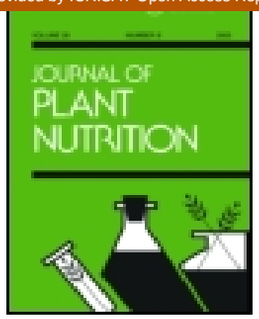

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Inheritance of iron deficiency chlorosis resistance in groundnut (*Arachis hypogaea* L.)

Santosh K. Pattanashetti [a,b], Gopalakrishna K. Naidu[a], Prakyath Kumar K.V.[a], Omprakash Kumar Singh[a], and Basavaraj D. Biradar[a]

[a]Department of Genetics and Plant Breeding, College of Agriculture, Vijayapur, University of Agricultural Sciences, Dharwad, Karnataka, India; [b]International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Telangana, India

ABSTRACT

Iron-deficiency chlorosis (IDC) is an important abiotic constraint affecting the growth and yield of groundnut in calcareous and alkaline soils worldwide. The present study investigated the inheritance of IDC resistance among four straight crosses of groundnut involving four IDC susceptible cultivars as females and a common IDC resistant male parent. The F_1's of all the four crosses were resistant to IDC indicating the dominant nature of IDC resistance. The F_2's of all the four crosses showed a good fit to the ratio of 15 (IDC resistant): 1 (IDC susceptible) and their behavior among the F_3's was as per the expected ratio of 7:4:4:1. The IDC resistance in groundnut is under the control of duplicate dominant genes wherein, the presence of a dominant allele at either of the loci results in IDC resistance, while duplicate recessive results in IDC susceptibility. This information would facilitate development of IDC resistant cultivars of groundnut.

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groundnut; genetics; inheritance; iron-deficiency chlorosis (IDC); peanut; resistance

Introduction

Iron (Fe) is an essential nutrient for all organisms (Zuo and Zhang 2011). In plants, Fe is involved in many physiological processes, including chlorophyll biosynthesis, respiration, and redox reactions (Mimmo et al. 2014; Ye et al. 2015; Zargar et al. 2015). Fe deficiency not only affects the growth and development of plants, but can also lead to anemia in animals and humans (Guerinot and Yi 1994). Iron-deficiency chlorosis (IDC) is common worldwide among crops grown in calcareous, alkaline, coarse textured, eroded and low organic matter containing, and cold region soils because Fe is mostly found in an insoluble form (Fe^{3+}). The available form (Fe^{2+}) does not exist much in this soil, which makes it less available for uptake by plants in these soils (Ye et al. 2015).

For Fe acquisition from the soils, plants adopt two types of mechanisms (Strategy I and II). Strategy-I is found among dicots and monocots, except graminaceous species, which adopt Strategy II. The Strategy I mechanism involves proton release at the rhizosphere that lowers the pH of soil solution and increasing solubility of Fe^{3+}, Fe(III) chelate reductase activity that reduces Fe^{3+} to more soluble Fe^{2+}, and transportation of Fe^{2+} into the root by metal transporters (Kim and Guerinot 2007). Groundnut (*Arachis hypogaea* L.) adopts strategy-I type of Fe-acquisition from the soil and its later translocation into plant parts. Groundnut is also found sensitive to Fe deficiency in alkaline and calcareous soils (Zuo and Zhang 2011; Sánchez-Alcalá et al. 2014).

CONTACT Santosh K. Pattanashetti santosh.pattanashetti@gmail.com Department of Genetics and Plant Breeding, College of Agriculture, Vijayapur, University of Agricultural Sciences, 586101, Dharwad, Karnataka, India.

Groundnut is an important food legume grown on 25.7 m ha area with a production of 42.3 m t globally (Faostat 2013). India stands first in groundnut area (5.20 m ha) but second in production (6.56 m t) after China (15.78 m t) due to very less productivity in India (1261 kg ha^{-1}) compared to China (3491 kg ha^{-1}) as it is affected by several abiotic and biotic stresses. In India, more than one-third of the soils are calcareous and spread mostly in the low rainfall areas of the western and central parts of the country, where groundnut is a major crop. Hence, IDC is prevalent in Saurashtra region of Gujarat, Marathwada region of Maharashtra, and parts of Rajasthan, Tamil Nadu and Karnataka states in India causing considerable reduction in pod yield (16–32%) (Singh et al. 1995; Singh 2001). IDC is also a common problem in groundnut-producing areas with calcareous soils in northern China (Gao and Shi 2007) and Pakistan (Imtiaz et al. 2010; Akhtar et al. 2013) causing significant reduction in yield. Severity of IDC will be usually quite high after excessive rainfall and also for groundnut grown under irrigation due to high bicarbonate ion concentration in the rhizosphere (Singh et al. 1995; Zuo et al. 2007).

