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Possibility for Exploitation and Identification of Rice Yield and Seed Quality Orthologs in Peanut (*Arachis hypogaea* L.)

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ABSTRACT

Background: The advancement in gene tagging and mapping in model crops such as Arabidopsis, rice andmaize has outpaced progress in major legume crops like groundnut, chickpea, redgram, greengram andsoybean, even in the post-genome release period of legume databases. To address this gap, a study investigated the transferability of gene tagged markers (GTMs) associated with rice yield, grain size andmicronutrient content (Fe and Zn) to groundnut.

Methods: This study utilized 17 diverse groundnut genotypes for molecular analysis, targeting 45 GTMs spanning 24 known functional genes.

Result: Remarkably, 31 out of the 45 markers (76%) demonstrated high transferability to groundnut, indicating significant conservation in functional regions across species. The amplification efficiency of rice GTMs varied among groundnut genotypes, ranging from 79.17% to 91.67%. Notably, 17 markers targeting 14 rice genes showed amplification across all 17 groundnut genotypes (100%) studied. These findings underscore the potential of leveraging knowledge from functionally characterized genes in molecular model crops and annotated orthologous genes in 'Omics' databases to enhance gene tagging efforts in crops like groundnut. By harnessing this approach, there is an opportunity to expand the molecular-level tagging of genes and improve crops like groundnut, which have seen limited progress in gene tagging. This strategy opens avenues for pyramiding desirable genes with precision, thereby enhancing crop traits with greater accuracy.

Key words: Gene tagged markers, Groundnut, Molecular breeding, Transferability.

INTRODUCTION

Peanut (*Arachis hypogaea* L.), a member of the Papilionaceae subfamily within the Fabaceae family, is renowned for its nutritional value, boosting high levels of digestible proteins, essential vitamins, minerals andphytosterols. Its importance as a staple food source for both human consumption and animal feed cannot be overstated. However, despite its nutritional prowess, the agricultural yield of peanut, along with many other crop plants, has reached a plateau since the post 'Green Revolution' era. Meeting the projected demand for peanut by 2050, estimated at 68 million tons, as outlined by Alexandratos and Bruinsma in (2012), necessitates a significant increase in productivity growth rates, as proposed by DGR Vision 2050.

To break free from this agricultural stagnation and realize future production targets, rapid advancements in crop improvement programs are essential. In the contemporary era of post-genome sequencing, the identification of genes governing desirable traits and the tagging of functional variants at the molecular level represent pivotal strategies for breeders. However, progress in this domain has been hindered in major legume crops like groundnut due to limited molecular genetic diversity. Challenges such as groundnut's tetraploid nature and low marker polymorphism have slowed the pace of genomic research. Nonetheless, leveraging comparative mapping across related species and genera offers promise, facilitating the exchange of molecular resources and the identification of orthologous genes. By harnessing insights from model crop genomes such as Arabidopsis and rice, the pace of crop improvement can be accelerated in under-researched legume crops like greengram, blackgram andgroundnut. This transferability of known gene-targeted markers between crop genomes paves the way for Marker Assisted Breeding, enabling precise enhancement of traits critical for food security and resilience in the face of climate challenges.

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MATERIALS AND METHODS

Plant material consists of a total of 17 groundnut genotypes released from RARS, Tirupati, Acharya N.G. Ranga Agricultural University (ANGRAU) and TAG-24, a popular variety released from BARC, Mumbai. A popular rice variety NLR34449 (Nellore Mahsuri) developed from cross IR72 ×BPT 5204, is a fine grain short duration (120-125 days) variety possessing Blast resistance that released from ARS, Nellore, ANGRAU in the year 2009 was used as control variety for molecular studies. Two wild relatives of groundnut *i.e.*, *Arachis glabrata* and *Arachis villosa* that are being maintained at RARS, Tirupati were used in the study as diploid wild source and work was carried out at Institute of Frontier Technology, RARS, ANGRAU, Tirupati with main emphasis to observe the molecular level similarities/ changes with respect to alloploid groundnut at the targeted loci.

Choice of markers

A total of 45 markers targeting 24 number of rice yield, grain size and micronutrient content (Fe and Zn) controlling genes were selected that were used in the rice crop improvement through marker assisted breeding programmes.

