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# Durability of Disease Resistance

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# ORIGIN AND UTILIZATION OF RUST RESISTANCE IN GROUNDNUT*

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## Summary

The groundnut (*Arachis hypogaea* L.) - groundnut rust (*Puccinia arachidis* Speg.) pathosystem appears to have coevolved in Peru, South America, where the host is known to have been cultivated for almost 4000 years. The groundnut spreaded to the rest of the world after the Spanish and Portuguese colonization of South America. Prior to 1969 the pathogen which was largely confined to South America, but it got firmly established in all the groundnut growing countries in a short span of time (a 're-encounter' phenomenon). The pathogen is highly host-specific and is known by its uredinial stage. Rust is an economically important disease on groundnut, often causing more than 50% yield losses in most groundnut growing areas. Rust resistant genotypes have been identified. The resistance is of a quantitative nature and its inheritance does not seem to be simple. Rust resistance in most genotypes is stable over a wide range of geographic locations except in a few locations, indicating possible variation in the pathogen, which needs confirmation. Rust resistance in groundnut fits neither typical race-specific nor race-non-specific patterns and appears to be an intermediate type falling in the continuum of these two extreme types.

## The host

### *Origin*

The cultivated groundnut (*Arachis hypogaea*) is believed to have originated somewhere along the eastern slopes of the Andes in southern Bolivia and northwestern Argentina (Krapovickas 1969). The species is subdivided into subspecies and botanical cultivars with a specific geographic distribution in South America. Six gene centers of *A. hypogaea* have been identified in relation to the distribution of subspecies and botanical cultivars. These gene centers include the Guarani region (river basins of Paraguay and upper Parana), Goias and Minas Gerais region (river basins of Tocantins and Sao Francisco in south eastern Brazil), Rondonia and northeastern Mato Grasso region (western Brazil), Bolivian region (eastern slopes of the Andes), Peruvian region (upper Amazon and west coast) and northeastern Brazil. The Bolivian region is believed to be the primary gene center of groundnut and the

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other regions to be the secondary gene centers (Gregory et al. 1980).

### *Distribution*

Groundnut is known to have been cultivated in Peru since ca. 2000 B.C (Hammons 1973). From its centers of origin, groundnut could have spread to the rest of the world only after the Spanish and Portuguese colonization of South America. There is no credible evidence for any pre-Columbian spread of groundnut from South America (Hammons 1973). Groundnut is now cultivated throughout the tropical, sub-tropical and warm temperate regions of the world, lying approximately between latitudes 40° N and 40° S. Groundnut is firmly established as one of the most important leguminous crops in these regions. In 1989, over 20 million ha worldwide were planted with groundnut and from that 22.6 million tonnes of dried pods were harvested, with an average yield of 1124 kg ha$^{-1}$. Asia was the largest producer (15.4 million t), followed by Africa (4.6 million t), North and Central America (2.0 million t), and South America (0.5 million t). Among individual countries, India was the largest producer (8.0 million t) of groundnut, followed by the People's Republic of China (5.4 million t), and the USA (1.83 million t). Approximately 90% of the world production comes from developing countries (FAO 1989).

## The pathogen

### *Occurrence and spread*

The first record of groundnut rust dates back to 1827 or 1828 in a collection made in Surinam (Hennen et al. 1987). Prior to 1969, the disease was largely confined to South and Central America, with occasional outbreaks occurring in the southern USA. Rust was also recorded from Mauritius in 1914 (Stockdale 1914) and from the People's Republic of China in 1934 (Tai 1937). A record of the occurrence of groundnut rust from the USSR (Jaczewski 1910) was reported to be erroneous (Tranzschel 1939). In the early 1970s groundnut rust spread rapidly to, and became firmly established in, many countries in Asia, Australasia and Oceania and Africa (Subrahmanyam and McDonald 1983). How do we explain this sudden wide spread of the disease? How were the fungal propagules carried to all these countries? Did the pathogen spread to all these countries from South America or from the People's Republic of China? We have no satisfactory answers to these questions. Although in the past it was thought that groundnut rust might have spread through exchange of germplasm, spread of the disease to almost all groundnut growing countries outside South America in such a short time is difficult to explain on this basis. There is no reliable evidence of groundnut rust being internally seedborne (Subrahmanyam and McDonald 1982; Mayee 1987).

