ORIGINAL ARTICLE

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Assessing variability for disease resistance and nutritional quality traits in an interspecific collection of groundnut (*Arachis hypogaea*)

Sandip K. Bera[1],[†] (ID) | Surendra S. Manohar[2],[†] | Murali T. Variath[2] | Sunil Chaudhari[2] | Shasidhar Yaduru[2] | Radhakrishnan Thankappan[1] | Manivannan Narayana[3] (ID) | Sadaiah Kurapati[2] | Manish K. Pandey[2] | Hari K. Sudini[2] | Saravanan Shanmugavel[3] | Ganesamurthy Kulandaivelu[3] | Rajeev K. Varshney[2] (ID) | Janila Pasupuleti[2] (ID)

[1]ICAR-Directorate of Groundnut Research (DGR), Junagadh, Gujarat, India

[2]International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Hyderabad, Telangana, India

[3]Tamil Nadu Agricultural University (TNAU), Coimbatore, Tamil Nadu, India

Correspondence
Pasupuleti Janila, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Hyderabad, Telangana, India.
Email: p.janila@cgiar.org

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Abstract

Rust and late leaf spot (LLS) resistance sources involving *Arachis batizocoi*, *A. duranensis*, *A. cardenasii* and *A.* sps Manfredi-5 were identified from field evaluation of interspecific derivatives (IDs) of groundnut in a disease nursery for two seasons. Although the sources displayed low levels of resistance compared to currently cultivated lines, they contribute allele diversity in groundnut breeding that has so far relied on alleles contributed from *A. cardenasii* for disease resistance. Multiple disease-resistant and agronomically superior IDs, ICGVs 11379, 10121, 10179, 05097, 02411 and 00248 involving *A. batizocoi*, *A. duranensis* and *A. cardenasii* can be used in breeding for groundnut improvement. Genetic variability for resistance to rust and LLS, yield and nutritional quality traits was influenced by genotype, environment and genotype × environment interaction effects in individual and pooled analyses. In case of *FAD* (fatty acid desaturase)-mutant alleles that govern high oleic trait, allele mining of IDs (110) showed that frequency of mutation in *ahFAD2B* is rare, whereas of *ahFAD2A* is common. High oleic lines were not detected among the IDs.

KEYWORDS
FAD2 gene, groundnut, interspecific derivatives, markers, multiple disease resistance, oleic acid

1 | INTRODUCTION

Cultivated groundnut (*Arachis hypogaea* L.) is an allotetraploid ($2n = 4x = 40$) belonging to the genus *Arachis* and family *Leguminosae*. It can be used as oil, food and feed crop and is cultivated in an area of 25.44 m ha globally with a total production of 45.22 m tons during 2013 (FAO stat, 2014). Globally, over 50% of the groundnut produce is crushed into oil for human consumption and industrial uses, and less than 40% is used directly as food.

Groundnuts are valued for their nutritional benefits as they are rich in oil (~50%) and protein (~25%), and also contain health-enhancing nutrients such as minerals, antioxidants and vitamins.

The genus *Arachis* contains 81 described species that include diploids and tetraploids (Leal-Bertioli et al., 2015; Valls, Costa, & Custodio, 2013; Valls & Simpson, 2005), classified into nine taxonomical sections based on morphological variation, geographical distribution and cross-compatibility (Krapovickas & Gregory, 1994). The other tetraploid species of the genus are *A. monticola* of section *Arachis* and *A. pseudovillosa*, *A. glabrata* and *A. nitida* from section *Rhizomatasae*, while all other species are diploid with $2n = 2x = 20$ or $2n = 2x = 18$ genome constitution. Differences in the ploidy levels

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[†]Contributed equally.

of cultivated and wild species have imposed crossing barriers resulting in low genetic variability for important biotic and abiotic stresses in the cultivated gene pool. Groundnut improvement programmes around the world have so far tapped the genetic variability from the primary gene pool that includes two tetraploid species, *A. hypogaea* and *A. monticola*. Both secondary and tertiary gene pools comprising diploid wild species are potential sources of new alleles for resistance to foliar fungal diseases (Dwivedi, Pande, Rao, & Nigam, 2002; Dwivedi et al., 2008; Pande & Rao, 2001), resistance to aflatoxin contamination (Xue, Isleib, Stalker, Payne, & Obrian, 2005), tolerance of abiotic stress (Nautiyal et al., 2008) and morpho-agronomic and nutritional quality traits (Upadhyaya, Dwivedi, Nadaf, & Singh, 2011). Majority of species from the secondary gene pool are cross-compatible with cultivated groundnut, while species from the tertiary gene pool are either weakly cross-compatible or cross-incompatible with cultivated groundnut. Despite the pre- and postfertilization barriers, triploids (Mallikarjuna, Pande, Jadhav, Sastri, & Rao, 2004) and synthetic tetraploids (Mallikarjuna, Senthilvel, & Hoisington, 2011) were developed through tissue culture techniques and used to introgress new alleles into cultivated groundnut. Molecular and genetic studies have led to identification of quantitative trait loci (QTL) from wild species contributing to genetic variation to groundnut productivity and adaptation traits (Fonceka et al., 2012), and resistance to disease (Leal-Bertioli et al., 2009). A full-length *AdTLP* gene from *A. diogoi*, a diploid wild species, was isolated and its protein was shown to impart significant resistance against fungal pathogens, salt and oxidative stress in transgenic plants (Singh, Rajesh Kumar, Kumar, Shukla, & Kirti, 2013), suggesting the potential of wild species to contribute new alleles.

Sources of resistance to two major foliar fungal diseases, late leaf spot (LLS) caused by *Phaeoisariopsis personata* (Berk. & M.A. Curtis) Van Arx and rust caused by *Puccinia arachidis* Speg., are available in cultivated groundnut. However, the genetic base can be broadened by utilizing new alleles from wild species. A few studies have reported sources of resistance to LLS and rust in interspecific derivatives (IDs) (Dwivedi et al., 2002; Pande, Rao, & Dwivedi, 2002; Shilpa et al., 2013).

