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Identification and validation of a major locus with linked marker for resveratrol content in culitivated peanut

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Abstract Resveratrol, a polyphenolic compound, is related with stress resistance or tolerance in plants and highly beneficial to human health. Peanut (*Arachis hypogaea* L.) is not only an important oilseed crop worldwide but also a key source of resveratrol from dietary food. In this study, a peanut recombinant inbred line (RIL) population consisting of 166 lines derived from a cross combination with a high resveratrol variety ICGV86699 and a normal resveratrol variety Zhonghua 5 as parents was assessed for resveratrol content across three environments. Broad phenotypic variation of resveratrol content ranging from 76.75 to 1617.00 μg/kg was observed among the RILs. From phenotyping resveratrol content and other traits, three elite lines (QT079, QT135, and QT141) were identified with resveratrol level as high as ICGV86699 while their seeds weights were around 1.5 times of ICGV8669. Nine additive QTLs with phenotypic variation explained (PVE) ranging from 6.66 to 11.33% were detected for resveratrol contnet, among which, *qRESA05.3* with 7.88–10.91% PVE was repeatedly detected. Furthermore, an InDel marker (InDel-A05-8,713,397) based on *qRESA05.3* could be detected in both the RILs and selected diverse peanut germplasm accessions possessing "aa" genotype, and the average resveratrol content of these "aa" accessions was significantly higher than that in the genotypes possessing "AA". The favorable allele was found to raise the resveratrol content by 292.15 ± 32.05 μg/kg in the diverse germplasm panel. This is the first report of stable marker for peanut resveratrol, which would be helpful for further fine-mapping the locus and developing marker-assisted selection strategy for high resveratrol peanut.

Keywords Peanut · Resveratrol · Quantitative trait locus · InDel marker

Introduction

Resveratrol is a naturally occurring stilbene phytoalexin phenolic compound that is found in a few edible materials, such as grape skins, peanuts, and red wine (Kpl et al. 2002). Resveratrol has been regarded to be beneficial to human health because of its roles in reducing risk of cancer, cardiovascular disease, and inflammatory reaction (Jang et al. 1997; Leonard et al. 2003; Fouad et al. 2013; Okamoto et al. 2018). In

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plants, resveratrol has been also found to be involved in resistance or tolerance to various biotical and abiotical stresses (Jeandet et al. 2002; Chung et al. 2003).

Peanut is a key sources of resveratrol from dietary food (Sales et al. 2014). As an important oilseed and cash crop, peanut is widely cultivated in more than 100 countries in the world and the production in 2019 was 48.76 million tonnes (FAOSTAT 2020), the highest one update. Peanuts are consumed as nuts, peanut butter, edible oil, and candies (Meredith et al. 2003; Varshney et al. 2013). Considerable variation of resveratrol content has been observed among different peanut varieties (Sanders et al. 2000; Wang et al. 2009). Lee et al. (2004) revealed a resveratrol content variation of 90–260 μg/kg among 15 peanut cultivars. Ogaki et al. (2003) found the resveratrol content in peanut cultivars cultivated in Japan ranging from 89 to 147 μg/kg. Wang et al. (2009) detected the air-dried seeds of 20 peanut germplasm accessions and found the resveratrol content ranging from 125 to 1626 μg/kg, with at least a ten-fold difference. As resveratrol content in peanut is highly variable, there would be a great potential for enhancing content of this interesting compound.

Genetically, resveratrol is a polygenic trait and the content can be easily influneced by environment (Luo et al. 2021). QTL mapping is an effective approach for genetic dissection of complex traits (Gupta et al. 2013). Previous studies on QTL mapping in peanut has mainly focused on pod size, seed size, oil content, and bacterial wilt resistance(Chen et al. 2016; Luo et al. 2018; Mondal et al. 2019; Liu et al. 2020; Luo et al. 2020), while less efforts have been made for resveratrol. Based on limited research results available, QTL for resveratrol have been identified on eight of the 20 chromosomes of cultivated peanut, with nine additive QTL were identified with 5.07–8.19% phenotypic variations explained (Luo et al. 2021). However, QTLs with large and stable PVE have not been reported, which retarded development of effective linked markers for marker-assisted selection. Therefore, it is necessary to identify stable and highly effective QTLs for resveratrol content and develop closely-linked markers for breeding application.

