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RESEARCH ARTICLE

Mapping of Quantitative Trait Loci for Yield and Grade Related Traits in Peanut (*Arachis hypogaea* L.) Using High-Resolution SNP Markers

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ABSTRACT Yield and grade are the key factors that affect production value of peanut. The objective of this study was to identify QTLs for pod yield, hundred-seed weight, and total sound mature kernel (TSMK). A total of 90 recombinant inbred lines, derived from Tamrun OL07 and a breeding line Tx964117, were used as a mapping population and planted in Brownfield and Stephenville, Texas. A genetic map was developed using 1,211 SNP markers based on double digest restriction-site associated DNA sequencing (ddRAD-seq). A total of 10 QTLs were identified above the permutation threshold, three for yield, three for hundred-seed weight and four for TSMK, with LOD score values of 3.7 - 6.9 and phenotypic variance explained of 12.2% - 35.9%. Among those, there were several QTLs that were detected in more than one field experiment. The commonly detected QTLs in this study may be used as potential targets for future breeding program to incorporate yield and grade related traits through molecular breeding.

Keywords Peanut (*Arachis hypogaea* L.), Groundnut, Yield, Quality, TSMK, QTL mapping

INTRODUCTION

Peanut (*Arachis hypogaea* L.) is the third most widely grown oilseed crop in the world, planted more than 26 million hectares in 2017 (https://apps.fas.usda.gov/psdonline/circulars/production.pdf). Peanut has an excellent nutrient profile, with high oil (40%-60%) and protein (20%-30%) content (Mallikarjuna and Varshney 2014). Among all crops in the USA, peanut is the eighth biggest crop and second biggest oilseeds crop by value, and accounts for more than US$1.6 billion production value in 2017 (http://usda.mannlib.cornell.edu/usda/current/CropValuSu/CropValuSu-02-23-2018.pdf). Texas is the second largest peanut producer in the US with 275,000 acres planting area in 2017. The average peanut production in major peanut producing states in the US is 3,941 pounds per acre, while it is 3,600 pounds per acre in Texas (https://www.nass.usda.gov/Quick_Stats/Ag_Overview/stateOverview.php?state=texas). In addition to yield, the other key aspect for peanut production is grade, which is the quality of the processed peanut. The grade of peanut can be separated into different components such as sound mature kernel (SMK), sound split kernel (SS), damage kernel (DK) and other kernel (OK), according to shelled kernel size, sound kernel rate, split kernel rate and damaged kernel rate. The importance of grade is not only to help capture higher market prices but also provides better storage conditions to prevent aflatoxin contamination (Whitaker *et al*. 2005). In the US peanut industry, percentage TSMK is the major criteria for peanut grading (https://www.ams.usda.gov/grades-standards/shelled-runner-type-peanuts-grades-and-standards). To improve peanut yield and quality, most previous studies have focused on field management, nematode resistance, disease resistance

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and other environmental controls (Wehtje *et al*. 1984; Faircloth and Prostko 2010; Wheeler *et al*. 2012; Burow *et al*. 2014; Arnold *et al*. 2017; Liang *et al*. 2017).

Peanut is an allotetraploid crop (AABB, 2n = 4x = 40) which hybridized naturally from two diploid wild species, *A. duranesis* (AA) and *A. ipaensis* (BB). The first SSR-based linkage map of cultivated peanut was developed in the last decade (Varshney *et al*. 2009). So far, however, there have been limited studies on improving peanut production and quality using genetic tools (Khedikar *et al*. 2010; Gautami *et al*. 2012; Wang *et al*. 2013; Burow *et al*. 2014). Compared with other major crops, research in peanut genetics is behind due to its genome complexity and low DNA polymorphism rates (Mallikarjuna and Varshney 2014).

