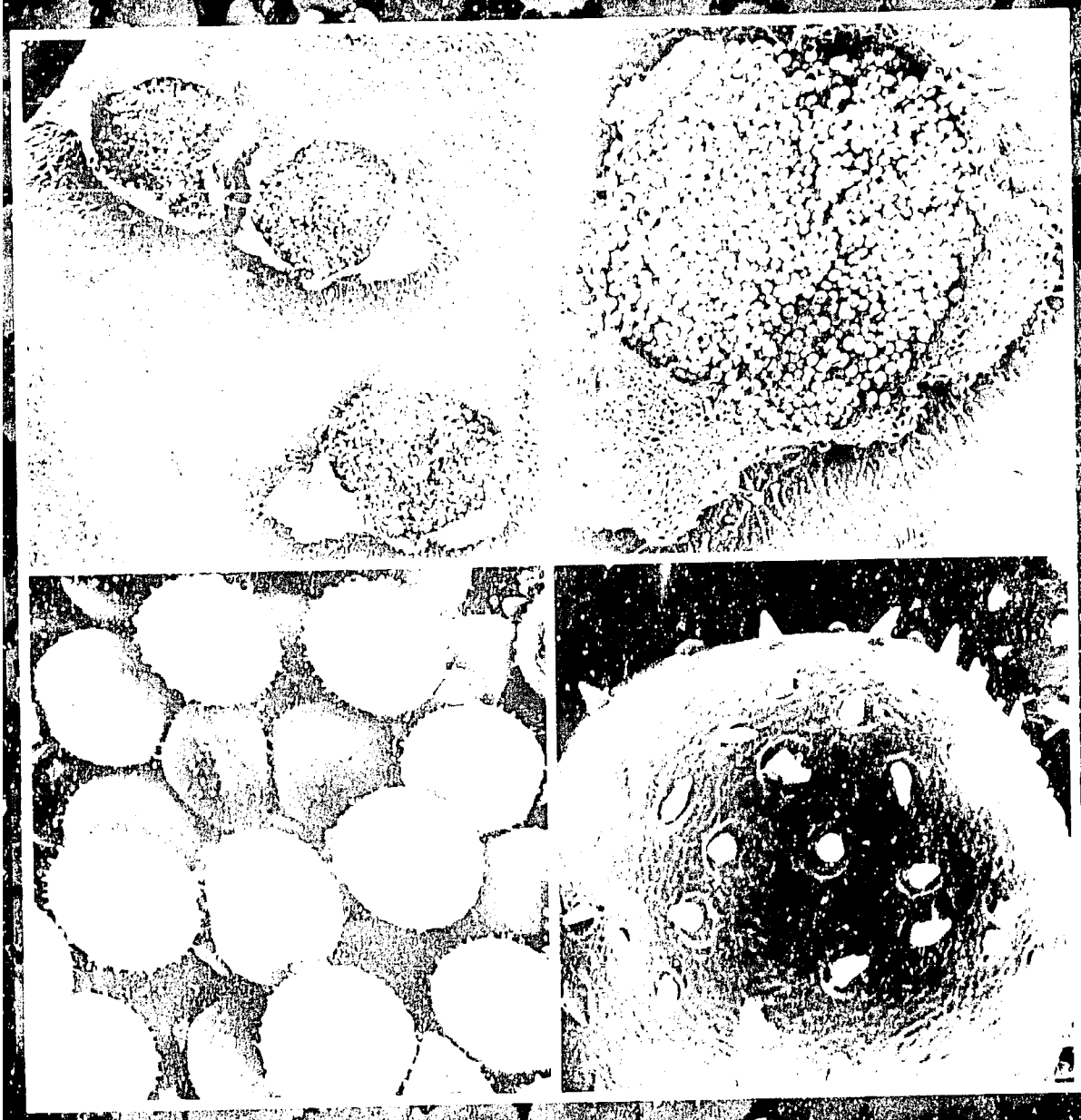
Groundnut Rust Disease



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Cover photo: Scanning electron micrographs of groundnut rust (*Puccinia arachis* Speg.) uridiniospores magnified × 72, × 172, × 1800, and × 9000

Groundnut Rust Disease

Proceedings of a Discussion Group Meeting

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Welcome to ICRISAT

C.R. Jackson
Director for International Cooperation,
International Crops Research Institute for the Semi-Arid Tropics.

It gives me great pleasure to welcome you to ICRISAT and to this conference on rust disease of groundnut. When I visited ICRISAT in 1980 I was impressed by the work being done on groundnut problems and, since coming to work here in 1983, I have similarly been impressed by the work on this and the other ICRISAT mandate crops. We are here to discuss groundnut rust, and I consider this to be both timely and appropriate. In comparison with leaf-spot diseases, very little is known about groundnut rust. A few years ago I tried to assemble the world literature on this subject and found it to be limited, the disease being regarded as a curiosity confined to the Caribbean and South America. I distinctly remember Ray Hammons, who is in our group today, going out to his groundnut plots in Georgia to see this "curiosity" of groundnut rust that had presumably been carried to our North American crop by the violent winds from the Caribbean.

While rust is still regarded as a visitor to the USA, it is no longer a curiosity there, and it is now established in Asia, Australia, and Africa. The spread around the world of groundnut rust in the past two decades has taken place despite quarantine precautions and care in the exchange of germplasm. Rapid air travel may have assisted the natural spread of the rust on winds and by storms. Irrespective of how it was spread, we now have to live with it. Groundnut rust is now an important disease in many countries of the world and therefore has high priority in our ICRISAT research program.

Our research has been carried out mainly at ICRISAT Center, but we also have established a program for groundnut research in southern Africa that is based in Malawi, and hope to initiate a similar unit in West Africa in the near future. We would like to establish a network of scientists concerned with research on groundnut rust throughout the world, and hope that you will consider yourselves as part of this group with interest in rust, and indeed, in other diseases of groundnut. I hope that you will give a great deal of thought to the groundnut rust problem over the next few days and that in the concluding session on Friday you will jointly determine the direction of the research on the disease at ICRISAT, and perhaps how your own research as cooperators should proceed.

I wish you every success in your deliberations.

Research on Groundnut Rust at ICRISAT

Origin, Distribution, and Taxonomy of *Arachis* and Sources of Resistance to Groundnut Rust (*Puccinia arachidis* Speg.)

V. Ramanatha Rao[1]

Abstract

The natural occurrence of the genus Arachis *is limited to five countries, i.e., Argentina, Bolivia, Brazil, Paraguay, and Uruguay. The headwaters of the Paraguay river in the region of Mato Grosso is considered to be the center of origin of the genus. The taxonomy of the genus is not well delineated and the grouping of species into seven sections is only tentative; there may be as many as 70 species in the genus* Arachis. *The cultivated groundnut,* Arachis hypogaea *L., originated in an area of southern Bolivia and northwestern Argentina on the eastern slopes of the Andes. This species is subdivided into subspecies and botanical varieties that have been found to have a specific geographic distribution in South America. Groundnut rust, caused by* Puccinia arachidis *Speg., is one of the major diseases of groundnut. It probably originated in South America and evolved along with the host species.*

Most of the 39 groundnut accessions identified as rust-resistant at ICRISAT belong to the ribbed valencia type and originated in Peru. So it is concluded that resistance to rust in the cultivated groundnut may have also originated in Peru. Hence there is a need for pointed collection in Peru to enrich and broaden the available gene pool. Wild Arachis *species belonging to different sections have been found to be either resistant or immune to rust. Efforts are under way to utilize such resistance for groundnut improvement. Observations in the native habitat have indicated that wild* Arachis *might be infected by rust and other diseases to a greater extent than expected. More research is required in South America to investigate possible pathogenic variation and resistance to rust in wild* Arachis *species.*

Résumé

Origine, distribution et taxonomie du genre Arachis et sources de résistance à la rouille de l'arachide (Puccinia arachidis Speg.) : *Le genre* Arachis *sous forme de végétation naturelle n'existe que dans cinq pays du monde : Argentine, Bolivie, Brésil, Paraguay et Uruguay. Le centre d'origine du genre serait dans la région de Mato Grosso où se trouve la source du fleuve Paraguay. La taxonomie du genre n'est pas bien délimitée; le groupement de ses quelques 70 espèces en sept sections étant encore provisoire. L'arachide cultivée,* Arachis hypogaea *L., est originaire de la zone recouvrant le sud de la Bolivie et le nord-est de l'Argentine sur le versant est des Andes.* A. hypogaea *est divisée en sous espèces et variétés botaniques ayant une distribution géographique spécifique en Amérique du Sud. La rouille de l'arachide due à* Puccinia arachidis *Speg. est une maladie importante attaquant cette culture. Elle serait également originaire de l'Amérique du Sud où elle a évolué avec sa plante-hôte.*

La plupart des 39 accessions ayant montré une résistance à la rouille appartiennent au type Valencia strié en provenance du Pérou. D'où la conclusion que la résistance à la rouille serait également originaire du Pérou. Il faut donc lancer un programme de collection bien défini au Pérou, en vue d'améliorer et d'élargir le pool génique existant. Certaines espèces sauvages d' Arachis *appartenant à différentes sections ont fait preuve d'une résistance ou même une immunité à la rouille. Les travaux en cours tentent d'incorporer cette résistance afin d'améliorer la culture d'arachide. L'étude de son habitat naturel indique que l'* Arachis

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sauvage serait plus exposé à l'attaque de la rouille et d'autres maladies qu'on aurait supposé. Des recherches approfondies effectuées en Amérique du Sud sont indispensables pour étudier la variation éventuelle du pathogène ainsi que la résistance à la rouille chez les espèces sauvages d' Arachis.

