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Breeding groundnut for rust resistance: A review

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ABSTRACT

Sustainable groundnut production can be realised through development and adoption of high yielding cultivars possessing durable rust resistance. Integrating conventional breeding with genomic tools in identifying candidate rust resistance genes, and introgressing the genes into adapted elite germplasm, with the aid of molecular makers, could enhance breeding for rust resistance. This review highlights breeding approaches for groundnut rust resistance, with emphasis on integrating conventional breeding with marker-assisted selection. The life cycle, symptoms and epidemiology of the pathogen are also discussed to understand the host-pathogen interaction and guide groundnut rust resistance breeding.

Key words: Epidemiology, Groundnut rust, Host resistance, Marker-assisted selection, *Puccinia arachidis.*

Groundnut (*Arachis hypogaea* L., AABB, 2n=4x=40), is the fifth world's most economically important oilseed crop after soybeans, cotton, rapeseed and sunflower. It is currently produced on about 26.54 million hectares per year with an annual production of ≈43.92 million tons of shelled grain providing about 16.55 t ha^{-1}across the tropics, subtropics and warm temperate agro-ecologies worldwide (FAOSTAT, 2014; Upadhyaya *et al.*, 2012). The African continent accounts for about 31.6% of the world's groundnut production and the import trade values for sub-Saharan Africa (SSA) is estimated to be at US$ 54 million by 2020 (Abate *et al.*, 2012). Despite the socio-economic and cultural importance of the crop, its productivity and quality are severely constrained by several biotic and abiotic stress factors, particularly fungal diseases including early leaf spot caused by *Cercospora arachidicola* Hori., late leaf spot (*Cercosporidium personatum* Berk. & Curtis.) and groundnut rust (*Puccinia arachidis* Speg*)* (Reddy *et al.*, 2003). Groundnut rust and late leaf spot cause up to 70% yield losses in susceptible cultivars, which most smallholder farmers in developing countries often rely on (Khedikar *et al.*, 2010).

Groundnut rust is an economically important disease that was previously prevalent in South and Central America, USSR and Mauritius with sporadic distributions in the People's Republic of China (Stockdale, 1914; Tai, 1937; Subrahmanyam *et al.*, 1984). The disease was later introduced and became established in Asia, Australia, Oceania, and Africa where frequent epidemics occurs (Subrahmanyam *et al.*, 1984). Groundnut rust has now become cosmopolitan, reducing seed yield and oil quality of susceptible genotypes globally. Damage symptoms associated with early attacks during the growing season includes early pod maturity, reduced seed size, increased pod senescence, and decreased oil content, while severe infection causes up to 57% economic losses (Mondal and Badigannavar, 2015).

There are various control options against groundnut rust including cultural practices, chemical control, use of biological agents and host plant resistance. Cultural practices such as early planting, fertilizer application, removal of volunteer plants, burning of crop residues and intercropping are widely applied to reduce carry-over of rust inoculum from crop to crop (Kokalis *et al.*, 1997; Mondal *et al.*, 2014). Rust can effectively be controlled through repeated applications of fungicides based on disease occurrence and severity. However, majority of smallholder farmers in sub-Saharan African countries cannot afford fungicides and do not have adequate skills to handle and utilize them without predisposing themselves to health and environmental risks. Breeding and adoption of rust resistant cultivars is the most sustainable control option that can safeguard the crop. Despite several breeding efforts against the disease by private, national and international research institutions, there are still very few improved rust resistant varieties reported globally. This could be due to knowledge gaps on the nature of inheritance of rust resistance, pathogenicity of the fungi and breeding approaches for successful selection and introgression of resistance genes. Therefore, the objective of this review was to summarize the pathogenicity of groundnut rust, inheritance of its resistance, control options and potential breeding methodologies to aid sustainable groundnut production and productivity.

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LIFE CYCLE OF GROUNDNUT RUST

The groundnut rust pathogen is a *Pucciniomycetes* classified among higher fungi whose life cycle evolves between haploid and dikaryotic stages that are further characterized by five spore stages such as the spemagonium, dikaryotic aecium, dikaryoticuredium, dikaryotic telium and dikaryotic and/or diploid basidium (Fig. 1) (Mondal and Badigannavar, 2015). Plasmogamy between two compatible spermatids and receptive hyphae form dikaryotic mycelium. The telial stage, basidium and basidiospores are not common in groundnut rust (Mondal and Badigannavar, 2015), which mainly exists as uredinia containing numerous pedicillate uredospores observed on leaf surfaces (Tashildar *et al.*, 2012). Due to the rare occurrence of the basidium (sexual stage), limited races or variants of groundnut rust have been reported so far, which could have evolved distinctly due to mutations.

Uredospores infect groundnut leaves form uredosori that matures, burst and release numerous uredospores that initiate several cycles of infection under production conditions. Telia containing numerous teliospores are often formed from uredospores under low temperature and nutrient stress, but the existence of teliospores of *P. arachidis*rarely occur in nature, hence their function remains unclear (Tashildar *et al.*, 2012; Mondal and Badigannavar, 2015). The teliospores and basidia, which are the sexual forms of the rust pathogen, as well as somatic recombination generates the limited genetic sequence variability existing among rust isolates and could cause evolution of new races or pathotypes in future (Tashildar *et al.*, 2012). Thus, breeders should constantly pyramid several minor effect genes into elite germplasm to develop durable resistance and safeguard varieties against resistance breakdown.