Quantitative trait loci (QTL) mapping has been used as one of the standard methods to ultimately identify the genes underlying the QTL in many crops, including rice, wheat and peanut (McCough and Doerge 1995; Buerstmayr *et al*. 2009). Up to now, only a few peanut QTL studies for yield and its components have been reported (Gomez Selvaraj *et al*. 2009; Liang *et al*. 2009; Varshney *et al*. 2009; Ravi *et al*. 2010; Shirasawa *et al*. 2012). Furthermore, no previous study has investigated QTLs corresponding to grade-related traits. Therefore, the major objective of the present study was to map QTLs affecting peanut yield and grade using the same RIL population and genetic map that we have used in our previous study in mapping QTL for leaf spot disease (Liang *et al*. 2017). The double digest restriction-site associated DNA sequencing (ddRAD-seq) genotyping method was used to produce the genetic map with high density SNP markers (Baird *et al*. 2008; Peterson *et al*. 2012). The RIL population was developed from a cross between an elite released cultivar, Tamrun 0L07, a runner type cultivar having high yield, good percentage of TSMK, and high oleic to linoleic fatty acid ratio (O/L) (Baring *et al*. 2006), and a Texas breeding line Tx964117, having high level of resistance to early and late leaf spot but only having average yield potential, poor percentage of TSMK, and normal O/L. Major QTLs detected in this study can be used as potential targets for future molecular breeding efforts to increase yield and grade in peanut.

MATERIALS AND METHODS

Plant materials

A RIL mapping population consisting of 90 lines that had been used in our previous study to identify QTLs for leaf spot disease (Liang *et al*. 2017), was used in this current study. The high oleic released cultivar Tamrun OL07, with high yield potential, high grade potential and resistance for *Tomato spotted wilt virus* (TSWV) and Sclerotinia blight was the female parent, and the breeding line Tx964117 with resistance to early and late leaf spot (unpublished data) was the male parent.

Field experiments and phenotyping

Phenotypic data were collected from experimental field stations in Brownfield and Stephenville, Texas in 2010 and 2012 using $F_{2:5}$ and $F_{2:6}$ mapping populations, respectively. Brownfield located in West Texas has an average of 24°C to 33°C daytime temperature and 6.1 cm precipitation per month during May to October, the growing season for peanut in this region. Stephenville has an average of 25.5°C to 35°C daytime temperature and 7.9 cm precipitation per month during the growing season. With no disease history and an ideal environment for peanut cultivation, Brownfield has become the best location to test yield potential and grade of peanut. On the other hand, the Stephenville nursery has mainly been used to conduct Sclerotinia blight disease experiments. Both experimental fields were conducted by randomized complete block design (RCBD) with three replications. Plots were two-rows wide measuring 1.83 m wide by 3.05 m in length. Both parents were replicated five times as controls in each replication in both years.

For phenotyping, yield, hundred seed weight, and total sound mature kernels (TSMK) were measured. Yield was measured as pod gram-weight per two-row plot. Hundred seed weight was one hundred mature seeds riding slotted screen. TSMK was calculated from sound mature kernels (SMK) and sound splits (SS). SMK and SS were measured as gram-weight of sound mature kernels riding slotted 0.64 cm × 1.9 cm screen plus sound splits, and removing damaged kernels. For each TSMK measurement, 250 g of pods were taken, shelled, and screened. TSMK was

calculated using the following formula:

$$TSMK\ \% = \frac{SMK\ (g) + SS\ (g)}{250\ (g)} \times 100\%$$

Genotyping

As previously reported in our study (Liang *et al*. 2017), our genotyping was performed using the restriction site association based method, ddRAD-seq (Peterson *et al*. 2012), digested DNA with two restriction enzymes, i.e. *PstI* and *MluCI*, with a library preparation of Peterson *et al*. (2012). The genotyping used Illumina HiSeq 2500v4 platform for sequencing. A total of 260,445,423 raw sequencing reads were processed, 17,341 SNPs were called, and 1,211 SNPs were used to construct the genetic map.