Very limited variability was reported for oleic acid concentration among wild *Arachis* species (Grosso, Nepote, & Guzman, 2000; Wang, Barkley, Chinnan, Stalker, & Pittman, 2010) and newly synthesized amphidiploid and auto-tetraploid groundnut (Shilpa et al., 2013). However, in a study involving 24 wild *Arachis* species, an *A. correntina* line with oleic acid concentration of 68% was reported by Tang et al. (2013). For oil concentration, variability ranging from 51% to 63% was reported among 72 wild *Arachis* accessions tested over 3 years (Huang et al., 2012). Thus, crossing cultivated groundnut with wild species can improve upon the genetic diversity and also introgress traits of interest into the cultivated gene pool. This study was conducted with an objective to explore variability for resistance to diseases, nutritional quality and yield parameters in a set of 110 IDs of groundnut developed at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Tamil Nadu Agricultural Research Station (TNAU), Vridhachalam and Indian Council of Agricultural Research-Directorate of Groundnut Research (ICAR-DGR), Junagadh, India, and to identify suitable IDs for use in breeding.

2 | MATERIALS AND METHODS

2.1 | Plant materials

A total of 110 IDs of which 50 from ICRISAT, Patancheru, 36 from DGR, Junagadh, and 24 from TNAU, Vridhachalam, were evaluated under field condition during 2013 and 2015 rainy season. The wild species involved in developing IDs are summarized in Table 1, and all the parents involved are given in Supporting information Table S1. ICGV 86590 is resistant control, and 'TMV2' is the susceptible control for foliar fungal diseases. SunOleic 95R, with oleic acid concentration of >80% and O/L ratio of >20, was used as the check for oleic acid.

2.2 | Field experiment

The IDs were evaluated in an alpha lattice design with two replications in precision fields on Alfisol (clayey-skeletal, mixed, isohyperthermic family of Udic Rhodustalfs) at Patancheru (17°53′N, 78°27′ E, and 545 m altitude), India, during 2013 and 2015 rainy season. The plot size was one row of 4 m length spaced at 30 cm between rows and 10 cm between plants. Recommended cultural management practices were followed during the cropping period. For disease screening, infector rows of a susceptible cultivar, 'TMV2', were planted along the border rows as well as after every ten rows of test material to maintain uniform and effective inoculum load. To promote disease development in the infector rows, rust and LLS-infected 'TMV2' plants from the greenhouse were transplanted to the field at 50 days after sowing (DAS). Also, both conidia of LLS and urediniospores of rust were sprayed at a concentration of 5×10^4 spores/ml on infector rows. Sprinkler irrigation was provided daily for 30 min/day for a period of one month starting from the day of field inoculation with the pathogen. The experimental field received 60 kg/ha P_2O_5 and 400 kg/ha gypsum. Eight supplemental sprinkler irrigations were provided with about 5 cm depth of water at each irrigation.

For artificial inoculation, 'TMV2' seeds were sown in the greenhouse and sprayed with urediniospores of rust and conidia of LLS at 5×10^4 spores/ml at 35 DAS. Water was sprinkled in and around the inoculated plants grown in the polybags, and the plants were covered with a polyethylene sheet during the nights for 7 days to maintain high humidity (95%).

2.3 | Recording disease reaction, nutritional quality and yield traits

The IDs along with checks were evaluated for disease reaction to LLS and rust, nutritional quality and yield traits. All plants in each plot were used to record observations on various qualitative and

TABLE 1 Wild *Arachis* species involved in developing groundnut interspecific derivatives

Wild species used	Interspecific derivatives (IDs)
A. cardenasii	ICGVs 00005, 01265, 02323, 03057, 03179, 04157 07086, 10004, 10150, 10221, 10290, 10291, 10332, 10340, 10342, 10349, 11008, 11009, 11010, 11015, 11367, 11368, 11370, 11417, 11447, 98373, 99085, 05100, NRCGCSs -151, -157, -158, -204, -212, -235, VGs 0401, 0410, 0411, 0430, 0437, 0438, 0512, 0515 and 0517
A. duranensis	NRCGCSs -146, -169, -172 and -317
A. batizocoi	VG 1002
A. villosa	NRCGCSs- 152, -170, -223 and -224
A. sps Manfredi-5	NRCGCS-161
A. paraguariensis	NRCGCS-227
A. stenosperma	NRCGCS-254 and VG 9406
A. kretschmeri	NRCGCSs -287, -289, -301, -305, -312 -353, and 289-1 purple,
A. diogoi	NRCGCSs-134, -137, -138 and -350
A. correntina	NRCGCS-354, VG 1007, VG 1008
A. oteroi	NRCGCS-355
A. batizocoi and *A. duranensis*	ICGVs 00248, 01361, 02411, 02446, 04071, 05097, 06157, 06175, 06285, 07213, 09012, 09138, 10002, 10179, 11003, 11379, 11464, 98293, 99052, 98290, NRCGCS-421, VG 0701 and VG 0706
A. cardenasii and *A. villosa*	VGs 1013, 1016, 9412 and 9411
A. cardenasii and *A. stenosperma*	VG 1012 and VG 1015
A. duranensis and *A. helodes*	NRCGCSs-415 and -416
A. duranensis and *A. monticola*	NRCGCS-417
A. duranensis and *A. pusilla*	NRCGCS-418
A. duranensis and *A. correntina*	NRCGCS-419
A. duranensis and *A. villosa*	VG 1004 and VG 1005
A. correntina and *A. helodes*	VG 1010
A. cardenasii and *Arachis* sps Manfredi-5	ICGV 00068
A. batizocoi, *A. duranensis*, and *A. cardenasii*	ICGV 10121

quantitative traits. Data were recorded on plot basis for pod and seed yield and converted into kg/ha. The shelling per cent (SH %) was estimated from a sample of 200 g of randomly selected pods, while a random sample of 100 mature seeds was used to record 100-seed weight. Protein, fatty acid and oil concentration were measured with near-infrared reflectance spectroscopy (NIRS) (NIR Systems model XDS monochromator, FOSS Analytical AB, Sweden, Denmark). About 100–150 seeds of each genotype from both the replications were scanned twice using NIRS. Calibration equations were developed in the laboratory and validated for estimation of oil, protein and fatty acid concentration in whole seeds of groundnut (Unpublished data). The regression coefficient (R^2) values of the calibration equations for predicting oil, protein and palmitic acid were 0.84, 0.88 and 0.89, respectively, while it was 0.96 for oleic and linoleic acid. For LLS and rust, disease scoring was done based on modified 9-point scale, where 1 = no disease and 9 = >80% diseases incidence with almost all leaves defoliated as given by Subrahmanyam et al. (1995). The disease scores of rust and LLS were recorded at 75 and 90 DAS.