Micronutrient content (Fe and Zn) controlling genes *i.e.*, YSL gene specific *Indels* were identified from RiceVarMap database (http://ricevarmap.ncpgr.cn/) and markers were designed by providing the specific ID of each*Indel* (*e.g*. vf0226164188, vf0226169288, vf0226164382) in the suit (http://ricevarmap.ncpgr.cn/primer_design_id/) wherein it consists of Primer3 as a backend engine. To design SSR markers, gene sequences for LOC02g43410 (YSL15), LOC04g44300(YSL13) with an additional 1kb sequence both upstream and downstream were downloaded from rice genomic database of Gramene (http://www.gramene.org). The microsatellite region of candidate genes were identified using SSRIT tool (http://archive.gramene.org/db/markers/ssrtool) and then primer designing was done using primer3 v.4.0.0, a primer designing tool (http://bioinfo.ut.ee/primer3-0.4.0/).

DNA preparation and PCR protocol

Total DNA was extracted from 17 cultivated varieties of groundnut, as well as two wild genotypes, Arachis glabrata and Arachis villosa, along with a rice genotype NLR34449 (Nellore Mashuri), utilizing the CTAB protocol devised by Lin *et al*. (2001). Following extraction, purification was carried out using 3M sodium acetate. The purity and integrity of both groundnut and rice DNA samples were evaluated through agarose gel electrophoresis and NanoDrop spectrophotometry. The amplified alleles were scored for groundnut genotypes, with respect to the allelic sizes of rice using a standard marker *i.e.* 50 bp ladder. Per cent Transferability of gene specific primers that can be from rice to groundnut genome was estimated trait/gene wise, based on the unambiguous amplification of markers at respective allele sizes. Further allele coding was assigned based on the presence of allele similar to rice.

RESULTS AND DISCUSSION

Standardization of markers with rice

All 45 markers targeting 24 rice yield and quality trait governing genes were initially standardized using rice genomic DNA from NLR34449 at temperatures ranging from 50 to 65°C. Out of these, 41 primers successfully amplified with NLR34449, while four primers did not yield amplification. The primers that amplified with rice DNA were subsequently tested for their transferability to groundnut genotypes to assess their applicability in genotyping groundnut.

Standardization of selected markers with peanut genotypes

The 41 markers amplified with rice were tested on wild (*Arachis glabrata* and *Arachis villosa*) and cultivated groundnut varieties. 31 markers (76%) amplified with cultivated groundnuts, except sd1-h. 25 markers amplified with wild groundnuts (Table 1). 10 markers amplified exclusively with rice. Cross-transferability of markers to groundnuts requires further analysis.

Cross transferability of markers between rice and peanut

During the course of crop evolution, the genome content across plant kingdom is proved to be conserved and is evident from many synteny studies across genera/families. Further, conservation of functional genes and important motifs are reported by many earlier research groups (Trivedi *et al*., 2013; Hussien *et al*., 2014). The transferability was analysed with similar allele sizes of groundnut genotypes to rice *i.e.* which are observed across the genotypes under study.

Plant height

In this study, the sd1-h marker, linked to the sd1 gene responsible for plant dwarfism and encoding gibberellin 20-oxidase (GA20ox-2), was examined. While previous

Table 1: Overview of the markers used in the study and their amplification status.

Crop	Rice yield markers		Groundnut oil quality markers		Total markers		% Amplification across genomes
	Markers screened (genes targeted)	Marker amplified	Markers screened (genems targeted)	Markers amplified	Markers used	Amplified	
Rice	45 (24)	41 (91%)	4 (2)	3 (75%)	50	44	88
Groundnut	41	31 (76%)	4	4 (100%)	46	36	78

reports (Monna *et al*., 2002) indicated the marker's association with specific allele sizes (843 bp) in rice varieties, amplification in wild peanut yielded a 190 bp product size, whereas cultivated peanut showed no amplification. This discrepancy may imply significant changes at the primer locus or complete loss of relevant alleles/gene during evolution.

Plant architecture

OsSPL14 (Squamosa Promoter Binding Protein-Like 14), also known as wealthy farmer s panicle/ideal plant Architecture 1, regulated by microRNA OsmiR156, plays a crucial role in rice grain productivity and plant architecture. In 11 groundnut genotypes, the marker predominantly amplified a 500bp allele, akin to rice, with exceptions in certain genotypes showing a 70 bp allele size and Greeshma exhibiting a 390bp allele (Fig 1). Functionally, OsSPL14 promotes heavy panicle formation and increased secondary branches in rice (Mohapatra *et al*., 2018). Exploring this gene in groundnuts offers potential for enhancing yield by modulating branching and flowering patterns, given the importance of secondary branch number in groundnut productivity.