The Genus *Arachis*

Origin and distribution

The natural occurrence of the genus *Arachis* is confined to that area of South America that is bounded by the Amazon river to the north, the la Plata river to the south, the Atlantic to the east, and by the foothills of the Andes to the west (Krapovickas 1969, Gregory et al. 1980) (Fig. 1a and b). However, plant explorations have yet to be made in many areas, and the distribution of the genus may eventually be found to be much wider (Simpson 1982, Valls 1983, Valls et al. 1985).

The geocarpic habit has largely determined the evolution of the genus. The aerially fruited genera of the subtribe *Stylosanthineae* are more widely distributed than *Arachis* (Gregory et al. 1973). Specific and supraspecific differentiation in *Arachis* follows the drainage basins and river beds of the continent, while the greatest diversity occurs in the headwaters of the Paraguay river in the region of Mato Grosso, Brazil. This region is considered to be the center of origin of the genus, the oldest forms occurring on the highlands of the Brazilian shield (Gregory et al. 1980).

The natural occurrence of *Arachis* species is restricted to Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Species belonging to all sections of the genus *Arachis* occur in Brazil, and four sections, *Ambinervosae*, *Caulorhizae*, *Extranervosae*, and *Triseminalae*, are known to occur only in Brazil.

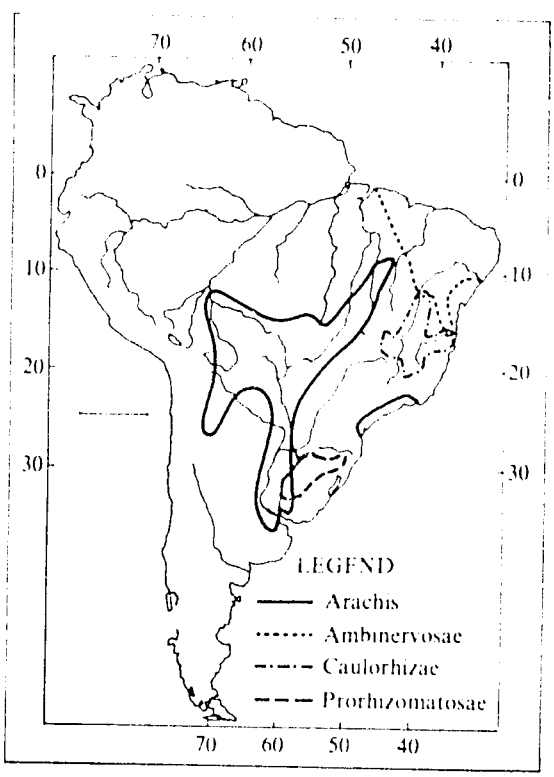

Figure 1a. Geographic distribution of *Arachis* in South America (group a) (after Valls et al. 1985).

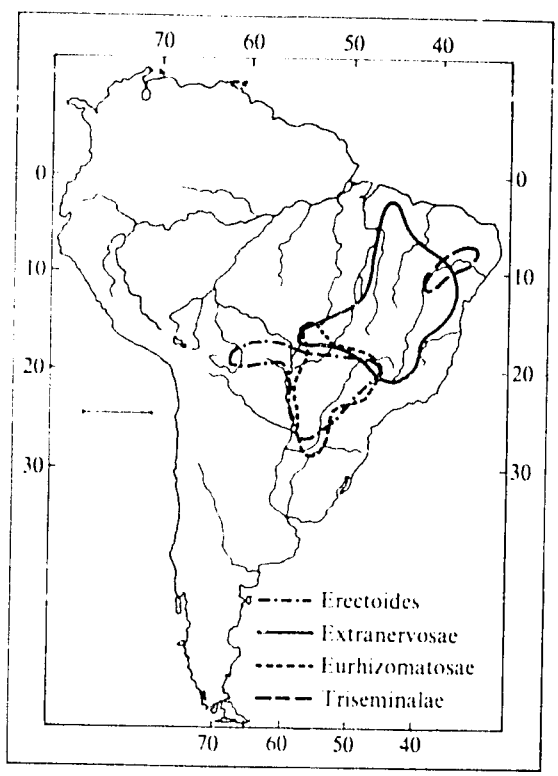

Figure 1b. Geographic distribution of *Arachis* in South America (group b) (after Valls et al. 1985).

Species in sections *Arachis* and *Rhizomatosae* occur in all five countries, but section *Erectoides* is not known to occur in Uruguay (Valls et al. 1985).

Taxonomy

Arachis hypogaea was first described as a species by Linnaeus (1753). Bentham (1841) associated *Arachis* for the first time with the genera *Stylosanthes* and *Chapmannia* in the tribe *Hedysareae* of the family *Leguminosae*. Taubert (1894) separated the tribe *Hedysareae* into six subtribes and *Arachis* was placed in the subtribe *Stylosanthineae*. Three genera of the subtribe *Stylosanthineae* i.e., *Chapmannia*, *Stylosanthes*, and *Arachis* have a distinct tubular hypanthium, pinnate leaves and a straight embryo. The genus *Arachis* differs from *Stylosanthes* and *Chapmannia* by having a geocarpic peg, an underground fruiting habit, and by producing most of its flowers at the lower nodes (Taubert 1894, Barkart 1939, Hoehne 1940). *Arachis* is now placed in the tribe *Aeschynomeneae* (Benth.) Hutch., formerly considered to be one of the subtribes of *Hedysareae* (Rudd 1981). The taxonomy of the genus is not well delineated and new and unidentified taxa are regularly reported.

The wild species show marked interspecific variation for various morphological features. Both annual and perennial forms occur and in some cases this character is difficult to ascertain. The genus is further subdivided into sections and series (Krapovickas 1969, 1973, Gregory et al. 1973), which are however, invalid according to the International Code of Botanical Nomenclature (Resslar 1980). Nevertheless, the section and series groupings have been used extensively in the literature and most groundnut workers are familiar with this system of grouping. The key (Table 1) to the seven sections in the genus *Arachis* is a tentative attempt to highlight certain morphological characters that have been used in the subdivision of the genus into sections and series. Before 1839 only one species of *Arachis* was described: the cultivated groundnut, *Arachis hypogaea*. Bentham (1841) described five species, and Chevalier (1934-35) recognized six. In the early taxonomic treatments by Chevalier (1934-35), Hoehne (1940), and Hermann (1954), only the above-ground parts were considered. Gregory et al. (1973) and Krapovickas (1973) recognized and emphasized the importance of underground parts of stem, root, and reproductive structures in the classification of *Arachis*. At present, there are 22 described species assigned informally to groups (sections and series) based on morphological structures and the cross-compatibility and fertility of hybrids (Table 2). Apart from validly published names, 12 specific names have been used in the literature (Resslar 1980). The use of invalid *Arachis* epithets has created much confusion. Therefore, until authentic descriptions of various species become available, it is convenient to refer to the genotypes accessions by their collector numbers. These, as well as more recently collected species, are expected to be formally described in the near future. The genus *Arachis* is likely to have 70 species (A. Krapovickas, IBONE, personal communication 1984). This number may be exceeded as more collections are made in South America.

Arachis hypogaea L.

Origin and distribution

The center of origin of the cultivated groundnut, *Arachis hypogaea*, has been discussed many times. Brazil was considered to be the center of origin by Bentham (1859). Mendes (1947) believed that the groundnut originated in the state of Mato Grosso, Brazil, which is generally recognized as a major center of diversity for the genus. However, Krapovickas (1969), who collected extensively in South America, postulated that *A. hypogaea* probably originated in Bolivia and northwest Argentina on the eastern slopes of the Andes. This area is a very important center of variation for *A. hypogaea* subsp *hypogaea*. *A. monticola*, another tetraploid species in section *Arachis*, also occurs in this region. *A. monticola*, which is fully cross-compatible with *A. hypogaea*, can be considered to be the closest wild relative of the cultivated form. This species resembles the cultivated greundnut closely and differs mainly in characters such as catenate pods (the segments of fruit are separated by a length of isthmus), and longer pegs, which enable it to survive in the wild. Krapovickas (1969) also considered ethnobotanical evidence, such as the diversity of the uses of groundnut in this region. Cardenas (1969) supported the Bolivian origin of groundnut and an independent origin in Brazil is unlikely (Gregory et al. 1981). In addition, six secondary centers of diversity are recognized, and a brief description of the genocenters is given below, following Krapovickas (1969) and Gregory et al. (1973).

Table 1. Key to sections/series of *Arachis* L. (after Krapovickas 1973, Gregory et al. 1973, Smartt and Stalker 1982, and A. Krapovickas, IBONE,—personal communication).