In the present study, a RIL population consisting of 166 lines was developed from a cross between Zhonghua 5 and ICGV86699. ICGV86699 is a breeding line derived from interspecific hybrid population in which two diploid species (*Arachis batizocoi* and *A. duranensis*) were involved in pedigree (Reddy et al. 1996), and was found to possess the highest resveratrol content among the peanut germplasm accessions tested in this laboratory. The two parental lines and 166 RILs were phenotyped in three environments and QTL analysis was performed for resveratrol content. The identified stable QTLs with linked markers would provide foundation for fine mapping and references for marker-assisted selection application.

Materials and methods

Plant materials and trait phenotyping

The peanut RIL population used in the present study consisteded 166 lines derived from a cross with Zhonghua 5 and ICGV86699 as parents (Zhou et al. 2014). The female parent Zhonghua 5 was a high yield variety, and the male parent ICGV86699 was an advanced breeding line from the International Crop Research Institute for Semi-Arid Tropic (ICRISAT, India) with higher resveratrol content than Zhonghua 5. The RILs in F_{11} and F_{12} were used for resveratrol content testing. The field planting trials were implemented for three environments including 2019WC, 2020WC, and 2020YL. In addition, a total of 400 diverse peanut germplasm accessions planted in Wuhan in 2017 and 2018, and Zhanjiang and Xiangyang in 2018, respectively, were also phenotyped for resveratrol content. After harvesting and drying, mature and round seeds were selected to measure resveratrol content using High Performance Liquid Chromatography (HPLC) (Xu et al. 2020).

Statistical analysis of phenotypic data

Statistical analysis for the phenotypic data of resveratrol content was conducted using IBM SPSS Statistics Version 22 software. Analysis of variance was performed to evaluate significant difference among RILs, environments, and RILs × environments interactions. The broad-sense heritability was estimated with the following formula: $H^2 = \sigma_g^2/(\sigma_g^2 + \sigma_{g\times e}^2/r + \sigma_\varepsilon^2/rn)$, where σ_g^2 is genotypic variance, $\sigma_{g\times e}^2$ is the genotype × environment interaction

variance, and σ_{ε}^2 is the residual variance, and r represents the number of environments and n represents the number of replications in each environment.

QTL mapping

A high density genetic map with 1685 loci distributed on 20 linkage groups was constructed based on the RIL population (Zhou et al. 2014). The QTLs were detected using the composite interval mapping method in Windows QTL Cartographer 2.5 (Wang et al. 2012). The threshold of LOD for declaring the presence of a QTL was determined by 1000 permutation tests at $P < 0.05$ (Churchill et al. 1994). QTLs were designated with an initial letter 'q' followed by trait name and linkage group. If two or more QTLs appeared on the same linkage group, a number was added after the linkage group in the corresponding QTL name. Epistasic QTL analysis was carried out using inclusive composite interval mapping (ICIM) method (Meng et al. 2015). The multiple-environment combined datasets were inputted to scan epistasic QTLs using MET function. The mapping step and P value for epistasis QTL scan were set to 5 cM and 0.0001, respectively. The LOD thresholds for all QTLs were determined by 1000-time permutation ($\alpha = 0.05$).

InDel marker development and validation

Based on the whole genome re-sequencing data of peanut, InDel loci of dimorphism were obtained in QTL physical interval by bioinformatics analysis. According to InDel loci, InDel markers were designed, each marker contained two upstream and downstream (F and R) primers, and primer design was completed by Premier 5 software package. PCR amplification was conducted in a 10 μl volume, containing 0.5 μL 0.5 μM primers, 2.5 μL 2 × Easy Taq PCR SuperMix, 5 μL ddH2O, and 2 μL DNA template. The reaction was performed using the following cycling conditions: at 95 °C for 3 min, followed 9 cycles of 95 °C for 30 s, touchdown starting at 65 °C for 30 s (decreasing − 1 °C per cycle), 30 cycles of 95 °C for 30 s, 55 °C for 30 s and 72 °C for 50 s, with a final extension at 72 °C for 10 min. After denaturation, The PCR products were separated on a 6% polyacrylamide gel and visualized by silver staining.