2.4 | DNA isolation and genotyping for FAD alleles and for resistance to rust and LLS

Leaf samples from unopened leaves of 10- to 15-day-old seedlings were collected and used to isolate the genomic DNA using modified CTAB-based method as described by Cuc et al. (2008). After DNA isolation, the quality and quantity of the DNA were checked on 0.8% agarose gel. The DNA concentration was then normalized to 5 ng/μl and used in genotyping with allele-specific markers of *ahFAD2A* and *ahFAD2B* genes (Chen, Wang, Barkley, & Pittman, 2010). The polymerase chain reactions (PCRs) were performed in 10 μl volume using 5 ng of genomic DNA, 0.5 μM of each forward and reverse primer, 1× PCR buffer (Sib-Enzyme, Russia), 5 mM MgCl₂, 0.03 U/μl of *Taq* DNA polymerase (Kapa Biosystems, Inc, Wilmington, MA), and 0.2 mM dNTPs. PCRs were performed following a touch-down PCR profile in an ABI thermal cycler (Applied Biosystems, Foster city, CA). The touch-down PCR amplification profile had initial denaturation step for 3 min at 94°C followed by first five cycles of 94°C for 20 s, 65°C for 20 s and 72°C for 30 s, with 1°C decrease in temperature after each cycle. Afterwards, 35 cycles of 94°C for 20 s with constant annealing temperature (59°C) for 20 s and primer extension at 72°C for 30 s and final extension at 72°C for 20 min were performed. The PCR products were separated on a 3.0% agarose gel (SeaKem LE® Agarose) in 1× TBE buffer by electrophoresis at 150 V for an hour. The agarose gels were stained with ethidium bromide and visualized under UV light. Separated fragments on the agarose gels were sized by referencing with a 100-bp DNA ladder (Life Technologies, Carlsbad, CA).

Four different SSRs, namely, GM1536, IPAHM103, GM2079, GM2301, were used to screen for rust and LLS-specific loci located on chromosome A03. Three different SSRs, namely, SEQ8D09, GM2032, and GM1009, were used for screening LLS resistance alleles present on chromosome A02 (Sujay et al., 2012). The genotyping method used is explained in Varshney et al. (2009). PCR products were resolved on 1.5% agarose gel to confirm amplification. The forward primers were dye labelled with FAM, VIC and NED, which were detected as blue, green and black colour peaks, respectively (Applied Biosystems, USA). The PCR products were denatured and

separated with capillary electrophoresis using ABI 3700 automatic DNA sequencer (Applied Biosystems). GeneMapper Software V (Applied Biosystems) was used for scoring of allele size.

2.5 | Statistical analysis

The mean data were used for analysis of individual and pooled variance using Genstat 17th edition for alpha lattice design (www.vsni.co.uk). The various genetic parameters including mean, range and coefficient of variation were evaluated as suggested by Federer (1956), and phenotypic and genotypic coefficient of variance was calculated using the formula suggested by Burton (1952). Broadsense heritability (H^2) was calculated using the following equation:

$$H^2 = \frac{\sigma_G^2}{\sigma_G^2 + \left(\frac{\sigma_{GE}^2}{e}\right) + \left(\frac{\sigma_e^2}{re}\right)}$$

where σ_G^2—genotypic variance, σ_{GE}^2—genotype–environment interaction variance, σ_e^2—residual variance, e—number of environments, r—replications per environment.

Genotypic and phenotypic correlation among the traits (Pearson, 1895) was estimated, and significance was tested comparing with critical values of t at <0.05 probability level using META R version 5.0.

3 | RESULTS

Disease incidence was severe in the experimental plots during 2013 and 2015 rainy seasons with 'TMV2' recording a score of 9.0 for rust and LLS at 90 DAS. Analysis of variance (ANOVA) presented in Table 2 revealed that the genotypic effects were significant for all the 14 traits during 2013 and 2015 rainy seasons. Pooled ANOVA over two seasons revealed significant differences among genotypes, environment and genotype × environment (G × E) interaction effects.

The pooled range, mean, coefficient of variation (CV), genotypic and phenotypic coefficient of variation (GCV and PCV) and heritability in broad sense for all the characters are given in Table 3. For resistance to diseases, yield and nutritional parameters, PCV values were found to be higher than the GCV. Higher GCV and PCV values coupled with high heritability were observed for LLS and rust at 75 and 90 DAS in individual as well as pooled across years, whereas low to moderate GCV and low to high PCV values were reported for yield traits. However, GCV and PCV values were low for all the nutritional quality parameters. The estimates of broad-sense heritability for yield and nutritional quality traits, and resistance to rust and LLS ranged from 33% to 89%.

The IDs recorded high variation for rust and LLS scores. Pooled analysis revealed that the disease score among the IDs at 90 DAS ranged from 3.2 to 7.6 for LLS, and from 2.1 to 5.6 for rust on a 1.0 to 9.0 scale. ICGVs 99052, 02411, 05097, 98293, 00248, 11379, 07213, 10121, 10179, 04071, 02323, 02446, 11417 and VGs 0517

and 1008 recorded lower mean disease score of 3.0 to 4.0 and were significantly superior compared to the resistant check ICGV 86590 with LLS score of 6.0 at 90 DAS. The LSD for LLS at 90 DAS was 0.89. For rust, ICGVs 98293, 11379, 00248, 10179, 02411, 99052, 11417, 10150, 11447 and 00068 recorded mean disease score of 2.0, similar to the resistant check (ICGV 86590). The LSD for rust at 90 DAS was 0.94. Among these derivatives, ICGVs 98293, 11379, 00248, 10179, 02411, 05097 and 99052 recorded disease scores of 3.0–4.0 for LLS and 2.0 for rust at 90 DAS (Table 4).