1 Plant with rhizomes	Section *Rhizomatosae* Krap. et Greg. *nom. nud.*
2 Rhizomes shallow; 2n = 2x = 20	Series *Prorhizomatosae* Krap. et Greg. *nom. nud.*
2′ Rhizomes thickened, deep; 2n = 2x = 40	Series *Eurhizomatosae* Krap. et Greg. *nom. nud.*
1′ Plants without rhizomes	
3 Plants mostly trifoliolate	Section *Trierectoides* Krap. *nom. nud* (= Ser. *Trifoliolatae* Krap. et Greg. *nom. nud.* under sect. *Erectoides* Krap. et Greg. *nom. nud.*)
3′ Plants mostly tetrafoliate	
4 Pegs almost vertical	
5 Tap-rooted; pegs without any roots	
6 Rooting at nodes common; mostly with hollow stems	Section *Caulorhizae* Krap. et Greg. *nom. nud.*
6′ Without any rooting at nodes; mostly with solid stems	
7 Red or purple markings on both the faces of the standard; 2n = 2x = 20	Section *Ambinervosae* Krap. et Greg. *nom. nud*
7′ Without any prominent markings on the back of the standard	Section *Arachis nom. nud.*
8 Plants annual or perennial; 2n = 2x = 20	
9 Usually annual; flowers smaller	Series *Annuae* Krap. et Greg. *nom. nud.*
9′ Usually perennial, flowers larger	Series *Perennes* Krap. et Greg. *nom. nud.*
8′ Plants annual or less than annual, short-lived, 2n = 2x = 40	Series *Amphiploides* Krap. et Greg. *nom. nud.*
5′ Commonly adventitious roots thickened; pegs usually with roots, red or purple color markings on the back of the standard	Section *Extranervosae* Krap. et Greg. *nom. nud.*
4′ Pegs almost horizontal	
10 Usually with prominent purple color markings on the front face of the standard; flowers small; fruits often 3 segmented	Section *Triseminalae* Krap. et. Greg. *nom. nud.*
10′ No purple markings on the front face of the standard, flowers larger	
11 Plants prostrate; tap-rooted, without any root thickenings	Section *Procumbensae* Krap. et. Greg. *nom. nud.* (= Ser. *Procumbensae* Krap. et Greg. *nom. nud.* under sect. *Erectoides* Krap. et. Greg. *nom. nud.*)
11′ Plants prostrate or erect, tap root thickened or not; sometimes with tuberiform hypocotyl	Section *Tetraerectoides* Krap. et. Greg. *nom. nud.* (= Ser. *Tetrafoliolatae* Krap. et Greg. *nom. nud.* under sect. *Erectoides* Krap. et Greg. *nom. nud.*)

1. The Guarani region

This region includes a large part of the river basins of Paraguay and Parana (bordering northeastern Argentina, eastern Paraguay, and southern Mato Grosso and western Sao Paulo in Brazil), probably extending up to Rio Grande de Sul, Brazil. This region is rich in subsp *fastigiata*; var *fastigiata* forms are more common than var *vulagaris* forms. A few subsp *hypogaea* forms also occur. There could have been some introgression within the subsp *fastigiata*, since some intermediate forms have been found. Both valencia and spanish forms could have evolved in this region.

Table 2. Valid *Arachis* epithets[1].

Section[2]	Series	Species ploidy level	Author citation
Arachis Annuae	*A. batizocoi* Krap. et Greg.	20	in Krapovickas et al. 1974
Perennes	*A. villosa* Benth.	20	Bentham 1841
	A. diogoi Hoehne	20	Hoehne 1919
	A. helodes Mart. ex Krap. et Rig.	20	Krapovickas and Rigoni 1957
Amphiploides	*A. hypogaea* L.	40	Linnaeus 1753
	A. monticola Krap. et Rig.	40	Krapovickas and Rigoni 1957
Caulorhizae	*A. repens* Handro	20	Handro 1958
Erectoides Trifoliolatae	*A. tuberosa* Benth	20	Bentham 1841
	A. guaranitica Chod. et Hassl.	20	Chodat and Hassler 1904
Tetrafoliolatae	*A. paraguariensis* Chod. et Hassl.	20	Chodat and Hassler 1904
	A. benthamii Handro	20	Handro 1958
	A. martii Handro	20	Handro 1958
Procumbensae	*A. rigonii* Krap. et Greg.	20	Krapovickas and Gregory 1960
Extranervosae	*A. prostrata* Benth.	20	Bentham 1841
	A. marginata Gard.	20	Gardner 1842
	A. villosulicarpa Hoehne	20	Heohne 1944
	A. lutescens Krap. et Rig.	20	Krapovickas and Rigoni 1957
Rhizomatosae			
Prorhizomatosae	*A. burkartii* Handro	20	Handro 1958
Eurhizomatosae	*A. glabrata* Benth.	40	Bentham 1841
	A. hagenbeckii Harms.	40	in Kuntze 1898
Triseminalae	*A. pusilla* Benth.	20	Bentham 1841

1. After Krapovickas 1973, Gregory et al. 1973
2. No species have been described in section *Ambinervosae*, though germplasm is available.

2. Southeastern Brazil (Goias and Minas Gerais)

This includes the river basins of Tocantins and São Franscisco. A predominance of subsp *fastigiata* forms was observed with an increasing frequency of spanish types.

3. West Brazil (Rondonia and northeastern Mato Grosso)

This region still needs to be explored properly. The so-called *A. nambyquarae*, which is now considered a form of *hypogaea* with variegated seed coat, and a few *fastigiata* forms with yellow seed coat, occur in this region. *A. villosulicarpa*, a diploid wild species with fairly large fruits, was found to be cultivated by natives of Juruena and Diamantino (Hoehne 1944, C.E. Simpson, personal communication 1985).

4. Bolivia (Eastern slopes of the Andes)

Var *hypogaea* forms predominate here, featuring extensive variability for various morphological characters. A few valencias have been found, and even fewer spanish forms. In this region, a great range of ecologically distinct groundnut-growing areas have been found at altitudes of up to 2000 m. There may have been significant introgression between subsp *hypogaea* and subsp *fastigiata* in this area.

5. Peru

Mostly primitive valencias (var *fastigiata*), characterized by constricted fruits with prominent beaks and highly reticulated, thick shells, occur in this region. Similar forms were observed in many pre-Columbian archaeological remains in coastal Peru, indicating that this type of groundnut was grown in the ancient agricultural system of Peru. Subsp *hypogaea* (both var *hypogaea* and var *hirsuta*) forms are also found and may still be cultivated on the Pacific coast. A few typical virginia runner forms were also found in this region but they may be later introductions from North America. Spanish (*vulgaris*) landraces have not been recorded.

6. Northeastern Brazil

Considerable variability exists in this region especially in the subsp *fastigiata*. Spanish forms predominate, some of which are typically large-seeded. A few *hypogaea* forms also occur in this region.

The progenitors of *A. hypogaea* are yet to be identified. On the basis of cytogenetic evidence, Husted (1936) suggested that *A. hypogaea* had an amphidiploid origin. Mendes (1947) concluded that it arose through spontaneous chromosome doubling of a diploid form. Krapovickas and Rigoni (1957), and Smartt and Gregory (1967) suggested that the derivation was directly from a wild allotetraploid. However, the wild amphidiploid could also have evolved from a hybrid between annual and perennial species within the section *Arachis* (Gregory and Gregory 1976) and the parents could have been similar to *A. cardenasii* Krap. et Greg. *nom. nud.* and *A. duranensis* Krap. et Greg. *nom. nud.* On the basis of karyotype studies, Smartt et al. (1978) suggested that *A. batizocoi* Krap. et Greg. *nom. nud.* and *A. cardenasii* Krap. et Greg. *nom. nud.* could be the probable ancestors. Singh and Moss (1982) also suggested that *A. cardenasii* Krap. et Greg. *nom. nud.* could be one of the parents for the tetraploid species. However, as Stalker (1980) indicated, many species have still to be collected and more basic information is required before the question of the putative parents of the cultivated groundnut can be resolved.

Though the cultivated groundnut originated in South America, it is now cultivated in many countries across the world, between latitudes 40° N and 40° S. In Peru, groundnut has been cultivated since 3000-2000 B.C. (Johnson 1964, D.J. Banks, OSU, personal communication 1985), but no form of wild *Arachis* has been reported from Peru. Cultivation of groundnut above the subsistence level of agriculture could be attributed only to the then level of civilization (Krapovickas 1969).

Groundnut could have spread to the old world only after the Spanish and Portugese colonization of South America. There is no credible evidence for any pre-Columbian spread of groundnut to Africa or Asia. Africa, where a considerable amount of variation exists, especially for var *hypogaea* types, has been tentatively described as a secondary center of diversity (Gibbons et al. 1972). However, the diversity in African germplasm is much less than that in South American germplasm, and hence it can be only a tertiary center of diversity.

Taxonomy

As in the case of interspecific taxonomy of the genus *Arachis*, intraspecific classification of *A. hypogaea* has received much attention by various workers. Most of the early systems were based on growth habit, presence or absence of dormancy, and maturity (Bouffil 1947). However, later attempts were based on branching pattern and location of fruiting branches. Gregory et al. (1951) presented a comprehensive study in which *A. hypogaea* was divided into two large botanical groups, i.e., virginia and spanish-valencia, on the basis of the branching pattern described by Richter (1894). The presence or absence of reproductive nodes on the main axis and the arrangement of reproductive and vegetative nodes on the laterals (alternate or sequential) were considered the most important criteria in this classification.

The subspecific classification of *A. hypogaea* is given below (after Krapovickas 1969).

A. hypogaea L. subsp *hypogaea* Krapovickas et Rigoni

1. var *hypogaea* Virginia type (western Brazil and Bolivia)

2. var *hirsuta* Kohler (Peru) subsp *fastigiata* Waldron

1. var *fastigiata* Valencia type (Guaranian, southeastern Brazil and Peru)

2. var *vulgaris* Harz Spanish type (Guaranian, southeastern Brazil, and northeast Brazil)

A few attempts have been made to relate the classification of the cultivated groundnut by Bunting (1955, 1958), extended by Smartt (1961), with the taxonomic treatment of Krapovickas and Rigoni (1960) and Krapovickas (1969). Gibbons et al. (1972)

described four cultivar groups in var *hypogaea*, one in var *fastigiata* and three in var *vulgaris*. Each of these cultivar groups was subdivided into a number of cultivar clusters based on various morphological characters such as plant habit, and pod and seed characters. This classification was based on a study of the material available in Africa. From the extent of variation, they considered that Africa was a secondary center of diversity. A somewhat similar classification was given by Verisai Muhammad et al. (1973a,b), in which they classified the available material into 45 different varietal groups. However, these classification systems fail to explain the extent of diversity in much larger collections. Moreover, considering the number of intermediate forms now available in the germplasm collection at ICRISAT, any agronomic classification will be cumbersome and one may end up with too many classes to be of any value.

Sources of Rust Resistance

Groundnut rust (*Puccinia arachidis*) is an important foliar disease causing substantial yield loss to groundnut in many countries (Subrahmanyam and McDonald 1983). Rust, in combination with leaf spots, can cause yield losses exceeding 50% (Gibbons 1980), and losses of over 70% have been recorded at ICRISAT Center (Subrahmanyam et al. 1980a,b and 1984). Although the disease can be controlled by fungicides, this approach is too expensive for many developing countries.