### *Life-cycle*

Groundnut rust is known almost exclusively by its uredinial stage. It is not known whether the fungus can produce pycnia and aecia or if any alternate host is involved in the life cycle. Urediniospores are the main means of dissemination and spread of groundnut rust. There are a few records of the occurrence of teliospores on the cultivated groundnut and on wild *Arachis* species (Hennen et al. 1987) in South America. There is no authenticated report of the occurrence of teliospores of groundnut rust from other countries.

The pathogen is highly host specific. There is no record of the occurrence of any host of groundnut rust outside the genus *Arachis* (Subrahmanyam and McDonald 1982). Because there is no knowledge of spermogonia, aecia, and hosts that basidiospores will infect, the life cycle of groundnut rust is unknown and the taxonomic position of the fungus is obscure and only tentative (Hennen et al. 1987).

### *A case of "re-encounter" phenomenon*

Groundnut rust is thought to have originated in South America along with the domestication of the groundnut in prehistoric times (Leppik 1971). The restricted distribution of the pathogen in South America until recently, and its host restriction to members of the genus *Arachis*, strongly support this hypothesis (Subrahmanyam et al. 1989). The groundnut rust was geographically separated from its host during several centuries in Asia, Africa, Australasia, and Oceania, before being reunited in the early 1970s. All groundnut cultivars grown by the farmers outside South America are susceptible to rust. A period of several centuries of separation of the host from the pathogen might have warranted re-ordering of host plant priorities to selection pressure in the new environments. The genes governing rust resistance might have been lost or their frequency greatly reduced in the absence of continual selection pressure by the pathogen leading to a genetic erosion phenomenon (Van der Plank 1963). However, this proposition seems to be less likely in self-pollinated and clonal crops (Buddenhagen and De Ponti 1984). It is possible that the early explorers might have introduced groundnut from South America including the rust-resistant genotypes, irrespective of their botanical type, pod type and seed colour. However, since most of the rust-resistant genotypes are primitive landraces with low yield potential and unacceptable pod and seed characteristics, they might have undergone conscious selection by farmers to meet their specific needs particularly for high yield, pod type, and seed colour. This could have further eroded rust resistance of the host populations outside South America.

### *Economic importance*

Rust is now an economically important disease in most groundnut-growing areas of the world, losses being particularly severe if the crop is also attacked by leaf spots (*Cercospora arachidicola* Hori and *Phaeoisariopsis personata* (Berk. and Curt.) v. Arx). In the Caribbean and Central America, commercial production of groundnut has been almost eliminated by the combined attack of rust and leaf spots (Hammons 1977). Losses from rust measured at two locations in Texas, USA, were 50 and 70% (Harrison 1973). Felix and Ricaud (1977) reported losses from rust amounting to 70% in Mauritius. In India, Subrahmanyam et al. (1980 and 1984) reported significant losses in groundnut yields from combined attack of rust and leaf spots, while rust alone was responsible for 52% reduction in pod yield. Ghuge et al. (1981), also from India, estimated that rust caused a 49% loss of pod yield and lowered the 100-seed weight to the extent of 19%. Zhou et al. (1980) recorded a loss of 20% for spring groundnut and 17% for autumn groundnut in the People's Republic of China. The early establishment of the disease is known to advance harvesting by about a month, resulting in poor pod filling (O'Brien 1977). In addition, haulm (hay) yields are lowered drastically.

### *Resistance to groundnut rust*

Although rust can be controlled effectively by certain fungicides (Smith and Littrell 1980), this is not economically feasible for the vast majority of smallholder farmers in developing countries. Hence, genetic control is decidedly the best solution (Gibbons 1980). Identification of sources of genetic resistance is therefore highly important. Recognition of this has stimulated research in many countries to exploit host plant resistance to rust.

### *Screening methods*

Effective field screening methods have been developed for use in areas where natural disease pressure is high or where such pressure can be artificially induced. Genotypes to be screened are sown in a disease nursery comprising infector rows of highly susceptible cultivars arranged systematically throughout the nursery. To enhance disease development, plants in infector rows are inoculated with suspensions of rust spores. This is most successful if done in the evening, following irrigation. Potted spreader plants heavily infested with rust are also placed systematically throughout the field to provide further sources of inoculum. As required by climatic conditions, fields may be irrigated frequently using overhead sprinklers until harvest. Some 10 days before harvest each genotype is scored for the development of rust using a 9-point scale (Subrahmanyam et al. 1982).