The plant architecture and yield 1 (PAY1) gene, known for improving plant architecture and grain yield, was examined using the PAY1SP6 marker to assess transferability from rice to peanut. Notably, an allele of 200bp was consistently observed across rice and both wild and cultivated peanut genotypes (Fig 1). Zhao *et al*. (2015) compared a wild rice introgression line, YIL55, with a mutant featuring modified plant architecture, PAY1, which exhibited superior traits such as increased plant height, reduced tiller number, thicker stems andlarger panicles. Analyses with NILs in Teqing or 9311 genetic backgrounds further confirmed PAY1′s role in shaping superior plant architecture and enhancing grain yield in rice, suggesting its potential as a key regulator. Characterizing genes like PAY1 offers opportunities for enhancing groundnut plant architecture and reproductive unit production.

Yield contributing genes

The grain number (GN2) gene, functioning as an OsWAK (Wall-Associated Kinase) receptor-like protein, is crucial for increasing grain number. In this study, the closely tagged marker RM3535 consistently amplified an 185bp fragment across all peanut genotypes, mirroring results observed in rice. Sequencing of this allele could further validate its utility for groundnut improvement breeding (Fig 1).

The *YLD* (yield) gene linked SSR marker RM223 amplified 165bp in all genotypes of rice and peanut (Fig 1). This marker also has tagged to aromatic/non-aromatic trait of rice as reported in Jewel *et al*. (2011).

The spikelet number (SPIKE) gene, linked to Narrow Leaf1 (NAL1), enhances spikelet number. The SPIKE-INDEL3 marker consistently amplified a 171 bp fragment in both rice and groundnut. However, in cultivated peanut genotypes, it showed non-specific amplification of a 250 bp fragment alongside the 171 bp fragment (Fig 1). Additionally, Erect Panicle 3 (EP3), associated with erect panicle formation, was noted. The S5-803 marker exclusively expressed a 243 bp allele size in rice (Piao *et al*., 2009).

SCM2/Aberrant panicle organization 1 (APO1) gene, crucial for rachis branching and culm diameter regulation, features a beneficial allele known as SCM2 found in the Habataki rice variety (Kim *et al.,* 2016). The SCM2 INDEL1 marker amplified consistently at 117bp in both rice and peanut genotypes, although with lower intensity in peanut, possibly due to primer site variations. Further primer design targeting different gene regions may confirm the presence of SCM2 ortholog in groundnut.

The DEP1 gene which encodes phosphatidyl ethanolamine binding protien (PEBP), regulates dense and erect panicle traits in rice, impacting grain number per panicle (Huang *et al*., 2009). Dep1s7 consistently amplified a 127 bp allele across rice and all peanut genotypes, indicating potential orthologous study from rice to peanut for identifying pod number increase per plant (Fig 1).

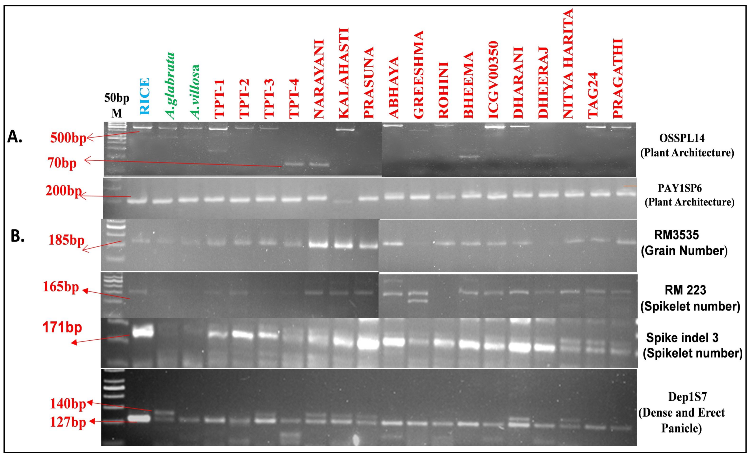

Fig 1: Amplification of groundnut genotypes with rice plant architecture (A) and yield gene tagged markers (B).

Seed quality genes (Seed Size and weight)

The GS2 gene plays a crucial role in regulating grain size and shape in rice, with the marker RM3212 associated with the medium-grain phenotype (Zhang *et al*., 2013). This marker consistently expressed an 181bp allele size in both rice and peanut. GS3, linked to markers RGS1, SF28, RGS2 andSR17, was not detected in African rice cultivars due to the domestication process. However, the wild rice relative *O. meridionalis* possesses unique alleles related to GS3, making it a candidate gene for genetic improvement in cultivated lines. Allelic variations at SF28, RGS1 andRGS2 loci within GS3 are strongly associated with grain length in Chinese rice germplasm. Meanwhile, SR17 marginally affects grain length (Wang *et al*.,2010). RGS1 and SR17 markers amplified 180bp/200bp and 1400bp allele sizes, respectively, exclusively in rice, underscoring their roles in regulating grain size and length.