To counter Fe deficiency in plants, application of Fe fertilizer in the form of inorganic, chelated, and organic formulations have been suggested (Laurie et al. 1991). Application of inorganic-Fe fertilizer to soil is of little benefit as the Fe ionizes and gets converted into insoluble Fe^{3+} compounds, while foliar application has the problem of poor translocation of applied Fe within the plant (Hüve et al. 2003). Organic-Fe fertilizer is readily adsorbed onto soil particles, which can reduce the fertilizer effect, hence often used in soilless cultivation and as a foliar spray (Cesco et al. 2000; Lucena, Garate, and Villen 2010). Chelated-Fe fertilizer is more expensive and often applied to high-value crops, hence economically not feasible in the semi-arid tropics where groundnut is mainly grown as a rainfed subsistence crop.

Development of micronutrient efficient genotypes can be a successive tool to overcome the micronutrient disorders in soil and also for the improvement in human health (Imtiaz et al. 2010). Genetic variability for IDC response has been reported earlier in groundnut (Samdur et al. 2000; Gao and Shi 2007; Akhtar et al. 2013; Su et al. 2015). It is necessary to understand the inheritance of IDC resistance trait in groundnut towards development of IDC resistant cultivars. Hence, the present study investigates the inheritance of IDC resistance among F_1, F_2 and F_3 generations of four crosses of groundnut involving IDC susceptible females (four) and IDC resistant common male parent.

Materials and methods

Experimental details

Four straight crosses were generated by involving four released cultivars of groundnut i.e., Dh 86, TAG 24, G 2-52 and GPBD 5 with varying degree of susceptibility to IDC as female parents, while ICGV 86031 as male parent (Table 1) that is resistant to IDC as reported earlier (Dwivedi et al. 1993) as well as based on our previous studies (Boodi, Pattanashetti, and Biradar 2015). All the generations, i.e., parents, F_1, F_2, F_2-derived F_3 ($F_{2:3}$) were evaluated in Fe-deficient calcareous soils [diethylenetriaminepentaacetic acid (DTPA) extractable Fe (Fe^{2+}) < 4 mg kg^{-1}] in the pot or field studies (Table 2) at College of Agriculture, Vijayapur and assessed for IDC resistance using associated traits like visual chlorotic rating (VCR) and SPAD values at 30, 60 and 90 days after sowing (DAS). The soil texture was analyzed by International pipette method (Piper 1966) (Table 2). The soil chemical properties were determined for the following parameters as described by Jackson (1967). The pH was determined in 1:2.5 soil water suspensions using digital pH meter [Systronics – 335, india]. The electrical conductivity was determined in 1:2.5 soil water extract using conductivity bridge i.e., digital direct reading conductivity meter [Systronics– 304, india]. The organic carbon content of soil water was determined by Walkley and Black's wet oxidation method. The $CaCO_3$ content in the soil was determined by the acid neutralization method. For estimation of calcium, Tri-ethanol amine solution (pH 8.2) was used to extract exchangeable calcium instead of using ammonium acetate to prevent over estimation of calcium in calcareous soil; extracted solution was titrated against versenate (disodium, dihydrogen, ethylene and diamine tetra acetic acid) using murexide as indicator. The available phosphorus (P) was

Table 1. Pedigree, salient features and IDC response of parents.

Parents	Institute, Year of Release	Pedigree	Features	Mean VCR[a]	Mean SPAD[a]	IDC Response
Females						
Dh 86	UAS Dharwad, 2005	Dh-40 × Dh-8	Tolerant to LLS and sucking pests	3.0	19.3	Susceptible
TAG 24	BARC Mumbai, 1992	TGS 2 × TGE 1	Early maturity, high harvest index	3.3	13.6	Susceptible
G 2-52	UAS Dharwad, 2015	EMS mutant of GPBD 4	High oil content and O/L ratio	2.3	23.7	Susceptible
GPBD 5	UAS Dharwad, 2010	TG 49 × GPBD 4	High pod and kernel yield	3.0	16.1	Susceptible
Male						
ICGV 86031	ICRISAT Patancheru, 1991	(F334A-B-14 × NC Ac 2214) F_2-B_1-8_3-B_2-B_3-B_2-B_3	Multiple insect pest resistant; resistant to bud necrosis disease and IDC; photoperiod insensitive	1.0	40.8	Resistant