Screening of germplasm for resistance to rust can also be done on a limited scale in the glasshouse using potted plants, or in the laboratory using detached leaves (Subrahmanyam et al. 1982, 1983a, and 1983b). A glasshouse or laboratory screening method could be useful in areas where rust epidemics do not occur regularly or where other foliar diseases or insect pests interfere with field screening. However, these techniques have limitations in identifying moderate levels of resistance and require further verification in the field.

### *Sources of resistance*

A number of sources of resistance to groundnut rust have been identified (Mazzani and Hinojosa 1961; McVey 1965; Bromfield and Cevario 1970; Cook 1972; Bromfield 1974; Moraes and Savy Filho 1983). At ICRISAT Center, India, an intensive research program was started in 1977 to confirm earlier reported sources of resistance and to search for additional sources of resistance for use in the breeding program to develop high yielding agronomically superior rust-resistant cultivars. A world collection of over 12,000 germplasm lines has been screened in the field for rust resistance during the period 1977 to 1990, and 124 rust-resistant and 29 rust and late leaf spot-resistant germplasm lines were identified (Subrahmanyam et al. 1989). Although many sources of resistance to rust have been identified from the available germplasm collections, not much is known about their genetic base. There is a need to study the genetic base of this material and diversify it further as diverse genotypes with rust resistance and superior agronomic traits are required for utilization in breeding programs.

### *Co-evolution of groundnut - groundnut rust pathosystem*

It is generally accepted that the centers of origin and domestication of cultivated plants are the best locations in which to find genuine sources of resistance to common pests and pathogens (Leppik 1970; Dinoor and Eshed 1984). During the coevolution of host and parasite, both participants develop complimentary genetic systems if they have long been associated in their centers of origin (Leppik 1970; Browning 1974; Harlan 1976; Anikster and Wahl 1979; Segal et al. 1980). The evolution of new or more virulent races of the pathogen may be counter-balanced by the development of higher levels of resistance in its host (Flor 1956). It is interesting to note that the grouping of the available rust-resistant *A. hypogaea* genotypes based on botanical type indicates that about 89% of them belong to var. *fastigiata*, 10% to var. *hypogaea*, and 1% to var. *vulgaris*. A study of all the available rust-resistant genotypes reveals that over 90% of them originated in South America or had South American connections and about 83% originated in Peru. The origin of other genotypes is not clearly documented. Available germplasm records indicate that the origin of resistant types could be traced to the Tarapoto region of Peru. The assumption that groundnut - groundnut rust pathosystem coevolved in Peru is further supported by the fact that Peru is a secondary gene center with predominance of primitive *fastigiata* types. A majority of rust-resistant groundnuts are primitive *fastigiata* types (Ramanatha Rao 1987; Subrahmanyam et al. 1989). Such types have been under cultivation since about 2000 B.C as evidenced by a number of archaeological findings (Hammons 1973). Why are the sources of rust resistance predominantly of Peruvian origin? Why does the rust resistance not occur in the primary center or in other secondary centers? Is it because the *fastigiata* types predominantly occur in the Peruvian region? If so, what are the levels of resistance available in *hirsuta* types which have cohabitated along with the *fastigiata* types in the Peruvian region? A better understanding of factors associated with these questions is important for genetic enhancement and rust resistance breeding programs.

### *Components of resistance*

Rust resistance is not correlated with either the frequency or the size of stomata, urediniospores germinate and germ tubes enter through stomata irrespective of whether a genotype is immune, resistant, or susceptible to rust. In immune genotypes (found only in wild *Arachis* species) the fungus dies shortly after entering the substomatal cavity.

The differences between resistance and susceptibility are associated with differences in rate and extent of mycelial development within the cavity and within leaf tissues (Subrahmanyam et al. 1980). Rust-resistant genotypes have increased incubation period, decreased infection frequency, and reduced pustule size, spore production and spore viability (Lin 1981; Sokhi and Jhooty 1982; Subrahmanyam et al. 1983a and 1983b; Lin et al. 1984). The effects of these components of resistance to rust appear to be cumulative over the course of the disease epidemic. In general, the disease on rust-resistant genotypes builds up slowly, and does little apparent damage to the foliage, as shown by the lower rates of disease development (r), and the area under disease progress curve (AUDPC). The pattern of inheritance and the number of genes governing these components of resistance is not known.