Screening for resistance to rust has been successfully carried out by numerous workers (Mixon et al. 1983). At ICRISAT a large collection of cultivated groundnut and its wild relatives has been assembled by the Genetic Resources Unit (Rao 1980, Rao and Sadasivan 1983). Intensive screening of the available germplasm for all the major groundnut pests and diseases was conducted in order to identify sources of resistance for incorporating genetic resistance into high-yielding cultivars. Screening of germplasm for resistance against rust and late leaf spot was carried out during 1977-84 under natural disease pressure in the field and several sources of resistance to rust and/or late leaf spot have been reported by Subrahmanyam et al. (1980a,b), Subrahmanyam et al. (1983), and Subrahmanyam and McDonald (these proceedings). Cultivated groundnut and wild *Arachis* species accessions with resistance to rust are listed in Tables 3 and 4 with details of their identity, origin, and botanical type.

Resistance in *A. hypogaea*

Out of about 9000 groundnut accessions screened so far, 39 have shown resistance to groundnut rust, but some appear to be duplicates (Hammons, these proceedings). However, various morphological characters indicate that they are not duplicates in the real sense (Reddy et al., these proceedings). Most of the resistant accessions belong to the botanical variety *fastigiata*, while less than 10% belong to var *hypogaea*, and none to var *vulgaris* (Table 3). It is not surprising that var *vulgaris* does not include rust-resistant types since spanish type landraces are not known from Peru (Krapovickas 1969). Among the *hypogaea* resistant types, two accessions from Honduras (ICG 7899 and 7900) originated from a cross with a resistant Tarapoto line (var *fastigiata*) from Peru as per the available germplasm records. These *fastigiata* types differ from normal valencia types in having a thick and highly reticulated shell and pods, which are constricted, prominently ridged and conspicuously beaked. The seeds of most of the resistant accessions are either purple or are variegated with splashes of purple, red, or tan. They generally have a long maturation period. Most of the rust-resistant accessions are poor yielders, and have other undesirable agronomic characters (Subrahmanyam et al. 1980a, Subrahmanyam and McDonald 1983).

The study also revealed that about 90% of the resistant genotypes are landraces from South America, or in some way related to such material, originating from Peru, which is a secondary center of diversity for the subsp *hypogaea* var *fastigiata* (Gregory et al. 1973). The origins of lines ICG 2716 (from Uganda) and ICG 6022 (from Sudan) are uncertain but plant and pod characters suggest that they were introductions from South America, probably from Peru. Even in the large collection at the Instituto Nacional de Tecnologia Agropecuaria (INTA), Manfredi, Argentina, the var *fastigiata* forms with characteristics of the resistant accessions described here come only from Peru, and may be separated taxonomically as var *peruviana* Krap. et Greg. *nom. nud.* (A. Krapovickas, IBONE, Personal communication 1984). So it is logical to assume that most of the rust resistant lines originate from Peru. Of all the cultivated germplasm accessions screened so far, only about 62 originate from Peru; about 50% of these are resistant to rust. The collection data indicate that almost all of these accessions could be traced to the Tarapoto region of Peru. Thus the existing evidence suggests that the resistance to rust in the cultivated groundnut has evolved in or around

Table 3. Rust-resistant cultivated groundnut accessions (after Subrahmanyam et al. 1980a,b).

ICG Number	Identity	Origin	Botanical variety	Seed color	Rust reaction
1697	NC Ac 17090	Peru	*fastigiata*	Light tan	MR
1703	NC Ac 17127	Peru	*fastigiata* stripes	Tan purple	MR
1704	NC Ac 17129	Peru	*fastigiata*	Light tan	MR
1705	NC Ac 17130	Peru	*fastigiata*	Tan	MR
1707	NC Ac 17132	Peru	*fastigiata*	Purple	MR
1710	NC Ac 17135	Peru	*fastigiata*	Purple	MR
1712	NC Ac 17142	Brazil	*fastigiata*	Tan	MR
2716	EC 76446(292)	Uganda[1]	*fastigiata*	Purple	R
3527	USA 63	-	*fastigiata*	Purple	R
3580	C. No 45-22	-	*fastigiata*	Tan	MR
4683	U 4-7-7	-	*fastigiata*	Tan	MR
4746	PI 298115	Israel/USA[2]	*hypogaea*	Off white	MR
4747	PI 259747	Peru	*fastigiata*	Purple	HR
4790	Krap. st.16	Argentina	*fastigiata*	Purple	R
4995	NC Ac 17506	Peru	*fastigiata*	Purple	MR
6022	NC Ac 927	Sudan	*fastigiata*	Purple	MR
6280	NC Ac 17124	Peru	*fastigiata* stripes	Tan purple	MR
6330	PI 270806	Zimbabwe	*fastigiata*	Purple	R
6340	PI 350680	Honduras[3]	*fastigiata*	Purple	R
7013	NC Ac 17133RF[4]	Peru	*fastigiata*	Purple	R
7881	PI 215696	Peru	*fastigiata*	Purple	R
7882	PI 314817	Peru	*fastigiata*	Light tan	R
7883	PI 315608	Israel/USA[2]	*hypogaea*	Purple	MR
7884	PI 341879	Peru	*fastigiata*	Purple	R
7885	PI 381622	Honduras[3]	*fastigiata*	Purple	R
7886	PI 390593	Peru	*fastigiata*	Light tan	R
7887	PI 390595	Peru	*fastigiata*	Purple	R
7888	PI 393516	Peru	*fastigiata*	White red	R
7889	PI 393517	Peru	*fastigiata*	Off white	R
7890	PI 393526	Peru	*hypogaea*	Red	M
7892	PI 393527 B	Peru	*fastigiata* stripes	Tan purple	R
7893	PI 393531	Peru	*fastigiata* stripes	L. tan purple	R
7894	PI 393641	Peru	*fastigiata* stripes	L. tan purple	R
7895	PI 393643	Peru	*fastigiata*	Tan	R
7896	PI 393646	Peru	*fastigiata*	Purple	R
7897	PI 405132	Ecuador-Venezuela[5]	*fastigiata*	Tan	MR
7898	PI 407454	Ecuador[5]	*fastigiata*	Tan	MR
7899	PI 414331	Honduras[6]	*hypogaea*	Tan	R
7900	PI 414332	Honduras[6]	*hypogaea*	Tan	MR

1. Given origins in Uganda and Sudan, respectively, uncertain, may be from Peru due to pod and plant characters.
2. Selection in Israel in material from USA. Exact origin not known.
3. Mazzani, origin not specified; sample source is Honduras.
4. Red flower selection at ICRISAT original population from Peru.
5. Origin uncertain; may be from Peru since it is also known as Tarapoto line.
6. Bred in Honduras, parents Florispan runner × Tarapoto (probably PI 259747 from Peru).

Table 4. Rust-resistant wild *Arachis* species/accessions (Subrahmanyam et al. 1983).

ICG Number	Name	Synonym[2]	Section[3] series[4]	Collection State	Area Country[5]	Rust reaction[6]
8124	*A. batizocoi*	K 9484	AR AN	Corrientes	ARG	I
8123	*A. duranensis*[1]	K 7988	AR AN	Salta	ARG	I
8138	*Arachis* sp	GKP 10038	AR AN	-	ARG	I
8196	*Arachis* sp	GK 30006	AR AN	Mato Grosso	BRA	I
8193	*Arachis* sp	GK 30011	AR AN	Mato Grosso	BRA	I
8216	*A. cardenasii*[1]	GKP 10017	AR PE	Robore	BOL	I
4983	*A. chacoensis*[1]	GKP 10602	AR PE	Puerto Casado	PRY	I
4985	*A. correntina*[1]	GKP 9548	AR PE	Corrientes	ARG	I
8132	*A. correntina*[1]	GKP 9530	AR PE	Corrientes	ARG	I
8134	*A. correntina*[1]	K 7897	AR PE	Corrientes	ARG	I
8140	*A. correntina*[1]	K 9530-1	AR PE	Corrientes	ARG	I
8125	*A. stenosperma*[1]	HLK 408	AR PE	Parana	BRA	HR
8126	*A. stenosperma*[1]	HLK 411	AR PE	Parana	BRA	HR
8137	*A. stenosperma*[1]	HLK 409	AR PE	Parana	BRA	HR
8144	*A. villosa*	PI 210554	AR PE	-	BRA	I
8952	*A. helodes*	GK 30031	AR PE	Mato Grosso	BRA	HR
8918	*Arachis* sp	Manfredi-5	AR PE	-	-	I
8954	*Arachis* sp	GK 30035	AR PE	Mato Grosso	BRA	HR
8130	*A. paraguariensis*	KG 11462	ER TE	Cordillera	PRY	I
8127	*A. appressipila*[1]	GKP 9990	ER PR	Mato Grosso	BRA	I
8128	*A. appressipila*[1]	GKP 9993	ER PR	Mato Grosso	BRA	I
8129	*A. appressipila*[1]	GKP 10002	ER PR	Mato Grosso	BRA	I
8142	*A. villosulicarpa*		EX	-	BRA	I
8149	*A. glabrata*	HLKHe 552	RZ EZ	S Mato Grosso	BRA	I
8150	*A. glabrata*	HLKHe 553	RZ EZ	S Mato Grosso	BRA	I
8153	*A. glabrata*	HLKHe 560	RZ EZ	S Mato Grosso	BRA	I
8155	*A. glabrata*	GKP 9566	RZ EZ	Trinidad	ARG	I
8167	*A. glabrata*	GKP 9806	RZ EZ	S Mato Grosso	BRA	I
8168	*A. glabrata*	GKP 9813	RZ EZ	S Mato Grosso	BRA	I
8902	*A. glabrata*	-	RZ EZ	-	-	I
8908	*A. glabrata*	A 3990	RZ EZ	S Mato Grosso	BRA	I
8933	*A. glabrata*	GKP 9797	RZ EZ	S Mato Grosso	BRA	I
8935	*A. glabrata*	GKP 9827	RZ EZ	S Mato Grosso	BRA	I
8936	*A. glabrata*	GKP 9830	RZ EZ	S Mato Grosso	BRA	I
8941	*A. glabrata*	GKP 9935-p49	RZ EZ	Mato Grosso	BRA	I
8165	*a. glabrata*	GKP 9649	RZ EZ		BRA	I
8170	*A. glabrata*	GKP 9834	RZ EZ	S Mato Grosso	BRA	I
8171	*A. glabrata*	GKP 9882	RZ EZ	S Mato Grosso	BRA	I
8938	*A. glabrata*	GKP 9893(a)	RZ EZ	Mato Grosso	BRA	I
8146	*A. hagenbeckii*	HL 486	RZ EZ	Campinas	BRA	I
8911	*A. hagenbeckii*	A44 11	RZ EZ	-	-	I
8922	*A. hagenbeckii*	HLKO 349	RZ EZ	Corrientes	ARG	I
8145	*Arachis* sp	HLO 333	RZ EZ	Corrientes	ARG	I
8154	*Arachis* sp	K 7934	RZ EZ	Misiones	PRY	I
8156	*Arachis* sp	GKP 9567	RZ EZ	Trinidad	PRY	I
8158	*Arachis* sp	GKP 9580	RZ EZ	Asuncion	PRY	I
8159	*Arachis* sp	GKP 9592	RZ EZ	Asuncion	PRY	I