EPIDEMIOLOGY OF GROUNDNUT RUST

Uredospores of the groundnut rust pathogen are dispersed by wind, rainfall or together with plant materials (Park and Wellings, 2012). Disease epidemiology is favored by continuous warm temperatures ranging between 20 and 30 °C and high humidity above 78 % (Peregrine, 1971; Mondal and Badigannavar, 2015). Uredospores were observed to remain viable for up to 20 days at 25–28 °C (Sunkad and Kulkarni, 2007).The disease progresses slowly at 10 °C or less and above 35 °C (Rao *et al.*, 1997). Controlled environment experiments can take advantage of these strict temperature and humidity requirements to manipulate the rate of inoculum accumulation. Allowing proper air movement can reduce the build-up and spread of inoculum under a given production condition. A prediction model developed by Gumpert *et al*. (1987) has been extensively used to describe the epidemic development of airborne foliar fungal diseases in different crops including soybean, groundnut and wheat. Environmental factors such as temperature, wind speed and direction and humidity affect airborne fungi distribution, infection and development (Pivonia and Yang, 2006). The following prediction equation has been commonly used in predicting disease severity (Gumpert *et al*., 1987):

$Y = b_0 + b_1x_1 + b_2x_2 + \ldots\ldots\ldots\ldots\ldots\ldots b_nx_n$

Where Y = Predicted disease severity

b_0 = intercept

b_1b_2……. bn= regression coefficients

x_1x_2…….. xn = independent or predictor variables

The groundnut rust pathogen's host range is confined to the genus *Arachis* making volunteer plants primarily responsible for disease carryover from season to season (Mallaiah and Rao, 1979; Kokalis *et al.*, 1997). In addition, overlapping crop seasons provide continuous inoculum build up and aerial propagation of uredospores. Rust epidemiology is dependent on the host's genotype and its severity, which is subject to genotype × environment interaction effects (Rao *et al.*, 1997). This suggests that rust resistance could be a complex trait that is conditioned by

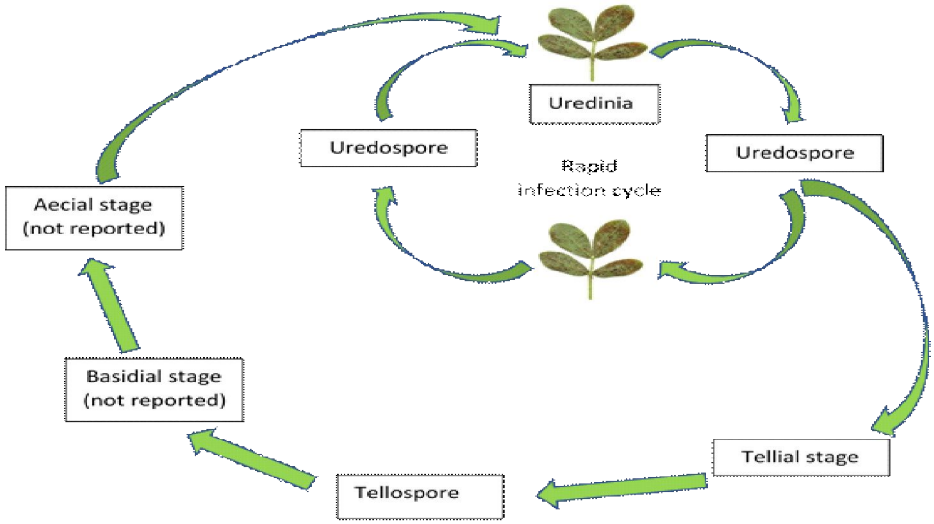

Fig 1: Schematic life cycle of groundnut rust (*Puccinia arachidis*).

numerous minor genes with additive genetic effect. Light rain showers favor disease dispersal, while heavy showers drastically reduce pore content in the canopy. Therefore, late sowing in the rainy season helps to reduces disease epidemic, whereas early sowing minimizes the severity of rust incidence during summer (Bulbule and Mayee, 1997). Spore trapping on the plant canopy is often higher in the morning than during evening hours (Savary and Janeau, 1986; Sunkad and Kulkarni, 2007).

GROUNDNUT RUST INFECTION PROCESS

Groundnut rust disease causes much damage during the flowering, fruiting and vegetative phases of crop growth. Uredospores of the groundnut rust pathogen geminates and protrudes a single unbranched germ tube of ~6 ìmin diameter and 100 to 200 ìm length from one of the equatorial germ pores on its wall (Das *et al.*, 1999). The germ tube grows across the leaf surface until it makes direct contact with the stoma, forming a thin walled ellipsoidal appressorium of about the same size as the spore from which it emerges (Mondal *et al.*, 2014). A thin cross wall then forms between the germ tube and the appressorium, confining the dense cytoplasm in the appressorium within 12 hrs of inoculation in susceptible genotypes. This is followed by the growth and penetration of a narrow infection peg from the appressorium through the stomatal apertures (Cook, 1980). After traversing the length of the stomatal passage, the infection peg swells and forms a vesicle in the substomatal chamber. Several infection dikaryotic hypha usually grow from the substomatal vesicle within 24 hrs of infection, from which simple knoblike haustoria develop within adjacent mesophyll cells. The pathogen then secretes hydrolytic enzymes like cellulases, glucanases and proteinase that cause dissolution of cell walls and plasma membranes. The infection foci later turn into cloronemic flecks that later develop into orange or reddish brown uredinia or pustules, on the lower surface of groundnut leaves (Fig. 2A). An ultrastructure study using a scanning electron microscope detected differences in spore reaction in the lower leaf surfaces of resistant (*A. stenosperma*cv V10309) and susceptible (*A. hypogaea* cv. IAC-Tatu) genotypes (Mondal and Badigannavar, 2015). The germ tube elongates sufficiently in susceptible genotypes within 24 hrs of inoculation and makes successful intercellular infection within 72 hrs (Mondal and Badigannavar, 2015).