The extent of rust damage to foliage is dependent on the physiological age of the plant. Young plants are most susceptible to rust attack and the susceptibility declines with age (Subrahmanyam and McDonald 1987).

Suryakumari et al. (1984) reported a strong association between the number of tannin sacs in leaves and rust resistance. The susceptible genotypes had few tannin sacs, but highly resistant or immune wild *Arachis* species had large numbers of them. Subba Rao (1987) found a correlation between the degree of resistance and the amounts of total phenolic compounds in leaf tissues. Biosynthesis of phytoalexins (methyl linolenate, dienic alcohols, tricarboxylic propanic acid, nonyl phenol and alkyl-bis-phenyl ether) was stimulated by infection in rust-resistant genotypes. Such a stimulatory response was also observed in rust-susceptible genotypes, but the amplitude was small and the response was usually delayed.

## *Utilization of resistance*

Most rust-resistant germplasm lines are primitive landraces, and have undesirable pod and seed characters such as dark testa colour, and heavily reticulated pods. At ICRISAT Center, more than 1500 single, two-way, and three-way crosses were made between lines with good agronomic characters and lines resistant to rust. Large $F_2$ populations, and subsequent generations, were grown in the field during the rainy season and screened for resistance using the infector row method. Several high-yielding, agronomically superior lines, with high levels of resistance to rust and moderate levels of resistance to late leaf spot were bred by pedigree and mass pedigree methods (Reddy et al. 1984). Backcrossing was also used in a few instances to improve pod, seed, and plant characters. Several of these resistant lines outyielded released susceptible cultivars when tested in multilocation trials and some are in advanced stages of testing in several countries. Two high-yielding cultivars ICG(FDRS) 10 and ICGV 86590 resistant to rust and moderately resistant to late leaf spot have recently been released for cultivation in the peninsular zone of India, where rust and late leaf spots cause severe yield losses (Reddy et al. 1992). Another high yielding cultivar ICG(FDRS) 4, with multiple resistances to rust, late leaf spot, stem and pod rots caused by *Sclerotium rolfsii* Sacc., leaf miner, and with low field incidence of bud necrosis disease has shown wide adaptability by outyielding local cultivars in India, Swaziland, Malawi, Myanmar, and The Philippines (Nigam et al. 1992). A foliar disease-resistant cultivar, Tifrust 2, jointly developed by USDA-ARS (University of Georgia, Tifton, U.S.A.), and ICRISAT has been released as 'Cardi Payne' in Jamaica.

Early generation breeding materials resistant to rust have been widely distributed to breeders and scientists in national and international programs to enable them to carry out further selection *in situ* under local agroclimatic conditions. This has resulted in the successful development and release of cultivars such as Girnar 1 and ALR 1 in India (Subrahmanyam et al. 1990).

## *Genetics of resistance*

Rust resistance in groundnut is reported to be governed by duplicate recessive genes (Bromfield and Bailey 1972; Knauft 1987). Depending on the resistant parents used in the study, Kishore (1981) observed both digenic and trigenic inheritance. Nigam et al. (1980) observed continuous segregation for rust resistance within the advanced generations of highly resistant progenies, refuting the validity of the two gene model. While, there is no clear agreement on the number of genes involved, all the workers have reported that resistance within cultivated species behaves as a recessive trait. Quantitative genetic analysis of parents, $F_1$, $F_2$, $BC_1$ and $BC_2$ generations of rust resistant x susceptible crosses using generation mean analysis at ICRISAT Center indicated that rust-resistance is predominantly controlled by additive, additive x additive, and additive x dominance gene effects (Reddy et al. 1987). These observations on the importance of both additive and nonadditive gene action in the rust inheritance is confirmed by other workers (Anderson et al. 1990; Varman et al. 1991). Wild *Arachis* spp. may have mechanisms of rust resistance that differ from those in the cultivated groundnut. In some diploid wild *Arachis* spp., rust resistance appears to be partially dominant (Singh et al. 1984), unlike in the cultivated groundnut, indicating that different genes may be involved. Combination of these resistances may result in more stable resistance in the cultivated groundnut