Oil concentration among the IDs varied from 45% to 54%, and protein concentration from 22% to 27%. Oleic acid concentration of the IDs varied from 34% to 49%, linoleic acid concentration varied between 30 and 43%, palmitic acid concentration from 11% to 13%, and stearic acid concentration from 1% to 3%. SunOleic 95R recorded oleic acid concentration of 82%, linoleic acid of 4% and O/L ratio >20 in this study. Pod yield per hectare varied from 1620 to 5598 kg, seed yield from 1074 to 3223 kg, shelling per cent from 57 to 70% and 100-seed weight from 21 to 56 g.

Phenotypic and genotypic correlations between the traits were calculated, and significant trait associations are presented in Table 5. Pod yield per hectare showed significant negative correlation with LLS and rust at 75 DAS ($r_p = -0.77$, $r_g = -0.98$ for LLS and $r_p = -0.67$, $r_g = -0.75$ for rust) and 90 DAS ($r_p = -0.79$, $r_g = -1.00$ for LLS and $r_p = -0.67$, $r_g = -0.89$ for rust), and positive association with seed yield per hectare ($r_p = 0.97$ and $r_g = 0.99$) and 100-seed weight ($r_p = 0.48$ and $r_g = 0.76$). Oil and protein concentration had significant negative association with each other but the magnitude was <0.5. Strong significant negative phenotypic and genotypic correlation was observed between oleic acid concentration and linoleic acid concentration ($r_p = -0.98$, $r_g = -0.99$), while significant positive correlation was found between linoleic acid concentration and palmitic acid concentration ($r_p = 0.83$, $r_g = 1.00$).

Allele mining was done for *ahFAD2A*- and *ahFAD2B*-mutant alleles in IDs (110 accessions) using allele-specific markers developed by Chen et al. (2010). Genotyping revealed mutation in A-genome (for *ahFAD2A*) among the genotypes ICGV 06175, NRCGS lines -227, -161, -157, -138, -421, and VG lines 0507, 1002, 1007, 1008, 1010 and 1016 but none with B-genome (for *ahFAD2B*) mutation.

Screening for rust and LLS alleles was done on 32 IDs. The rust score of the derivatives varied from 2 to 3 for rust and 3 to 7 for LLS at 90 DAS. GPBD 4, a rust- and LLS-resistant genotype derived from *A. cardenasii*, was used to characterize the IDs. SSR markers, namely, GM1536, IPAHM103, GM2079 and GM2301 for rust and LLS screening showed similar peaks to GPBD 4 in 23 IDs, of which nine are from *A. cardenasii*, 13 are derived from *A. batizocoi* and *A. duranensis*, and one was derived from *A. cardenasii*, *A. batizocoi* and *A. duranensis* (Tables 6 and 7). Five derivatives (ICGV 10221, ICGV 11009, VG 0410, VG 0411 and VG 0430) from *A. cardenasii* showed different alleles for GM1536 and IPAHM103; while ICGVs 04157, 06157, 00068 and VG 0437 had a different allele only for GM1536. For LLS, with the exception of VG 0437 which indicated a different peak for GM1009, all the remaining derivatives showed

TABLE 2 Individual and combined analysis of variance (mean squares) for different traits of interspecific derivatives of groundnut from field studies conducted at ICRISAT, Patancheru

Source of variation	df	PYH	SYH	SH (%)	HSW	LLS 75 days	LLS 90 days	Rust 75 days	Rust 90 days	OC (%)	PC (%)	PAC (%)	SAC (%)	OAC (%)	LAC (%)
Rainy 2013															
Replication	1	519,188	674,631	62.23	107.61	0.64	0.02	4.86*	8.64*	38.43*	15.16*	0.05	1.36*	5.4	0.71
Rep × Block	14	7,953,449*	4,156,953*	62.71*	213.40*	11.03*	8.46*	9.82*	11.81*	34.75*	8.46*	0.68*	0.42*	55.26*	36.38*
Genotype	104	2,377,785*	1,168,386*	44.18*	96.50*	1.73*	1.46*	1.40*	1.85*	10.53*	2.21*	0.68*	0.18*	33.23*	25.28*
Residual	104	292,146	16,2547	17.5	5.92	0.22	0.36	0.33	0.34	2.79	0.92	0.15	0.08	2.66	1.95
Total	223	1,746,817	884,704	32.98	61.65	1.61	1.38	1.45	1.8	8.56	2.06	0.43	0.15	20.23	14.98
Rainy 2015[a]															
Replication	1	177,250	181,484	6.89	1.99	0.30	2.52	0.04	2.74	0.33	6.83	0.03	0.01	3.29	0.22
Rep × Block	14	9,538,609*	2,728,740*	68.09*	129.90*	4.35*	14.04*	5.55*	14.32*	38.40*	7.66*	4.04*	0.76*	93.93*	64.64*
Genotype	97	1,227,455*	367,196*	30.68*	54.50*	0.98*	2.21*	0.87*	3.07*	5.96*	4.07*	0.88*	0.23*	32.16*	25.73*
Residual	97	326,972	178,641	11.53	6.26	0.3	0.43	0.37	0.5	1.01	0.85	0.14	0.03	2.9	2.39
Total	209	1,361,231	436,986	24.19	36.91	0.89	2.18	0.94	2.63	5.81	2.83	0.75	0.17	22.58	17.39
Pooled															
Genotype	111	4,275,989*	1,745,647*	52.4*	158.7*	4.1*	5.5*	3.7*	6.9*	19.9*	5.7*	1.5*	0.3*	70.7*	53.6*
Environment	1	4,964,845*	22,909,114*	7472.3*	5636.8*	22.7*	85.1*	35.4*	79.6*	552.9*	113.2*	156.2*	38.9*	1544.8*	5059*
G × E	104	1,600,884*	718,660*	34.5*	23.2*	0.5*	1.0*	0.5	1.0*	4.7*	2.3*	0.7*	0.2*	7.9*	5.9*
Residual	216	312,437	171,969	14.8	7.2	0.3	0.4	0.4	0.5	2.0	1.0	0.1	0.1	2.7	2.1
Total	433	1,559,795	703,106	45.2	61.8	1.3	2.0	1.3	2.3	8.5	2.7	1.0	0.2	24.7	27.1

Notes. *Represents significance at <0.001 probability level.