[a]Mean across three stages i.e., 30, 60, 90 days after sowing (DAS)

determined by Olsen's method. Potassium (K) was determined by flame photometer after extracting the soil with neutral normal ammonium acetate. The available sulphur (S) was determined by turbidometric method using 0.15% $CaCl_2$ as an extractant. The nitrogen (N) content was determined by alkaline potassium permanganate distillation method as described by Subbaiah and Asija (1956) using Kjeldahl flasks. The available Fe (Ferrous, Fe^{2+}), zinc (Zn), manganese (Mn) and copper (Cu) were determined by atomic absorption spectrophotometer after extracting the soil with DTPA (Lindsay and Norvell 1978).

The F_1 plants of all the four crosses were raised in pots during summer season of 2013–14. For raising F_1 plants, cement pots (45 cm diameter, 45 cm height) filled with 75 kg of Fe-deficient calcareous soil obtained from the field (Table 2) was used. In each pot, 3 cross seeds of respective cross were sown in triangular fashion and required number of pots for each F_1's were used. The recommended dose of

Table 2. Soil texture and chemical properties of the experimental site.

Parameter	Values
Soil texture[a]	
Soil type	Shallow black
Coarse sand (%)	29.1
Fine sand (%)	7.1
Silt (%)	10.8
Clay (%)	40.5
Soil chemical properties	
pH	8.33
Electrical conductivity (dsm^{-1})	0.23
Organic carbon (%)	0.25
Available N ($kg\ ha^{-1}$)	269.7
Available P_2O_5 ($kg\ ha^{-1}$)	45.6
Available K_2O ($kg\ ha^{-1}$)	296.2
Available Ca (Cmol (p^+) kg^{-1})	43.7
Available Mg (Cmol (p^+) kg^{-1})	18.13
Available sulphur ($mg\ kg^{-1}$)	7.44
Free lime (%)	27.0
Cation exchange capacity (Cmol (p^+) kg^{-1})	95.1
Base saturation (%)	67.0
DTPA-extractable Zn ($mg\ kg^{-1}$)	2.26
DTPA-extractable Fe ($mg\ kg^{-1}$)	3.91
DTPA-extractable Cu ($mg\ kg^{-1}$)	1.97
DTPA-extractable Mn ($mg\ kg^{-1}$)	2.95

[a]12.5% difference in total (%) is due to dissolution of $CaCO_3$ granules during estimation of different soil particles

N (25 kg ha^{-1}), P (75 kg ha^{-1}) and K (25 kg ha^{-1}) fertilizer were added at the time of sowing, while Fe containing fertilizers were not added. Measured quantity of water was applied equally to all the pots regularly to get the better expression of IDC. The plants were grown in the pot up to harvest (105–110 days). All the four F_2 populations and respective parents were grown in field having calcareous soil (shallow black, clay texture) (Table 2) during rainy season of 2014, while F_2-derived F_3 ($F_{2:3}$) progenies and respective parents were grown during rainy season of 2015 with an inter and intra-row spacing of 30 × 10 cm and row length of 3 m. Required number of rows were used for growing the F_2 population and $F_{2:3}$ families of all the four crosses. The female and male parents of the respective cross were sown as first and last row flanking F_2 population and $F_{2:3}$ progenies. The recommended cultivation practices were followed to raise a good crop and protective irrigation was provided under severe moisture stress. All the major nutrients (N, P and K) were supplied in the form of urea, diammonium phosphate and muriate of potash fertilizers as per recommended dose. Micronutrients like Zn, Mn, and Mg were applied in the form of $ZnSO_4$, $MnSO_4$ and $MgSO_4$ to avoid the complexity of overlapping deficiency symptoms with Fe. But, fertilizers containing Fe were not applied to maintain the Fe-deficiency status. The plants matured in 105–110 days and were harvested on individual plant basis in F_1, F_2 and F_3 generations.