## *Stability of resistance*

Stability of host resistance is an important objective of breeding programs. Some of the rust-resistant genotypes identified/assembled at ICRISAT Center are being tested in different locations in the International Groundnut Rust Diseases Nursery (IGRDN). The results obtained indicate that rust resistance of most genotypes is stable over a wide range of geographic locations (e.g., USA, Niger, Malawi, and India). However, the results from the People's Republic of China and Taiwan were different from those of other countries. The genotype NC Ac

17090, is highly resistant to rust at ICRISAT Center, only moderately resistant in the People's Republic of China, and susceptible in Taiwan. In contrast, the genotype PI 298115, is only moderately resistant at ICRISAT Center, but is highly resistant in the People's Republic of China and in Taiwan. Although this indicates the possibility of variation in the pathogen, there is no authenticated report on the occurrence of races.

### Possible occurrence of races

Hennen et al. (1987) speculated that the fungus completes its sexual life cycle in South America and genetic diversity of the pathogen is predicted to have accumulated there. In fact, the susceptibility of several wild *Arachis* species to groundnut rust in their natural habitats in South America strongly supports this hypothesis. All these *Arachis* species are found to be immune or highly resistant to groundnut rust in India (Subrahmanyam et al. 1983c), and elsewhere (Bromfield and Cevario 1970; Hammons 1977). The results obtained from the People's Republic of China and Taiwan also indicate the possible occurrence of races of groundnut rust. There is a need for systematic identification of races and determination of their geographical distribution. Recently a set of preliminary differential hosts has been proposed (P. Subrahmanyam, unpublished).

### How durable is the rust resistance in groundnut?

The genetic composition of rust resistance in groundnut is not conclusively established. There are indications tho rust-resistance is controlled by a fev major genes, a situation typical o race-specific resistance (Van der Plank 1963). However, quantitative genetic analysis of parents and progenies indicated that rust resistance is predominantly controlled by additive, additive x additive, and additive x dominance gene effects with duplicate epistasis (Reddy et al. 1987). These findings suggest that rust resistance does not fit a typical race specific pattern. It is probably an intermediate type exhibiting smaller race-specific effects as indicated in other pathosystems (Parlevliet 1981). The majority of rust-resistant groundnut genotypes typically show fully developed rust lesions, which are small and only sparsely sporulating. However, in certain genotypes, although lesions are initially fully developed, they show some necrosis around the lesions at later stages of development resembling a hypersensitive reaction. These observations suggest two types of resistance, the latter one possibly being of a race-specific nature. When resistance is conferred by the action of a single gene, preventing the development of the pathogen during or immediately after penetration, there is strong selection pressure on the pathogen population. However, the resistance that is governed by the additive effects of several genes, retarding several aspects of pathogen development, exerts a weaker selection pressure. This kind of resistance may not be subject to sudden "breakdown" and is more likely to be durable.

Durability of disease resistance can best be identified by growing a resistant-cultivar on a large scale for a long period of time in an environment favouring the disease (Johnson 1984). The stability of groundnut rust resistance found in different geographical locations is only an indication of durability, and there is no strict causal relation between stability and durability. The majority of rust-resistant genotypes identified in recent years are not agronomically acceptable and can not meet the farmers' and trade's demands for yield and quality. However, these genotypes have served as sources of resistance in rust resistance breeding programs in many countries and several agronomically superior rust-resistant cultivars have been developed. When recently released rust-resistant groundnut cultivars are grown by farmers on larger areas we may obtain reliable information as to the durability of resistance. The role of these cultivars in stabilizing the pathogen evolution (Leonard and Czochor 1980) needs to be examined.

Most of the world's groundnuts are grown in developing countries (FAO 1989) under subsistence agriculture in diverse agro-environments. Agronomic practices such as intercropping, mixed cropping and use of cultivar mixtures may also influence the durability of disease resistance.

There are many gaps in our knowledge of the groundnut - groundnut rust pathosystem. The occurrence of races of the pathogen, the gene-for-gene relationship, and host-pathogen specificity need to be clearly established to provide a better understanding of the durability of resistance.

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