



Genetic mapping of tolerance to iron deficiency chlorosis in peanut (*Arachis hypogaea* L.)

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Abstract Iron deficiency chlorosis (IDC) under calcareous and alkaline soils is a significant abiotic stress affecting the growth and yield of peanut. In this study, the genomic regions governing IDC tolerance were mapped using a recombinant inbred line (RIL) population derived from TMV 2 (susceptible to IDC) and TMV 2-NLM (tolerant to IDC), which was phenotyped during the rainy seasons of 2019 and 2020 in the iron-deficient calcareous plots. The best linear unbiased prediction (BLUP) values for IDC tolerance traits like visual chlorotic rating (VCR), and SPAD chlorophyll meter reading (SCMR) were used for QTL analysis along with a genetic map carrying 700 GBS-derived SNP, AhTE and SSR markers. In total, 11 and 12 main-effect QTLs were identified for VCR

and SCMR, respectively. Among them three QTLs were major with the phenotypic variance explained (PVE) of 10.3–34.4% for VCR, and two QTL were major for SCMR with PVE of 11.5–11.7%. A region (159.3–178.3 cM) on chromosome Ah13 carrying two QTLs (one each for VCR and SCMR) was consistent with the previous report. A SNP marker, Ah14_138037990 identified from single marker analysis for VCR was located in the intronic region of the gene *Arahy.QA0C1*, which is important for protein-binding. Overall, this study identified new QTLs and also validated QTL for IDC tolerance. These genomic resources could be useful for genomics-assisted breeding of peanut for IDC tolerance.

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Introduction

Peanut (*Arachis hypogaea* L.) is a major legume food and oilseed crop mainly grown on sandy, loamy, and clayey soils (Zhao et al. 2015) across the globe. Peanut grown on clay soils suffers from iron deficiency chlorosis resulting in yellowing and stunted growth symptoms and pod yield loss of 16–32% (Singh 2001). These symptoms are generally related to the important roles of iron in photosynthesis, respiration, nitrogen fixation, hormone production, chlorophyll formation apart from being a component of various redox and iron-sulphur enzymes in plants (Zheng 2010). Acute iron deficiency can lead to plant death and even complete crop failure. Foliar application of salicylic acid and sodium nitroprusside (a nitric oxide donor) could reduce the IDC symptoms and promote iron uptake, translocation and activation (Kong et al. 2014). The treatment also modulated the balance of mineral elements and protected iron deficiency induced oxidative stress.

The mechanisms which reduce the adverse effects of iron deficiency by increasing the soluble iron have been identified (Römheld & Marschner 1986). Molecular components of iron uptake and transport have also been characterized. In peanut, the full-length cDNA of *AhFRO1* was isolated and found to code for Fe(III)-chelate reductase, a membrane protein with role in iron uptake (Ding et al. 2009). Later, *AhNRAMP1*, coding for a functional iron transporter, was found to be induced by iron deficiency in both roots and leaves. The study also suggested its role in iron acquisition in peanut plants (Xiong et al. 2012).

Recent genomics studies using the RIL population of TAG 24×ICGV 86,031 and a map of 191 SSR markers identified two major QTLs for VCR with the highest PVE of 31.8% and a single major QTL for SCMR with a PVE of 11.0% (Pattanashetti et al. 2020). Subsequently, Pandey et al. (2021) improved the genetic map for TAG 24×ICGV 86,031 using 1028 SNP loci genotyped with a high-density 58 K “*Axiom_Arachis*” array and 177 SSR markers. The genome-wide QTL analysis identified a single major

main-effect QTL for VCR with a PVE of 33.9% and two major main-effect QTLs for SCMR with the highest PVE of 22.4%. These identified QTLs shared a common genomic region on chromosome B03 on diploid genome corresponding to Ah13 of tetraploid genome.

TMV 2 and TMV 2-NLM differ for IDC tolerance (our unpublished data). The RIL population derived from TMV 2 and TMV 2-NLM has demonstrated its utility in mapping complex traits (Hake et al. 2017; Jadhav et al. 2021) since the latter parent is an EMS-derived mutant of the former, and helps in subtracting out a major genomic portion common to both the parents. Therefore, an effort was made in this study to map the genomic regions governing IDC tolerance using a RIL population derived from TMV 2 and TMV 2-NLM.

Materials and methods

Population Development and phenotyping A RIL population developed (Pattanashetti 2005) from the cross between TMV 2, an elite variety of peanut and its EMS-mutagenized derivative TMV 2-NLM (**N**arrow **L**eaf **M**utant) (Prasad et al. 1984) was used for mapping the tolerance to iron deficiency chlorosis. TMV 2 is a Spanish bunch cultivar with susceptibility to IDC (Boodi et al. 2016), while TMV 2-NLM (Prasad et al. 1984) is a semi-spreading cultivar with tolerance to IDC. Phenotypic and genotypic differences between TMV 2 and TMV 2-NLM have been previously reported by Hake et al. (2017).