Results

Phenotypic variation of resveratrol content in RILs

The resveratrol content in seeds of the RILs derived from Zhonghua5 × ICGV86699 and their two parents harvested from environments were quantified using HPLC. As shown in Fig. 1, the resveratrol content of Zhonghua 5 (299.79 ± 43.25 μg/kg) was significantly lower than that of ICGV86699 (1370.25 ± 274.46 μg/kg). Broad phenotypic variation of resveratrol among the RILs was observed with in each environment (Table 1). The resveratrol content of the 166 RILs varied from 62.5 to 1795.01 μg/kg in 2019WC, from 50.63 to 1258.86 μg/kg in 2020WC, from 84.37 to 1797.12 μg/kg in 2020YL. The phenotypic values of the RILs showed continuous distribution with transgressive segregation (Fig. 2). The Shapiro–Wilk normality test indicated that the phenotypic data of the RILs across three environments were non-normally distributed (Table 1). Among the RILs, the overall mean resveratrol content were 420.35 ± 230.28 μg/kg, 281.14 ± 197.53 μg/kg and 329.37 ± 202.71 μg/kg in 2019WC, 2020WC and 2020YL, respectively (Table 1). The resveratrol content across different environments showed a moderate correlation (Fig. 2), with correlation coefficients ranging from 0.499 to 0.720, indicating that the resveratrol content could be much affected by environments. The broad-sense heritability of resveratrol content was estimated to be 0.75, indicating that resveratrol content was mainly controlled by genetic factors. Variance analysis across three trials revealed that genetic, environmental effects and genotype × environment interactions significantly influenced the resveratrol content (Table 2).

Identification of additive QTLs for resveratrol content

Based on the genetic map of the RILs (Zhou et al. 2014), a total of nine QTLs were identified on chromosomes A03, A05, A07, B07, and B10, explaining 6.66–11.83% of the phenotypic variation of resveratrol content across multiple environments (Table 3). The additive effects of seven QTLs (*qRESA05.1, qRESA05.2, qRESA05.3, qRESA07, qRESB07.1, qRESB07.2, and qRESB10*) were negative, indicating that the alleles for enhancing

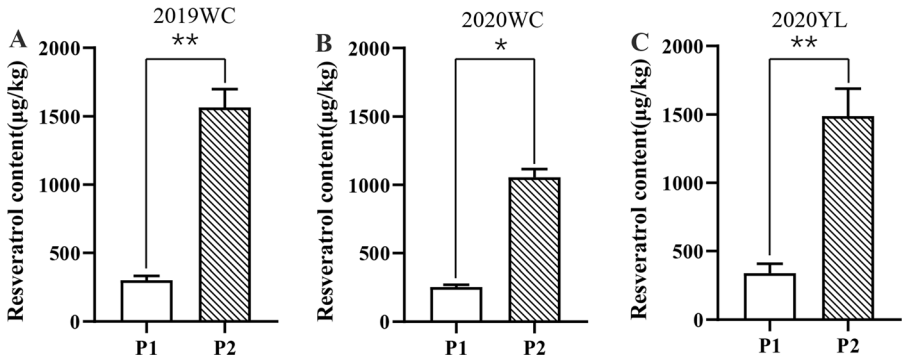

Fig. 1 Phenotypic comparison of resveratrol content between P1 and P2 in different environments. P1, Zhonghua5; P2, ICGV86699; **, Significant at $P < 0.01$; *, Significant at $P < 0.05$

Table 1 Description of phenotype analysis for resveratrol content in the RIL population

Environment	Range (μg/kg)	Mean (μg/kg)	SD (μg/kg)	Skew	Kurt	W-test (sig)
2019WC	62.5–1795.01	420.35	230.28	2.28	8.62	0.84 (0.000)
2020WC	50.63–1258.86	281.14	197.53	2.84	9.57	0.71 (0.000)
2020YL	84.37–1797.12	329.37	202.71	3.65	20.1	0.72 (0.000)

SD, standard deviation; Kurt, kurtosis; Skew, skewness; W-test, Shapiro–Wilk normality test

resveratrol content were from ICGV86699. The additive effects of the remaining two QTLs were positive, indicating that the alleles for enhancing resveratrol content were from Zhonghua 5. Furthermore, among these QTLs, *qRESA05.3* was repeatedly detected in two environments (Fig. 3) with 7.88% and 10.91% of the phenotypic variation in 2019WC and 2020YL, respectively.