SYMPTOMATOLOGY

Rust symptoms starts to appear 8 to10 days after infection with the occurrence of whitish flecks on the abaxial surface followed by yellowish flecks on the upper leaf surface (Fig. 2B). Orange colored pustules then form on the lower surface of the leaves (Fig. 2A). Elliptical pustules of 0.3 to 2.0 mm diameter rupture after about 2 days of appearance and expose circular or oval urediniospores, which are dark orange at first but become cinnamon brown with maturity (Leal-Bertioli *et al.*, 2009). Pustules occasionally develop on the upper leaf surface but are not as numerous as on the lower. Necrotic areas occur around the pustules and later coalesce causing leaf desiccation. The disease commonly develops in a radiating pattern from a single spot and increase in size in wet and warm weather. Rust spores can clearly be seen with naked eye on above ground parts including the stems and leaves, while it is not easy to diagnose on the seed because the pathogen is internally seed born.

CONTROL STRATEGIES OF GROUNDNUT RUST

Cultural control: Prevention of the outbreak or proliferation of *P. arachidis* in farmers' fields should be prioritized to minimize any damage to the crop and to minimize costs associated with other control strategies. Introduction and spread of the inoculum to areas where it has not been can be avoided through regulating the movement of groundnut plant materials across regions or boarders by enforcing strict phyto-sanitary inspections at quarantine stations. In groundnut producing areas where rust is a constant threat, adoption of crop rotations involving cereals or other non-host species is effective to avoid disease carryover (Mondal *et al.*, 2014). Small-scale farmers particularly in the semi-arid tropics often intercrop groundnuts with either pigeon pea (*Cajanus cajan*L.), sorghum (*Sorghum bicolor*), cassava (*Manihot esculenta* Crantz), pearl millet (*Pennisetum*

Fig 2: Groundnuts rust pustule at the lower (A) and upper (B) parts of the leaf.

glaucum) or maize (*Zea mays* L). Eradicating volunteer plants, which are often initial sources of inoculum and implementing fallow periods to break the disease cycle also help to suppress the inoculum since the pathogen is biotrophic. These should be complemented by maintaining field sanitation through weeding and proper spacing of plants (Kokalis *et al.*, 1997). Where a new crop has to be planted later during the growing season, adequate isolation distances from old crops should be maintained depending on the direction of the wind and whether the old crop has is infected or not. Cultural control options are however ineffective in the event of severe and unexpected outbreaks or infection, hence the need for constant field inspection and application of fungicides once the economic threshold level is reached.

Chemical control: Frequent applications of fungicides at 2 week intervals from the time that signs of rust infection are first observed effectively minimizes crop damage (Kokalis *et al.*, 1997). Regular application of chlorothalonil, tridemorph, combinations of mancozeb and zinc, hexaconazole, strobilurinsterol-inhibitors and other Sulphur based fungicides effectively reduce groundnut ruts incidences (Kokalis *et al.*, 1997). Early application of chemicals is more effective in reducing rust epidemics than applications later during the season. However, this should be based on regular monitoring and forecasting according to prevailing weather conditions. Trials conducted at Naliendele Research Institute in Tanzania found Chlorothalonil (Daconil) to be the most effective fungicide in controlling groundnut rust(NARI, 2001). Fungicides that are effective against both rust and leaf spot diseases such as chlorothalonil and tebuconazole are required in areas where leaf spot and rust occur together (Kokalis *et al.*, 1997).The use of costly crop protection chemicals is not economical, cause environmental and health hazards and often leads to resistance build-up among pathogen strains. Since doing away with fungicides is inevitable, proper rotation of fungicides belonging to different chemical groups is required to reduce the chances of resistant mutants. Environmentally friendly interventions such as the use of biological control agents and adoption of resistant cultivars could be more sustainable.

Biological control: Biocontrol agents such as the fungi *Verticillium lecanii* Zimmerm. *and Penicillium islandicum* Sopp. have been reported to inhibit the germination of urediniospore of *P. arachidis* and the severity of rust infection, hence can serve as bio-fungicides (Kokalis *et al.*, 1997).*Verticillium lecanii*proliferates within *P. arachi dis*spores, subsequently causing the spores to rupture (Kokalis *et al.*, 1997). This antagonistic fungi is a potential biological control agent against groundnut rust, early and late leaf spot, which often occur together (Podile and Kishore, 2002). Treatment of groundnut leaves with the fungus *A.obclavatum* reduces the number of pustules and uredospores, delays maturity and opening of uredosori, and reduces viability of uredospore resulting in significant preservation of seed yield and oil quality (Gowdu and Balasubramanian, 1993). The biocontrol agent survives on the crop until the pathogen establishes and is carried along with the rust fungal spores when they are liberated from the pustule (Podile and Kishore, 2002). Knowledge gapes still exist on how best to enhance the virulence of different biocontrol agents against the groundnut rust pathogen. Exploring more invasive variance that share similar

Table 1: Sources of groundnut rust resistance reported globally.

