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Genetic mapping of drought tolerance traits phenotyped under varying drought stress environments in peanut (*Arachis hypogaea* L.)

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Abstract Genomic regions governing water deficit stress tolerance were identified in peanut using a recombinant inbred line (RIL) population derived from an elite variety TMV 2 and its narrow leaf mutant TMV 2-NLM, which was evaluated over six-seasons at Dharwad (non-stress) and Tirupati (water-stress) in India. Stress condition could differentiate the RILs much better than the non-stress condition for the physiological traits. A linkage map with 700 markers was used to identify the quantitative trait loci (QTLs). Three sets of best linear unbiased predictions (BLUPs) were estimated for the drought tolerance traits for the rainy and post-rainy seasons at Dharwad and post-rainy seasons at Tirupati, and employed for single marker analysis, composite interval mapping and multiple QTL mapping. Of the 305 significant marker-trait associations for the 11 traits, only 21 were of major effect for pod yield per plant (PYPP), specific dry weight at 70 days after sowing (SDW_70) and specific leaf area at 70 DAS (SLA_70). Three major main effect QTLs were identified for PYPP with the highest phenotypic variance explained (PVE) of 10.5%. Nine QTLs with the highest PVE of 18.4% were identified for SDW_70, of which four QTLs were also governing SLA_70 with

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the highest PVE of 15.7%. A few of them were also involved in epistatic interactions, and formed multiple QTL mapping models. Five major QTLs for SDW_70 were stable over both the locations. Candidate genes with SNPs and *AhMITE1* insertion were identified for the major QTL regions. A rare nonsynonymous SNP at Ah02_1558700 within the gene *ArahyW1P0U6* governing PYPP was detected. Functional analysis of these candidate genes may be useful for future genetic modifications in addition to validating and using the linked markers for improving drought tolerance in peanut.

Keywords Peanut · Drought tolerance · Multi-environment phenotyping · BLUP · QTLs and candidate genes

Introduction

Peanut (*Arachis hypogaea* L.) is an important grain legume serving as a source of protein and oil. It is grown globally on an area of 31.6 million hectares with a production of 53.6 million tons (FAOSTAT 2020) (https://www.fao.org/faostat/en/#data/QCL/visualize) and productivity of 1699 kg/hectare. It is widely grown under rainfed conditions in more than 100 countries, which are characterized by inconsistent rainfall followed by severe drought especially in Asia and Africa. Water deficiency is known to reduce peanut yield by 70% (Manjonda et al. 2018; Prasad et al. 2010). Flowering and pod setting stages are considered most critical for water stress in peanut (Xiong et al. 2016). Prolonged drought can cause reduction in root growth and density, curling of leaves, reduced inter-nodal length which in turn affect the absorption activity and efficient water usage resulting in delayed flowering and anthesis, reduced flower and pod number (Zhang et al. 2012; Yang et al. 2019). Biochemically, photosynthesis and ATP biosynthesis are affected, which leads to a significant reduction in productivity (Liu et al. 2013).

Significant progress has been made in understanding the intrinsic mechanisms of drought tolerance in peanut through integrated approaches encompassing physiology and productivity (Nigam et al. 2005; Ratnakumar et al. 2009). Root traits are identified as drought adaptive traits; however, their use as selection criteria for drought resistance is limited as they require elaborate phenotyping protocols (Janila et al. 2016). Transpiration efficiency (TE), specific leaf area (SLA), SPAD chlorophyll meter reading (SCMR) and relative water content (RWC) have been recognized as important surrogate traits of water stress tolerance contributing to yield variation under drought stress in peanut (Krishnamurthy et al. 2007). Studies also reported SCMR and total dry matter content (TDMC) as better pertinent traits than SLA for the selection of genotypes due to their significant correlation with pod yield under drought stress (Kalariya et al. 2017).

Low heritability and high genotype × environment interaction among afore-mentioned surrogating traits limit conventional breeding techniques to improve drought tolerance in peanut (Wright et al. 1996; Basu and Nautiyal 2004). Despite the fact that wild *Arachis* species such as *Arachis duranensis*, *Arachis stenosperma*, and *Arachis magna* have shown contrasting early responses to dehydration (Vinson et al. 2018; Dutra et al. 2018), the challenge for gene introgression from wild to cultivated peanut due to time-consuming, intricate breeding techniques, ploidy level difference, and linkage drag limits gene transfer (Simpson 2001).

In the past few years, considerable efforts have been made to map drought tolerance traits using genome-wide markers in peanut (Manjonda et al. 2018). Identification of QTLs for transpiration efficiency, SCMR, shoot dry weight, leaf area, pod yield per plant (PYPP) were reported (Varshney et al. 2009; Ravi et al. 2011; Gautami et al. 2012) though with low-density maps. Genetic mapping of drought tolerance using a dense map was recently reported by Pandey et al. (2021). These studies used the RILs derived from the drought resistant (ICGV 86031, ICGS 44, ICGS 76 and CSMG 84-1) and drought susceptible (TAG 24) genotypes.

Identifying the genomic regions governing drought tolerance traits in peanut is still important considering the low or moderate phenotypic variance explained (PVE) and/or stability of the QTL detected so far. A recombinant inbred line (RIL) population derived from an elite variety TMV 2 and its narrow leaf mutant TMV 2-NLM showed considerable variability for drought tolerance while demonstrating its high utility in identifying the genomic regions for the contrasting traits (Hake et al. 2017). Therefore, this RIL population was evaluated under six environments with varying levels of moisture stress. An improved

linkage map (Jadhav et al. 2021) constructed using single nucleotide polymorphic (SNP), simple sequence repeats (SSR) and *Arachis hypogaea* Transposable Elements (AhTE) markers was used to map the main effect and epistatic effect QTLs for drought tolerance in peanut.

Materials and methods

RIL population of TMV 2 × TMV 2-NLM

A mapping population consisting of 432 recombinant inbred lines (RILs) (Pattanashetti 2005) of F_{19-23} generations, derived from TMV 2 and its mutant TMV 2-NLM (Prasad et al. 1984) was used for mapping drought tolerance traits. TMV 2 (https://tnau.ac.in/ors-tindivanam/varieties-released), a Spanish bunch variety of peanut, was released in 1940, which got popularized due to its wider adaptability. This elite variety is drought susceptible probably due to low transpiration rate and low diffusive resistance compared to more tolerant cultivars (Ratnakumar and Vadez 2011). But its mutant TMV 2-NLM is characterized by narrow leaves and high SCMR (Hake et al. 2017).