The genetic interval of *qRESA05.3* was 9.44 cM, Through mapping sequences of the flanking marker linked to QTL into the A05 of the cultivated peanut (*Arachis hypogaea.* L) (Bertioli et al. 2019), 134 putative genes were detected in a 2.25 Mb physical interval (8,548,250–10,835,503 bp). A total of 104 genes were annotated, whereas another 30 genes were reported to be unknown proteins (Table S1). Gene Ontology (GO) enrichment analysis showed that genes were mainly enriched in biological process and molecular function terms (Fig. S1). Among the genes involved in molecular functions, binding was the most frequent GO term and followed by activity. For biological processes, 20 GO terms were enriched, including regulation of RNA biosynthetic process, RNA metabolic process, cellular metabolic process, and metabolic process.

Detection of epistatic QTLs for resveratrol content

Epistatic QTLs interactions were explored using QTL IciMapping. Totally, 11 pairs of epistatic QTLs were detected on 11 chromosome (Table S2). The effect of additive by additive interaction varied from 213.68 to 291.30 μg/kg and the PVE of two-locus interaction ranged from 4.30 to 9.21%. All pairs of epistatic interaction occurred in the same linkage group. Besides, three epistatic QTLs which could interact with other loci did had individual additive effects in the present study, while the remaining epistatic QTLs did not have individual additive effects.

Estimation of phenotypic effect of QTLs in the RILs

Among the nine QTLs identified in the present study, *qRESA05.3* could be repeatedly detected. To validate the effect of *qRESA05.3* in different environments, the SNP marker (Ahsnp487) tightly linked to this locus was selected. Under different environments, the resveratrol content of lines with allele C of Ahsnp487 locus was significantly higher than that in the lines with allele T (Fig. 4). The differences ranged from