Continued

Table 4. *Continued.*

ICG Number	Name	Synonym[2]	Section[3] series[4]	Collection State	Area Country[5]	Rust reaction[6]
8160	*Arachis* sp	GKP 9618	RZ FZ	Itobati	PRY	I
8161	*Arachis* sp	GKP 9634	RZ FZ	S Mato Grosso	PRY BRA	I
8162	*Arachis* sp	GKP 9645	RZ FZ	S Mato Grosso	BRA	I
8166	*Arachis* sp	GKP 9667	RZ FZ	S Mato Grosso	BRA	I
8172	*Arachis* sp	1960 No.100	RZ FZ	-	-	I
8916	*Arachis* sp	2A5 301	RZ FZ	-	-	I
8925	*Arachis* sp	GKP 9553	RZ FZ	Corrientes	ARG	I
8929	*Arachis* sp	GKP 9591	RZ FZ	Asuncion	PRY	I
8937	*Arachis* sp	GKP 9893(p1)	RZ FZ	Mato Grosso	BRA	I
8959	*Arachis* sp	GKBSPScZ30085	RZ FZ	Portacheulo	BOL	I
8131	*A. pusilla*	GKP 12922	TR	Bahia	BRA	I

1. *nomina nudum*
2. Collectors: B = Banks, C = Costebal, G = Gregory, H = Hammons, He = Hemsy, K = Krapovickas, L = Langford, O = Ojeda, P = Pietrarelli, S = Simpson, Sc = Schinini, Z = Zarucha
3. Sections: AR = *Arachis*, ER = *Erectoides*, EX = *Extranervosae*, RZ = *Rhizomatosae*, TR = *Triseminalae*
4. Series: AN = *Annuae*, PE = *Perennes*, EE = *Extrafoliolatae*, PR = *Procumbentes*, FZ = *Fabizomatosae*
5. Countries: ARG = Argentina, BOL = Bolivia, BRA = Brazil, PRY = Paraguay.
6. Reaction: HR = highly resistant, I = immunity

Peru and taxonomically such cultivars are probably distinct from other groundnuts.

More recent collections from Peru are arriving at ICRISAT and preliminary observations indicate that some of the accessions have resistance to rust.

Resistance in wild *Arachis* species

Most of the accessions tested in the section *Arachis* were either immune or highly resistant to rust (Table 4). The probable ancestral species, *A. batizocoi nom. nud.*, *A. cardenasii nom. nud.*, and *A. chacoensis nom. nud.* were immune to the disease. However, *A. monticola*, probably the closest relative to *A. hypogaea*, was susceptible. The species from sections *Erectoides*, *Extranervosae*, *Rhizomatosae*, and *Triseminalae* that were tested were immune to rust although the number of accessions tested in sections *Erectoides*, *Extranervosae*, and *Triseminalae* were very few (Subrahmanyam et al. 1983). Several herbarium specimens at CENARGEN EMBRAPA, Brasilia, Brazil were examined by the author and rust pustules were observed on several specimens of species in sections *Arachis*, *Erectoides*, *Extranervosae*, and *Rhizomatosae*. No pustules were observed on specimens belonging to the sections *Ambinervosae*, *Caulorhizae*, and *Triseminalae*. A number of specimens of *A. glabrata* had rust pustules. A similar situation was reported for specimens of *A. glabrata* collected by W.A. Archer and A. Ghert (Bromfield 1971).

Mild to very severe rust symptoms were observed by the author on species belonging to sections *Arachis*, *Erectoides*, and *Rhizomatosae* when on a collection expedition during April 1984 in the state of Matto Grosso do Sul, Brazil. Rust was also observed on a few plants of *A. glabrata* in a screen house.

Very little information is available on the occurrence of pests and diseases of wild *Arachis* in their natural habitats. Observations on herbarium material and on live plants by the author (both on plants in the screen house and on natural populations during collection expeditions) indicate that *Arachis* species may be infected, to a greater degree than expected, by a number of pathogens including rust. Hence it may be necessary to gather more information on such natural occurrence of pathogens and their pathogenicity. Differential reactions were also observed in *A. monticola* (Bromfield and Cevario 1970, Hammons 1977). These differences could be due to variation in the pathogen, host-pathogen-environment interactions, or even to confusion in the identification or to intraspecific variation (Subrahmanyam et al. 1983). As *A. monticola* is highly variable and it is difficult to maintain its genetic identity since it introgresses easily with the cultivated groundnut (Gregory et al. 1973), the variation in rust reaction in this species is probably due to variability in the host. In any case a number of wild

species of *Arachis* are presently available with varying degrees of resistance to groundnut rust.

Conclusions

Much has still to be done to elucidate the origin and taxonomy of the genus *Arachis*. The authentic description of several species is an immediate need. A proper understanding of the taxonomic level of material available is essential for the exploitation of the genus. The origin of *Arachis* was probably in the planaltine region of South America. The cultivated groundnut probably originated in south Bolivia and northwestern Argentina on the eastern slopes of the Andes. More information is needed to understand the intrasectional relationships in *Arachis* and the ancestry of the cultivated groundnut.

Resistance to rust in the cultivated groundnut appears to have originated in Peru. The evidence available indicates that the genes for rust resistance in *A. hypogaea* are nonrandomly distributed in the region of Peru. These sources of rust resistance in *A. hypogaea* are already being exploited at ICRISAT and elsewhere. More recent collections from Peru are presently becoming available at ICRISAT, and preliminary observations in the quarantine nurseries indicate that a number of them may possess rust resistance. Pointed collections should be carried out in Peru and in surrounding areas to find more germplasm having resistance to rust. Such a search may also result in obtaining accessions with yields beyond the postulated yield resistance barrier (Subrahmanyam et al. 1984) as some introgression may have occurred in this secondary center of diversity.

A number of *Arachis* species accessions are immune or highly resistant to groundnut rust. More species accessions, especially in sections other than *Arachis* and *Rhizomatosae*, are presently becoming available and should be screened for rust resistance. Attempts are being made to transfer this character from wild relatives to the cultivated groundnut. Wild species may have different mechanisms of resistance and so provide the possibility of combining rust resistance of wild and cultivated, to give more effective and stable resistance. More input to understand the possible variation in the pathogen, specially in the wild, in South America, is essential. This has significance not only in groundnut improvement, but also in the context of international exchange of germplasm, specially the non- or poor seed producing species that need to be transferred in the form of cuttings or live plants.

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Breeding Groundnut Cultivars Resistant to Rust (*Puccinia arachidis* Speg.)

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Abstract

An array of rust-resistant groundnut breeding lines has been generated at ICRISAT Center, from selection within segregating natural hybrids received from the United States, and from many crosses made between rust-resistant germplasm accessions and agronomically superior but rust-susceptible parents. Advanced breeding lines, with good yield potential, have been entered in national trials in India. The resistant lines are suitable for oil expressing but pod and seed characters need to be improved for their use as confectionery products. Some of the breeding lines also have resistance to other biotic and abiotic stresses. Preliminary studies on the genetics of rust resistance indicate that two or three duplicate recessive genes are involved in conferring resistance. Quantitative data revealed significant additive, additive × additive, and additive × dominant gene effects involved in resistance.

Résumé

Sélection de cultivars d'arachide résistants à la rouille (Puccinia arachidis Speg.) : *Au Centre ICRISAT, en Inde, on a produit une diversité de lignées de sélection résistantes à la rouille à partir d'hybrides naturels en ségrégation provenant des États-Unis et d'un grand nombre de croisements effectués entre des accessions résistantes et des géniteurs sensibles mais à bons caractères agronomiques. Les lignées en sélection avancée ayant un haut potentiel de rendement, ont été inscrites aux essais nationaux en Inde. Les lignées résistantes possèdent de bons caractères pour l'extraction de l'huile, il faut cependant améliorer les caractères de la gousse et des graines avant de les destiner à la confiserie. Certaines lignées de sélection présentent également une résistance à d'autres stress biotiques et abiotiques. Les études préliminaires sur la génétique de la résistance mettent en évidence deux à trois gènes récessifs doubles qui transmettent cette résistance. Les données quantitatives ont révélé des effets additifs significatifs : additif × additif et additif × gène dominant.*

Groundnut rust, caused by the fungus *Puccinia arachidis* Speg., is a serious foliar disease in many groundnut-growing countries (Bromfield 1974, Hammons 1977, Subrahmanyam et al. 1980) causing severe yield losses (Burger 1921, Muller 1950). At ICRISAT Center, rust in conjunction with late leaf spot can cause yield losses of over 70% in susceptible cultivars, while rust disease on its own is capable of causing up to 50% yield loss (Subrahmanyam et al. 1980). In addition to the direct yield losses, rust disease can lower seed quality by reducing seed size (Arthur 1929, South 1912) and oil content (Castellani 1959).