IDC response

IDC response was assessed based on two related traits, such as VCR and SPAD values. For VCR, the 1–5 scale proposed by Singh and Chaudhari (1993) based on severity and coverage of interveinal chlorosis in entire plant was followed (1) normal green leaves with no chlorosis, (2) green leaves with slight chlorosis on some leaves, (3) moderate chlorosis on several leaves, (4) moderate chlorosis on most of the leaves and (5) severe chlorosis on all the leaves (Figure S1). The chlorophyll meter SPAD 502 (Soil plant analysis development meter, Konica Minolta, india) measures the abssorbance of the leaf in the red and near infrared region. Using these two transmittances, it calculates a numerical SPAD value, which is proportional to the chlorophyll present in the leaf and is negatively related to chlorosis of the plants. The SPAD values were recorded in interveinal area of the standard leaf (third fully opened leaf from the top) of the plants using SPAD 502. Each plant of all the generations (parents, F_1, F_2 and $F_{2:3}$) of the four crosses were scored for VCR and SPAD values at three different stages i.e., 30, 60 and 90 DAS. Based on the VCR score and SPAD values at most severe stage (at 60 DAS), plants were classified as IDC resistant (VCR 1 to 2; SPAD > 25) or susceptible (VCR >2 to 5; SPAD < 25), respectively.

Statistical analysis

The observed number of plants showing IDC resistance or susceptibility in F_2 and $F_{2:3}$ progenies of the four crosses along with expected number of plants or progenies based on predicted phenotypic ratio were subjected to Chi-square (χ^2) test to assess the goodness of fit of the predicted ratio (Pearson 1900). If the χ^2 test was non-significant, the predicted ratio was accepted and probability values were estimated using web resources at http://www.socscistatistics.com/.

Results

Inheritance of IDC resistance among four crosses of groundnut

The results pertaining to IDC response of parents, F_1, F_2 and $F_{2:3}$ generation plants or progenies among the four crosses and the expected inheritance pattern of IDC resistance among these crosses are presented in this section.

In the cross, Dh 86 × ICGV 86031, all the true F_1 plants (12) were IDC resistant with lesser VCR score (1.7) and higher SPAD value (41.9). Segregation in the F_2 generation (377 IDC resistant: 21 IDC susceptible) showed a good fit to the predicted ratio of 15:1 (IDC resistant: IDC susceptible) as evident from non-significance of chi-square test ($\chi^2 = 0.644$, $p = 0.422$) (Table 3). The F_2 derived F_3 families

Table 3. Inheritance of IDC resistance in four crosses of groundnut.

Cross	Gen.	No. of Progeny	Observed IDC Response		Predicted Ratio[a]	Chi-square	df	Probability
			Resistant	Susceptible				
Dh 86 × ICGV 86031	F_1	12	12	–	–	–	–	–
	F_2	12	377	21	15:1 (R:S)	0.644	1	0.422
	F_3	162	1084	0	BT (Res)	–	–	–
		96	557	177	3:1 (R:S)	0.307	1	0.580
		79	1220	80	15:1 (R:S)	0.021	1	0.886
		21	0	104	BT (Sus)	–	–	–
	Total	358	–	–	7:4:4:1	1.973	3	0.578
TAG 24 × ICGV 86031	F_1	3	3	–	–	–	–	–
	F_2	3	106	6	15:1	0.152	1	0.696
	F_3	44	345	0	BT (Res)	–	–	–
		25	191	52	3:1 (R:S)	1.680	1	0.195
		20	318	20	15:1 (R:S)	0.064	1	0.800
		6	0	59	BT (Sus)	–	–	–
	Total	95	–	–	7:4:4:1	0.802	3	0.849
GPBD 5 × ICGV 86031	F_1	1	1	–	–	–	–	–
	F_2	1	67	4	15:1	0.046	1	0.830
	F_3	22	124	0	BT (Res)	–	–	–
		17	93	24	3:1 (R:S)	1.256	1	0.262
		13	207	13	15:1 (R:S)	0.044	1	0.835
		3	0	12	BT (Sus)	–	–	–
	Total	55	–	–	7:4:4:1	1.042	3	0.791
G 2-52 × ICGV 86031	F_1	3	3	–	–	–	–	–
	F_2	3	38	2	15:1	0.107	1	0.744
	F_3	12	36	0	BT (Res)	–	–	–
		8	65	20	3:1 (R:S)	0.098	1	0.754
		5	80	5	15:1 (R:S)	0.020	1	0.889
		2	0	15	BT (Sus)	–	–	–
	Total	27	–	–	7:4:4:1	0.746	3	0.862