Multi-environment evaluation of RIL population for drought tolerance

The mapping population was evaluated along with the parents TMV 2 and TMV 2-NLM in two locations (Dharwad and Tirupati). RILs were evaluated under non-stress condition during four seasons, namely, rainy 2019 (2019R), post-rainy 2019 (2019PR), rainy 2020 (2020R) and post-rainy 2020 (2020PR) at the University of Agricultural Sciences, Dharwad, India (15.4889° N, 74.9813° E). The mapping population was evaluated during the post-rainy 2018 (2018PR) and post-rainy 2020 (2020PR) under drought stress at the Regional Agricultural Research Station, Acharya N. G. Ranga Agriculture University, Tirupati, India (13.6250° N, 79.3728° E). Plants were sown at a spacing of 30 × 10 cm in the field in two replications, and recommended agronomical practices were followed for raising a healthy crop. At Tirupati, drought stress was induced in both the seasons by withholding the irrigation at flowering stage at 40 days after sowing (40 DAS) and the water stress was allowed to continue till the plants showed wilting. On 80th day after sowing, the plants were watered and observed for the recovery. Observations were recorded for the physiological traits like SCMR, SLA, specific dry weight (SDW), TDMC, RWC and canopy temperature (CT) in different growth stages like days to fifty percent flowering (DFF), 70 DAS and 100 DAS. Productivity was measured using PYPP.

Data analysis

Analysis of variance (ANOVA) was performed for each trait across the seasons and locations to test the significant difference among the RILs. In addition, four sets of combined ANOVA (Set I: rainy seasons at Dharwad, Set II: post-rainy seasons at Dharwad, Set III: post-rainy seasons at Tirupati and Set IV: across all seasons and locations) was performed to check for the genotype × environment interactions for the traits. Genetic parameters like genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), genetic advance over mean (GAM) (Johnson et al. 1955) and broad sense heritability (h^2_{BS}) were calculated using the first three sets of combined ANOVA. All the statistical analyses were carried out using R (R Core Team 2021).

Best linear unbiased predictions (BLUPs) were calculated for the drought tolerance traits separately for the two rainy seasons at Dharwad (Set I), two post-rainy seasons of Dharwad (Set II) and the two post-rainy seasons of Tirupati (Set III) using the lme4 package (Bates et al. 2011) of R, which helps fit linear and generalized linear mixed effects models. Pearson's correlation coefficient analysis and multiple regression analysis (where PYPP was used as the dependent variable and other traits were used as the independent variables) were performed using these sets of BLUPs.

Linkage map

The genetic map previously constructed by Hake et al. (2017) using AhTE markers, and later improved by incorporating SNP and SSR markers by Jadhav et al. (2021) was used in this study. This

map of 2438.2 cM carried 700 loci including 553 SNPs, 8 SSRs and 139 AhTEs markers.

Single marker analysis

Marker-trait association was tested using single marker analysis (SMA) which was carried out using "mr" method of r/qtl package (Broman and Sen 2009) of R. SMA for the 700 markers was performed for the traits separately over the three sets of BLUPs with 1000 permutations to calculate the logarithm of odd (LOD) and PVE.

Main-effect and epistatic QTL analysis

Main effect QTL analysis was carried out for the three sets of BLUPs using scanone() function of r/qtl package. For composite interval mapping, "ehk" method was employed with "Kosambi" mapping function. Threshold LOD scores were calculated for each trait at 5% significance using 1000 permutations. The significant QTLs with LOD more than the threshold and PVE more than 10% were identified as the major main effect QTLs, and those with PVE less than 10% were considered as minor main effect QTL (Collard et al. 2005). Naming of QTLs was done sequentially starting with '*q*' followed by the name of the trait, the growth stage at which it was observed, followed by the season (R: rainy and PR: post-rainy) and location (D: Dharwad and T: Tirupati), and followed by the chromosome number on which it was mapped. For example, a QTL for specific leaf area observed at DFF in rainy season at Dharwad on chromosome Ah16 was denoted as *qSLADFFRD-Ah16*.

Epistatic QTLs were identified by two-way genome search using scantwo() function in r/qtl package. Five threshold LODs (over 1000 permutations) namely *full* (likelihood ratio that compares the full model with identified QTL on both chromosomes to the null model), *fv1* (likelihood ratio that compares the full model with identified QTLs on both chromosomes to the single QTL model), *int* (likelihood ratio that compares the full model with identified QTLs on both chromosomes to the additive model QTLs on both the chromosomes), *add* (is the analogous for the additive model) and *av1* (likelihood ratio that compares the additive model with identified QTLs on both chromosomes with the single QTL model with one QTL on each chromosome) were calculated for each trait. Any two QTLs with $LOD_{full} \geq full$ and $LOD_{fv1} \geq fv1$ or $LOD_{int} \geq int$ were considered as epistatic.

Results

Phenotypic variability in the mapping population

Skewness, kurtosis and Shapiro–Wilk test statistics showed normal distribution for all the traits across the seasons and locations except for SLA_70 during 2018PR and SDW_70 during 2020PR at Tirupati (Supplemental Table S1). ANOVA for each trait (within seasons and locations) showed significant differences among the RILs. Combined ANOVA showed significant F values for the lines and the line × season interactions for all the traits in Set I, Set II and Set III (Supplemental Table S2). Line × season × location interactions were also significant for the traits in Set IV (Supplemental Table S3). At Dharwad, TMV 2-NLM was significantly superior over TMV 2 for SCMR_DFF, while it was marginally superior for SCMR_70, SCMR_100, SDW_DFF and SDW_70 as compared to TMV 2 across locations and seasons (Supplementary Table S4). However, TMV 2 had higher SLA and PYPP when compared to TMV 2-NLM across the seasons and locations. Transgressive segregants were identified for all the physiological and productivity traits in the RIL population across the seasons and locations.