Linkage map construction and QTL analysis

The genetic map was constructed by MSTMAP software (Wu *et al*. 2008) as described in our previous study (Liang *et al*. 2017). Windows QTL cartographer 2.5 (Wang *et al*. 2012) was used to perform QTL analysis. Composite interval mapping (CIM) analysis was performed using Kosambi map function with Ri1 cross type (recombinant inbred line, derived by selfing), and forward and backward regression method was used with F-in and F-out equal to 0.01 selection criteria. Five markers were set for background control with window size of 10 cM. Permutations of 1,000 iterations were used to determine the QTL threshold. According to Lander and Kruglyak (1995) and Van Ooijen (1999), however, a LOD value just below the threshold can be used to show "suggestive linkage" of a locus that can then be compared to other studies to support if it is a real effect or not. Hence, in this study, QTLs with a LOD value of 3.0 were still presented for QTL comparison purposes, although they were not included in the final count of 10 significant QTLs detected in this study. When doing QTL analysis for experimental data from Stephenville, Sclerotinia disease severity score (DSR) was set as "other trait" to act as a covariate in the analysis.

RESULTS

Phenotypic analysis of yield and grade related traits

ANOVA across locations and years revealed that yield, hundred-seed weight, and TSMK had significant genotypic effect, environment effect, and genotype-by-environment effect, with $P \leq 0.001$. Therefore, all phenotypic data were analyzed separately. The average yield across three environments was 2,450 g per two-row plot. However, the distribution of yield had a high variance in the three environments with an average of 1,577 g in Stephenville in 2010, 2,406 g in West Texas in 2010 and 3,366 g West Texas in 2012 (Fig. 1A) with heritability ranging from 0.36 to 0.57. The yield for the elite cultivar Tamrun OL07 was 2,389 g, 2,539 g and 3,906 g in the three environments, respectively; while Tx964117 had a plot yield of 1,598 g, 2,387 g and 3,425 g, respectively. The average hundred-seed-weight in three environments were 54.3 g in Stephenville in 2010, 63.2 g in West Texas in 2010, and 62.5 g in West Texas in 2012 (Fig. 1B) with consistent high heritability of 0.79. On average, Tamrun OL07 had 74.1 g weight whereas Tx964117 had 50.3 g. Both parents had higher hundred-seed weight in West Texas in both years, which was similar to the trend of the mapping population. TSMK was calculated as a percentage with an average of 66.8% from the measurements of 65.1%, 65.5% and 69.6% in the three environments, respectively (Fig. 1C). Across environments, the heritability of TSMK ranged from 0.51 to 0.60 and the average TSMK of Tamrun OL07 and Tx964117 were 73.6% and 65.3%, respectively.

QTLs for yield-related traits

In total, three QTLs for pod yield were detected above the permutation threshold across three environments (Table 1, Fig. 2) with the LOD values and phenotypic variance explained (R^2) ranging from 3.7 - 6.3 and 12.2% - 23.2%, respectively. Two QTLs, *qY7* and *qY14.1*, were detected in two field experiments. *q14.1* was the largest QTL being detected for yield in this study, with a LOD value of 6.3 and 3.7 and R^2 of 23.2% and 12.2%, in Stephenville 2010 and West Texas 2010, respectively. *qY7* had a LOD score of 4.6 and 3.9 and R^2 of 15.2% and 16.3%, in Stephenville 2010 and West Texas 2012, respectively.