[a]Seven interspecific derivatives were missing in rainy 2015 season.

75 days, and 90 days indicate the disease score recorded at 75 and 90 days after sowing; df: degree of freedom; HSW: hundred seed weight (g); LAC: linoleic acid concentration; LLS: late leaf spot; OAC: oleic acid concentration; OC: oil concentration; PAC: palmitic acid concentration; PC: protein concentration; PYH: pod yield hectare (kg/ha); SAC: stearic acid concentration; SH: shelling per cent; SYH: seed yield hectare (kg/ha).

Trait	Mean±SE	CV%	Range among IDs	GCV (%)	PCV (%)	Heritability (%)
PYH (kg/ha)	3190 ± 393.1	17.52	1620–5598	24.34	31.49	59.7
SYH (kg/ha)	2036 ± 261.7	20.36	1074–3223	22.91	31.13	54.2
SH (%)	64.0 ± 1.7	5.999	57.2–69.7	3.239	5.6	33.5
HSW (g)	34.8 ± 2.1	7.723	21.5–56.2	16.78	18.15	85.5
LLS (75 days)	3.4 ± 0.4	15.98	1.9–5.1	27.72	29.69	87.2
LLS (90 days)	5.9 ± 0.4	10.91	3.2–7.6	17.44	19.43	80.6
Rust (75 days)	2.4 ± 0.4	25.95	1.4–4.3	36.97	39.98	85.5
Rust (90 days)	3.6 ± 0.5	19.19	2.1–5.6	33.11	35.99	84.6
OC (%)	48.7 ± 0.9	2.891	44.6–53.9	4.012	4.587	76.5
PC (%)	24.4 ± 0.5	4.045	21.9–26.7	3.541	4.734	56.0
PAC (%)	12.4 ± 0.2	3.015	11.3–13.2	3.397	4.762	50.9
SAC (%)	2.0 ± 0.1	12.96	1.4–2.5	9.473	14.59	42.2
OAC (%)	41.2 ± 1.3	3.967	34.4–48.6	9.64	10.22	88.9
LAC (%)	36.9 ± 1.1	3.924	30.1–42.9	9.378	9.939	89.0

TABLE 3 Pooled means, range, CV, GCV, PCV and broad-sense heritability for 14 traits of interspecific groundnut derivatives evaluated at ICRISAT, Patancheru

Notes. 75d, and 90d indicate the disease score recorded at 75 and 90 days after sowing; CV: coefficient of variation; GCV: genotypic coefficient of variation; HSW: hundred seed weight (g); LAC: linoleic acid concentration; LLS: late leaf spot; OAC: oleic acid concentration; OC: oil concentration; PAC: palmitic acid concentration; PC: protein concentration; PCV: phenotypic coefficient of variation; PYH: pod yield hectare (kg/ha); SAC: stearic acid concentration; SE: standard error; SH: shelling per cent; SYH: seed yield hectare (kg/ha).

similar peaks to GPBD 4 for the markers SEQ8D09, GM2032 and GM1009 (Table 7).

4 | DISCUSSION

The wild species used in this study represented four diverse gene pools, primary, secondary, tertiary and quaternary. Thirty-nine of these derivatives involved more than one wild species in their pedigree (Table 1). Of the fourteen wild species involved, thirteen were diploids *viz.*, *A. villosa*, *A. cardenasii*, *A. correntina*, *A. duranensis*, *Arachis* sps Manfredi-5, *A. paraguariensis*, *A. stenosperma*, *A. kretschmeri*, *A. diogoi*, *A. helodes*, *A. pusilla*, *A. oteroi* and *A. batizocoi*, while *A. monticola* was the only tetraploid species. They belonged to four sections and represent five different genomes, *viz.*, AA, BB, EE, AABB and AM. Information on the genome constitution and section of *Arachis* sps Manfredi-5 is not reported in the available literature. The diploid species *A. batizocoi* is a B-genome species; *A. parguariensis*, *A. oteroi* and *A. kretschmeri* have E-genome; *A. pusilla* has AM-genome; and other diploids are A-genome species as per genome assignment given by Bechara et al. (2010). *A. paraguariensis* and *A. oteroi* belongs to section *Erectoides* and *A. pussila* to section *Heteranthae* and both these sections come under fourth gene pool. *A. kretschmeri* belongs to section *Procumbentes* of the tertiary gene pool, and the other ten species belong to section *Arachis* of primary and secondary gene pools (Bechara et al., 2010; Huang et al., 2012; Singh & Simpson, 1994).

Morphologically, the IDs were similar to the cultivated groundnut in growth habit (erect or decumbent) and branching pattern (Spanish Bunch). However, a few irregular branching types were also observed.

4.1 | Variation for rust and LLS resistance and yield parameters among the IDs

Individual and pooled analysis revealed the existence of genetic variability for resistance to LLS and rust diseases among the IDs (Table 3; Figure 1). Over 50% of the genotypes recorded disease scores in the range of 5–8 for LLS and 3–6 for rust at 90 DAS in both the seasons. The genotypes, ICGVs 99052, 02411, 05097, 98293, 00248, 11379, 07213, 10121, 10179, 04071, 02323, 02446, 11417, VG 0517 and VG 1008, recorded lower mean disease score (3–4), compared to resistant check, ICGV 86590 with LLS score of 6 at 90 DAS. The ICGV derivatives and VG 0517 involved either *A. cardenasii* or both *A. batizocoi* and *A. duranensis* in their pedigree or a combination of them, while VG 1008 is a derivative involving *A. correntina*. Hence, both A (*A. cardenasii*, *A. duranensis* and *A. correntina*) and B-genome species (*A. batizocoi*) contributed to LLS resistance among the IDs.