Gen. – Generation; df – Degrees of freedom; R – IDC Resistant; S – IDC Susceptible; BTR – Breeding True for IDC Resistance; BTS – Breeding True for IDC Susceptibility

[a]F2 ratio – 15 (IDC Resistant): 1 (IDC Susceptible); $F_{2:3}$ ratio – 7 (BTR): 4 (3R:1S): 4 (15R:1S): 1 (BTS)

($F_{2:3}$) (358) also showed a good fit to the expected ratio of 7:4:4:1 i.e., Breeding true for IDC resistance (BTR): 3:1 (IDC Resistant: IDC Susceptible): 15:1 (IDC Resistant: IDC Susceptible): Breeding true for IDC susceptibility (BTS) based on the non-significance of chi-square test (χ^2 =1.973, $p = 0.578$).

All the F_1 plants (3) in the cross, TAG 24 × ICGV 86031 were IDC resistant with lesser VCR (1.6) and higher SPAD value (36.6). Segregation in the F_2 generation (106 IDC resistant: 6 IDC susceptible) was in accordance with the predicted ratio of 15:1 (IDC resistant: IDC susceptible) based on the non-significance of chi-square test ($\chi^2 = 0.152$, $p = 0.696$) (Table 3). The $F_{2:3}$ families (95) showed a good fit to the predicted ratio of 7:4:4:1 [BTR : (3R:1S) : (15R:1S) : BTS] as described for previous cross based on the non-significance of chi-square test ($\chi^2 = 0.802$, $p = 0.849$).

The only F_1 plant recovered from the cross, GPBD 5 × ICGV 86031 was IDC resistant with lesser VCR (1.3) and higher SPAD value (36.9). Segregation in the F_2 generation (67 IDC resistant: 4 IDC susceptible) was in agreement with the predicted ratio of 15:1 (IDC resistant: IDC susceptible) based on the non-significance of chi-square test ($\chi^2 = 0.046$, $p = 0.830$) (Table 3). The $F_{2:3}$ families (55) also showed a good fit to the predicted ratio of 7:4:4:1 [BTR : (3R:1S) : (15R:1S) : BTS] evident from the non-significance of chi-square test (χ^2=1.042, $p = 0.791$).

All the F_1 plants (3) of the cross, G 2-52 × ICGV 86031 were also IDC resistant with lesser VCR (1.6) and higher SPAD value (36). Segregation in the F_2 generation (38 IDC resistant: 2 IDC susceptible) was in agreement with the predicted ratio of 15:1 (IDC resistant: IDC susceptible) based on the non-significance of chi-square test ($\chi^2 = 0.107$, $p = 0.744$) (Table 3). The $F_{2:3}$ families (27) also showed a good fit to the predicted ratio of 7:4:4:1 [BTR : (3R:1S) : (15R:1S) : BTS] evident from the non-significance of chi-square test ($\chi^2 = 0.746$, $p = 0.862$).

Discussion

Phenotyping for IDC response

The VCR and chlorophyll content estimation are widely used for selecting IDC resistant groundnut genotypes in the field (Gao and Shi 2007; Samdur et al. 1999). The utility of SPAD chlorophyll meter for rapid and *in situ* screening of genotypes for IDC resistance has been evident from significant positive correlation between SPAD readings and chlorophyll content observed earlier (Samdur et al. 2000). Hence, in the present study, VCR and SPAD readings were used to phenotype the IDC response of parents, F_1, F_2, and $F_{2:3}$ generation plants or progenies at three different stages (30, 60 and 90 DAS). Since, the most severe symptoms were observed at 60 DAS, the same data was used to classify the plants as IDC resistant (VCR 1 to 2; SPAD > 25) or susceptible (VCR >2 to 5; SPAD < 25). Gao, Shi, and Zhou (2009) also observed highest chlorosis scores for susceptible cultivars during 50–65 days after emergence as noted in this study.