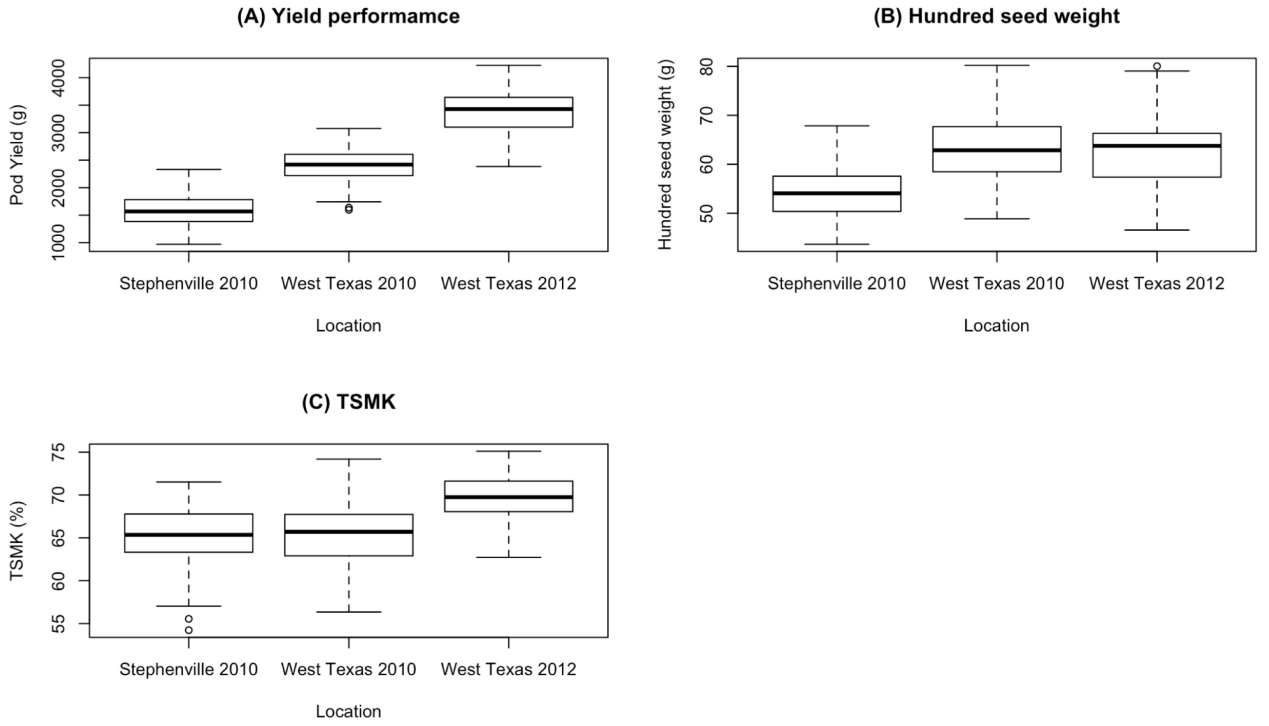

Fig. 1. Performance of the RIL population in each environment. (A) Boxplot of plot yield. (B) Boxplot of TSMK. (C) Boxplot of plot hundred seed weight.

Table 1. QTL identified for yield in the RIL mapping population in 2010 and 2012.

Location and year	QTL	Chr.	QTL region (cM)	Marker closest to LOD peak	Increased Allele[z)]	LOD[y)]	Add.	R^2 (%)
Stephenville 2010	*qY4*	4	0.0-5.3	Aradu.A04_87285618	A	3.4	108.0	14.3
	qY14.1	14	205.0-220.2	Araip.B04_133148884	A	6.3**	23.2	23.2
West Texas 2010	*qY4*	4	0.0-5.3	Aradu.A04_87285618	A	3.2	99.1	10.1
	qY7	7	38.6-45.1	Aradu.A07_37970368	B	4.6**	174.5	15.2
	qY12	12	237.7-265.7	Araip.B02_13294474	B	4.0**	213.8	12.7
	qY14.1	14	216.4-216.5	Araip.B04_133148884	A	3.7*	117.6	12.2
	qY14.2	14	220.2-237.9	Araip.B04_133148957	A	3.4	114.3	11.2
West Texas 2012	*qY6*	6	123.4-153.8	Aradu.A06_1542476	B	3.1	166.7	16.8
	qY7	7	41.0-45.1	Aradu.A07_37970368	B	3.9*	215.4	16.3

[z)]Allele A indicates the allele from Tamrun OL07, and B indicates the allele from Tx964117.
[y)]"*" for *P*-value $\leq$ 0.05 and "**" for *P*-value $\leq$ 0.01 according to 1000 times permutation.

qY12 was only detected in West Texas 2010, with a LOD value of 4.0 and R^2 of 12.7%. In addition to the three main QTLs, there were four suggestive QTLs detected below the permutation threshold but above the LOD score of 3.0. These QTLs were also presented in Table 1 for QTL comparison purposes. One of these QTL, *qY4*, was detected in Stephenville 2010 and West Texas 2010, with LOD values of 3.4 and 3.2 and R^2 of 14.3% and 10.1%, respectively. Among these seven QTLs, the yield-increased allele of *qY4*, *qY14.1* and *qY14.2* were from elite parent Tamrun OL07. On the other hand, Tx964117 contributed the allele for increasing yield in *qY6*, *qY7* and *qY12* loci.