F₁₉₋₂₀ generations of the 432 RILs together with the parents were grown during the Rainy-2019 and Rainy-2020 at College of Agriculture, Vijayapur, University of Agricultural Sciences, Dharwad, India. During each season, the RILs were grown in two replications with a spacing of 30×10 cm with recommended agronomic practices. Soil properties of experimental sites during Rainy-2019 and Rainy-2020 are given in **Supplemental Table S1**. The climatic factors during the crop period (June to October) at Vijayapur in 2019 and 2020 information given (**Supplemental Table S2**). Visual chlorotic rating (VCR) at 30, 60 and 90 days after sowing (DAS) was recorded as per the scale proposed by Singh and Chaudhari (1993) based on the severity and the spread of interveinal chlorosis on the leaves where 1

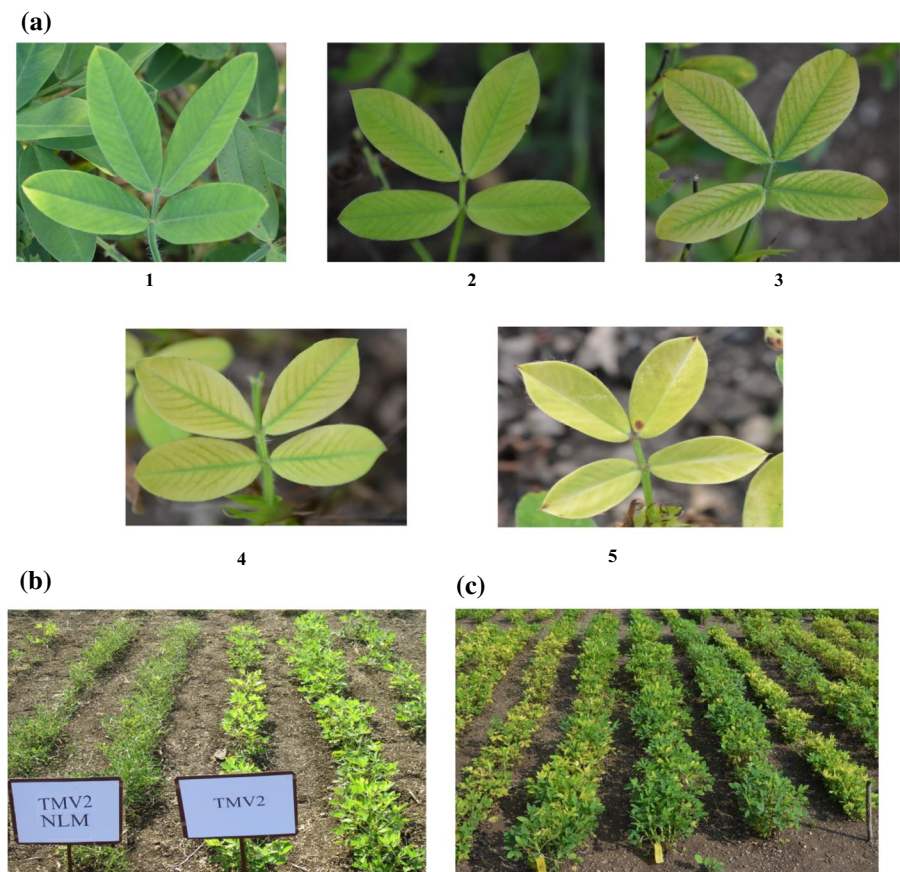
is normal green leaves with no chlorosis, 2 is green leaves but with slight chlorosis on some leaves, 3 is moderate chlorosis on several leaves, 4 is moderate chlorosis on most of the leaves and 5 is severe chlorosis on all the leaves on an overall line basis (Fig. 1a). SPAD chlorophyll meter reading (SCMR) was recorded at 30, 60 and 90 DAS using SPAD 502 (Konica Minolta, Japan).

Analysis of variance (ANOVA) was performed for each trait to test for the significant differences among the RILs. Phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV) and broad sense heritability (h^2_{BS}) were estimated using the plant breeding package Windostat ver. 8.5 (Indostat Services, Hyderabad, India, <https://www.indostat.org/agriculture.html>). Pearson's correlation coefficients (r) among the different traits were estimated over the seasons using the 16th version of SPSS. For further analysis, best linear unbiased prediction (BLUP) values for VCR and SCMR at the three stages (30, 60 and 90 DAS) across the seasons were calculated

using the lme4 package (Bates et al. 2011) of R, which helps fit linear and generalized linear mixed-effects models.