Genotype	Variety /pedigree	Source/origin	Reference
ICGV99003	Virginia	ICRISAT	Singh *et al.* (2003)
ICGV87165	Spanish	ICRISAT	
ICGV99005	Virginia	ICRISAT	
ICGV86699	Virginia	ICRISAT	Mace *et al.* (2006)
ICG11325	Spanish	India	
ICG 11485	Spanish	Peru	
ICG 10975	Spanish	Peru	
ICG 1185	Spanish	Argentina	
ICG11312	Spanish	India	
ICGV950084	Spanish	ICRISAT	
ICGV950166	Spanish	ICRISAT	
ICGV99051	Virginia	ICRISAT	
ICGV99052	Virginia	ICRISAT	
ICGV99019	Spanish	ICRISAT	
ICGV87157	Valencia	ICRISAT	
AB-ICGS76-7-1	ICGS 76× ISATGR 278-18	ICRISAT	Kumari *et al.* (2014)
AB-ICGS76-18-4	ICGS 76× ISATGR 278-18	ICRISAT	
AB-ICGS76-40-6	ICGS 76× ISATGR 278-18	ICRISAT	
AB-DH 86-47-1	DH 86× ISATGR 278-18	ICRISAT	
AB-DH 86-8-4	DH 86× ISATGR 278-18	ICRISAT	

ICRIAST: International Crop Research Institute for the Semi-Arid Tropic

Table 2: Quantitative trait loci (QTL) conferring resistance to groundnut rust.

QTL	Marker interval	Position (cM)	LOD Value	Reference
QTL_{R4}-$Rust_{03}$	GM2009–GM1536	6.01	5.41–69.75	Sujay *et al.* (2012)
QTL_{R5}-$Rust_{01}$	GM1536–GM2301/GM2079	12.51	8.61–53.61	
QTL_{R5}-$Rust_{02}$	IPAHM103–GM1954	16.51–22.51	11.92–78.41	
QTL_{R5}-$Rust_{03}$	GM2009–GM1536	0.01	7.12–36.45	
QTL_{R5}-$Rust_{04}$	IPAHM103–GM1954	5.41–13.41	5.66–30.78	
QTL_{R5}-$Rust_{03}$	RN16F05–GM1988	124.11	5.01–6.19	
QTL_{R5}-$Rust_{04}$	TC6E01–RN16F05	107.81	5.84	
QTL_{rust}01	IPAHM103-pPGSseq19D6	0–12	4.35–44.32	Khedikar *et al.* (2010)
QTL_{rust}02	PM436-Lec-1	46	3.22–3.51	
QTL_{rust}03	TC11A04-IPAHM524	16	3.51	
QTL_{rust}04	TC1B02-TC9F04	0-14	2.86–4.91	
QTL_{rust}05	TC4E09-IPAHM121	24	2.59	
QTL_{rust}06	pPGSseq13E6-PM3	20	4.24	
QTL_{rust}07	pPGSseq19G7-TC2C07	76	3.15	
QTL_{rust}08	TC2G05-TC9H09	2	3.09	
QTL_{rust}09	GM624-TC4G10	14	2.94–3.87	
QTL_{rust}10	PM434-TC4F02	4	3.16	
QTL_{rust}11	TC9H09-GM624	12	2.80	
QTL_{rust}12	PM377-TC1A01	0	2.53	

environmental requirements as the pathogen is a potential study area. Otherwise, integrating host plant resistance into the rust management system will enhance the efficacy of biological control and reduce costs associated with fungicide application.

Host resistance: Adoption of groundnut genotypes that possess inherent resistance against groundnut rust is a sustainable management alternative that can mitigate the shortcomings of other control strategies. To date, several rust resistant groundnut genotypes have been bred by different national and international crop breeding institutions, including the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (Singh *et al.*, 2003; Mace *et al.*, 2006). Table 1 presents some of the key genotypes possessing significant levels of rust resistance that can still be used as key sources of genes. Some of the genotypes were released for cultivation in Asian and African countries or have been used as parents in national breeding programs (Singh *et al.*, 2003; Mace *et al.*, 2006). Significant durable resistance could be achieved if different resistance genes harbored in elite cultivated materials could be introgressed into genotypes adapted to various production regions through backcross breeding. In this case, hybridization of elite or superior cultivars or lines will not be hindered by cross incompatibility issues or linkage drag associated with undesirable traits. However, high levels of resistance to late leaf spot and rust are often reported in wild peanut species of groundnut compared to *A. hypogaea* (Singh, 2004; Mondal and Badigannavar, 2015). Some of these genetic stocks can be utilized through the development interspecific hybrids and interspecific derivatives such as GPBD 4, developed from the parental genotype ICGV 86855, which is an interspecific derivative of *A. hypogaea* × *A. cardenasii* showing resistance to both late leaf spot and rust (Stalker, 1997). However, the use of resistance from wild species is limited because of associated linkage drag, resulting in delayed maturity and undesirable pod and kernel features, requiring several cycles of backcrossing to the recurrent parent with the help of foreground and background selection using genetic makers. Also, ploidy barriers between wild and cultivated species, genetic isolation of several wild species, and genetic incompatibility complicate the use of wild *Arachis* species as sources of resistance (Pasupuleti *et al.*, 2013).