The *GS5* gene, governing grain width (Li *et al*., 2011) in rice, consistently amplified a 67 bp allele with GS5-INDEL1 in both rice and peanut genotypes, indicating potential transferability of the marker and suggesting wide grain size (Kim *et al*., 2016). Additionally, RM574 expressed a 240bp allele associated with low grain width, which could be useful in rejecting undesirable traits in rice breeding (Bidanchi *et al*., 2018). Exploring GS5 in groundnut could reveal key allelic variants influencing kernel size (Fig 2).

The *GW2* gene, integral to grain width and weight regulation, was analyzed utilizing the GW2SNP2 marker, which consistently revealed a 51 bp allele in both rice and peanut genotypes (Fig 2), mirroring previous findings of Zhang *et al*. (2015). Furthermore, investigation into the *GW5* gene, associated with grain width, employed the RM3328 and RMw513 markers. RM3328 exhibited a 119 bp product in rice and a 95 bp allele in cultivated peanut genotypes, while no alleles were detected in wild groundnut. Conversely, RMw513 showcased a 600bp allele in both rice and cultivated peanut genotypes, with the wild peanut revealing a 700 bp allele (Fig 2). Further exploration of GW5 orthologs in peanut holds promise to unravel seed size variation.

The *SW5* (Seed Width) gene, targeted by the N1212 marker, is linked to increased grain width. Contrary to findings of Zhang *et al*., (2015), our study revealed a 65bp product as the major allele in both rice and peanut genotypes (Fig 2).

GLW7 (Grain Length and Width), governed by the OsSPL13 transcription factor, regulates cell size in grain hulls, enhancing grain length and yield belongs to *Squamosa Promoter Binding Protein (SBP)* family. This marker consistently expressed a 140bp size in both rice and peanut genotypes, with some cultivated peanut genotypes displaying a 160bp allele, indicating potential locus variations among groundnut genotypes. Further research on this gene could elucidate its function in peanut.

Another marker, RM505, linked to *qgrl7* responsible for grain length, exhibited varying (500 and 180bp) amplification patterns in different rice and peanut genotypes, with cultivated peanut genotypes displaying a 490 bp allele (Fig 3). Sequencing the major allele may clarify the gene's orthologous nature in groundnut. RM21945, associated with grain length, grain weight (GW), length and width ratio and Gel Consistency (Verma *et al*.,2015), consistently expressed a 292bp allele in all rice and peanut genotypes, but with lower intensity in peanut. These findings suggest potential transferability from rice to peanut, pending analysis with additional markers.

Seed filling

Shelling percentage, a vital trait in groundnut, prompted an examination of the rice GIF1 (GRAIN INCOMPLETE FILLING 1)

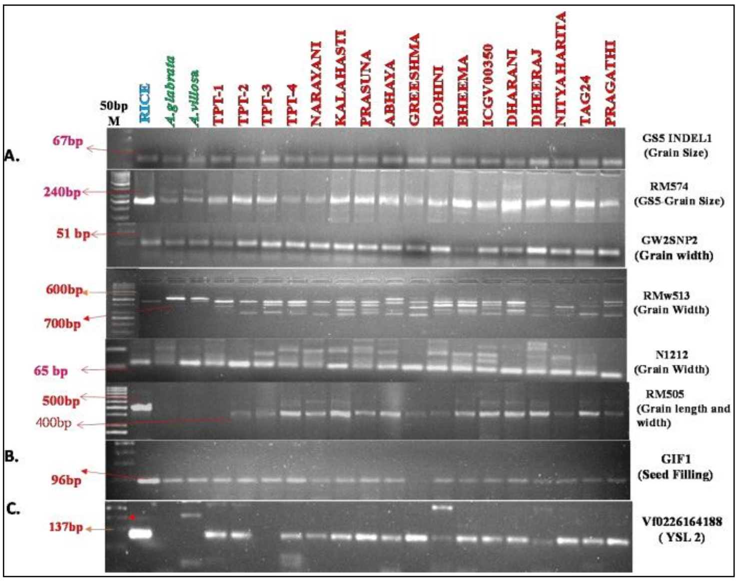

Fig 2: Amplification pattern of groundnut genotypes with rice seed quality (A), Seed filling (B) and seed micronutrient (Fe and Zn, yellow stripe Like 2 -YSL 2) (C) gene tagged markers.

gene, known for its role in grain filling. The GIF1 marker revealed a consistent 96bp allele across all rice and peanut genotypes, indicating potential transferability for seed filling/ size regulation (Fig 2).