Genetic variability was estimated from the first three sets separately (Supplemental Table S5). PYPP showed the highest PCV (23.3–32.1%) and GCV (22.4–29.3%) in all the three sets. TDMC showed high PCV and GCV in Set II. In general, SLA, SCMR and SDW showed moderate to low variability in all the sets. PYPP (67.9–92.7%) followed by SCMR (86.2%) and SLA_70 (71.1%) showed high broad sense heritability in one or more sets. PYPP (44.5–55.7%) followed by TDMC (16.9%) showed high genetic advance over mean (GAM).

Multiple regression analysis for the Set I BLUPs showed that none of the physiological traits influenced PYPP (Supplemental Table S6). However, it showed that PYPP was significantly influenced by TDMC and RWC_70 in Set II and Set III, respectively (Supplemental Tables S7 and S8). Correlation coefficients calculated using BLUPs showed that

SCMR, SLA and SDW were positively correlated between the stages in Set I (Supplemental Tables S9). SLA showed negative correlations with SCMR and SDW in all the three sets. PYPP was significantly positively correlated with SLA_DFF, while it was significantly negatively correlated with SDW_DFF in Set I and Set II (Supplemental Table S10). PYPP was significantly negatively correlated with TDMC in Set II. In Set III (Supplemental Table S11), RWC_70 and CT_70 were significantly negatively correlated with each other, and PYPP showed a significantly positive correlation with RWC_70, and a significantly negative correlation with CT_70.

Marker trait associations identified using single marker analysis (SMA)

Marker trait associations (MTAs) were studied for all 700 markers using the BLUP values. A total of 305 (111 in Set I, 72 in Set II and 122 in Set III) significant marker-trait associations were identified using SMA (Supplemental Table S12). Out of them, a total of 21 (7 in Set I and 14 in Set III) associations were found to be major (PVE more than 10%). Only three traits (SDW_70, PYPP and SLA_70) were involved in the major associations. It was SDW_70 which contributed 10 major MTAs among the 14 MTAs of Set III with the highest PVE of 18.2%. The remaining four MTAs involved SLA_70 with the highest PVE of 15.5%. In total, 10 markers were engaged in the 14 MTAs, of which six were associated with SDW_70 and four were associated with both SDW_70 and SLA_70. The marker AhTE0120 showed the highest PVE for both SDW_70 (18.2%) and SLA_70 (15.5%). Of the seven major MTAs for PYPP in Set I, six associations involved SNP markers that were located within a 1.37 Mb region on chromosome Ah02. All seven MTAs were stable over Set II with minor effects. Similarly, five AhTE markers associated with SDW_70 in Set III were also stable over Set II with minor effects.

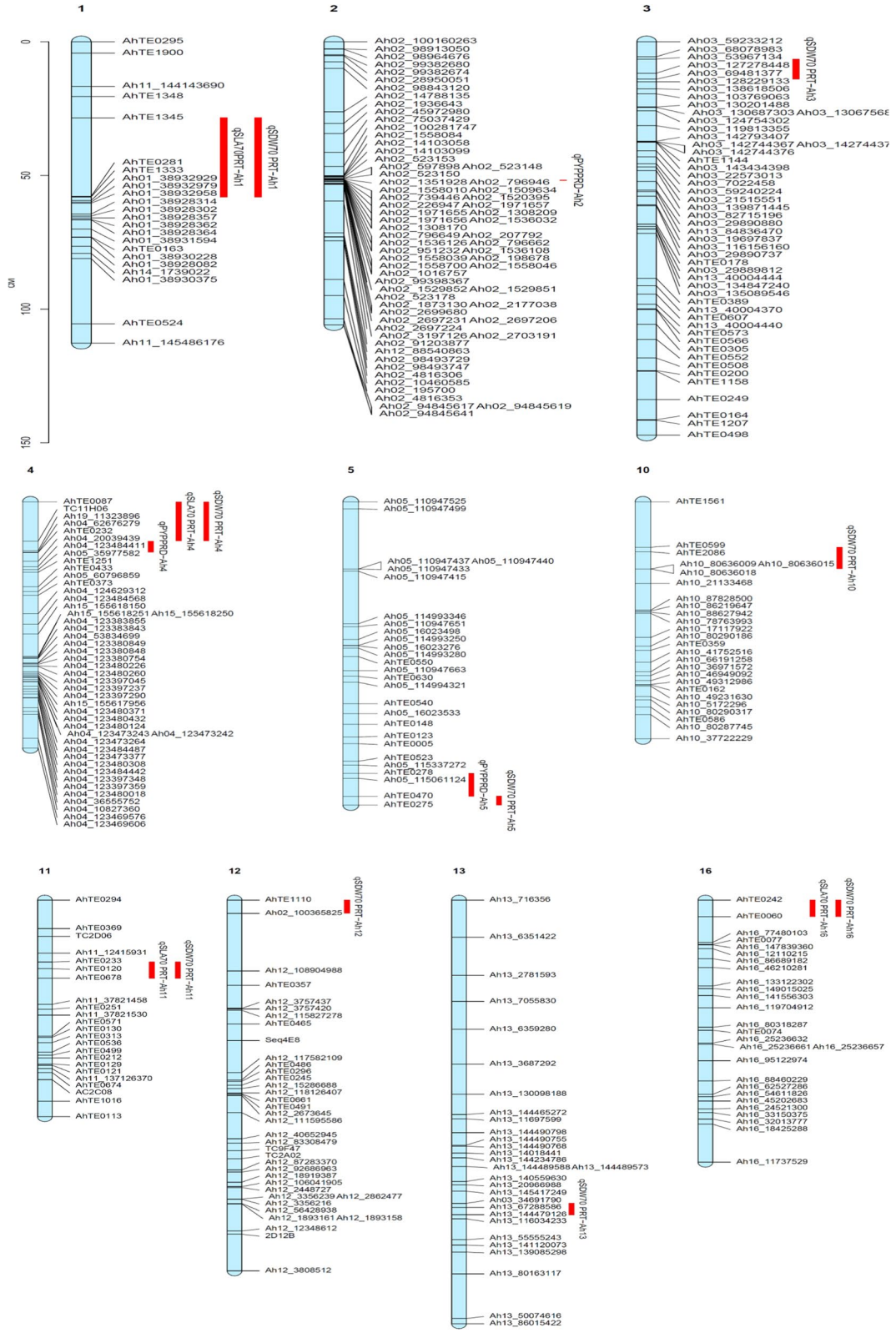
Main effect QTLs for drought tolerance related traits

QTL analysis using the three sets of BLUPs could identify 23, 19 and 46 significant main effect QTLs from Set I, II and III, respectively for all the traits except for TDMC (Supplemental Table S13). Of them, three and nine were major QTLs (Fig. 1) which were identified from Set I and Set III, respectively for the three traits (PYPP, SLA_70 and SDW_70) (Table 1). Of the three QTLs identified for PYPP in Set I, *qPYPPRD-Ah2* flanked by Ah02_198678 and Ah02_1558700 on Ah02 showed the highest PVE of 10.5% with a LOD of 9.7. The favourable allele for this QTL was contributed by TMV 2-NLM parent, and all the three QTLs were stable over Set II with minor effects (7.2–8.5%).