Population genotyping and map construction, QTL and candidate gene discovery The genetic map with 700 mapped markers (SNP, AhTE and SSR) previously constructed by Jadhav et al. (2021) was used for QTL mapping. The main-effect QTL analysis was carried out using the “Composite Interval Mapping (CIM)” approach (Zeng 1994) with Model 6 and a scanning distance of 1.0 cM between markers and moving window size of 10.0 cM using Windows QTL Cartographer version 2.5 (Wang et al. 2007). Forward-backward stepwise regression method was used to set the marker cofactors for the background selection. Highest peak was considered to locate QTL where the distance between the peak and the QTL was less than 5.0 cM. Permutation (1,000) test was performed to work out the threshold and identify the significant QTL. The QTLs with > 3.0 LOD and phenotypic variance explained

Fig. 1a Visual chlorotic rating used for visual screening for iron deficiency chlorosis in peanut
b Response of parent for iron deficiency chlorosis
c Response of the RIL population for iron deficiency chlorosis



(PVE) > 10% were considered major effect QTLs for a particular trait. Those with a PVE < 10% were considered as minor effect QTLs. Based on the trait name and chromosome number, the QTLs were named, where the first letter ‘q’ indicated the QTL and the abbreviated capital letters indicated the trait followed by the chromosome number and the numerical number indicating the serial number of the QTL for a trait. For instance, *qVCR30_Ah04-1* the first QTL for visual chlorotic rating 30 days after sowing was detected on chromosome Ah04.

Analysis for the epistatic QTL (Q×Q) was conducted using the function “two-dimensional scanning ICIM-EPI” implemented in inclusive composite interval mapping (ICIM) software version 4.1 (Wang et al. 2014) with 5 cM step and 0.001 probability mapping parameters in stepwise regression. The minimum threshold LOD value for significant epistatic QTL was set at 3.0. Multiple QTL Mapping was performed with the *r/ql* package’s stepwise *ql* () function (<https://rql.org/>). Association of the markers with the VCR and SCMR was tested by single marker analysis (SMA) using the *lm*() function (linear regression) of R programme. Putative genes were identified for the major QTL clusters and selected markers using the GBrowse [https://](https://www.peanutbase.org/gb2/gbrowse/arahy.Tifrunner.gnm2/)

www.peanutbase.org/gb2/gbrowse/arahy.Tifrunner.gnm2/) at PeanutBase.

Results

IDC tolerance-related traits such as VCR and SCMR across the stages (30, 60 and 90 DAS) showed normal distribution (Fig. 2) in the rainy seasons of 2019 and 2020. ANOVA showed significant differences for VCR and SCMR among the RILs (Supplemental Tables 3 and 4). Across the years, TMV 2 showed susceptible response to IDC over all the three stages with VCR ranging from 3.0 to 4.0 and SCMR ranging from 17.1 to 29.9, while TMV 2-NLM was found to be tolerant to IDC with VCR ranging from 1.0 to 2.0 and SCMR ranging from 28.3 to 40.2 (Table 1). Wide variation was observed among the RILs for VCR, which ranged from 1.0 to 5.0 over the three stages across the years, while SCMR ranged from 2.8–52.9 (Fig. 1b and c; Table 1). The average VCR score increased from VCR30 to VCR60, but it decreased in VCR90 with the recovery of some of the RILs. The average SCMR reduced from SCMR30 to SCMR60, but increased in SCMR90 again with some RILs showing recovery (Fig. 2).