BREEDING FOR GROUNDNUTS RUST RESISTANCE

Genetics of groundnut rust resistance: Resistance to groundnut rust has been reported to be predominantly governed by recessive genes that are expressed in a homozygous state (Bromfiel and Bailey, 1972; Tiwari *et al.*, 1984; Paramasivam *et al.*, 1990). This imply the need to use marker-assisted selection to ensure efficient selection and to reduce hybridization cycles during backcrossing by eliminating the need for test crossing to confirm the presence of the recessive gene. Bromfiel and Bailey (1972) reported of digenic inheritance controlled by recessive resistance genes among F_2 segregants of a natural cross between a rust-resistant female parent, PI 298115, and an unknown pollen parent. Similarly, the recessive nature of groundnut rust resistance was confirmed using F_3 derivatives of the same cross at ICRISAT. Other studies at ICRISAT using F_2 genotypes reported digenic inheritance in some crosses and trigenic inheritance in others (Kishore, 1981). Continued segregation observed among highly-resistant progenies also suggests that more than two genes influence resistance to groundnut rust (Nigam *et al.*, 1980). Based on the F_2

segregation ratios, Joel *et al*. (2006) observed that rust resistance was recessive and controlled in monogenic (3:1), digenic (15:1) and trigenic (63:1) manners. Further studies are required to ascertain the number of genes that govern groundnut rust resistance. Preliminary investigations on the inheritance of rust resistance derived from diploid wild species indicated that F_1 hybrids between *A. hypogaea* and diploid species showed resistant reactions to rust, suggesting that the resistance was governed by a partially dominant gene (Singh and Moss, 1984). The crosses involving wild relatives and wild derivatives often indicate partially dominant or dominant gene actions, which would possibly simplify backcross breeding (Mondal *et al.*, 2008). Other studies reported partial resistance, which is described as slow rusting type involving several minor genes that cause decreased infection frequency, pustule size, spore production, and spore viability as well as increased incubation period. (Wynne *et al.*, 1991; Kokalis *et al.*, 1997). Genetic analysis according to Hayman (1958) revealed preponderance of non-additive, additive × additive, and additive × dominance gene effects on the expression of groundnut rust resistance. Ghewande (2009) reported that resistance to rust was conditioned by additive, additive x additive, and additive x dominance gene effects.

Few studies reported the gene regulation or transcript up-regulation in response to *P. arachidis*. Proite *et al*. (2007) identified 35 putative non-redundant resistance gene analogs (RGAs) and 26 pathogenesis related expressed sequence tags (ESTs) from a rust resistant accession of *A. stenosperma*. Bertioli *et al*. (2003) also reported 78 RGAs based on the nucleotide-binding site (NBS) regions involving *A. hypogaea* and four wild relatives (*A. duranensis, A. cardenasii, A. stenosperma, and Arachis simpsonii*).

Phenotyping for groundnut rust resistance: Accurate phenotyping for rust resistance is important for efficient genotype screening since most critical breeding decisions rely on results obtained from phenotyping (Pasupuleti and Nigam, 2013). Selection of plants with a desired combination of traits is a challenging task in breeding programs because a large number of plants and traits are considered and recorded. Further, imposed screening conditions for one trait often have confounding effect(s) on the other. For instance, the rust pathogen being obligate in nature fails to establish and survive on leaf tissues that are already dead following leaf spot pathogen infection making rust screening difficult. Occurrence of chance escapes that get selected also compromises the reliability and reproducibility of phenotyping, particularly when relying on natural infection and limited number of replications (Mondal and Badigannavar, 2010). Thus, artificial inoculation under controlled environments is key during initial screening to ensure even distribution of inoculum. Transfer of resistance to the rust disease through hybridization often rely on phenotyping, hence the need to properly define rust symptoms and other traits associated with resistance or susceptibility. Under these circumstances, newly emerging biotechnological tools like marker-assisted selection can play a crucial role in ensuring efficient selection and introgression of genes for disease resistance.

Genotyping of groundnut for rust resistance: Molecular markers are useful in diseases resistance breeding as they can complement phenotypic screening in the early phase of breeding programs. They allow identification of resistant lines at juvenile stage saving time and cost of screening and, allow easy identification, transfer, and tracking of both dominant and recessive genes. Use of both foreground and background selection could help to reduce linkage drag by aiding in the elimination of undesirable traits in a much shorter time than with conventional breeding alone. Several marker systems including Random Amplified Polymorphic DNA (RAPDs), Amplified Fragment Length Polymorphism (AFLPs) and Microsatellites or Simple Sequence Repeat (SSRs) have been used in tagging of genes and selecting genotypes for rust resistance in groundnut. SSR markers are often preferred due to their co-dominance, simplicity, high polymorphism, repeatability, abundance, multi-allelic nature and their transferability within the genus *Arachis* (Moretzsohn *et al.*, 2005; Pandey *et al.*, 2012; Wang *et al.*, 2012).