Out of the 9 QTLs from Set III, four were commonly mapped for SLA_70 and SDW_70, while the remaining five were mapped exclusively for SDW_70. The QTL *qSLA70PRT-Ah11* on Ah11 flanked by AhTE0233 and AhTE0120 recorded the highest PVE of 15.7% (Lod of 14.9) and 18.4% (LOD of 17.8) for SLA_70 and SDW_70, respectively. The favourable allele at this QTL was contributed by TMV 2 (Fig. 2). Of the four common QTLs for SLA_70 and SDW_70, three QTLs also governed CT with minor effects (5.6–9.5%) in Set III. They were also stable over Set II for SDW with minor effects (3.8–5.1%). Similarly, two of the five exclusive QTLs for SDW_70 were also stable over Set II with minor effects (3.8–4.3%). The QTL region 0–15.3 cM on Ah04 governing SLA and SDW was co-localized with the QTL region (15.4–19.7 cM) for PYPP. Likewise, the QTL region 115.3–118.7 cM on Ah05 contributing for SDW was co-localized with the region 106.2–115.3 cM for PYPP.

Epistatic QTL analysis

Thirty-four QTL interactions were identified for the eight traits (except for SLA_DFF, SLA_70 and RWC_70) (Supplemental Table S14) (Fig. 3). Among them, 27 interactions mapping four traits were major. Five of the major QTLs identified through composite interval mapping were involved in the epistatic interactions. Highest PVE of 23.3% was observed for the interaction mapped for SDW_70 involving one major QTL *qSDW70PRT-Ah16* and the region at 73.5 cM on Ah 12. This location on Ah12 also had an intra-chromosomal interaction with another major QTL *qSDW70PRT-Ah12* with a high PVE of 21.1% for SDW_70. The third major QTL for SDW_70 *qSDW70PRT-Ah3* showed significant interaction with two genomic regions at 115.9 cM and 42.2 cM on Ah15 and Ah18, respectively. The position on Ah18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Ah16_25236661 Ah16_25236657
Ah16_95122974
Ah16_88460229
Ah16_62527286
Ah16_54611826
Ah16_45202683
Ah16_24521300
Ah16_33150375
Ah16_32013777
Ah16_18425288
Ah16_11737529
qSLA70 PRT-Ah16
qSDW70 PRT-Ah16

◂**Fig. 1** QTL plot illustrating main effect major QTLs identified for drought tolerance and productivity traits in RIL population of TMV 2 and TMV 2-NLM of peanut

(42.2 cM) carried a minor effect QTL for SDW_70 *qSDW70PRT*-Ah18.

The fourth major QTL *qPYPPRD-Ah2* showed significant interactions with three other epiQTLs located on Ah06, Ah10 and Ah12 with a PVE of 16.3%, 15.6% and 15.5%, respectively for PYPP. The fifth major QTL *qPYPPRD-Ah4* showed significant interactions with regions on Ah06, Ah08, Ah12 and Ah14 with the PVE of 15.5%, 15.3%, 15.2% and 15.2%, respectively for PYPP.

The remaining major interactions were mapped for the traits SCMR_DFF, SDW_70, PYPP and CT_70. Among those, an intra-chromosomal interaction (between 52.9 cM and 111.1 cM) was observed for SDW_70 on Ah09 with a PVE of 14.7%. For CT_70, two minor main effect QTLs (*qCT70PRT-Ah5 and qCT70PRT-Ah14*) *on* Ah05 and Ah 14, respectively showed major epistatic interaction with the PVE of 11.6%.

Multiple QTL mapping

Multiple QTL mapping (MQM) was attempted for those three traits (PYPP, SLA_70 and SDW_70) which showed a major main effect QTLs (Supplemental Table S15). Multiple QTL models were developed using the 'stepwiseqtl()' function of r/qtl package. The best models were selected based on the penalized LOD score calculated using 1000 permutation tests to avoid the false positives. The LOD and PVE values for each QTL in the model were estimated using 'fitqtl()' function. MQM analysis for SLA_70 using the BLUPs of Set III showed a model which consisted of nine significant QTLs, of which two were also interacting. This model showed a LOD of 139.5 with a PVE of 79.7%. However, none of these QTLs were identified as main effect major QTL by composite interval mapping (CIM). However, two minor main effect QTLs (Q3 and Q8) on Ah12 (*qSLA70PRT_Ah12*) and Ah18 (*qSLA70PRT_Ah18*) were detected in this model with the PVE of 6.4% and 4.9%, respectively.

In the same set (Set III), the MQM for SDW_70 could identify a model (PVE of 29.9%) consisting of four main effect QTLs which also included a major main effect QTL *qSDW70PRT-Ah16* on Ah16 (Q2). Another main effect minor QTL *qSDW70PRT-Ah18* and one marker associated with SDW_70 Ah12_117582109 (73.5 cM) on Ah12 were also included in this model. Q4 corresponding to the genomic region on Ah19 (81.4 cM) was identified as a major epistatic QTL. MQM for Set I identified a model with four main effect QTLs for PYPP with a LOD of 6.1 and a PVE of 6.7%. Q1 corresponded to the major main effect QTL *qPYPPRD-Ah2* identified by CIM.

Identification of putative candidate genes

For candidate gene discovery, the QTLs and the markers (identified by SMA) with major effects towards PYPP, SLA_70 and SDW_70 were considered (Tables 2 and 3). For the QTLs, the regions between the two flanking markers were scanned to identify the genes and their functions using PeanutBase (https://peanutbase.org) (Dash et al. 2016). For the markers identified by SMA, the genomic positions were checked for gene content. Of the 12 major main effect QTLs, only 10 were flanked by the markers which showed co-linearity between the physical map and genetic map.