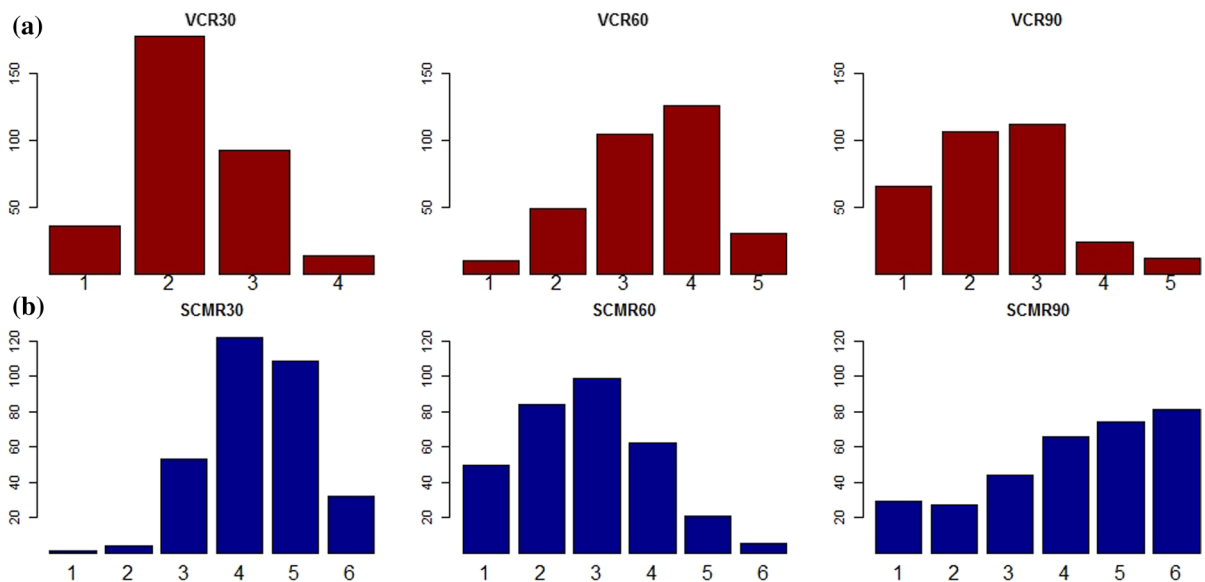


Fig. 2 Frequency distribution of RILs for VCR and SCMR **a** frequency of RILs and parents for VCR score (1 to 5) across three stages (30, 60 and 90 DAS) over two years **b** frequency

of RILs and parents (number) for SCMR groups (6) across three stages (30, 60 and 90 DAS) over two years

Table 1 Estimates of genetic variability for tolerance to iron deficiency chlorosis among the RILs of TMV 2 and TMV 2-NLM of peanut

Traits	Parents		RILs		PCV (%)	GCV (%)	h ² _{BS} (%)	GA	GAM (%)
	TMV 2	TMV 2-NLM	Mean	Range					
VCR30	3.0	1.0	1.5	1.0–4.0	10.8	9.0	68.7	0.2	15.3
VCR60	4.0	2.0	2.0	1.0–5.0	16.7	16.0	91.5	0.6	31.5
VCR90	4.0	2.0	1.9	1.0–5.0	31.1	30.8	98.0	1.2	62.8
SCMR30	29.9	40.2	30.5	4.0–47.4	11.2	8.2	52.9	3.7	12.2
SCMR60	17.1	28.3	21.2	2.8–48.8	17.6	12.7	51.9	4.0	18.8
SCMR90	20.1	32.3	28.4	2.8–52.9	18.2	16.3	80.2	8.5	30.0
NPPP	7.8	3.1	6.1	1.3–17.4	29.7	26.6	80.4	3.0	49.2
PYPP	5.6	2.4	4.0	0.4–15.1	28.1	23.4	69.2	1.6	40.0

PCV: Phenotypic coefficient of variation (%); GCV: Genotypic coefficient of variation (%); h²_{BS}: Heritability in broad sense (%); GAM: Genetic advance as percent of mean (%); VCR30: Visual chlorosis rating at 30 days after sowing (DAS); VCR60: Visual chlorosis rating at 60 DAS; VCR90: Visual chlorosis rating at 90 DAS; SCMR30: SPAD chlorophyll meter reading at 30 DAS; SCMR60: SPAD chlorophyll meter reading at 60 DAS; SCMR90: SPAD chlorophyll meter reading at 90 DAS; NPPP: Number of pod per plant and PYPP: Pod yield per plant

Phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) for VCR and SCMR increased over the stages. Highest PCV and GCV observed for VCR were 31.1% and 30.8%, respectively. SCMR showed the highest PCV and GCV of 18.2% and 16.3%, respectively. Heritability and genetic advance over mean (GAM) also increased over the stages for VCR and SCMR. The highest heritability and GAM recorded for VCR were 98.0% and 62.8%, respectively, while SCMR showed the highest heritability and GAM of 80.2% and 30.0%, respectively.

VCR across the stages showed positively significant correlations (0.3–0.7). SCMR also showed positively significant correlations (0.3–0.5). However, VCR and SCMR were significantly negatively correlated across all the three stages (–0.2 to –0.8) (Table 2). VCR across the stages showed a significantly negative correlation with the number of pods per plant (NPPP) and pod yield per plant (PYPP), while SCMR showed significantly positive correlations with productivity traits. Multiple regression analysis showed the significant coefficients for VCR60 and SCMR30 with the model showing a multiple R² of 16.2% (F of 10.1 with p value < 0.05).