A total of three QTLs were detected above the permutation threshold for hundred-seed-weight, i.e. *qWT4*,

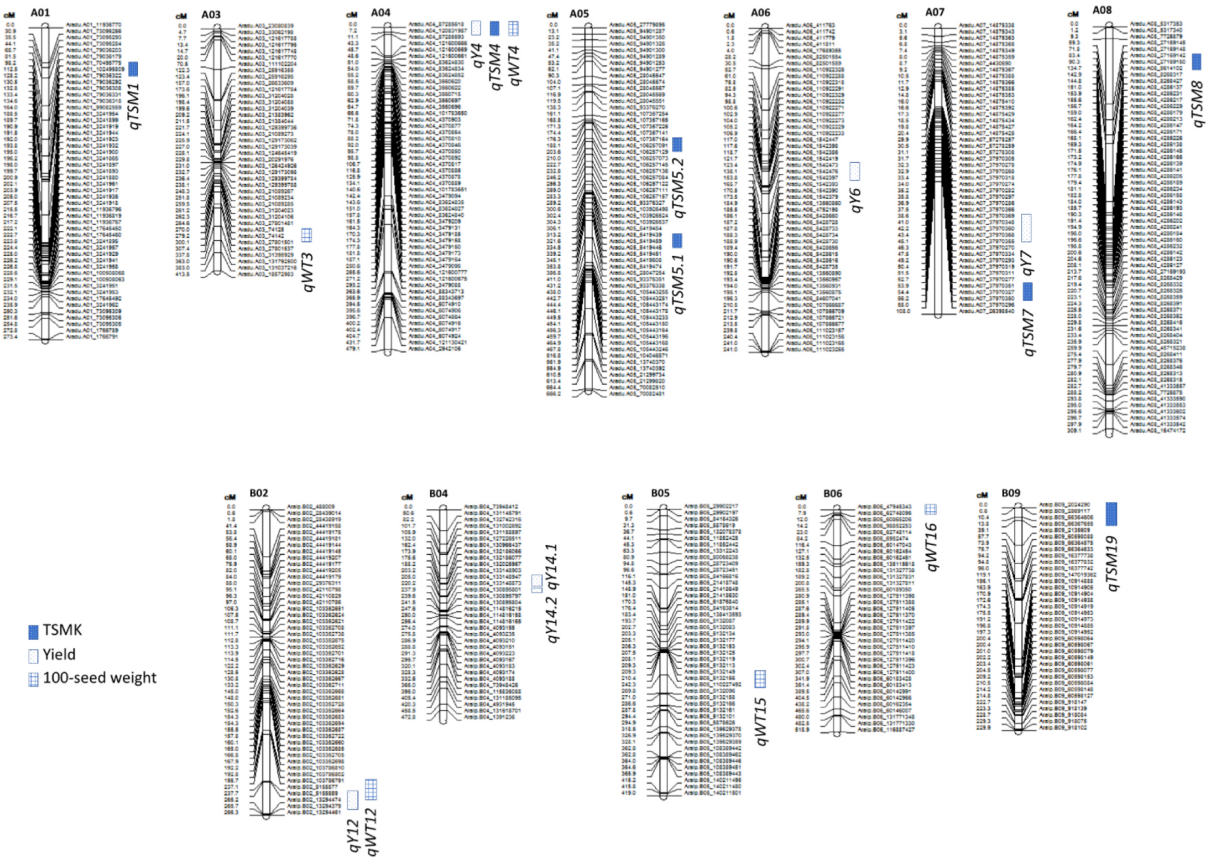

Fig. 2. Linkage map of the RIL population. The mapping population ($F_{2:7}$) derived from a cross between Tamrun OL07 and Tx964117 along with the positions of QTLs for TSMK, yield, and 100-seed weight, which are indicated by the different bars.