Flowering time

Groundnut farming in India relies on rainfed conditions, making early flowering crucial. Heading date genes like Hd3a and RFT1 (RICE FLOWERING LOCUS T) accelerate flowering under different day lengths (Yano *et al*., 2000). Hd1AGC and Hd3a showed 140 bp and 90 bp alleles consistently across rice and peanut genotypes. This suggests the presence of similar genes in groundnut, aiding in the development of groundnut varieties with preferred flowering times.

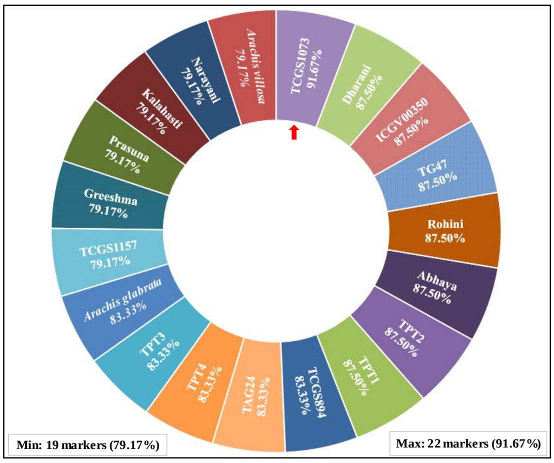

Fig 3: Comparison of individual groundnut genotypes for amplification status (%) with reported rice gene tagged markers.

Seed micronutrient content

Fe and Zn are important micronutrients towards human health, thus needs to be focused in research of food crops. For Fe and Zn content, primers using primer 3 software were designed for 3 reported genes *viz*., *YSL2*, *YSL13* and *YSL15* which belongs to Yellow-Stripe Like gene family. *YSL2* gene reported for preferential expression in the leaf tissues which suggests that this *YSL2* functions as transporter which is responsible for the phloem transport of iron. The other gene *YSL15* proved for its significant expression in root and rhizome type of tissues indicating its role in the uptake/absorption of iron from the source (Menna *et al*., 2011). Out of the five *indel* markers used, only one marker (vf0226164188) tagged to *YSL2*gene amplified alleles (137 bp) in both rice and peanut (Fig 2).

Assessment of cross transferability across genotypes

The assessment revealed that 76% of rice gene markers successfully amplified in groundnut, indicating high conservation between the two crops (Fig 3 and Fig 4). Genotype-level analysis (Table 2) showed common allele sharing ranging from 79.17% to 91.67% among groundnut genotypes (Fig 3). Seventeen markers from 14 genes showed consistent amplification across all groundnut genotypes (Fig 4), while two markers (Dep1 INDEL 1 and Hd1) exhibited limited amplification. Some markers showed lower intensity but retained rice allele size, suggesting the need for alternative marker regions to address amplification challenges.