Pandey *et al*. (2012) studied variation among parental lines and identified microsatellite markers associated with rust resistance in groundnut that can be used in future marker assisted selection and gene introgression. Mace *et al*. (2006) fingerprinted 117 F_2 lines segregating for rust resistance derived from the resistant parent VG 9514 and the susceptible parent TAG 24 and tagged the RAPD marker J171300 tightly linked to a rust resistance gene at a genetic distance of 18.5 cM using the modified bulk segregant analysis (BSA).Another study conducted by Mondal *et al*. (2008) revealed more diagnostic markers associated with rust resistance genes. Analysis of molecular variance (AMOVA) and Kruskal–Wallis one-way ANOVA identified candidate SSR loci that could be valuable for mapping rust and LLS resistance (Kokalis *et al.*, 1997; Mace *et al.*, 2006). Varma (2005) screened 23 SSR markers using 22 groundnut genotypes with varying levels of rust resistance and reported 52% polymorphism with high PIC values (≥ 5%). Table 2 presents some quantitative trait loci (QTL) conferring resistance to groundnut rust. Khedikar (2010) screened parental genotypes using 1,089 polymorphic SSR markers and identified a major QTL (QTLrust01) associated with rust resistance, contributing to 6.90–55.20% of the observed variation. Varshney *et al*. (2014) successfully introgressed a major QTL for rust resistance, through marker-assisted backcrossing, in three popular Indian peanut cultivars and generated several promising introgression lines with enhanced rust resistance and higher yield.

Mating design and genetic analysis of groundnut rust resistance: The choice of a mating design for estimating genetic variances is dictated by the objectives of the study, time, space, cost and other biological considerations. Jogloy *et al.* (1999) used the NCD II design involving high yielding and rust resistant lines to generate crosses for genetic analysis of rust resistance and associated agronomic traits. Another genetic study of rust resistance using line x tester mating design was conducted at the Centre for Plant Breeding and Genetics, TNAU, Coimbatore-3 (Tamil Nadu), India and revealed that resistance was recessive and governed in either monogenic, digenic or trigenic manners. Combining ability analysis using half diallel crosses and their parents revealed an additive type of gene action, implying that selection for high yield and for foliar disease resistance should be effective at later selection generations (Joel *et al.*, 2006). Breeders often use diallel mating schemes to estimate the potential value of genotypes and their combining ability effects for resistance to foliar diseases in groundnut using either a fixed or randomly chosen set of parental lines.

Combining ability studies provide a guideline for selecting of elite parents or crosses. It helps to choose parents and design crosses to accumulate fixable genes and to identify specific cross combinations for use in development of high-yielding rust resistant cultivars. Both specific combining ability (SCA) and general combining ability (GCA) effects have been reported to control resistance to foliar diseases of groundnut (Adamu *et al.*, 2008). This suggests that resistance to foliar diseases is controlled by additive and non-additive genetic effect, hence, can be improved through hybridization and selection.

CONCLUSION

Developing rust resistant groundnut germplasm requires effective screening techniques and marker-assisted selection in order to identify good source of resistance. ICRISAT scientists identified different molecular markers useful for genomic-assisted breeding of groundnut. Furthermore, several rust resistant varieties were identified through hybridization with landraces or wild relatives possessing QTL associated with groundnut rust resistance. Genetic control of rust resistance is still not clearly understood, therefore, studying the gene action influencing this trait is important. Further, groundnut rust and Late Leaf spot (LLS) often occur together, hence, their resistance should be selected for simultaneously.

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REFERENCES

Abate, T., Alene A.D., Bergvinson D., Shiferaw B., Silim S., Orr A. *et al.* (2012a) Tropical Grain Legumes in Africa and South Asia. Knowledge and Opportunities. TL II *Research Report* No. 1

Adamu, A., Olorunju P., Ado S., Alabi S. (2008) General and specific combining ability estimates for rosette resistance, early maturity and other agronomic traits in groundnut (*Arachis hypogaea* L.). *Int. J. Pure. Appl. Sci.* **2**: 33-41.

Bertioli, D., Leal-Bertioli S., Lion M., Santos V., Pappas G., Cannon S. *et al.* (2003) A large scale analysis of resistance gene homologues in Arachis. *Mol. Genet. Genom.* **270**: 34-45.

Bromfiel, K., and Bailey W. (1972) Inheritance of resistance to puccinia-arachidis in peanut. *Phytopathol.***62**: 748-760.

Bulbule, S., and Mayee C. (1997) Influence of weather parameters on the deposition pattern of urediniospores of groundnut rust. *Indian J. Mycol. Pl. Path.***27**: 170-174.

Cook, M. (1980) Host-parasite relations in uredial infections of peanut by *Puccinia arachidis*. *Phytopathol.***70**: 822-826.

Das, S., Raj S., Sen C. (1999) Temporal and spatial epidemic development of groundnut rust (*Puccinia arachidis* Speg.) as a function of altered date of sowing. *Trop. Agr.***76**: 45-50.