qWT3, and *qWT12* (Table 2, Fig. 2). Additionally, there were two suggestive QTLs detected below the permutation threshold, but both of them having LOD values of 3.0. However, none of the QTLs were detected in more than one field experiment. There were three QTLs detected in Stephenville 2010; the largest one was *qWT4*, having LOD 3.8 and R^2 of 16.4%, with the increased allele from Tamrun OL07. Of the other two QTLs, one was derived from Tamrun OL07 and the other one was from Tx964117. In West Texas, only one QTL was detected in each year; in West Texas 2010, *qWT3* was detected, having LOD 4.1 and R^2 of 16.6 %; the increased allele was from Tamrun OL07; while in West Texas 2012, *qWT12* was detected with LOD 5.6 and R^2 was 35.9%. Interestingly, the increased allele effect of *qWT12* came from Tx964117.

QTLs for the grade-related trait TSMK

A total of four QTLs for TSMK were detected above the permutation threshold across three environments, i.e. *qTSM4*, *qTSM1*, *qTSM5.1*, and *qTSM19* (Table 3, Fig. 2), having a range of LOD scores of 3.8 - 6.9 and R^2 of 12.2% - 28.1%. Additionally, there were three suggestive QTLs detected below the permutation threshold but having LOD scores of at least 3.0. All of the increased alleles were from Tamrun OL07 with the exception of *qTSM1*, *qTSM7*, and *qTSM5.2* where the beneficial alleles came from Tx964117. One of the QTLs, *qTSM4*, was the largest QTL for TSMK, having LOD scores of 6.9 and 4.7 and R^2 of 28.1 and 20.5 in Stephenville 2010 and West Texas 2012, respectively. Meanwhile, *qTSM8* was detected in two field experiments but below the permutation threshold, having LOD scores of 3.0 and 2.7 and R^2 of 28.1% and 20.5% in

Table 2. QTL identified for hundred-seed-weight in the RIL mapping population in 2010 and 2012.

Location and year	QTL	Chr.	QTL region (cM)	Marker closest to LOD peak	Increased Allele[z)]	LOD[y)]	Add.	R^2 (%)
Stephenville 2010	*qWT4*	4	0.0-5.3	Aradu.A04_87285618	A	3.8*	2.4	16.4
	qWT15	15	209.2-242.3	Araip.B05_5132156	B	3.0	2.0	1.6
	qWT16	16	0.0-6.0	Araip.B06_47945343	A	3.0	1.9	10.2
West Texas 2010	*qWT3*	3	270.0-282.2	Aradu.A03_74226	A	4.1*	3.1	16.6
West Texas 2012	*qWT12*	12	192.8-262.2	Araip.B02_5155559	B	5.6**	5.1	35.9

[z)]Allele A indicates the allele from Tamrun OL07, and B indicates the allele from Tx964117.
[y)]"*" for *P*-value ≤ 0.05 and "**" for *P*-value ≤ 0.01 according to 1000 times permutation.

Table 3. QTL identified for TSMK in the RIL mapping population in 2010 and 2012.

Location and year	QTL	Chr.	QTL region (cM)	Marker closest to LOD peak	Increased Allele[z)]	LOD[y)]	Add.	R^2 (%)
Stephenville 2010	*qTSM4*	4	0.0-5.3	Aradu.A04_87285618	A	6.9**	2.1	28.1
	qTSM8	8	85.8-131.2	Aradu.A08_27169150	A	3.0	1.4	13.0
West Texas 2010	*qTSM1*	1	98.2-128.2	Aradu.A01_102495809	B	4.4**	3.4	14.6
	qTSM5.1	5	315.0-334.5	Aradu.A05_5419497	A	4.7**	1.8	15.3
	qTSM7	7	53.9-56.2	Aradu.A07_37970327	B	3.2	1.7	10.3
	qTSM8	8	85.8-131.2	Aradu.A08_27169150	A	2.7	1.7	23.2
	qTSM19	19	0.6-13.8	Araip.B09_66364606	A	3.8*	1.9	12.2
West Texas 2012	*qTSM4*	4	0.0-5.3	Aradu.A04_87285618	A	4.7*	1.4	20.5
	qTSM5.2	5	179.5-195.1	Aradu.A05_106257091	B	3.5	1.2	11.4

[z)]Allele A indicates the allele from Tamrun OL07, and B indicates the allele from Tx964117.
[y)]"*" for *P*-value ≤ 0.05 and "**" for *P*-value ≤ 0.01 according to 1000 times permutation; Italic indicates the QTL has LOD value between 2.5-3.0, but detected significantly in different environment.