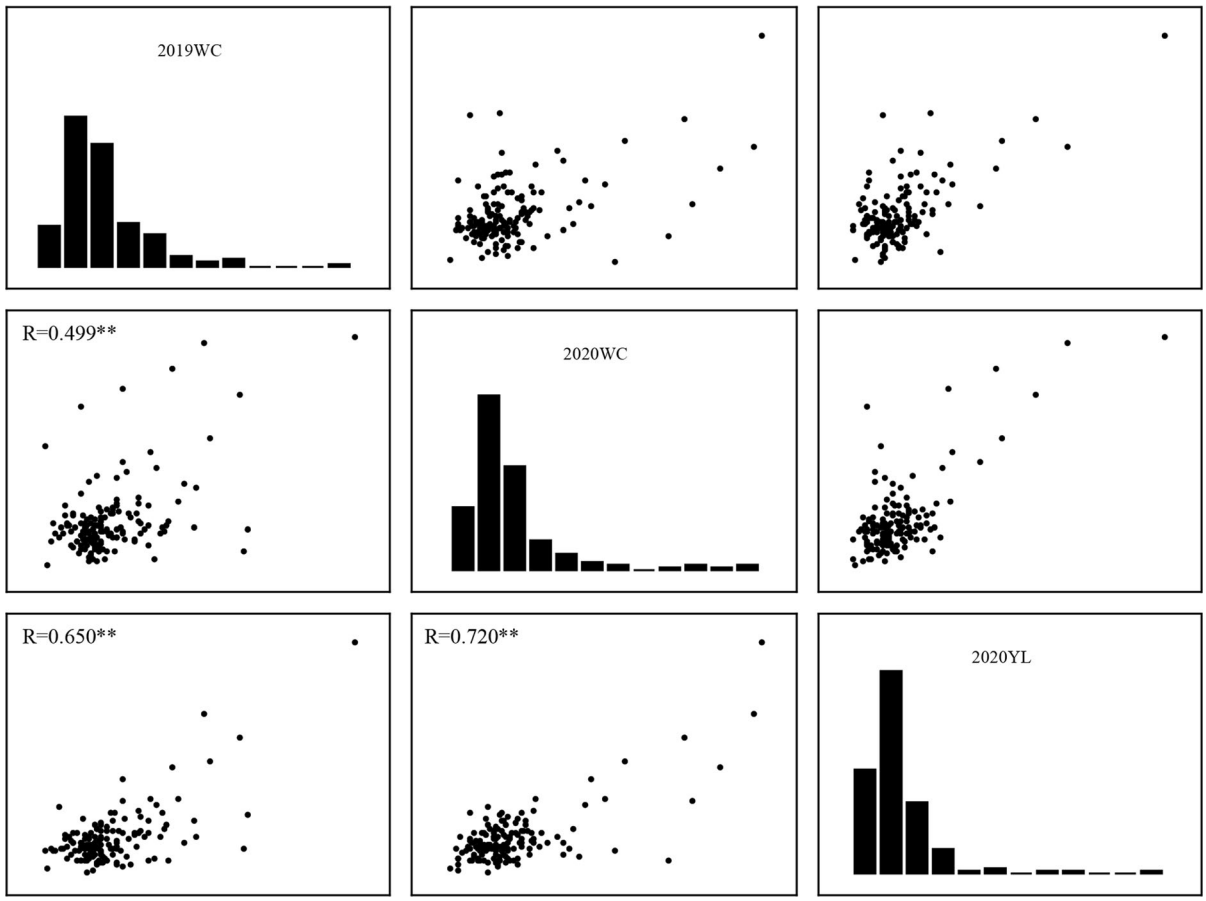

Fig. 2 Phenotypic distribution and Correlation coefficient of resveratrol content among different environments in the RIL population

Table 2 Analysis of variance for resveratrol content across multiple environments

Source	DF	SS	MS	F value	*P* value	H2
Genotype	164	51,672,018	315,073.3	60.5	< 0.0001	0.75
Environment	2	5,142,943	2,571,472	494.1	< 0.0001	
Genotype × Environment	322	25,266,193	78,466.44	15.1	< 0.0001	
Error	970	5,048,718	5204.86			

DF degree of freedom, *SS* sum of squre, *MS* mean squre, *H2* broad-sense heritability

80.63 to 229.01 μg/kg, with an average of 144.16 μg/kg for the three environments. Three elite lines (QT079, QT135, and QT141) with high resveratrol content possessed allele C at this locus and exhibited superiority over ICGV86699 in the trait of seed length and hundred seed weight (Table 4).

Development and validation of marker for resveratrol content

Based on the whole genome re-sequencing data of biparental, we developed an InDel marker in QTL *qRESA05.3* physical interval. This marker could detect polymorphism between Zhonghua 5 and ICGV86699 (the genotypes derived from Zhonghua

Table 3 Information on additive QTLs for resveratrol content in the three environments

QTL	LG	Environment	Position(cM)	Marker interval	LOD	Additive_effect	PVE (%)
qRESA03.1	A03	2020WC	57.61	Ahsnp1230-Ahsnp1477	5.14	87.68	11.33
qRESA03.2	A03	2020YL	59.41	Ahsnp11-Ahsnp807	3.4	95.89	7.84
qRESA05.1	A05	2020YL	40.71	Ahsnp1567-Ahsnp957	4.12	− 87.53	7.78
qRESA05.2	A05	2020YL	48.41	Ahsnp91-Ahsnp1623	6.66	− 113.21	11.83
qRESA05.3	A05	2019WC	60.21	Ahsnp392-Ahsnp487	3.89	− 81.73	7.88
		2020YL	60.11	Ahsnp487-Ahsnp269	5.93	− 108.89	10.91
qRESA07	A07	2020WC	70.61	Ahsnp1188-Ahsnp1182	3.11	− 56.75	6.66
qRESB07.1	B07	2019WC	17.41	Ahsnp248-GA24	3.45	− 82.86	8.78
qRESB07.2	B07	2019WC	23.21	GA24-GM624	3.15	− 75.91	7.83
qRESB10	B10	2020YL	56.31	Ahsnp1592-Ahsnp2027	3.31	− 106.59	9.17