FAOSTAT (2014) Statistical data on crops, groundnut, area, production quantity of Tanzania, Africa & World,.*http://faostat.fao.org*.

Ghewande, M. (2009) Rust of Groundnut-An Overview. *APH Publishing Corp., New Delhi,* pp 326–334.

Gowdu, B.J., Balasubramanian R. (1993) Biocontrol potential of rust of groundnut by Acremonium obclavatum. *Can. J. Bot.***71**: 639-643.

Gumpert, F.-M., Geiger H., Stähle U. (1987) A mathematical model of the epidemics in homogeneous and heterogeneous host stands. *J. Plant Dis. Prot.* **94**: 206–215 .

Hayman, B. (1958) The separation of epistatic from additive and dominance variation in generation means. *Heredity.* **12**: 371-390.

Joel, A., Sumathi P., Raveendran T. (2006) Genetics of rust (*Puccinia arachidis* Speg.) and its association with rust related traits in groundnut (*Arachis hypogaea* L.). *Plant Arch.***6**: 553-556.

Jogloy, S., Trisuvanwat W., Wongkaew S., Patanothai A. (1999) Combining ability and heritabilty of rust resistance and agronomic traits in peanut (*Arachis hypogaea* L.). *Thai. J. Agr. Sci.***47**: 777-780.

Khedikar, Y., Gowda M., Sarvamangala C., Patgar K., Upadhyaya H., Varshney R. (2010) A QTL study on late leaf spot and rust revealed one major QTL for molecular breeding for rust resistance in groundnut (*Arachis hypogaea* L.). *Theor. Applied Genet.* **121**: 971-984.

Khedikar, Y., Gowda M., Sarvamangala C., Patgar K., Upadhyaya H., Varshney R. (2010) A QTL study on late leaf spot and rust revealed one major QTL for molecular breeding for rust resistance in groundnut (*Arachis hypogaea* L.). *Theor. Appl. Genet.***121**: 971-984.

Kishore, B. (1981) Rust inheritance studies in groundnut (*Arachls hypogaea* L.). Masters Thesis, Andhra Pradesh Agricultural University, India.

Kokalis, Porter D.M., Rodriguez-Kabana R., Smith D., Subrahmanyam P. (1997) Compendium of peanut diseases. *Am. Phytopathol*.**2**: 31-333.

Kumari, V., Gowda M., Tasiwal V., Pandey M.K., Bhat R.S., Mallikarjuna N. *et al*. (2014) Diversification of primary gene pool through introgression of resistance to foliar diseases from synthetic amphidiploids to cultivated groundnut (*Arachis hypogaea* L.). *Crop Journal*. **2**: 110-119.

Leal-Bertioli, S.C., José A.C.V., Alves-Freitas D.M., Moretzsohn M.C., Guimarães P.M., Nielen S. *et al*. (2009) Identification of candidate genome regions controlling disease resistance in *Arachis*. *BMC Plant Biol*.**9**: 1-12.

Mace, E., Phong D., Upadhyaya H., Chandra S., Crouch J. (2006) SSR analysis of cultivated groundnut (*Arachis hypogaea* L.) germplasm resistant to rust and late leaf spot diseases. *Euphytica*. **152**: 317-330.

Mallaiah, K., and Rao A. (1979) Groundnut rust: factors influencing disease development, sporulation and germination of uredospores. *Indian. Phytopathol*.**32**: 382-388.

Mondal, Badigannavar A. (2010) Molecular diversity and association of SSR markers to rust and late leaf spot resistance in cultivated groundnut (*Arachis hypogaea* L.). *Plant Breeding*. **129**: 68-71.

Mondal, Badigannavar A. (2015) Peanut rust (*Puccinia arachidis* Speg.) disease: its background and recent accomplishments towards disease resistance breeding. *Protoplasma*. **252**: 1409-1420.

Mondal, Badigannavar A.M., Murty G. (2008) RAPD markers linked to a rust resistance gene in cultivated groundnut (*Arachis hypogaea* L.). *Euphytica*. **159**: 233-239.

Mondal, Hande P., Badigannavar A.M. (2014) Identification of transposable element markers for a rust (*Puccinia arachidis* Speg.) resistance gene in cultivated peanut. *J. Phytopathol*.**162**: 548-552.

Moretzsohn, M., Leoi L., Proite K., Guimaraes P., Leal-Bertioli S., Gimenes M. *et al*. (2005) A microsatellite-based, gene-rich linkage map for the AA genome of Arachis (*Fabaceae*). *Theor. Appl. Genet*.**111**: 1060-1071.

NARI (2001) Annual Report. 2000.

Nigam, S., Dwivedi S., Gibbons R. (1980) Groundnut breeding at ICRISAT. *ICRISAT*. **1**: 62-68.

Pandey, M.K., Monyo E., Ozias-Akins P., Liang X., Guimarães P., Nigam S.N. *et al*. (2012) Advances in Arachis genomics for peanut improvement. *Biotechnol. Adv*.**30**: 639-651.

Paramasivam, K., Jayasekhar M., Rajasekharan R., Veerabadhiran P. (1990) Inheritance of rust resistance in groundnut (*Arachis hypogaea* L.). *Madras Agr. J*.**77**: 50-52.

Park, R.F., and Wellings C.R. (2012) Somatic hybridization in the Uredinales. *Ann. Rev. Phytopathol*.**50**: 219-239.