Stephenville 2010 and West Texas 2010, respectively.

DISCUSSION

Phenotype variation for three traits across three environments

The data analysis showed that yield and hundred-seed weight were not as good in Stephenville as in West Texas (Fig. 1). The pod yield average in West Texas was 2886 g; however, it was only 1,577 g in Stephenville, resulting in a 45% decrease in yield in Stephenville. The trend stays the same for the hundred-seed weight, the average in West Texas was 62.8 g in comparison of 54.3 g in Stephenville. The poor yield performance in Stephenville is largely due to the prevalence of Sclerotinia blight. This results coincided with previous study, which revealed that Sclerotinia blight is one of the most destructive disease for peanut which may cause more than 50% yield loss (Porter and Melouk 1997).

In contrast, for TSMK, there was no significant difference between Stephenville and West Texas in 2010, but it was significantly higher in West Texas in 2012 ($P \leq 0.001$). A possible explanation for the difference could be the environmental effect. The environmental effect across the three experiments of TSMK was as significant as the genotypic effect (data not shown). Moreover, TSMK, yield and seed weight all were measured slightly different, yet were interrelated, as aspects of yield components and quality. Even though the correlations between the three traits were highly significant, the correlation coefficients were still lower than 0.5 (Fig. 3).

Consistent QTLs across different traits or different environments

Our results showed that *qY4*, *qWT4* and *qTSM4* were detected on the same region of the top of chromosome A04 (Fig. 2). Moreover, *qY4* and *qTSM4* were detected in more than one field experiment (Tables 1, 2). However, *qY4* was detected slightly below the permutation threshold (LOD values of 3.4 and 3.2). The source of the trait-enhancing allele of these three QTLs was from the elite parent Tamrun OL07. Additionally, the three traits were significantly correlated with each other (Fig. 3). Whether these three QTLs were closely linked or pleiotropic, needs further study. Likewise, *qY12* and *qWT12* shared a partially overlapping region on the distal end of chromosome B02 (Fig. 2). Whether they were the same or different QTLs needs further investigation. The QTLs *qY14.1* and *qY14.2* were identified closely in tandem. However, in this case, *qY14.2* was detected slightly below the permutation threshold (a LOD value of 3.4). The beneficial alleles of the two QTLs were derived from Tamrun OL07. Compared to our previous leaf spot study (Liang *et al*. 2017), *qY14.1* overlapped with the leaf spot resistant QTL *qLS14.2*. The increased allele for yield was from Tamrun OL07, whereas the leaf spot resistant allele was from Tx964117. This indicated that the QTL conferring leaf spot resistance may also cause a yield and grade penalty. A previous study had shown that the disease resistance allele caused yield loss when there is no disease prevalence (Brown 2002). At this point, it is unclear whether this relationship is due to closely-linked genes (Worland *et al*. 1990) or a pleotropic effect of the disease resistant gene(s) (Sharp *et al*. 2002). If those traits are controlled by different genes but closely linked, the negative linkage drag could be possibly broken by increasing the size of the population. Otherwise, we could also develop lines that are higher yielding, but these lines cannot be deployed in the regions with high prevalence of leaf spot disease.

QTL comparison with previous publications

In a previous QTL study it was reported that the released cultivar Tamrun OL01 has a hundred-seed weight QTL linked to the SSR marker PM375 (Gomez Selvaraj *et al*. 2009). The primer sequences of PM375 marker are: 5'-CGGCAACAGTTTTGATGGTT-3' and 5'-GAAAA TATGCCGCCGTTG-3' (He *et al*. 2005). Since two of the whole genome references of peanut cultivars are available (AA and BB genomes), we can simply perform BLAST