Table 2 Pearson correlation coefficients for iron deficiency chlorosis related traits among the RILs of TMV 2 and TMV 2-NLM of peanut

Traits	VCR30	VCR60	VCR90	SCMR30	SCMR60	SCMR90
VCR30	1.0					
VCR60	0.3**	1.0				
VCR90	0.3**	0.7**	1.0			
SCMR30	–0.5**	–0.3**	–0.2**	1.0		
SCMR60	–0.3**	–0.8**	–0.6**	0.3**	1.0	
SCMR90	–0.3**	–0.6**	–0.8**	0.3**	0.5**	1.0
NPPP	–0.1	–0.3**	–0.2**	0.2**	0.2**	0.1**
PYPP	–0.0	–0.3**	–0.2**	0.2**	0.2**	0.2**

** Correlation is significant at the 0.01 level (2-tailed);

VCR30 Visual chlorosis rating at 30 days after sowing (DAS); VCR60 Visual chlorosis rating at 60 DAS; VCR90 Visual chlorosis rating at 90 DAS; SCMR30 SPAD chlorophyll meter reading at 30 DAS; SCMR60 SPAD chlorophyll meter reading at 60 DAS; SCMR90 SPAD chlorophyll meter reading at 90 DAS; NPPP Number of pod per plant and PYPP Pod yield per plant

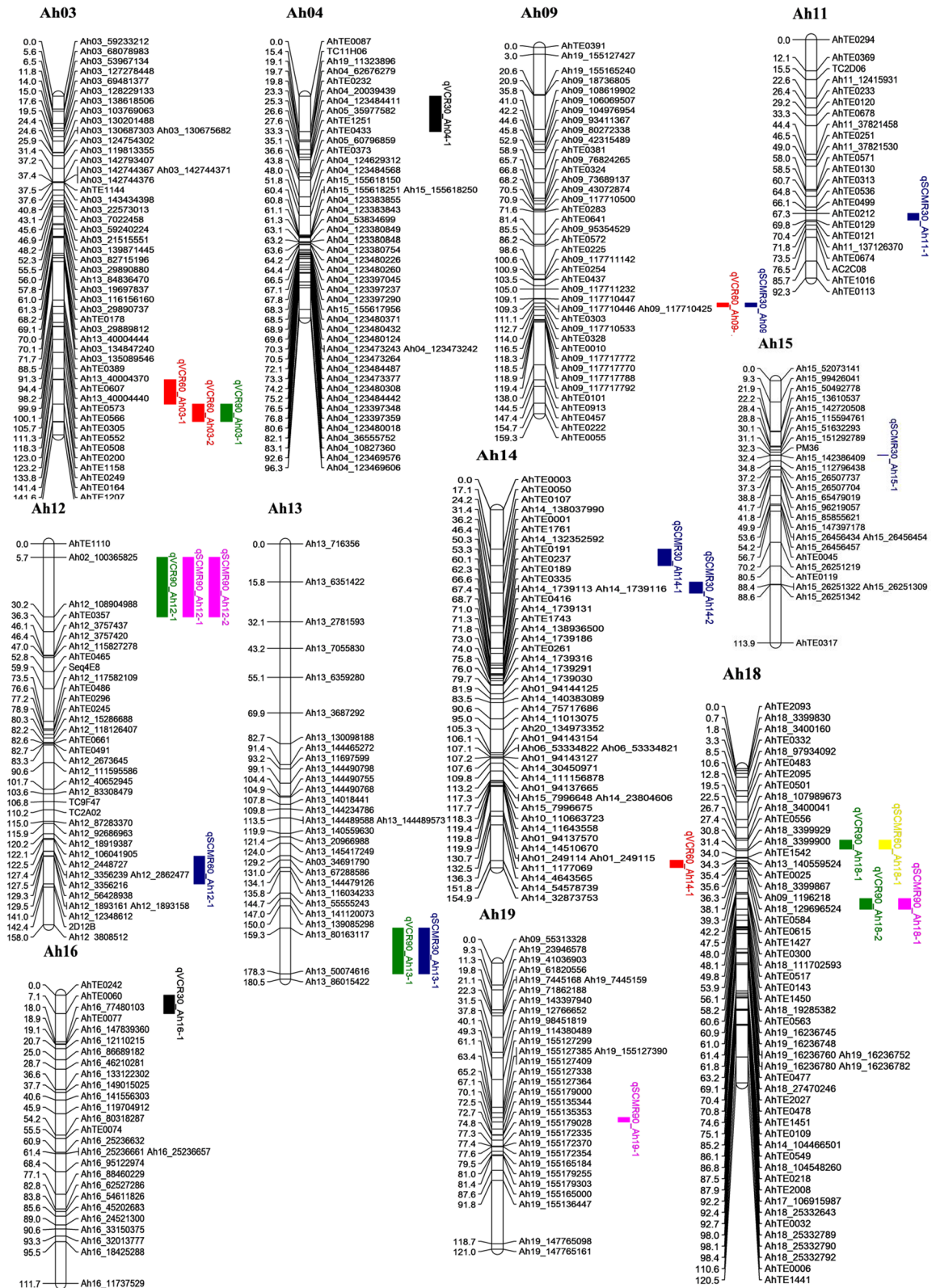


Fig. 3 Genetic map showing location of QTL in different chromosome for iron deficiency chlorosis related traits among the RILs of TMV 2 and TMV 2-NLM