Prior to the establishment of the Groundnut Improvement Program at ICRISAT, a few rust-resistant sources had been reported (Mazzani and Hinojosa 1961, Bromfield and Cevario 1970, Bailey et al. 1973). Extensive field screening of over 9000 accessions from the world collection of groundnut germplasm at ICRISAT Center, where severe rust disease epidemics occur in the rainy season, has resulted in the identification of new sources of resistance and resistant genotypes are currently available (Subrahmanyam et al. 1980; Subrahmanyam and McDonald 1983). In addition, 61 wild *Arachis* species accessions have been screened for rust resistance

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and most of them were found to be immune; 6 being highly resistant and 2 susceptible to the pathogen (Subrahmanyam et al. 1983).

It was considered that the development of disease-resistant cultivars would be the most effective and practical solution for resource-limited peasant farmers in the semi-arid tropics. This paper describes the breeding efforts that are under way in the development of rust-resistant cultivars with special emphasis on agronomic evaluation of resistant sources, breeding methodology, selection procedures, yield levels, and the stability of yield, and resistance of the advanced resistant selections. In addition genetic studies of rust resistance have been initiated.

Evaluation of Rust-resistant Germplasm

As knowledge of the variability available within a given gene pool is a prerequisite for its effective utilization, the 41 germplasm accessions identified as rust-resistant (V.R. Rao, these proceedings) were evaluated in replicated trials for various morphological and agronomic characters including yield and yield attributes. Considerable variation within the rust-resistant germplasm was observed for most of the characters studied (Table 1). Yield trials were conducted at ICRISAT Center in the rainy season when rust disease is severe, and in the postrainy season when it is not. Trials were also conducted at Bhavanisagar where rust is not a serious problem in the rainy season. These trials showed that some of the rust-resistant lines had good yield potential (Table 2). However, they also had some undesirable pod and seed characteristics, including hard shells (which were difficult to open), deep constrictions, and dark purple or variegated seeds.

The choice of the parents in a hybridization program is very important for proper resource utilization, and in an international program where the main goal is to generate broad-based breeding populations it is essential to use diverse parents in the crossing program. Mahalanobis' D^2 analysis and canonical analysis were employed to assess the magnitude of divergence in the rust-resistant germplasm. These analyses, based on 14 different agronomic and morphological characters, resulted in the identification of 5 clusters based on rust resistance. The first

Table 1. Range of variability within the rust-resistant groundnut germplasm.

Character	Range
Plant height (cm)	49.0-20.4
Plant width (cm)	67.0-34.8
No. of primary branches (N+1s)	9.2- 3.1
No. of secondary branches (N+2s)	14.8-0
No. of nodes main stem	23.9-14.9
No. of nodes N+1 branch	22.5-12.9
Pegs/node	2.1- 1.2
No. of pegs/plant	84.8-12.1
Internode length (cm) main stem	2.7- 0.7
Internode length (cm) N+1 branch	5.8- 1.1
Leaf area (cm²)	44.6-21.7
Fresh haulm wt/plant (g)	89.3-30.8
Pod weight/plant (g)	29.5-13.7
No. of mature pods/plant	16.3- 7.2
No. of immature pods/plant	5.3- 0.3
No. of mature seeds/plant	39.0-11.4
No. of immature seeds/plant	10.8- 0.9
Seed weight/plant (g)	17.8- 9.5
Days to 75% flowering	
Rainy season	25-33
Postrainy season	30-42
Pod yields (kg ha⁻¹)	
Rainy season	2580-840
Postrainy season	8139-3694
100-Seed weight (g)	
Rainy season	47.6-22.2
Postrainy season	88.1-41.9
Shelling percentage (Rainy season)	72-45

Table 2. Mean pod yields (kg ha⁻¹) of some germplasm lines resistant to foliar diseases.

Pedigree	ICRISAT Center: Rainy season, 1983	ICRISAT Center: Postrainy season, 1983/84	Bhavanisagar: Postrainy season, 1983/84
PI 407454	2146	8139	2100
Krap.St.16	2583	6514	2800
PI 393531	2115	7194	2233
PI 390593	2229	7361	1667
PI 393646	1958	7208	1908
PI 341879	2031	6389	2300
PI 393641	2094	6271	1983
PI 270806	1938	6174	2150
PI 350680	2323	6000	1916
PI 381622	1917	5694	2167
Robut 33-1 (Sus. cultivar)	1094	4653	1850
J 11 (Sus. cultivar)	990	4639	633
SE	±178	±44	±484
CV %	15	7	25

Table 3. Intra- and intercluster average D^2 values of rust-resistant lines based on Mahalanobis' D^2 analysis and canonical analysis.

	I (33)[1]	II (2)	III (4)	IV (1)	V (1)
I	7.4	12.9	15.5	15.1	13.8
II		5.2	12.8	10.3	10.2
III			9.1	15.3	10.3
IV				0.0	17.1
V					0.0

1 Figures in parentheses refer to number of genotypes representing each cluster.

cluster consisted of 33 genotypes, the second of 2 genotypes, the third of 4 genotypes, and the fourth and fifth clusters of 1 genotype each (Table 3). Although the first cluster consisted of 33 genotypes, the intra-cluster average D^2 value (7.9) was less than that of the third cluster (9.1) consisting of only 4 genotypes. This indicates that cluster III is more variable than cluster I. The inter- and intracluster D^2 values are taken into consideration when selecting parents.

Utilization

Methodology (Fig. 1)

Over 700 single, double, and triple crosses were made using the rust-resistant germplasm lines and high-yielding but susceptible released cultivars from various countries. A wide array of rust-resistant breeding populations were generated and supplied to cooperators. At ICRISAT Center, the F_1s were generally grown at wide spacing in the postrainy season to get maximum seed return. From the F_2 to F_5 generations, the material was grown in the disease nursery using an infector-row method (Subrahmanyam and McDonald, these proceedings). The truncation method of selection for resistance was adopted and plants that received scores of less than 5 on the 9-point disease scale were classified as resistant. Plants with scores of 5 to 6 were classed as moderately resistant, and those with scores greater than 6 as susceptible. The three categories were further subdivided into high-yielding, moderately-yielding, and low-yielding bulks on the basis of an eyeball index. Only the susceptible and low-yielding bulks were rejected in the early generations. In the F_6 generation, sister lines were bulked on the basis of

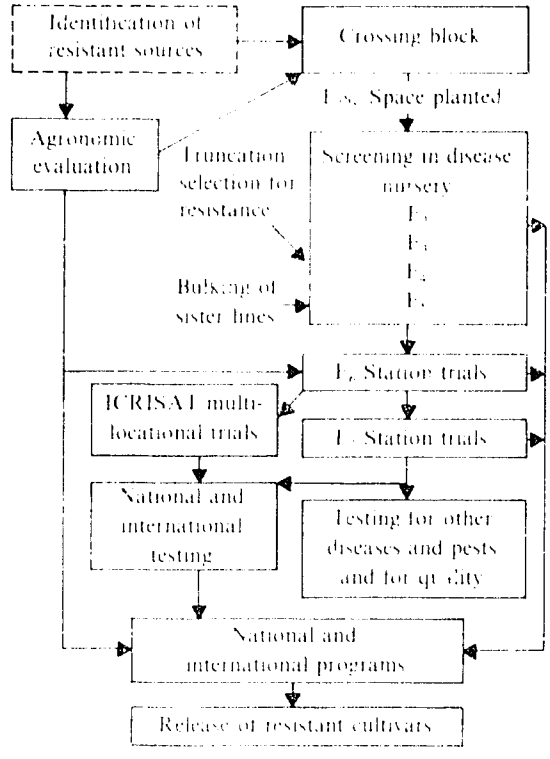

Figure 1. Basic scheme for development of rust-resistant groundnut cultivars.

their levels of resistance, visual yield, pod, and seed characteristics. The F_7 bulks were evaluated at ICRISAT Center under both high-input (60 kg P_2O_5 ha^{-1}; supplemental irrigation and insecticide sprays when required) and low-input (20 kg P_2O_5 ha^{-1}; rainfed and no insecticide sprays) conditions during the rainy season. In the postrainy season the trials were conducted only under high-input conditions.

The stability of yield performance and rust-resistance of the promising lines identified at ICRISAT Center was checked by conducting multilocational tests within India at Bhavanisagar (red gravelly Alfisol; 11° N latitude), Dharwad (Vertisol; 15° N latitude), Anantapur (shallow Alfisols, drought-prone area; 14° N latitude) and Hisar (sandy loam; 29° N latitude). To identify lines with broad adaptability and lines suited to specific agroecological zones, advanced rust-resistant breeding lines are also being extensively tested in India through the All India Coordinated Research Project on Oilseeds (AICORPO).

Most of the rust-resistant advanced breeding lines have also been evaluated for their reaction to other major diseases and pests, and for seed quality.

