar, were obtained from Shandong Academy of Agricultural Sciences (Jinan, China). A cross was made between the two cultivars at the Experimental Field of Shandong Academy of Agricultural Sciences in Jinan in 2006. One F_1 plant was picked based on morphological markers, such as flower color, to produce the F_2 generation. All F_2 plants were advanced separately to produce JRB1F_2 using the single seed descent method population. Thus, the JRB1F_2, consisted of 170 plants, which was derived from this cross. The female parent, Huapidou, is a soybean landrace from Shandong. The male parent, Qihuang26, is a released soybean cultivar from Shandong in 1999, with a plant height of approximately 75 cm and protein content and oil contents of approximately 46% and 18%, respectively. Huapidou, Qihuang26 and the JRB1F_2 plants were planted with high whitefly density at the Experimental Field of the Shandong Academy of Agricultural Sciences in Jinan, China (E1 environment) and Base Seed Production Farm in Guanxian, Shandong Province, China (E2 environment) from 2008 to 2010. Parents and JRB1$F_{2:3}$ were planted with three replicates in each environment. Each material was planted in three rows using single seed sowing; each row is 1 m, with 50 cm row spacing and 10 cm plant spacing. Conventional field management was carried out. Result of whitefly diseases were not observed at Guanxian in 2008. Soybean whitefly test is carried out at late August to mid-September, where the whitefly density is highest in the Shandong Province.

The relationship between different resistance indices was also comprehensively analyzed according to Xu et al. (2009). We investigated MWPL using 5-plant plot random measurements to determine the number of 2–4 instar nymphs in the middle-leaflet of the trifoliolate of the main stem of each plant.

SSR molecular marker analysis

Simple sequence repeat (SSR) primers were synthesized according to the sequences published by Cregan et al. (1999), Song et al. (2004) and SoyBase (http://www.129.186.26.94/ssr.html). A total of 600 SSR primers distributed throughout the 20 soybean chromosomes were initially analyzed for polymorphism using parental DNA. The 170 JRB1F_2 plants were genotyped using a selected set of polymorphic markers. Ninety-three SSR primers with polymorphism between parents were obtained, accounting for 16% of the total primers screened. Total genomic DNA from the JRB1F_2 population and both parents was extracted according to the method described by Ma et al. (2011), with the PCR reaction adjusted to 20 ng/μl. The 10 μl PCR reaction buffer composed of 20 ng total DNA, 0.4 μM forward and reverse primers, 200 μM of each dNTPs, 1 × PCR buffer (10 mM of Tris-HCl, pH 8.3, 50 mM of KCl), 2 mM of $MgCl_2$ and 0.5 U of Taq DNA polymerase. PCR was programmed with an initial denaturing at 94°C for 3 min, followed by 30 cycles at 94°C for 30 s, 55°C for 60 s, 72°C for 1 min, with a final extension at 72°C for 8 min. PCR reactions were performed using an MJ Research PTC 225 DNA engine thermal cycler (Bio-RAD, USA). Amplified products were fractionated by electrophoresis through 8% non-denaturing polyacrylamide gels, stained and visualized via silver staining and scored as either parental (1 or 2), heterozygous (3) alleles or missing data (-).

Construction of genetic map and QTL analysis

The genetic linkage map was constructed using MAPMAKER/ EXP VER3.0. Associations between traits and markers were analyzed using composite interval mapping introduced in WinQTLCartographer 2.5 (Wang et al., 2012). Threshold was determined using the permutation method (1000 times; $P<0.05$) (Churchill and Doerge, 1994). A putative QTL was detected between the markers when the LOD score was larger than the threshold. The differences of phenotypic values between marker genotypes were calculated in each environment according to the flank markers of a QTL. A significant interaction between QTL and the environment was observed when the difference between the two environments was significant at 5% probability level using the *t*-test. Standard errors and free degrees for the *t*-test were calculated via a scaling test (Mather and Jinks, 1982).

Conclusion

Our results indicate that 8 QTLs directly associated with whitefly resistance were localized. This information would benefit the understanding of the genetic mechanism of the different whitefly ability between resistance and susceptible soybean cultivar. The genotypes with good whitefly response can be selected using DNA markers that are tightly linked to these QTLs. These identified QTLs would be beneficial for MAS of whitefly resistant soybean varieties.

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