QTL analysis using the BLUPs over two seasons identified a total of 11 and 12 QTLs for VCR and SCMR, respectively (Fig. 3; Table 3). Among the 11 QTLs for VCR, two, four and five QTLs were detected for VCR30, VCR60 and VCR90, respectively. Among them *qVCR30_Ah04-1* on chromosome Ah04 was a major QTL for VCR30 with a PVE of 20.0% and LOD value of 4.4. TMV 2-NLM contributed the favourable allele at this QTL for VCR. Two major QTLs (*qVCR90_Ah13-1* and *qVCR90_Ah12-1*) on chromosome Ah13 and Ah12 were detected for VCR90 with a PVE of 34.4% and 10.3% and LOD values of 4.3 and 4.3 respectively.

Among the 12 QTLs for SCMR, six, two and four QTLs were detected for SCMR30, SCMR60 and SCMR90, respectively (Fig. 3; Table 3). Among them, *qSCMR30_Ah13-1* on chromosome Ah13 was a major QTL for SCMR30 with a PVE of 11.5%. Likewise, *qSCMR90_Ah12-1* on chromosome Ah12 was a major QTL for SCMR90 with a PVE of 11.7%. Of the two QTLs detected for SCMR60, the highest PVE of 3.7% was observed for *qSCMR60_Ah12-1*.

In total, two QTL clusters were identified for VCR and SCMR. Cluster 1 of 24.5 cM (5.7–30.2 cM) flanked by Ah02_100365825 and Ah12_108904988 on Ah12 chromosome was common for VCR90 and SCMR90. It showed the maximum PVE of 10.3% and 11.7% for VCR90 and SCMR90, respectively. Cluster 2 of 19 cM (159.3–178.3 cM) region flanked by Ah13_80163117 and Ah13_50074616 on chromosome Ah13 controlled VCR90 and SCMR30 with the PVE of 34.4% and 11.5%, respectively (Table 3).

Single marker analysis showed the significant association (LOD more than the threshold calculated using 1,000 permutations) of four markers (AhTE1144, AhTE0087, AhTE0120 and AhTE0242) for VCR30. The marker AhTE1144 showed the highest PVE of 7.7% followed by AhTE0242 (7.4%). AhTE0087 with a PVE of 6.3% was found in the vicinity of the major QTLs *qVCR30_Ah04-1* (**Supplemental Table S5**). An attempt was made to find epistatic QTLs for VCR and SCMR. However, genomic regions with epistatic interactions were not identified. Multiple QTL mapping could identify the same major QTLs for all the traits.

Candidate gene discovery resulted in the identification of 300 genes in cluster 1 flanked by Ah02_100365825 and Ah12_108904988 and 259 genes in cluster 2 flanked by Ah13_80163117 and Ah13_50074616 (**Supplemental Tables S6 and S7**). All the markers showing significant association with VCR30 through single marker analysis were non-genic. However, an SNP marker Ah14_138037990, which showed a PVE of 4.3% with a LOD score of 3.0 for VCR30 was located in the intronic region of *Arahy.QA0C1* (on chromosome Ah14) which is known to have protein binding function.

Discussion

This study reports identification of QTL for IDC-related traits like VCR and SCMR in peanut using an existing genetic map from a RIL population of TMV 2 and TMV 2-NLM and the phenotypic data collected over two seasons in iron deficient soils. With the normal distribution of VCR and SCMR, they showed significant association with the productivity traits like NPPP and PYPP though a few RILs recovered from the IDC stress at 90 DAS. This recovery could be due to the enzymatic activities of the efficient RILs (Römheld & Marschner 1983). VCR60 and SCMR30 together contributed for 16.2% variation at PYPP, indicating the influence of VCR and SCMR on productivity. TMV 2 (Spanish type) and TMV 2-NLM clearly show susceptible and tolerance responses, respectively. High PCV and GCV were recorded for VCR and SCMR among the RILs indicating the presence of substantial variability. In peanut, Spanish bunch types were found to be more tolerant to IDC than the other botanical types (Pattanashetti et al. 2018), and the pod yield was positively correlated with chlorophyll content as reflected by SCMR (Singh et al. 2018). SCMR was successfully used as an indicator of IDC tolerance (Samdur et al. 1999). High heritability and GAM indicated a high proportion of phenotypic variance which is heritable and the extent of improvement in the mean genotypic value, respectively for VCR and SCMR during the three stages (30, 60 and 90 DAS).