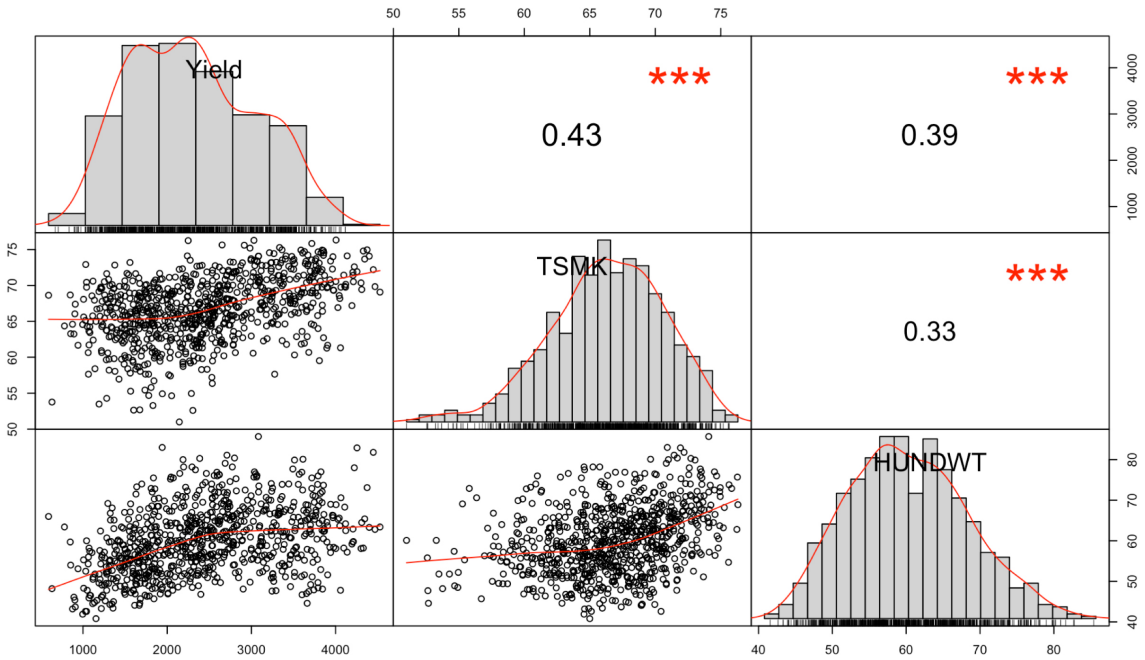

Fig. 3. Pearson correlations among yield, TSMK and 100-seed weight. ***Significant at *P*-value ≤ 0.001.

search of the SSR primer sequences to identify the marker position on the chromosome. The results show that PM375 marker is located on chromosome A04. Based on the pedigree, Tamrun OL01 and Tamrun OL07 have common parents, SunOleic 95R, a high O/L ratio donor, and recurrent parent Tamrun 96, with high yield potential (Smith *et al*. 1998; Simpson *et al*. 2003; Baring *et al*. 2006). Our QTL for hundred-seed weight, *qWT4*, is also located at the same chromosome. As described above, this QTL was in a cluster with two other QTLs underlying increased yield and TMSK (*qY4* and *qTSM4*). The results of our current study validate that the hundred-seed weight QTL on chromosome A04 is linked to the marker PM375.

In the same report, a QTL for hundred-pod weight was also mapped and linked to the SSR marker Ah-041. It was also demonstrated that there was very highly significant correlation (0.92) between pod weight and seed weight (Gomez Selvaraj *et al*. 2009). After performing BLAST the primer sequences of Ah-041: 5'-CGCCACAAGATTAAC AGCACC-3' and 5'-GCTGGGATCATTGTAGGGAAG G-3' (Moretzsohn *et al*. 2004), the result suggests that Ah-041 is positioned on chromosome A03. This result also coincides with our seed weight QTL *qWT3*, which is also located on the same chromosome.

Only a very few QTL studies have been reported on yield and quality related traits. In our study, the two QTLs described above are the only ones that most likely coincide with previous reported QTLs. The rest of the QTLs that we have identified are potentially novel. Some of these QTLs, especially the ones that have high phenotypic contribution and/or in a cluster with one or more other beneficial QTLs can be used as targets for molecular breeding.

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