LG linkage group, *LOD* logarithm of odds, *PVE* phenotypic variation explained

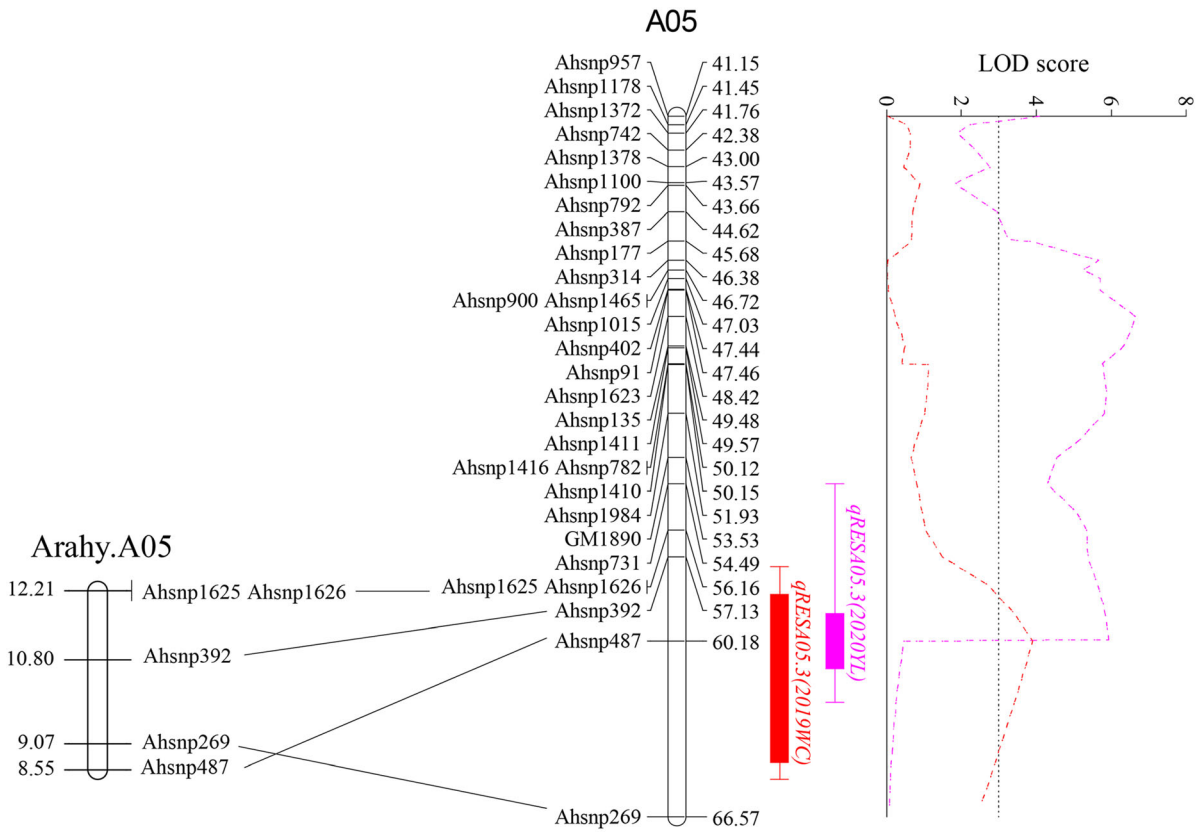

Fig. 3 QTL and their LOD values for resveratrol on chromosome A05

5 were designated as ''AA'', and those from ICGV86699 were designated as ''aa'') (Table 5). In the RILs, the resveratrol content of lines with "AA" genotype (325.33 ± 142.00 μg/kg) was significantly lower than that of the lines with "aa" genotype (417.04 ± 288.76 ug/kg). A total of 46 extremely germplasm accessions in resveratrol content were selected from 400 germplasm accessions including 23