Though 11 QTL were identified for VCR, only three QTL; *qVCR30_Ah04-1* for VCR30, and *qVCR90_Ah13-1* and *qVCR90_Ah12-1* for VCR90 were major regions with a PVE of 20.0%, 34.4%

Table 3 Identification of main effect QTLs for iron deficiency chlorosis related traits among the RILs of TMV 2 and TMV 2-NLM of peanut

Trait	Chr	Position (cM)	Flanking distance	Left marker	Right marker	LOD	PVE	Additive effect
<i>VCR30</i>								
<i>qVCR30_Ah04-1</i>	Ah04	9.2	0.0–15.4	AhTE0087	TC11H06	4.4	20.0	-0.007
<i>qVCR30_Ah16-1</i>	Ah16	2.0	0.0–7.1	AhTE0242	AhTE0060	5.7	6.9	0.013
<i>VCR60</i>								
<i>qVCR60_Ah03-1</i>	Ah03	130.2	123.2–133.8	AhTE1158	AhTE0249	3.1	6.5	0.042
<i>qVCR60_Ah03-2</i>	Ah03	135.8	133.8–141.4	AhTE0249	AhTE0164	4.3	5.7	0.039
<i>qVCR60_Ah09-1</i>	Ah09	111.1	111.1–112.7	AhTE0303	Ah09_117710533	3.6	3.4	-0.030
<i>qVCR60_Ah14-1</i>	Ah14	153.8	151.8–154.9	Ah14_54578739	Ah14_32873753	4.5	5.6	-0.043
<i>VCR90</i>								
<i>qVCR90_Ah03-1</i>	Ah03	136.8	133.8–141.4	AhTE0249	AhTE0164	5.0	8.4	0.120
<i>qVCR90_Ah12-1</i>	Ah12	19.7	5.7–30.2	Ah02_100365825	Ah12_108904988	4.1	10.3	0.003
<i>qVCR90_Ah13-1</i>	Ah13	163.3	159.3–178.3	Ah13_80163117	Ah13_50074616	4.3	34.4	0.005
<i>qVCR90_Ah18-1</i>	Ah18	27.4	27.4–30.8	AhTE0556	Ah18_3399929	4.0	3.8	0.082
<i>qVCR90_Ah18-2</i>	Ah18	50.8	49.8–53.9	AhTE0517	AhTE0143	4.4	7.5	0.117
<i>SCMR30</i>								
<i>qSCMR30_Ah09-1</i>	Ah09	111.1	111.1–112.7	AhTE0303	Ah09_117710533	4.4	4.1	0.314
<i>qSCMR30_Ah11-1</i>	Ah11	67.3	67.3–69.8	AhTE0212	AhTE0129	4.8	4.6	-0.328
<i>qSCMR30_Ah13-1</i>	Ah13	161.3	159.3–178.3	Ah13_80163117	Ah13_50074616	5.1	11.5	-0.461
<i>qSCMR30_Ah14-1</i>	Ah14	24.1	17.1–24.2	AhTE0050	AhTE0107	5.0	5.1	0.357
<i>qSCMR30_Ah14-2</i>	Ah14	32.5	31.4–36.2	Ah14_138037990	AhTE0001	4.1	7.3	0.415
<i>qSCMR30_Ah15-1</i>	Ah15	32.3	32.3–32.4	PM36	Ah15_142386409	3.6	3.8	-0.330
<i>SCMR60</i>								
<i>qSCMR60_Ah12-1</i>	Ah12	129.5	129.5–140.9	Ah12_1893158	Ah12_12348612	4.0	3.7	0.526
<i>qSCMR60_Ah18-1</i>	Ah18	27.4	27.4–30.8	AhTE0556	Ah18_3399929	3.6	3.3	0.252
<i>SCMR90</i>								
<i>qSCMR90_Ah12-1</i>	Ah12	21.2	5.7–30.2	Ah02_100365825	Ah12_108904988	3.8	11.7	-0.251
<i>qSCMR90_Ah12-2</i>	Ah12	27.7	5.7–30.2	Ah02_100365825	Ah12_108904988	4.2	5.6	-0.834
<i>qSCMR90_Ah18-1</i>	Ah18	49.8	49.8–53.9	AhTE0517	AhTE0143	3.6	3.3	0.582
<i>qSCMR90_Ah19-1</i>	Ah19	65.2	65.2–67.1	Ah19_155127338	Ah19_155127364	3.8	3.5	0.659