The QTL *qSDW70PRT-Ah10* governing SDW_70 consisted of two genes (*Araip.1CJ82 and Araip.ESI8G*). The QTL for SDW_70, *qSDW70PRT-Ah03* carried four genes; *Araip.13K1T* coding for ATP synthesis protein, *Araip.XG2Y6* coding for peptide transfer, *Araip.4QA2R* coding for secretary carrier membrane protein and *Araip.440M0* coding for PAP-specific phosphatase HAL2-like protein. The other two QTLs *qSDW70PRT-Ah05* and *qSDW70PRT-Ah12* governing SDW_70 had seven and five genes, respectively. The two QTLs *qPYPPRD-Ah02* and *qPYPPRD-Ah05* governing PYPP had 125 and 17 genes, respectively. Two QTLs on Ah11 and Ah16 governing both SLA_70 and SDW_70 had 25 and 415 genes, respectively.

Of the 17 major effect markers involved in 21 MTAs, a total of 14 showed co-linearity, of which 10 (8 SNP and 2 AhTE) were in the genic regions of seven genes. Of them, four genes were associated with PYPP, and three were associated with SLA_70 and SDW_70. Of the four genes associated with PYPP, three were located on Ah02 chromosome.

Table 1 Major effect QTLs for physiological and productivity traits identified in TMV 2 × TMV 2-NLM RIL population across the rainy and post-rainy seasons at Dharwad and Tirupati, India

Set	Trait	Chr	position (cM)	Flanking distance	LOD	PVE	Left marker	Right marker	Effect	Source of favorable allele
I	*PYPP*									
	qPYPPRD-Ah2	2	51.7	51.7–51.9	9.7	10.5	Ah02_198678	Ah02_1558700	0.93 ± 0.13	TMV 2-NLM
	qPYPPRD-Ah4	4	19.1	15.4–19.7	9.3	10.1	Ah19_11323896	Ah04_62676279	0.77 ± 0.15	TMV 2-NLM
	qPYPPRD-Ah5	5	108.2	106.2–115.3	9.6	10.4	Ah05_115061124	AhTE0470	0.38 ± 0.10	TMV 2-NLM
III	*SLA_70*									
	qSLA70PRT-Ah1	1	57.9	28.4–58.1	9.9	10.7	AhTE0281	AhTE1333	2.36 ± 0.41	TMV 2-NLM
	qSLA70PRT-Ah4	4	0.0	0.0–15.3	13.1	13.9	AhTE0087	TC11H06	3.27 ± 0.41	TMV 2-NLM
	qSLA70PRT-Ah11	11	29.3	26.4–33.3	14.9	15.7	AhTE0233	AhTE0120	− 2.21 ± 0.41	TMV 2
	qSLA70PRT-Ah16	16	0.0	0.00–7.09	13.6	14.4	AhTE0242	AhTE0060	− 3.42 ± 0.41	TMV 2
III	*SDW_70*									
	qSDW70PRT-Ah1	1	57.9	28.4–58.1	12.5	13.3	AhTE0281	AhTE1333	− 0.00 ± 0.00	TMV 2-NLM
	qSDW70PRT -Ah3	3	11.8	6.5–14.0	11.2	12.0	Ah03_53967134	Ah03_127278448	0.00 ± 0.00	TMV 2
	qSDW70PRT -Ah4	4	0.0	0.0–15.3	16.1	16.7	AhTE0087	TC11H06	− 0.00 ± 0.00	TMV 2-NLM
	qSDW70PRT -Ah5	5	118.7	115.3–118.7	9.3	10.1	AhTE0470	AhTE0275	0.00 ± 0.00	TMV 2
	qSDW70PRT -Ah10	10	19.6	17.8–26.3	9.4	10.2	AhTE0599	AhTE2086	− 0.00 ± 0.00	TMV 2-NLM
	qSDW70PRT -Ah11	11	29.3	26.4–33.3	17.8	18.4	AhTE0233	AhTE0120	0.00 ± 0.00	TMV 2
	qSDW70PRT -Ah12	12	0.0	0.0–5.6	13.3	14.2	AhTE1110	Ah02_100365825	− 0.00 ± 0.00	TMV 2-NLM
	qSDW70PRT -Ah13	13	131.0	129.2–134.1	10.8	11.6	Ah03_34691790	Ah13_67288586	0.00 ± 0.00	TMV 2
	qSDW70PRT -Ah16	16	0.0	0.0–7.0	15.7	16.5	AhTE0242	AhTE0060	0.00 ± 0.00	TMV 2

Chr Chromosome; *LOD* Logarithm of odds; *PVE* Phenotypic variance explained; *PYPP* Pod yield per plant; *SLA_70* Specific leaf area at 70 days after sowing (DAS) and *SDW_70* Specific dry weight at 70 DAS