Pasupuleti, J., Nigam S., Pandey M.K., Nagesh P., Varshney R.K. (2013) Groundnut improvement: use of genetic and genomic tools. *Front. Plant Sci*.**4**: 23.

Peregrine, W. (1971) Groundnut rust (*Puccinia arachidis* Speg.) in Brunei. *Pest Articles & News Summaries*. **17**: 318-319.

Pivonia, S., and Yang X. (2006) Relating epidemic progress from a general disease model to seasonal appearance time of rusts in the United States: Implications for soybean rust. *Phytopathol*. **96**: 400-407.

Podile, A.R., and Kishore G.K. (2002) Biological control of peanut diseases. *Biological control of crop diseases'.(Ed. SS Gnanamanickam) pp*. 131-160.

Proite, K., Leal-Bertioli S.C., Bertioli D.J., Moretzsohn M.C., da Silva F.R., Martins N.F. *et al*. (2007) ESTs from a wild Arachis species for gene discovery and marker development. *BMC Plant Biology*. **7**: 7.

Rao, A., Donald D., Ramachandra Reddy K. (1997) Effect of temperature on rust and leaf spot disease development in groundnut. *J. Oilseeds Res*.**14**: 249-255.

Reddy, Reddy, Anbumozhi (2003) Physiological responses of groundnut (*Arachis hypogaea* L.) to drought stress and its amelioration: A review. *Acta Agron. Hung*.**51**: 205-227.

Savary, S., and Janeau J.-L. (1986) Rain-induced dispersal in *Puccinia arachidis*, studied by means of a rainfall simulator. *Neth. J. Plant Pathol*.**92**: 163-174.

Singh (2004) Growth and physiology of groundnut. *Groundnut Res. Ind*.**1**: 178-212.

Singh, Dwivedi S.L., Pande S., Moss J.P. (2003) Registration of rust and late leaf spot resistant peanut germplasm lines. *Crop Sci*.**43**: 440.

Singh, A., and Moss J. (1984) Utilisation of wild relatives in the genetic improvement of Arachis hypogaea L. *Theor. Appl Genet*. **68**: 355-364.

Stalker, H. (1997) Peanut (*Arachis hypogaea* L.). *Field Crop. Res*.**53**: 205-217.

Stockdale, F. (1914) Report of work of Division of Phytopathology. *Mauritius. Department of Agriculture. Annual Report*. **1913**: 7-9.

Subrahmanyam, P., Williams J., McDonald D., Gibbons R. (1984) The influence of foliar diseases and their control by selective fungicides on a range of groundnut (*Arachis hypogaea* L.) genotypes. *Ann. Appl. Biol*.**104**: 467-476.

Sujay, V., Gowda M., Pandey M., Bhat R., Khedikar Y., Nadaf H. *et al*. (2012) Quantitative trait locus analysis and construction of consensus genetic map for foliar disease resistance based on two recombinant inbred line populations in cultivated groundnut (*Arachis hypogaea* L.). *Mol. Breeding*. **30**: 773-788.

Sunkad, G., and Kulkarni S. (2007) Studies on perpetuation and carry over of groundnut rust (*Puccinia arachidis* Speg.) in northern Karnataka. *Karnataka. J. Agri. Sci*.**20**: 297-300.

Tai, F. (1937) A list of fungi hitherto known from China. *Sci. Rep. Tsing-Hua Univ. Ser. B*.**2**: 492.

Tashildar, C., Adiver S., Chattannavar S., Palakshappa M., Kenchanagaudar P., Fakrudin B. (2012) Morphological and isozyme variations in *Puccinia arachidis* Speg. causing rust of peanut. *Karn. J. Agr. Sci.***25**: 0972-1061.

Tiwari, S., Ghewande M., Misra D. (1984) Inheritance of resistance to rust and late leaf spot in groundnut (*Arachis hypogaea* L.). *J. Cytol. Genet.***19**: 97-101.

Varma, T., Dwivedi S., Pande S., Gowda M. (2005) SSR markers associated with resistance to rust (Puccinia arachidis Speg.) in groundnut (Arachis hypogaea L.). SABRAO *J. Breed. Genet.* **37:** 107-119.

Varshney, R.K., Pandey M.K., Janila P., Nigam S.N., Sudini H., Gowda M. *et al.* (2014) Marker-assisted introgression of a QTL region to improve rust resistance in three elite and popular varieties of peanut (Arachis hypogaea L.). *Theor. Appl. Genet*. **127:** 1771-1781.

Upadhyaya, H.D., Mukri G., Nadaf H.L., Singh S. (2012) Variability and stability analysis for nutritional traits in the mini core collection of peanut. *Crop Sci.***52**: 168-178.

Wang, H., Penmetsa R.V., Yuan M., Gong L., Zhao Y., Guo B. *et al.* (2012) Development and characterization of BAC-end sequence derived SSRs, and their incorporation into a new higher density genetic map for cultivated peanut (*Arachis hypogaea* L.). *BMC Plant Biol.***12**: 10.

Wynne, J., Beute M., Nigam S. (1991) Breeding for disease resistance in peanut (*Arachis hypogaea* L.). *Ann. Rev. Phytopathol.***29**: 279-303.