Chr Chromosome; *LOD* Logarithm of odds; *PVE* Phenotypic variance explained;

VCR30 Visual chlorosis rating at 30 days after sowing (DAS); *VCR60* Visual chlorosis rating at 60 DAS; *VCR90* Visual chlorosis rating at 90 DAS; *SCMR30* SPAD chlorophyll meter reading at 30 DAS; *SCMR60* SPAD chlorophyll meter reading at 60 DAS and *SCMR90* SPAD chlorophyll meter reading at 90 DAS

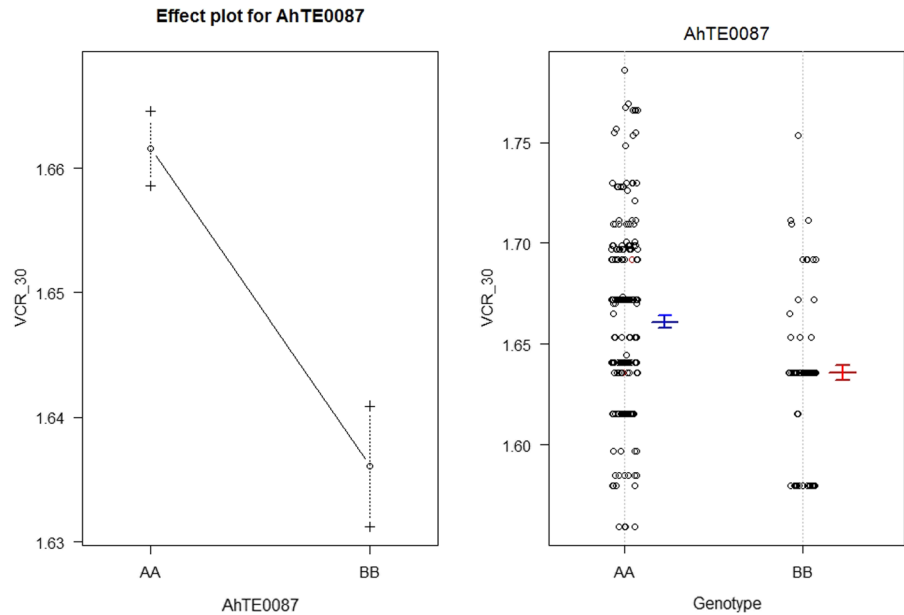
The naming of QTL is as follows *qVCR30_Ah04-1* 'q' indicates QTL identified for VCR at 30 DAS on chromosome Ah04 and 1 showing no of QTLs on same chromosome

and 10.3%, respectively. Of the 12 QTLs detected for SCMR, *qSCMR30_Ah13-1* for SCMR30 and *qSCMR90_Ah12-1* for SCMR90 were two major regions with PVE of 11.5% and 11.7%, respectively. *qVCR30_Ah04-1* was also supported by a marker (AhTE0087) (Fig. 4) identified through single marker analysis. However, none of these five major QTL showed epistatic interaction with other genomic regions. A QTL for VCR30 and VCR60 identified on

Ah04 was found to govern NPPP from the previous study using the same mapping population (Jadhav et al. 2021). Similarly, a QTL on Ah14 for SCMR30 was common with NPPP thus indicating the scope for improving the productivity using these IDC traits.

Of the five major QTL, four were clustered in two genomic regions; a 24.5 cM region on Ah12 chromosome with 300 predicted genes carried one QTL each for VCR90 and SCMR90, and a 19 cM region

Fig. 4 Mean of the genotypic classes and the additive effect for AhTE0087



on chromosome Ah13 with 259 predicted genes carried one QTL each for VCR90 and SCMR30. The cluster 2 on Ah13 was consistent as it was also identified for VCR90 by Pattanashetti et al. (2020), while Pandey et al. (2021) identified a QTL cluster on Ah13 for VCR30, SCMR60 and SCMR90. These regions can be the targets for further fine-mapping. A marker (Ah14_138037990) identified with a PVE of 4.3% for VCR30 using single marker analysis was located in the intronic region of the gene *Arahy. QA0C1*, which is known to have protein binding function. Further fine-mapping and candidate gene discovery, as it has been reported in soybean (Merry et al. 2019; Assefa et al. 2020) and mungbean (Prathet et al. 2012), could be useful for gene-based methods of improving peanut for IDC tolerance. Overall, this study validated the results of the previous studies in a different mapping population, and also provided more evidence for the QTL, especially for VCR and SCMR influencing tolerance to iron deficiency chlorosis in peanut.

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Declarations

Conflict of interest Authors confirm disclosure of potential conflicts of interest. This research does not involve Human Participants and/or Animals and all the authors are informed and consent is obtained.

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