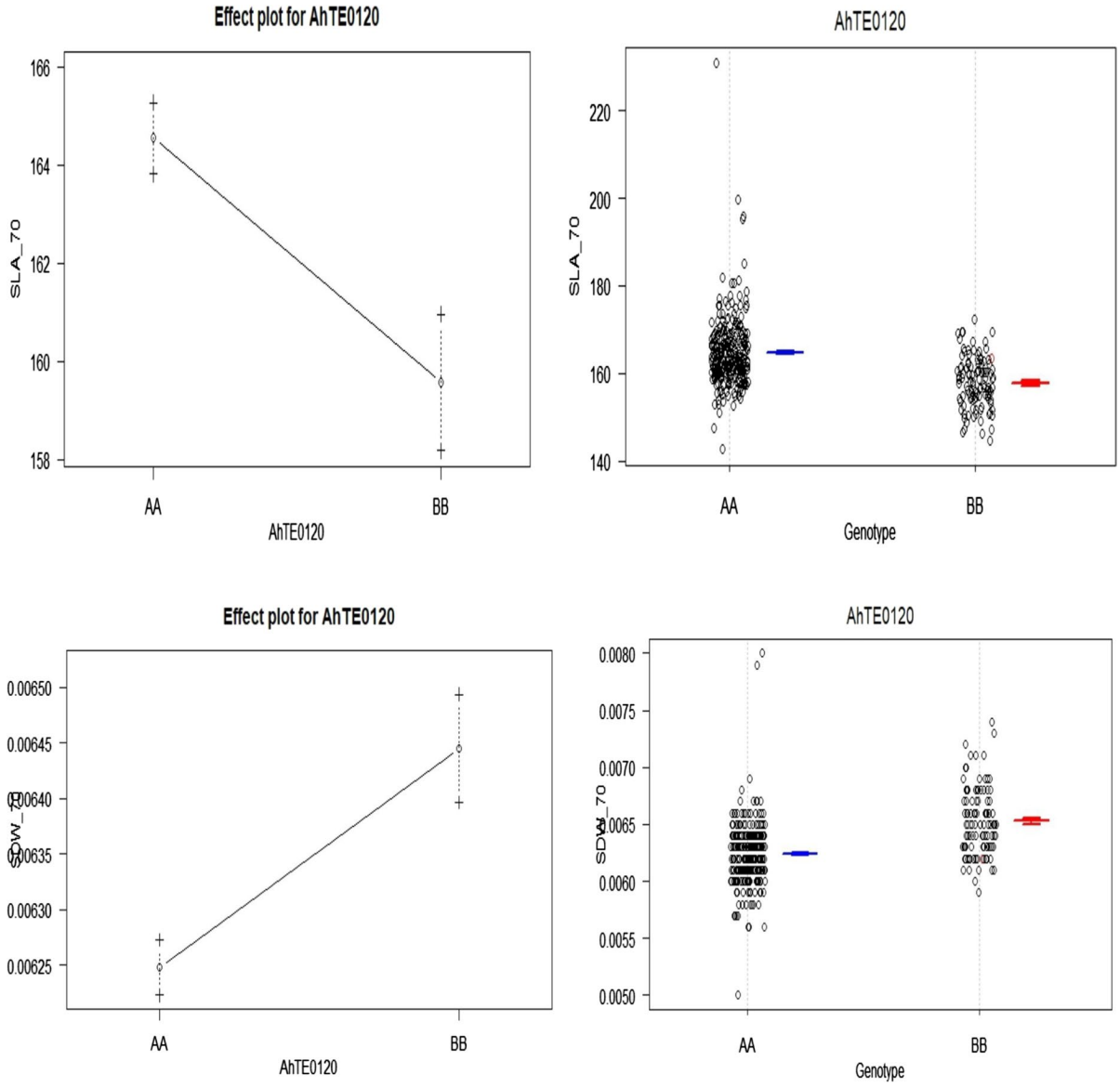

Fig. 2 Means of SLA_70 and SDW_70 for the genotypic classes at AhTE0120

An effort was made to identify the superior RILs for drought stress recovery. In total, 14 RILs along with TMV 2-NLM were identified as early recovering at RARS, Tirupati when the plants were watered after subjecting to water deficit stress for 40 days. Fifteen late recovering RILs were also identified (Supplemental Table S16). These lines significantly differed for SCMR_70, SLA_70, SDW_70, RWC_70 and PYPP, indicating their potential application in improving drought tolerance.

Discussion

This study reports mapping of QTLs and markers for drought tolerance in peanut by evaluating a RIL population derived from TMV 2 and its mutant TMV 2-NLM in six seasons over two locations, comprising of both normal and drought stress conditions. Previously, this mapping population has been used for mapping the taxonomic traits (Hake et al. 2017), quality traits (Jadhav et al. 2021) and iron deficiency