Progress

Infra- and intrasubspecific hybridization

From crosses involving predominantly valencia-type rust-resistant germplasm and some high-yielding rust-susceptible virginia and spanish cultivars, a large number of high-yielding, rust-resistant lines with commercially acceptable pod and seed characteristics have been bred. Several of these advanced breeding lines outyielded the popular Indian cultivars Robut 33-1 and JL 24 under both high- and low-input conditions (Table 4). In the high input trial in the rainy season some rust-resistant lines such as ICG(FDRS) 29 and ICG(FDRS) 30 produced over 4000 kg ha^{-1} compared to 2890 kg ha^{-1} from the best rust-susceptible check cultivar JL 24. These lines were also superior to JL 24 in the low-input trial (Table 5). Even in the postrainy season when rust disease is negligible, some of the resistant breeding lines yield well (Table 6). A few advanced rust-resistant lines such as ICG(FDRS) 11, 21, 10, 22 and 27 showed consistently higher yields across years and seasons at ICRISAT Center than the rust-susceptible cultivar Robut 33-1 (Table 7).

Table 4. Summary of the rust-resistant advanced groundnut lines yield trials, ICRISAT Center, rainy season 1983.

Trial	No. of resistant selections tested	Number of lines significantly outyielding			
		Robut 33-1		JL 24	
		HI[1]	LI[2]	HI	LI
F_{8}	21	9	3	16	20
F_{9}	35	25	3	14	30
F_{9}	60	52	13	56	57
F_{10}	37	10	6	8	31
F_{10} (Rainfed selections)	15	0	2	4	14
F_{11}	22	7	1	13	13
F_{11} (Rainfed selections)	19	3	6	3	17
Multilocational trial	46	14	1	10	39
FDRVT	17	3	3	9	9
Total	272	123	38	133	227

1. HI = High input (60 kg P_2O_5 ha^{-1} with irrigation and insecticide sprays when necessary) trial.
2. LI = Low input (20 kg P_2O_5 ha^{-1}, rainfed and no insecticide sprays) trial.

Table 5. Pod yields of foliar-diseases resistant advanced lines, ICRISAT Center, rainy season 1983.

Identity	Pod yield (kg ha^{-1})		Rust Score[3]
	HI[1]	LI[2]	
ICG(FDRS) 19	3710	2610	3.3
ICG(FDRS) 20	3800	2540	3.2
ICG(FDRS) 23	3990	2500	3.8
ICG(FDRS) 29	4290	2220	3.3
ICG(FDRS) 30	4260	2050	3.0
Robut 33-1 (Sus. check)	2600	2150	7.8
JL 24 (Sus. check)	2890	1340	8.7
SE	±203	±148	±0.4
CV (%)	12	13	17.6

1. HI = High input trial (60 kg P_2O_5 ha^{-1} with irrigation and insecticide sprays when necessary)
2. LI = Low input trial (20 kg P_2O_5 ha^{-1}, rainfed, and no insecticide sprays).
3. Scored on a 9-point scale; 1 = no disease and 9 = 50 to 100% of foliage destroyed.

Table 6. Pod yields of foliar-diseases resistant lines, ICRISAT Center, postrainy season 1983/84.

Trial	Identity	Yield (kg ha^{-1})	Rust score[1]
F_{11}	(GAUG-1 × EC76446(292)-F11B	8320	3.2
	(JH 60 × PI 259747)-F11B	7890	2.8
	(Ah 8254 × NC Ac 17090)-F11B	7860	3.0
	Robut 33-1	6630	8.7
	SEM	±322	±0.3
	CV (%)	8.4	16.5
F_{9}	(NC.Fla 14 × 17090)-F9B	8150	2.5
	Robut 33-1	6740	6.7
	SEM	±246	±0.4
	CV (%)	6.6	20.5
MLT[2]	(NC Ac 2190 × 17090)-F10B	8330	4.3
	(SM 1 × EC 76446(292)-F11B	8170	4.5
	Robut 33-1	6260	7.0
	SEM	±229	±0.4
	CV (%)	6.3	17.6

1. Scored from 1983 rainy season trials on a 9 point scale; 1 = no disease and 9 = 50 to 100% foliage destroyed.
2. MLT = Multilocational Trial.

Table 7. Pod yields (kg ha^{-1}) of some rust-resistant selections over seasons and years at ICRISAT Center.

Identity	1982 R	1983 R		1983-84 PR	1984 R	
		HI[1]	LI[2]		HI	LI
ICG(FDRS) 11	2680	3010	2560	3640	5850	1080
	(1350)[3]	(2730)	(2250)	(3250)	(4690)	(610)
ICG(FDRS) 21	2260	3530	2310	6720	5990	920
	(1510)	(2600)	(2150)	(6260)	(4690)	(610)
ICG(FDRS) 10	3020	3540	3250	3620	5620	1030
	(1350)	(2730)	(2250)	(3250)	(4690)	(610)
ICG(FDRS) 22	2400	3040	2290	7100	5880	990
	(1350)	(2600)	(2150)	(6260)	(4690)	(610)
ICG(FDRS) 27	2320	3760	1670	6130	5700	970
	(1510)	(2410)	(1010)	(6125)	(4690)	(610)

1 HI = High input trial (60 kg P_2O_5 ha^{-1} with irrigation and insecticide sprays when necessary)
2 LI = Low input trial (20 kg P_2O_5 ha^{-1}, rainfed and no insecticide sprays).
3 Figures in parentheses refer to yields of the susceptible cv Robut 33-1.
R = Rainy season, PR = Postrainy season

Exploitation of natural hybrids

Although natural outcrossing poses problems in maintaining the purity of cultivars, it can also serve as a source of additional genetic variation that can be profitably exploited, especially in a crop such as groundnut where artificial crossing is tedious. Several workers (Hammons 1964, Gibbons 1971, Hildebrand and Smartt, 1980) have indicated the usefulness of natural hybrids in groundnut improvement. Recently at ICRISAT, Nigam et al. (1983) demonstrated the usefulness of natural hybrids in developing high-yielding lines.

In 1973 the United States Department of Agriculture and the Virginia Agricultural Experiment Station released 14 rust-resistant selections made from the progeny of a single natural hybrid between PI 298115 (Israel 136) and an unknown pollen donor (Bailey et al. 1973). These fourteen F_3-derived rust-resistant lines (referred to as FESR lines) were received by ICRISAT in 1977 and their progeny segregated for rust reaction and for some morphological characters. All the lines were progeny-rowed in the next generation when they were again segregated for rust reaction. Several hundred selections were purified and advanced to the F_8 generation by which stage they were fairly uniform and more or less true breeding. Some of these F_7 rust-resistant lines were also found to be highly resistant to late leaf spot (Nigam et al. 1980; Subrahmanyam et al. 1980). While these FESR selections in general were low yielding compared to popular, high-yielding, susceptible, Indian cultivars such as Robut 33-1, they served as excellent parental sources of multiple resistance to rust and late leaf spot. One of the advanced FESR selections, ICG(FDRS) 14, that showed consistently superior yield performance over the check cultivars at ICRISAT Center is currently being tested in several Indian locations by AICORPO.

Mutation breeding

The direct use of mutations is a valuable supplementary approach to plant breeding, particularly when used to improve a few easily identifiable characters in an otherwise well-adapted variety.

The rust-resistant genotype NC Ac 17090 is widely adapted and has good yield potential. However, it possesses the undesirable pod characteristics of thick shells, and long, reticulated pod. In an attempt to eliminate these undesired characteristics NC Ac 17090 was treated with gamma rays (25 kr, 35 kr), ethyl methane sulphonate (0.1% and 0.2%) and nitrosomethyl urea (0.001% and 0.003%). The progenies are currently in the M_3 generation and some useful pod mutants have been identified and are being further evaluated.

Stability of yield performance of rust-resistant lines

To test the stability of yield performance, 40 rust-resistant advanced breeding lines and 6 breeding lines with combined resistance to rust and late leaf spot, were evaluated together with the rust-resistant genotype NC Ac 17090 and 2 rust-susceptible cultivars, JL 24 and Robut 33-1, in 5 environments in India. Sixteen resistant lines gave higher mean yields than the highest-yielding susceptible cultivar Robut 33-1, and 3 lines were better than the resistant parent NC Ac 17090. A stability analysis was carried out according to the method of Eberhart and Russel (1966). Two breeding lines with combined resistance to rust and late leaf spot, (Var 2-5 × PI 259747) F10B and (GAUG-1 × PI 259747) F9B(S2) showed regression coefficients close to unity and nonsignificant deviations (S values) indicating that they are more stable than the adapted susceptible cultivars (Table 8). Similarly several rust-resistant lines showed better stability across the five environments than the susceptible cultivars.

Yield performance of resistant lines in national trials

In India, the rust-resistant breeding lines developed at ICRISAT are being tested extensively in the Foliar Diseases Resistance Varietal Trial (FDRVT) conducted by AICORPO. To date, 38 rust-resistant lines have been entered in these trials. The yield advantage of rust-resistant lines varied from location to location, and the best line, ICG(FDRS) 10, showed a 17% yield advantage over the highest yielding rust-susceptible cultivar JL 24 on the basis of overall mean yield during the 1983 rainy season (Table 9). The AICORPO requires four stages of testing before any cultivar is released for general cultivation. Currently ICG(FDRS) 4 is in the third

Table 8. Stability parameters for yield (kg ha⁻¹) of the rust- and late leaf spot-resistant advanced lines.

Identity	Mean over 5 environments	Regression coefficient	Significance
(HH 335 × NC Ac 17090)F9B	2986	1.51	35179
(HH 171 × NC Ac 17090)F8B	2980	1.42	565929**
(Var 6-29 × PI 259747)F9B	2848	1.58	240261*
(NC Ac 2190 × NC Ac 17090)F8B (S1)	2628	1.07	270742*
(NC Ac 2190 × NC Ac 17090)F8B (S2)	2620	1.25	176366
(Var 2-5 × PI 259747)F10B	2586	0.93	142899
(GAUG-1 × PI 259747)F9B (S2)	2512	0.90	118662
NC Ac 17090 (Resistant check)	2788	1.54	588078**
Robut 33-1 (Susceptible check)	2484	0.64	340360**
JL 24 (Susceptible check)	2350	1.23	639484**

Table 9. Pod yields (kg ha⁻¹) of some rust-resistant lines in the foliar diseases resistance varietal trial, India, rainy season 1983.