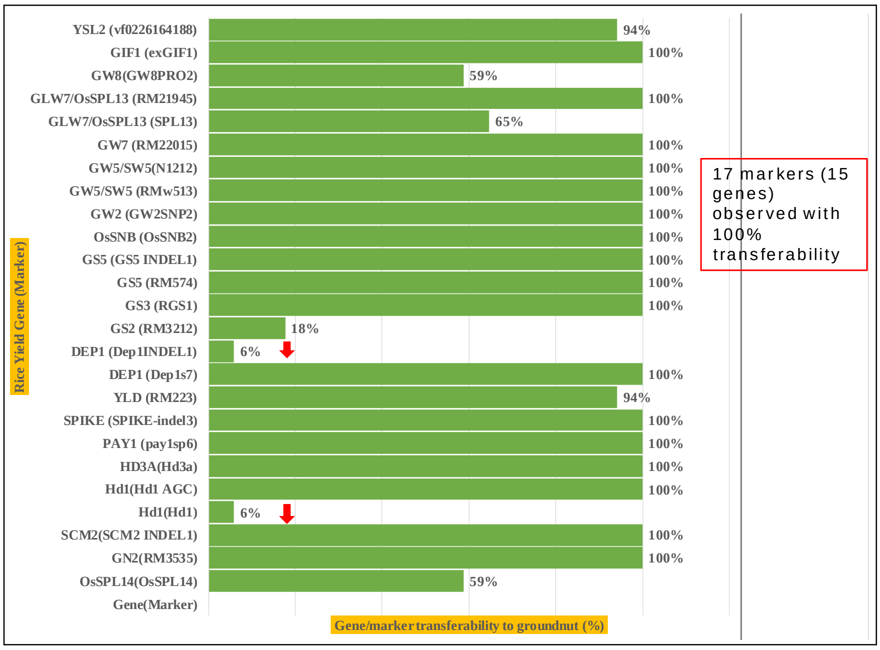

Fig 4: Estimation of transferable efficiency of rice gene targeted markers to groundnut and possibility of presence of rice ortholog genes

Table 2: Alleles generated with rice yield gene tagged markers among groundnut genotypes under study and their allele codes.

Rice Yield Gene (Marker)	Rice	*A. glabrata*	*A. villosa*	TPT1	TPT2	TPT3	TPT4	Narayani	Kalahasti	Prasuna	Abhaya	Greeshma	Rohini	Bheema	ICGV00350	Dharani	Dheeraj	Nithya Haritha	TAG24	Pragathi	TGSR*	Allele code			
																						A	B	C	D
OsSPL14(OsSPL14)	A	A	A	A	A	A	C	C	A	NA	A	B	A	C	A	A	C	NA	A	A	10	500	390	70	-
GN2(RM3535)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	185	-	-	-
SCM2(SCM2 INDEL1)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	117	-	-	-
Hd1(Hd1)	A	A	A	NA	D	NA	NA	NA	NA	NA	NA	NA	NA	D	NA	A	D	NA	C D	B	1	100	260	250	110
Hd1(Hd1 AGC)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	140	-	-	-
HD3A(Hd3a)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	90	-	-	-
PAY1 (pay1sp6)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	200	-	-	-
SPIKE (SPIKE-INDEL3)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	171	-	-	-
YLD (RM223)	A	A	A	A	A	A	A	A	A	A	B C	B C	NA	A	A	A	A	A	A	A	16	165	240	140	-
DEP1 (Dep1s7)	A	A B	A	A	A	A B	A	A B	A B	A B	A	A	A	A	A	A B	A	A B	A	A	17	127	140	-	-
DEP1 (Dep1INDEL1)	A	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	A	NA	NA	1	1031	-	-	-
GS2 (RM3212)	A	A	NA	NA	B	NA	NA	NA	NA	B	500	NA	A	A	NA	NA	NA	NA	NA	NA	3	181	400	-	-
GS3 (RGS1)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	180	-	-	-
GS5 (RM574)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	240	-	-	-
GS5 (GS5 INDEL1)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	63	-	-	-
OsSNB (OsSNB2)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	50	-	-	-
GW2 (GW2SNP2)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	51	-	-	-
GW5/SW5 (RMw513)	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	600	700	-	-
GW5/SW5(N1212)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	65	-	-	-
GW7 (RM22015)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	176	-	-	-
GLW7/OsSPL13 (SPL13)	A	A	A	A	A	A	B	NA	B	A	B	A	A	A	A	A	A	B	A	B	11	140	160	-	-
GLW7/OsSPL13 (RM21945)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	292	-	-	-
GW8(GW8PRO2)	A	NA	NA	A	A	A	NA	A	NA	NA	A	NA	A	A	A	NA	A	NA	NA	A	10	861	-	-	-
GIF1 (exGIF1)	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	17	96	-	-	-
YSL2 (vf0226164188)	A	NA	B C	A	A	NA	A	A	A	A	A	A	A	A	A	A	A	A	A	A	16	137	200	300	-
Total number of Alleles similar to rice#		20	19	21	21	20	20	19	19	19	21	19	21	21	21	21	22	19	20	20					

TGSR*: Total number of groundnut genotypes that amplified alleles similar to rice. #: Total number of alleles exhibited by individual groundnut genotype. NA: not amplified.

CONCLUSION

Slow progress in groundnut gene characterization is due to its complex genome and limited molecular diversity. However, the high transferability of gene markers from rice to peanut, as observed in this study, suggests potential for rapid gene improvement in groundnut by leveraging existing knowledge and databases from molecular model crops and widens the scope to improve the orphan crops with low molecular progress like peanut by pyramiding of desirable genes in short span of time by the breeders.

Conflict of interest

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

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