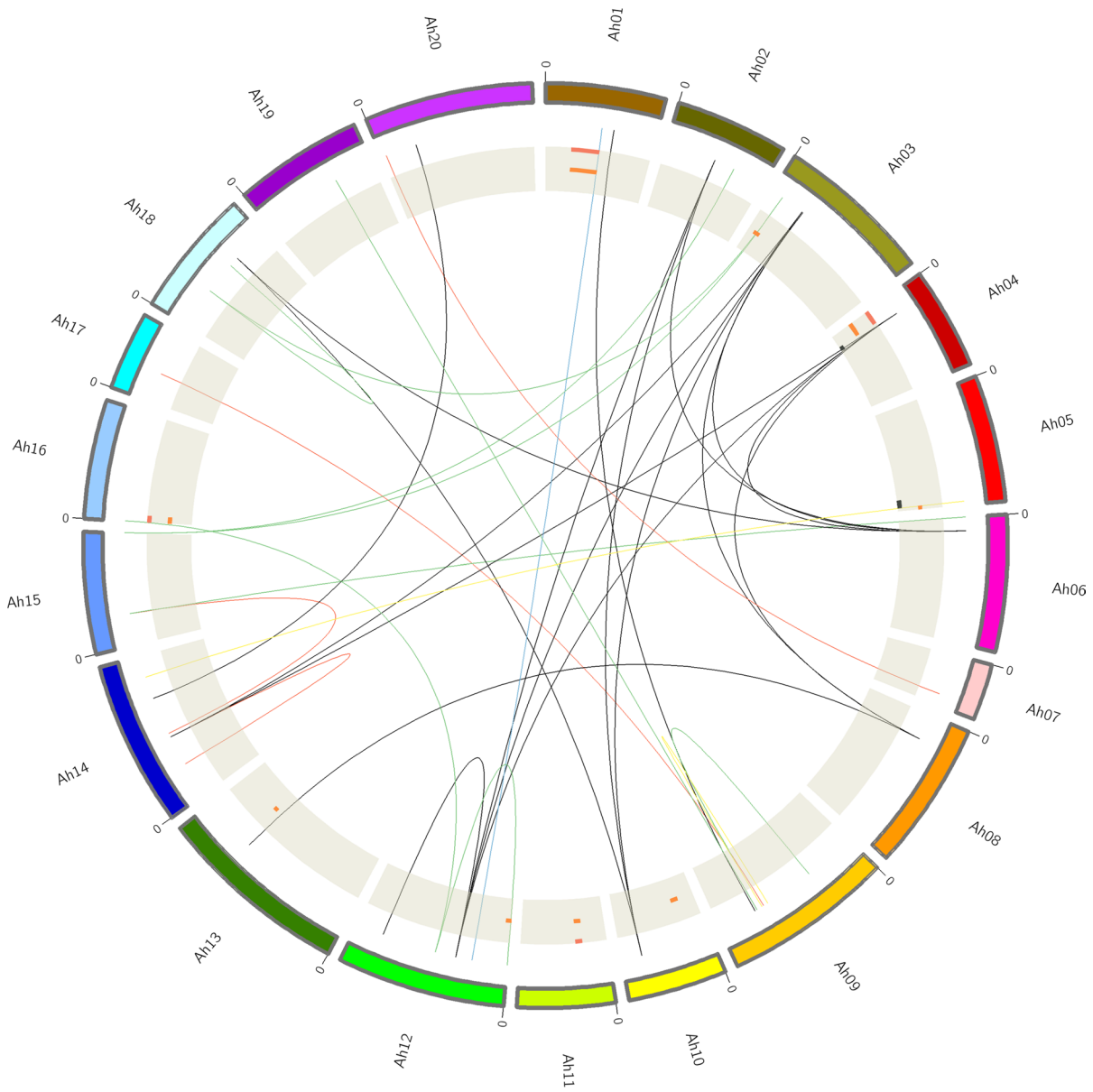

Fig. 3 Main effect major QTLs with their epistatic interactions for drought tolerance and productivity traits in TMV 2×TMV 2-NLM RIL population

tolerant traits (Tayade et al. 2022), and this success could mainly be attributed for the small genomic region differing between the two parents (TMV 2 and its own mutant), and also due to the availability of a fairly dense genetic map. TMV 2 and TMV 2-NLM also differed for a few drought tolerance and productivity traits.

Normal distribution of most of the drought stress-related traits like SCMR, SLA, SDW RWC and CT showed quantitative gene control. Large differences between PCV and GCV were observed for SLA_DFF, SLA_70, SDW_DFF, SDW_70 in Set I, SLA_DFF, SDW_DFF and TDMC in Set II and CT_70 in Set III, indicating the influence of environment. The pattern of correlations between the productivity

Table 2 Putative genes identified for major QTLs detected for productivity and physiological traits in TMV 2×TMV 2-NLM RIL population in peanut

Trait	QTL	Chromosome	Flanking markers	Flanking distance	Total number of genes
PYPP (Set I)	*qPYPPRD-Ah2*	Ah02	Ah02_198678-Ah02_1558700	51.7–51.9	125
	qPYPPRD-Ah5	Ah05	Ah05_115061124-AhTE0470	106.2–115.3	17
SDW_70 (Set III)	qSDW70PRT-Ah03	Ah03	Ah03_53967134-Ah03_127278448	6.5–14.1	4
	qSDW70PRT-Ah05	Ah05	AhTE0470-AhTE0275	115.2–118.7	7
	qSDW70PRT-Ah10	Ah10	AhTE0599-AhTE2086	17.8–26.2	2
	qSDW70PRT-Ah12	Ah12	AhTE1110-Ah02_100365825	0.0–5.6	5
SDW_70, SLA_70 (Set III)	*qSLA70PRT-Ah11/qSDW70PRT-Ah11*	Ah11	AhTE0233-AhTE0120	26.4–33.3	25
	qSLA70PRT-Ah16/qSDW70PRT-Ah16	Ah16	AhTE0242-AhTE0060	0.0–7.1	415

PYPP Pod yield per plant; *SLA_70* Specific leaf area at 70 days after sowing (DAS) and *SDW_70* Specific dry weight at 70 DAS

Table 3 Putative genes and positions identified for major markers detected by SMA for productivity and physiological traits in TMV 2×TMV 2-NLM RIL population in peanut

Trait	Marker	Chr	Position	Gene ID	Function
PYPP	Ah02_198678	Ah02	Intron	*Arahy.H3LZVP*	Mediator of RNA polymerase II transcription subunit 12-like isoform X2
	Ah02_1558700	Ah02	Exon	*Arahy.W1P0U6*	Putative disease resistance RPP13-like protein 1-like isoform X7
	Ah02_1558039	Ah02	Intron	*Arahy.W1P0U6*	Putative disease resistance RPP13-like protein 1-like isoform X7
	Ah02_1558046	Ah02	Intron	*Arahy.W1P0U6*	Putative disease resistance RPP13-like protein 1-like isoform X7
	Ah02_1558010	Ah02	intron	*Arahy.W1P0U6*	Putative disease resistance RPP13-like protein 1-like isoform X7
	Ah02_1016757	Ah02	5' UTR	*Arahy.23PCL8*	Protein kinase superfamily protein; IPR011009 (Protein kinase-like domain)
	Ah05_115061124	Ah05	Exon	*Arahy.85VNG6*	Oxidoreductase family protein
SDW_70	Ah03_127278448	Ah03	Non-genic		
	AhTE0275	Ah05	Non-genic		
	Ah12_117582109	Ah12	Exon	*Araip.SJ8UT*	LRR and NB-ARC domain disease resistance protein
	AhTE1110	Ah12	Non-genic		
	Ah13_67288586	Ah13	Non-genic		
SDW_70, SLA_70	AhTE0120	Ah11	Intron	*Araip.03APC*	Phospholipase D P2
	AhTE0242	Ah16	Intron	*Araip.8SB48*	Receptor-like kinase 1

Chr Chromosome; *PYPP* Pod yield per plant; *SLA_70* Specific leaf area at 70 days after sowing (DAS) and *SDW_70* Specific dry weight at 70 DAS

traits and the physiological traits differed between the water-stressed and non-stressed conditions. RWC was found to have a significant influence on PYPP under stressed conditions in a correlation study and multiple regression analysis. Similar pattern of association between pod yield and RWC was also observed under stress condition in peanut by Aninbon et al. (2021). We also observed a strong association between PYPP and RWC in a multi-parent advanced generation intercross (MAGIC) population of peanut under water stressed condition (unpublished data).

In order to have better prediction accuracies (Meher et al. 2022; Piepho et al. 2008), BLUPs were used to identify the MTAs by SMA and QTL analysis in this study. Set I BLUPs were calculated for the eight traits using the means of two rainy seasons at Dharwad, while Set II BLUPs were worked out for the five traits using the means of two post-rainy seasons at Dharwad. Set III BLUPs were estimated for the six traits using the means of two post-rainy seasons at Tirupati. Varying levels of possible water deficit stress across the seasons and the environment was considered as the basis to calculate three separate sets of BLUPs as reported earlier by Hamidou et al. (2012). Though 305 significant MTAs were detected for the 11 traits across the three sets, only 21 were major (PVE ≥ 10%) for the three traits; with the highest PVE of 10.5% for PYPP, 18.2% for SDW_70 and 15.5% for SLA_70. Overall, it was observed that the stress condition could differentiate the RILs much better than the non-stress condition for the physiological traits like SLA_70 and its inverse trait SDW_70. Eight markers (AhTE0281, AhTE0087, AhTE0275, AhTE0120, AhTE1110, AhTE0242, AhTE0060 and Ah003_127278448) associated with SDW_70 in this study were also associated with protein content (Jadhav et al. 2021) and tolerance to iron deficiency chlorosis (Tayade et al. 2022) in peanut in the previous studies.