The rust scores of the IDs ranged from 2 to 6 and from 2 to 7 during rainy seasons 2013 and 2015, respectively. In the pooled analysis, about 27 IDs recorded rust score of 2, which was similar to the resistant check ICGV 86590, and were derived from eight wild species, namely, *A. cardenasii*, *A. batizocoi*, *A. stenosperma*, *A. correntina*, *A. duranensis*, *A. villosa*, *A. helodes* and *Arachis* sps Manfredi-5. The diversity among the wild species involved in providing rust resistance indicates the possibility of mining new alleles for this trait. A few earlier studies on groundnut have also reported resistance to rust and LLS in IDs (Dwivedi et al., 2002; Pande et al., 2002; Shilpa et al., 2013).

Among the yield parameters, pod yield per hectare varied from 1620 to 5598 kg, seed yield per hectare from 1074 to 3223 kg, shelling per cent from 57% to 70% and HSW from 21 to 56 g in the

TABLE 4 Characterization of promising genotypes of groundnut interspecific derivatives with better performance for yield and disease scores

Genotypes	PYH	SYH	SH %	HSW	LLS-90[a]	Rust-90[a]	OC (%)	PC (%)
ICGV 11379	5,598	3,186	62.9	44.3	3.9	2.1	49.9	24.5
ICGV 10121	5,400	3,223	62.5	44.7	4.2	2.4	52.1	25.1
ICGV 10179	5,174	2,971	61.6	41.4	4.4	2.1	50.2	24.7
ICGV 05097	4,905	2,951	61.9	37.7	3.7	2.4	50.9	24.8
ICGV 00248	4,876	3,075	63.1	38.6	3.7	2.1	53.0	24.6
ICGV 02411	4,746	2,843	60.8	35.8	3.5	2.1	52.8	24.6
ICGV 99052	4,596	2,721	60.5	39.9	3.2	2.1	51.0	25.5
ICGV 07213	4,521	3,056	65.5	37.2	4.2	2.6	49.7	24.7
ICGV 02323	4,309	2,871	66.6	39.6	4.4	2.4	50.4	25.6
ICGV 04071	4,263	2,812	64.8	42.5	4.4	2.4	50.9	24.5
ICGV 98293	4,231	2,501	66.3	33.4	3.7	2.1	48.3	24.2
ICGV 02446	4,136	2,592	63.1	35.5	4.4	2.4	53.9	25.1
VG1008	3,970	2,762	67.2	42.1	4.4	2.4	50.4	26.1
ICGV 86590 (RC)	2,848	1,758	61.8	31.4	6.0	2.4	46.9	24.4

Notes. [a]LSD for LLS 90 and rust 90 days are 0.89 and 0.94, respectively. The best entries were significantly superior for LLS-90 score, while for Rust-90 score entries were at par with resistance check (ICGV 86590).

75 days and 90 days indicate the disease score recorded at 75 and 90 days after sowing; HSW: hundred seed weight (g); LLS: late leaf spot; OC: oil concentration (%); PC: protein concentration (%); RC=resistant check for LLS and RUST. The disease score of 'TMV2', a susceptible check, was 9.0 for both LLS and rust at 90 days after sowing (DAS); PYH: pod yield hectare (kg/ha); SH: shelling per cent; SYH: seed yield hectare (kg/ha).

pooled analysis (Table 3). Variability for pod and seed yield, HSW, harvest index and shelling per cent were earlier reported among IDs (Bera, Kumar, Radhakrishnan, Sojitra, & Gedia, 2010) and cultivated groundnut (Zaman, Tuhina-Khatun, Ullah, Moniruzzamn, & Alam, 2011).

4.2 | Multiple disease-resistant interspecific derivatives

About 13 IDs, namely, ICGVs 99052, 02411, 05097, 98293, 00248, 11379, 10121, 10179, 04071, 02323, 02446, 07213 and VG 1008, had low rust (score 2) and LLS (score 3–4) score at 90 DAS, and

TABLE 5 Phenotypic and genotypic correlation coefficient between some important pairs of traits in interspecific derivatives of groundnut

S. No.	Trait Association	Correlation	Correlation coefficient
1	LLS disease score at 75 DAS and PYH	r_g	−0.98*
		r_p	−0.77*
2	LLS disease score at 90 DAS and PYH	r_g	−1.00*
		r_p	−0.79*
3	Rust disease score at 75 DAS and PYH	r_g	−0.75*
		r_p	−0.67*
4	Rust disease score at 90 DAS and PYH	r_g	−0.89*
		r_p	−0.67*
5	SYH and PYH	r_g	0.99*
		r_p	0.97*
6	PYH and HSW	r_g	0.76*
		r_p	0.48*
7	Rust disease score at 75 DAS and LLS disease score at 75 DAS	r_g	0.67*
		r_p	0.79*
8	Rust disease score at 90 DAS and LLS disease score at 90 DAS	r_g	0.67*
		r_p	0.79*
9	Oil concentration and protein concentration	r_g	−0.35*
		r_p	−0.13
10	Linoleic acid and oleic acid concentration	r_g	−0.99*
		r_p	−0.98*
11	Linoleic acid and palmitic acid concentration	r_g	1.00*
		r_p	0.83*
12	Linoleic acid and stearic acid concentration	r_g	0.50*
		r_p	0.32*

Notes. *Represents significance at <0.05 probability level.
75 days and 90 days indicate the disease score recorded at 75 and 90 days after sowing; HSW: hundred seed weight (g); LLS: late leaf spot; PYH: pod yield hectare (kg/ha); SYH: seed yield hectare (kg/ha).

recorded superior pod yield performance (Table 4). They were derived from four different wild species (*A. batizocoi*, *A. duranensis*, *A. cardenasii* and *A. correntina*) and might possibly contain new alleles for rust and LLS, which needs to be further studied. For the yield parameters of these 13 IDs, pod yield per hectare varied from 3970 to 5598 kg, seed yield per hectare from 2501 to 3223 kg, shelling per cent from 60% to 67% and 100-seed weight from 33 to 45 g. The superior performance of IDs may in part be attributed to the protection offered to the yield loss by disease resistance. The oil and protein concentration (%) of these lines varied from 48 to 54% and 24% to 26%, respectively.