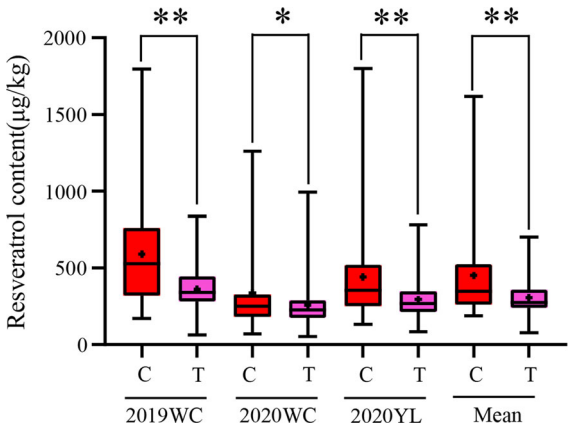

Fig. 4 Phenotypic effect of *qRESA05.3* in the three environments. " + " represent mean value; **, Significant at $P < 0.01$; *, Significant at $P < 0.05$

accessions with high resveratrol content ranging from 717.64 to 996.33 μg/kg and 23 accession with low resveratrol content ranging from 177.29 to 308.82 ug/kg (unpublished data). The InDel marker was validated in a panel of 46 peanut germplasm accesssions. The resveratrol content of these 46 accessions ranged from 177.29 to 996.33 μg/kg on average over four environments, with a mean of 556.02 μg/kg(Table S3). In the 46 accessions, the resveratrol content of those possessing the "aa" genotype (676.59 ± 232.39 μg/kg) were significantly ($P < 0.01$) higher than that in the accessions possessing the "AA" genotype (384.69 ± 182.95 μg/kg) (Fig. 5). There results would be highly valuable for marker-assisted in high resveratrol breeding.

Discussion

Resveratrol has been found to be beneficial to human health, and peanut is among the plants with relatively high resveratrol content (Ogaki et al. 2003). Since being crucial for human health and stress reaction in plants, resveratrol has attracted much research efforts. Wang et al. (2009) found three peanut accessions containing a high amount of resveratrol (1058–1626 μg/kg). Wang et al. (2013) also detected the seeds of 102 accessions within the U.S. peanut mini-core collection and found that the resveratrol content varied from 30 to 260 μg/kg. Luo et al. (2021) reported that the resveratrol content of a RIL population were 3.61–282.69 μg/kg. In the present study, a large phenotypic variation of resveratrol (76.75–1617.00 μg/kg) among the RILs over three environments was revealed. In addition, three lines

Table 4 Information of resveratrol content and yield traits of three elite lines

Accession	Allele	2019WC (μg/kg)	2020WC (μg/kg)	2020YL (μg/kg)	SL (cm)	SW (cm)	HSW (g)
Zhonghua 5	T	303.11 ± 25.51	254.97 ± 12.41	341.28 ± 54.24	1.81 ± 0.09	1.12 ± 0.11	88.65 ± 6.32
ICGV86699	C	1565.33 ± 108.53	1056.03 ± 42.45	1489.4 ± 161.13	1.38 ± 0.04	0.86 ± 0.03	48.09 ± 5.60
QT079	C	1678.46 ± 138.06	1392.21 ± 126.11	1742.08 ± 54.76	1.55 ± 0.07	0.94 ± 0.10	68.52 ± 7.17
QT135	C	1376.73 ± 346.75	1011.39 ± 105.63	1021.15 ± 66.72	1.56 ± 0.07	0.92 ± 0.09	61.71 ± 5.26
QT141	C	1004.93 ± 55.67	1175.43 ± 58.72	1268.14 ± 24.75	1.76 ± 0.13	0.92 ± 0.08	69.27 ± 6.96

SL seed length, *SW* seed width, *HSW* hundred seed weight

Table 5 Information of InDel markers

InDel marker	Sequence of primer (5′–3′)	Annealing temperature (°C)	Target fragment size (bp)	No. of InDel base
Indel-A05-8,713,397	Forward: AAGTGCAGTGATACAACGTC Reverse: TTTTCTGATGATGGTGCTAT	55	417	5