Inheritance of IDC resistance

The F_1's of all the four crosses were resistant to IDC, which indicate that IDC resistance is a dominant trait in groundnut. The segregation in the F_2 and $F_{2:3}$ generations of all the four crosses suggest that IDC resistance is under the control of duplicate dominant genes (A and B) wherein, the presence of a dominant allele at either of the loci (A_B_, A_bb, aaB_) results in IDC resistance, while duplicate recessive (aabb) results in IDC susceptibility. Earlier in groundnut, Fe absorption efficiency has been suggested to be governed by a basic gene with two or four inhibitory complementary genes showing F_2 ratios of 21 efficient: 43 inefficient, and 525 efficient: 499 inefficient wherein, the trait is governed by a dominant basic gene but presence of dominant inhibitory genes make them inefficient (Gowda et al. 1993). Using six generation mean analysis, Samdur, Manivel, and Mathur (2005) studied the genetic basis of IDC resistance in groundnut in the cross ICGV 86030 × ICGV 86031. The F_1 mean was significantly higher than the mid-parental and better parental values for carotenoids, indicating the dominance of this character; Out of four scaling tests, at least two were found significant for all the related characters indicating the presence of non-allelic interactions for their inheritance. Six-parameter model indicated the presence of significant additive × dominance epistatic interaction for chlorophyll *a*, chlorophyll *b*, and total chlorophyll at both 35 and 50 days after emergence. These reports support the dominance nature of the IDC resistance trait in groundnut as noted in this study.

This is the first study wherein inheritance of IDC resistance in groundnut has been elucidated based on behavior in the F_2 and F_3 generations. The results indicated duplicate dominant genes governing of IDC resistance in groundnut. Several traits in groundnut are found to be governed by duplicate or multiple genes due to allotetraploid nature consisting of two genomes *viz.*, A and B, which are genetically similar (Hammons 1973; Wynne and Coffelt 1982; Kochert et al. 1991). In addition, IDC resistance or Fe absorption efficiency has been reported to be governed by one or two dominant genes in several legumes like soybean (Weiss 1943), dry beans (Coyne et al. 1982), mungbean (Srinives et al. 2010), chickpea (Toker et al. 2010) and lentils (Ali, Riaz-ul-haque, and Bhatti 1997). IDC resistance has also been suggested to be polygenically inherited with additive effect in soybean (Cianzio and Fehr 1982) and tomato (Dasgan et al. 2004).

In groundnut, high correlations observed between root Fe reduction and field chlorosis scores suggested that Fe-reduction capacity as a better physiological indicator for screening Fe-efficient genotypes (Gao and Shi 2007). In addition, the soil or foliar application of sodium nitroprusside, a NO donor has shown to increase the available Fe in the soil by reducing the pH of the soil, increase the H^+-ATPase and Fe^{3+} reductase activities, increase the total Fe concentration in the leaves and antioxidant activities in groundnut (Kong et al. 2014). In the light of this, the physiological basis of IDC resistance in the parent ICGV 86031 need to be established through further detailed studies, such as change in the pH, Fe-reduction capacity and translocation efficiency.

The Fe-efficient genotypes able to respond to the Fe-limited condition and delay the onset or minimize the impact of IDC, whereas the inefficient genotypes respond slow or lack the ability to respond.

The genes and gene families that are involved in Fe uptake under Fe-deficient conditions have been identified and further characterized in *Arabiopsis* and other crop species (Kim and Guerinot 2007). In peanut, Fe responsive genes such as *AhIRT1*, encoding an Fe-uptake transporter (Ding et al. 2010); *AhFRO1*, encoding ferric-chelate reductase (Ding et al. 2009), and; *AhNRAMP1*, encoding a functional Fe transporter (Xiong et al. 2012) have been identified. Hence, it is necessary to investigate the role of these identified genes and also homologues of other genes to understand the basis of IDC resistance in ICGV 86031. Molecular markers significantly associated with IDC resistance genes have been identified in soybean (Charlson, Cianzio, and Shoemaker 2003) and mungbean (Srinives et al. 2010). We are developing recombinant inbred populations from the crosses used in this study; further mapping using these populations would be helpful in identification of genomic regions and tightly linked markers associated with IDC resistance and further genomics assisted improvement of IDC resistance in groundnut in particular and legumes in general.

Conclusions

The inheritance of IDC resistance among four straight crosses of groundnut indicated the dominant nature of the trait as all the F_1's were IDC resistant. The segregation in the F_2 and $F_{2:3}$ generations of all the four crosses suggested that IDC resistance is under the control of duplicate dominant genes. This information would be useful towards development of IDC-resistant cultivars of groundnut in particular and legumes in general.

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ORCID

Santosh K. Pattanashetti http://orcid.org/0000-0001-9869-081X

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