4.3 | Variation for nutritional quality traits among the IDs

The IDs recorded good variability for oil, protein and fatty acids concentration (Table 3). The IDs ICGVs 02446, 00248, 06175, 02411,

TABLE 6 Rust-resistant alleles in interspecific derivatives using specific markers linked to the QTL governing rust resistance

Source of resistance	Genotypes	Rust score Range (90 DAS)	Chromosome A03			
			GM1536	IPAHM103	GM2079	GM2301
A. cardenasii	GPBD 4	2.0–3.0	+	+	+	+
	ICGVs 00005, 01265, 02323, 03057, 10150, 10290, 11417, 11447 and 98373	2.0–2.2	+	+	+	+
	ICGV 04157, VG0437	2.7	*	+	+	+
	ICGVs 10221, 11009 and VGs 0410, 0411 and 0430	2.2–3.2	*	*	+	+
A. batizocoi & A. duranensis	ICGVs 00248, 01361, 02411, 04071, 05097, 06175, 07213, 99052, 09138, 10179, 11379, 11464 and 98293	2.00–2.52	+	+	+	+
	ICGV 06157	2.2	*	+	+	+
A. cardenasii & A. sps Manfredi-5	ICGV 00068	2.0	*	+	+	+
A. batizocoi, A. duranensis & A. cardenasii	ICGV 10121	2.6	+	+	+	+

Notes. "+" indicates the presence of GPBD 4 specific peaks; "*" indicates different peak compared to GPBD 4.

FIGURE 1 The susceptible and resistant interspecific derivatives in disease screening nursery at 90 DAS during 2015 rainy season at ICRISAT-Patancheru

10121, 10342, and 10290 recorded ≥52% oil concentration, whereas ICGVs 10221, 11447, 11370, 02323, 99052; VGs 1010, 1007, 1008, 0438, 9406, 9412 and NRCGCS 421 had higher protein concentration of ≥26%. VG 9406 was derived from *A. stenosperma*

(A-genome), VG 1010 was derived from *A. correntina* (A-genome) and *A. helodes* (A-genome), VG 1007 and 1008 were derived from *A. correntina*, VG 9412 was derived from *A. cardenasii* (A-genome) and *A. villosa* (A-genome), while the others involved either *A. cardenasii* or *A. batizocoi* (B-genome) and *A. duranensis* (A-genome) or their combinations. In earlier studies, a mean oil concentration of 41%–61% and protein concentration of 15%–31% was reported among 160 cultivated elite breeding lines evaluated over six environments (Janila, Manohar, Nagesh, Variath, & Nigam, 2016). Given the vast genetic variability available in cultivated gene pool, the IDs can be useful if they contribute new alleles to oil and protein concentration not available in cultivated gene pool. Oil concentration of 48%–50% and protein concentration of 29%–31% were reported in a subset of best 18 accessions belonging to *A. hypogaea* subsp. *fastigiata* and subsp. *hypogaea* selected from 184 accessions of minicore collection at ICRISAT (Upadhyaya, Mukri, Nadaf, & Singh, 2012). Huang et al. (2012) reported oil concentration in the range of 51%–63% among 72 wild *Arachis* accessions tested over 3 years.

Variability was also observed for oleic, linoleic and palmitic fatty acids but no high oleic lines were detected. The high oleic check SunOleic 95R recorded an oleic acid concentration of 82% in the study. Oleic acid concentration of the IDs varied from 34 to 49%. Palmitic acid, stearic acid and linoleic acid concentrations varied between 11.2%–13.2%, 1.4%–2.5% and 30.1%–42.9%, respectively, among the IDs.

Allele mining studies using allele-specific markers for *ahFAD2A* and *ahFAD2B* revealed that the derivatives ICGV 06175, NRCGCSs -227, -161, -157, -138, -421 and VGs 0517, 1002, 1007, 1008, 1010 and 1016 had *ahFAD2A*-mutant allele with oleic acid concentrations ranging from 36% to 49%. They were derived from nine different wild species with either AA-, BB- or EE-genomes (Table 1). No IDs were reported with *ahFAD2B*-mutant allele. The nonavailability of high oleic lines among the IDs indicates that both *ahFAD2A*- and *ahFAD2B*-mutant alleles are important for the high oleic trait in groundnut.

TABLE 7 LLS-resistant alleles in interspecific derivatives using specific markers linked to the QTL governing LLS resistance

Source of resistance	Genotypes	LLS score Range (90 DAS)	Chromosome A03				Chromosome A02		
			GM1536	IPAHM103	GM2079	GM2301	SEQ8D09	GM2032	GM1009[a]
A. cardenasii	GPBD 4	2.0–3.0	+	+	+	+	+	+	+
	ICGVs 00005, 02323, 10150, 11417 and 11447	4.3–4.5	+	+	+	+	+	+	+
	ICGVs 01265, 03057, 10290 and 98373	5.0–5.8							
	ICGVs 10221, 11009, and VGs 0410, 0411 and 0430	6.0–6.5	*	*	+	+	+	+	+
	VG 0437, ICGV 04157	6.0	*	+	+	+	+	+	*/+
A. batizocoi & *A. duranensis*	ICGVs 00248, 02411, 04071, 05097, 06175, 07213, 99052, 09138, 10179, 11379 and 98293	3.0–4.5	+	+	+	+	+	+	+
	ICGVs 11464 and 01361	4.8–6.0							
	ICGV 06157	5.5	*	+	+	+	+	+	+
A. cardenasii & *A.* sps Manfredi-5	ICGV 00068	4.8	*	+	+	+	+	+	+
A. batizocoi, A. duranensis & A. cardenasii	ICGV 10121	4.0	+	+	+	+	+	+	+

Notes. "+" indicates the presence of GPBD 4 specific peaks; "*" indicates different peak compared to GPBD 4.
[a]Different peak observed only for VG 0437.