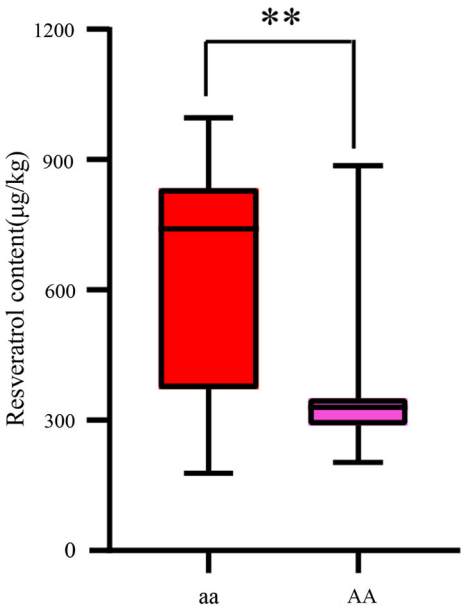

Fig. 5 Phenotypic different among two genotypes of InDel-A05-8,713,397. **, Significant at $P < 0.01$

from the RILs with higher resveratrol content were identified, and they possessed large hundred seed weight compared to ICGV86699 (around 1.5 times higher). In this study, the broad-sense heritability of the resveratrol content was 0.75, even significant variations across environments including locations and seasons were obsvered. The results suggested that varieties, locations and seasons could greatly influenced the resveratrol content in peanut.

The resveratrol content in peanut is regulated by a complex system in which multiple genes are involved. Complex quantitative traits in peanut are normally regulated and controlled by multiple genetic and environmental factors (Sarvamangala et al. 2011; Baring et al. 2013; Yu et al. 2020), QTL mapping could provide a foundation for genetic improvement of these traits. In the current study, nine additive QTL with 6.66–11.83% PVE for resveratrol content were identified on three chromosomes (A03, A05 and A07) of the A subgenome and two chromosomes (B07 and B10) of the B subgenome. Among these nine additive QTLs, only *qRESA05.3* was repeatedly detected in two environments, explained 7.88% and 10.91% of the phenotypic variation in two environments, respectively. Based on the high-quality reference genome of cultivated peanut (Bertioli et al. 2019), *qRESA05.3* located in a 2.25-Mb interval containing 134 genes. The synthesis of resveratrol in peanut mainly depends on the function of stilbene synthases (STS) gene in phenylalanine pathway. The peanut STS gene might be located at ∼ 13 Mb on B04 or ∼ 11 Mb on A04 (Shomura et al. 2005), which was outside of the identified QTL in this study. Therefore, the production and accumulation of resveratrol in peanut seeds would be a more complex regulatory process. Luo et al. (2021) detected nine QTLs for resveratrol content in eight chromosomes with 5.07–8.19% PVE, but no QTL was repeatedly detected in two or more environments. Comparing with results from Luo et al. (2021), the *qRESA05.3* was a novel and valuable QTL. In addition to additive effects, epistatic interaction might also contribute a considerable portion of the genetic variation. A total of 11 pairs of epistatic interactions were detected in the present study. The results suggested that resveratrol was a complex and polygenic trait.

The Ahsnp487 marker was used to evaluate the effect of *qRESA05.3*, a favorable allele of the locus in the RILs could increase 144.16 μg/kg resveratrol content across multiple environments. Three RILs had high resveratrol content (equivalent to ICGV86699), and they possessed the favored alleles of 6–9 identified QTL from both parents (Table S4). The above results demonstrated that it might be valuable in the introgression of the high-resveratrol allele into peanut cultivars. An InDel marker was developed in the study, and 46 diversified genotypes and two parents were used for validating the identified marker. This interesting marker exhibited valuable deployment potential in molecular breeding for enhancing resveratrol contnet.

Conclusion

In this study, three elite peanut lines with high resveratrol were identified from the RILs derived from cross combination in which ICGV86699 was involved. Nine QTLs for resveratrol were detected across three environments, explained 6.66–11.83% of the phenotypic variation. A novel reliable QTL for resveratrol content, *qRESA05.3*, was identified. An InDel marker (Indel-A05-8,713,397) was developed based on *qRESA05.3* and consequently verified in other diversified germplasm panel. The identified QTL and InDel marker from this study would be highly

valuable in further fine mapping the locus and developing marker-assisted selection approach in peanut breeding.

Authors contribution JG, NL and HJ conceived and designed the research. XZ and WC developed the RIL population. LH, WL and HC planted the materials and conducted field management. JG, HC and BW performed the measurement of resveratrol content. JG analyzed the data and wrote the manuscript. NL, HL, DH, YL, BL and HJ revised the manuscript and improved the English writing. All the authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The experiments were performed in compliance with the current laws of China.

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