A few markers with minor MTAs showed association with multiple traits (up to four). However, four markers with major MTAs showed association with SDW_70 and SLA_70. Eleven markers involved in major MTAs were also found to be the flanking markers for the QTL regions with major effects. Four genes were found for PYPP and three genes were found for SLA_70 (and its inverse trait, SDW_70). Of the four genes for PYPP, three were located in a genomic region of 1.37 Mb, which also corresponded with a QTL region (*qPYPPRD-Ah02*) for PYPP. Of those three genes, *Arahy.W1P0U6* coding for putative disease resistance RPP13-like protein 1-like isoform X7, carried four SNPs (Ah02_1558010, Ah02_1558039, Ah02_1558046 and Ah02_1558700), all of which had major effect for PYPP. Ah02_1558010, Ah02_1558039, Ah02_1558046 were in the intronic region of *Arahy.W1P0U6*, while Ah02_1558700 was in the exonic region with a non-synonymous SNP effect (base change from cytosine to thymine leading to amino acid change from leucine to phenylalanine). *Arahy.W1P0U6* and *Araip.SJ8UT* genes though code for disease resistance proteins, previous reports showed their induction under drought stress in peanut (Khan et al. 2020; Deng et al. 2018) and maize (Yang et al. 2021). The SNP at Ah02_1558700 was found to be rare since it was detected only between TMV 2 and TMV 2-NLM but not among any of the 179 accessions of peanut (Bhat et al. 2022). Other two genes, *Arahy.H3LZVP* and *Arahy.23PCL8* in the same QTL region code for mediator of RNA polymerase protein and protein kinase super-family protein, respectively. Two SNPs (Ah02_198678 and Ah02_1558046) which were associated with PYPP with major and stable effects were also found to be associated with SCMR, shoot dry weight and TDMC under both stress and non-stress conditions in a MAGIC population (our unpublished data).

Of the three (*qPYPPRD-Ah02, qPYPPRD-Ah04* and *qPYPPRD-Ah05*) major main effect QTLs for PYPP, the first two were involved in the epistatic interactions, and the last two were previously reported to govern tolerance to iron deficiency chlorosis (Tayade et al. 2022), and number of pods per plant and oil content (Jadhav et al. 2021). Since the favourable allele at all the three loci were contributed by TMV 2-NLM which is generally low yielding than TMV 2, the importance of other genomic regions contributing for PYPP could be expected. Two major effect QTLs on Ah12 (0.0–5.7 cM) and Ah16 (0.0–7.1 cM) governed SLA_70 and SDW_70 through their main effects and epistatic interactions with a genomic region on Ah12 (73.5 cM). The region on Ah04 (0.0–19.7 cM) carrying two co-localized QTLs *qPYPPRD-Ah04* and *qSLA70PRT-Ah04/qSDW70PRT-Ah04* was also previously reported to govern drought tolerance traits like transpiration, total dry matter and SCMR (Varshney et al. 2009; Ravi et al. 2011). Another genomic region (106.2–118.7 cM) on Ah05

carrying two colocalized major QTLs for PYPP and SDW_70 was also previously reported to govern transpiration efficiency, total dry matter and shoot dry weight by Gautami et al. (2012).

Genomic regions on Ah01 (28.5–58.1 cM) and Ah11 (26.4–33.3 cM) governing SLA_70 and SDW_70 in this study were also reported to contain epiQTL and main effect, respectively for SLA by Gautami et al. (2012). Similarly, another major QTL region (0.0–7.1 cM) on Ah16 governing both SLA_70 and SDW_70 was also reported to carry QTLs for SCMR under well-watered (Faye et al. 2015; Ravi et al. 2011) and drought stress condition (Varshney et al. 2009). All five major QTLs that govern SDW_70 were linked to one or more drought tolerance traits such as SCMR, CT, SLA, and shoot dry weight (Ravi et al. 2011; Faye et al. 2015; Gautami et al. 2012).

Again, the stress condition provided better opportunity to identify genomic regions for drought stress-related physiological traits as compared to non-stress condition in this study. Greater contribution of these traits towards drought tolerance under mid stress and severe stress condition over non-stress condition was also previously reported by Songsri et al. (2009).

Four major QTLs (on Ah03, Ah05, Ah10 and Ah12) governing SDW_70 were predicted to carry two to seven genes. For example, the major QTL on Ah10 *qSDW70PRT-Ah10* carried two genes, of which *Araip.1CJ82* codes for FKBP-like peptidyl-prolyl *cis–trans* isomerase family protein, and *Araip.ESI8G* codes for unknown protein. Overexpression of FKBP-like peptidyl-prolyl *cis–trans* isomerase family protein in Arabidopsis could enhance tolerance to ABA, drought, heat and salt stress (Alavilli et al. 2018). Of the four genes residing in the QTL region *qSDW70PRT-Ah03*, the gene *Araip.440M0* coding for PAP-specific phosphatase HAL2-like protein has previously been reported to act as a signaling molecule under oxidative stress like drought and high light conditions, and thereby regulating nuclear gene regulation in *Arabidopsis* (Estavillo et al. 2011).

Overall, this study identified the drought responsive QTLs and plant-type QTLs, markers and a few candidate genes from a dense genetic map and extensive phenotypic data from stress and non-stress conditions for the physiological and productivity traits related to drought in peanut. Some of the markers and QTLs were also stable across environments, and consistent with other reports. Validation of some of the markers in a MAGIC population certainly extends their utility in molecular breeding. The candidate genes identified in this study can be subjected to functional analysis for future genetic modifications. These genomic regions and the candidate genes could significantly contribute for improving drought tolerance in peanut.

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Conflict of interest Authors confirm disclosure of potential conflicts of interest.

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