4.4 | Trait association

Negative significant phenotypic and genotypic correlation was observed between pod yield per hectare and disease score of LLS at 75 and 90 DAS (Table 5). Thus, pod yield under disease pressure can be used as selection criteria. The incidence of rust was positively correlated with LLS at different stages of observation. This strong correlation can be corroborated with identification of a major QTL governing rust resistance which was also found to govern LLS resistance in groundnut (Khedikar et al., 2010; Pandey et al., 2017).

Pod yield per hectare showed a strong positive association with seed yield per hectare and also with HSW. Thus, selection of genotypes combining high pod yield, seed yield and HSW is possible in early generations. Oil concentration was negatively correlated with protein concentration. The inverse relationship between oil and protein concentration was earlier reported in several studies (Jivani et al., 2012). Among the fatty acids, linoleic acid showed a strong negative correlation with oleic acid concentration and positive correlation with palmitic acid concentration. Thus, increasing the oleic acid concentration in groundnut will result in concomitant reduction in linoleic acid and palmitic acid concentration.

4.5 | Mining for rust- and LLS-resistant alleles

Genotyping for major effect QTLs governing rust and LLS on A02 and A03 chromosomes was performed on a set of 32 IDs derived from four wild species (*A. batizocoi*, *A. duranensis*, *A. cardenasii* and *Arachis* sps Manfredi-5), with GPBD 4 as the control. All the derivatives showed peaks similar to GPBD 4 for the linked markers on A03 (GM2079 and GM2301) (Table 6). However, ICGVs 04157, 06157, 00068 and VG 0437 had different peaks for GM1536, while ICGV 10221, ICGV 11009, VGs 0410, 0411 and 0430 had different peaks for GM1536 and IPAHM103. The phenotypic score of the selected IDs varied from 2.0 to 3.2 indicating that all the selected derivatives are resistant to rust. The selected ICGV and VG lines involved single or combinations of the four wild species, *A. batizocoi*, *A. duranensis*, *A. cardenasii* and *Arachis* sps Manfredi-5, indicating their potential to contribute alleles for rust resistance. The results based on this preliminary analysis showed similarity between the resistance alleles of IDs derived from *A. cardenasii* and GPBD 4, a cultivated genotype carrying the resistance alleles from *A. cardenasii*. Nevertheless, it will be interesting to conduct further sequence-based analysis to see whether these lines also share similar sequence variations in resistance genes controlling foliar disease resistance. A total of nine germplasm accessions belonging to subspecies *hypogaea* botanical variety *hypogaea* were reported as resistant to rust using validated molecular markers (Yole, Upadhyaya, & Uzun, 2016).

A recent study in groundnut has reported that resistance for LLS is conferred by two genomic regions located on chromosome A03 and A02 (Pandey et al., 2017). The rust-resistant markers on chromosome A03 also explained upto 67.98% PVE for LLS (Sujay et al., 2012). A total of seven markers, four on chromosome A03 and three

on chromosome A02, were used to screen 32 IDs (score 3.0–6.5) for LLS resistance. Screening the set using three LLS-specific markers on A02 did not reveal any peak differences with GPBD 4, except for VG 0437 for the marker GM1009 (Table 7). When the markers linked to chromosome A03 was compared to GPBD 4, several IDs exhibited similar peaks as GPBD 4, but they recorded a disease score of 4.0–6.0 (Table 7). Some derivatives VG 0410, VG 0411, VG 0430, VG 0437, ICGVs 10221, 11009, 04157, 06157 and 00068 did not exhibit the resistant peak for the A03 region and recorded a disease score of 4.8–6.5. All the LLS-resistant derivatives have shown similar peaks to GPBD 4. The ICGVs 01265, 03057, 10290, 98373 derived from *A. cardenasii*, in spite of their similarity to GPBD 4, showed higher susceptibility to LLS (score 5.0–5.8). The conditioning for minor QTLs in GPBD 4 may have contributed to the higher level of resistance to LLS compared to the IDs that conform to the same QTL region. Both major and minor QTLs were reported to be involved in governing resistance to rust and LLS in groundnut (Khedikar et al., 2010; Pandey et al., 2017). Our recent study on introgression lines derived from GBPD 4 in the background of TAG 24, JL 24 and ICGV 91114 also suggests significant contribution of minor QTLs for resistance besides the major effect QTL (Janila, Pandey et al., 2016).

5 | CONCLUSION

Evaluation of the IDs identified foliar fungal disease-resistant sources derived from three different wild species other than *A. cardenasii*. ICGVs 05097, 02411, 11379, 10121, 10179 and 00248 with multiple disease resistance and superior pod yield performance were identified for use as parents in breeding programmes. These lines were derived from two different wild species with either AA (*A. duranensis* and *A. cardenasii*) or BB-genome (*A. batizocoi*) and it may be possible that new alleles for resistance or yield may be identified from these derivatives. These IDs can be directly utilized in breeding programme.

Allele mining studies for *ahFAD2*-mutant alleles of A- and B-genomes in ID revealed that *ahFAD2A* mutation is common, whereas *ahFAD2B* is rare. Genotypes positive for *ahFAD2A*-mutant allele are derived from nine different wild species. Oleic acid concentration in these lines varied from 36% to 49%. Genotyping identified few rust-resistant lines with different alleles from GPBD 4, which needs to be studied further prior to their utilization in breeding. The alleles for LLS were not found to confer better resistance among the IDs than GPBD 4 or ICGV 86855 (parent of GPBD 4).

AUTHOR CONTRIBUTIONS

PJ, SKB and TR designed the experiment. SSM, MTV, PJ, SC, SK and HKS conducted the experiment, recorded observations, and analysed the data. SSM analysed the data. PJ, SKB and SSM interpreted the results. SKB, SSM, MTV, PJ, TR, MKP, RKV and SC did manuscript writing and editing. SKB and TR developed NRCGCS lines. SS, MN and KG developed VG lines. YS, MKP and RKV collected leaf samples and conducted genotyping.

ORCID

Sandip K. Bera http://orcid.org/0000-0003-1140-6762
Manivannan Narayana http://orcid.org/0000-0001-5918-1799
Rajeev K. Varshney http://orcid.org/0000-0002-4562-9131
Janila Pasupuleti http://orcid.org/0000-0003-2583-9630

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.