Identity	Center						
	Ahyar-nagar	Dharwad	Kadiri	ICRISAT	Tirupati	Vriddha-chalam	Mean
ICG(FDRS) 10	2400	4240	2640	3250	1800	1770	2683
ICG(FDRS) 2	1930	3090	2500	1860	2110	2640	2355
ICG(FDRS) 4	1220	2720	2150	2620	1960	2480	2192
ICG(CG,FDRS) 17	1990	2470	2140	3540	1850	1830	2303
JL 24 (Sus. cultivar)	1800	3080	2810	1840	2040	2140	2285
SE	±232	±394	±123	±189	±83	±46	
Trial mean	1550	2970	2380	2160	1730	1850	
CV (%)	21	20	10	17	0.3	6	

stage of testing in the Peninsular Zone of India. Lines ICG(FDRS) 1, ICG(FDRS) 10 and ICG(FDRS) 23 are in the second stage of evaluation in all six testing zones of India. Another eight lines are in the first stage of testing.

In the Philippines the rust-resistant lines showed from 4 to 36% yield advantage over the local rust-susceptible check cultivar Biyaya in a trial conducted by the San Miguel Corporation. The resistant lines also had larger seed and a higher shelling percentage than Biyaya.

Reaction of rust-resistant lines to other diseases and pests

Several rust-resistant breeding lines were found to have resistance to late leaf spot (incited by *Phaeoisariopsis personata* (Berk. and Curt.) v. Arx). During the 1983 rainy season when the late leaf spot disease was severe, 30 lines showed late leaf spot severity scores of less than 5 on the 9-point disease scale at ICRISAT Center.

Genotype ICG(FDRS)4 showed tolerance to peanut mottle virus: less than 10% yield loss compared to about 40% yield loss in TMV 2, a susceptible check cultivar, when artificially inoculated. Seed of one of the FESR lines supported production of only very low levels of aflatoxin although it was readily colonized by *Aspergillus flavus*. Three FESR lines showed tolerance to termites (Table 10). About 250 rust-resistant breeding lines were evaluated for their resistances to drought, leafhoppers, leafminer, and bud-necrosis disease. Six lines showed tolerance to terminal drought stress in two years of testing (Table 10). Several lines showed good levels of resistance to leafhoppers, bud-necrosis disease, and leafminer. Screening is continuing to confirm these resistances.

Table 10. Some rust-resistant lines with other useful attributes.

Identity	Remarks
ICG(FDRS) 4	Tolerant to peanut mottle virus
FESR 12-P6-B_1-B_1-B_1	Low aflatoxin-producing line
[(G 37 × EC 76446(292))F_2]B	Drought tolerant
(JH 60 × PI 259747)F_2B	Drought tolerant
(M 145 × PI 259747)F_{11}B	Drought tolerant
(JH 335 × NC Ac 17090)F_2B	Drought tolerant
(NC Ac 400 × NC Ac 17090)F_2B	Drought tolerant
(G 37 × NC Ac 17090)F_2B	Drought tolerant
(Ah 8254 × PI 259747)F_{11}B	Resistant to jassids
(Ah 6279 × PI 259747)F_{11}B(S1)	Resistant to jassids
(M 13 × DHU 200)F_2B	Resistant to jassids
(Ah 6279 × PI 259747)F_{11}B(S2)	Resistant to jassids
(GAUG 1 × NC Ac 17090)F_2B	Resistant to jassids
MGS 9 × EC 76446(292)F_2B	Resistant to jassids
MGS 8 × NC Ac 17090 F_2B	Resistant to jassids
Ah 65 × NC Ac 17090 F_2B	Resistant to jassids
FESR 1-P3-B_1-B_1-B_1	Tolerant to termites
FESR 1-P9-B_1-B_1-B_1	Tolerant to termites
FESR 2-P3-B_1-B_1-B_1	Tolerant to termites

Quality aspects of rust-resistant lines

The quality attributes of advanced breeding lines are routinely monitored to ensure that they are not inferior to existing commercial cultivars. The most advanced rust-resistant lines from trials at three different locations in India were analysed for oil and protein contents of seeds. The oil contents of seeds of rust-resistant lines were slightly higher than those of rust-susceptible check cultivars and the protein contents were almost identical (Table 11).

Genetics of rust resistance

Observations in the USA by Bromfield and Bailey (1972) on F_2 plants of a natural cross between a rust-resistant female parent, PI 298115 and an unknown pollen donor indicated digenic inheritance, with resistance being recessive. Further studies on advanced derivatives (F_3 derived FESR families) of the same cross at ICRISAT Center confirmed the recessive nature of the resistance, but continued segregation within the highly-resistant progenies suggested that more than two genes were involved (Nigam et al. 1980). Later studies at ICRISAT on F_2 plants from crosses involving three susceptible and three resistant parents suggested digenic inheritance (15 susceptible : 1 resistant) in some crosses and trigenic inheritance (63 susceptible : 1 resistant) in others (Kishore, 1981). Based on studies of F_2 and F_3 generations from crosses between three resistant and one susceptible cultivar Knauft and Norden (1983) reported the involvement of two recessive duplicate genes in the inheritance of rust resistance. Recent studies at ICRISAT (Nigam, personal communication) have supported this interpretation in some crosses.

Genetic analysis of parents, F_1, F_2, BC_1 and BC_2

Table 11. Oil and protein content of the groundnut entries in the foliar-diseases resistant varietal trial, rainy season 1983.

Genotype	Location							
	ICRISAT		Aliyarnagar		Tirupati		Mean over locations	
	Oil %	Protein %	Oil %	Protein %	Oil %	Protein %	Oil %	Protein %
ICG(FDRS) 1	45.1	23.3	50.6	24.4	46.7	29.0	47.5	25.6
ICG(FDRS) 2	41.1	23.5	46.3	24.5	43.0	29.4	43.5	25.8
ICG(FDRS) 4	45.3	24.9	48.7	25.2	46.6	29.1	46.9	26.4
ICG(FDRS) 5	41.8	23.7	46.1	28.1	46.1	25.6	44.7	25.8
ICG(FDRS) 6	46.5	23.4	47.8	25.3	44.3	30.4	46.2	26.4
ICG(FDRS) 7	45.5	24.3	46.8	28.2	43.2	31.1	45.2	27.9
ICG(FDRS) 8	48.7	22.7	48.2	22.9	46.2	29.0	47.7	24.9
ICG(FDRS) 9	45.9	25.4	49.8	25.0	45.1	33.0	46.9	27.8
ICG(FDRS) 10	46.7	25.1	49.6	26.1	46.8	28.5	47.7	26.6
ICG(FDRS) 11	42.0	22.9	47.1	25.3	43.1	29.9	44.1	26.0
ICG(FDRS) 12	42.9	24.2	47.2	25.1	43.1	31.1	44.4	26.8
ICG(FDRS) 13	40.5	23.3	43.1	26.8	41.8	30.1	41.8	26.7
ICG(FDRS) 14	51.2	24.0	49.7	29.2	48.4	32.4	49.8	28.5
ICG(FDRS) 15	41.7	23.9	48.8	23.4	46.0	29.6	45.5	25.6
ICG(FDRS) 16	45.1	23.4	47.4	23.4	43.6	30.9	45.4	25.9
ICG(FDRS) 17	44.7	26.4	44.7	28.4	46.4	31.9	45.3	28.9
ICG(FDRS) 18	47.6	26.9	47.7	27.2	46.6	31.7	47.3	28.6
J 11	42.2	23.8	48.3	24.5	43.0	30.8	44.5	26.4
JL 24	38.4	30.7	45.0	31.7	44.0	30.8	42.5	31.1
Robut 33-1	39.2	26.1	45.2	24.4	43.2	28.8	42.5	26.4
SE	±0.8	±0.7	±0.7	±0.9	±1.0	±1.7		
CV%	3.6	5.8	2.8	6.8	2.3	5.7		

Table 12. Estimates of various components for rust disease score and percentage leaf-area damage in six crosses of groundnut, by Jinks and Jones' (1958) six-parameter model.

Parameter	Rust score		Leaf area damage		Rust score		Leaf area damage		Rust score		Leaf area damage	
	Gangapuri × NC Ac 17090				Gangapuri × EC 76446(292)				Gangapuri × PI 259747			
m	8.3**	+0.74	83.7**	+ 7.4	6.7**	+0.7	69.5**	+ 6.5	4.2**	+0.7	49.1**	+ 7.2
d	2.4**	+0.05	29.4**	+ 0.3	2.4**	+0.08	24.4**	+ 1.1	2.9**	+0.03	27.0**	+ 0.6
h	1.5	+2.00	14.8	+20.0	2.2	+1.7	23.0	+16.6	9.4**	+1.8	68.8**	+19.8
i	1.7**	+0.74	23.1**	+ 7.5	0.14	+0.6	3.9	+ 6.4	1.8**	+0.7	13.7	+ 7.2
j	0.32	+0.60	8.7	+ 5.9	0.6	+0.5	10.3**	+ 5.0	3.0**	+0.5	15.9**	+ 6.0
l	2.1	+1.28	18.7	+13.1	0.10	+1.0	2.5	+10.3	4.9**	+1.2	13.0**	+13.0
	J 11 × NC Ac 17090				J 11 × EC 76446(292)				J 11 × PI 259747			
m	7.4**	+0.5	71.0**	+ 4.4	8.3**	+0.7	77.8**	+ 8.6	6.9**	+0.6	69.8**	+ 6.6
d	3.1**	+0.07	27.9**	+ 0.8	2.7**	+0.09	32.9**	+ 0.74	2.4**	+0.07	24.7**	+ 1.1
h	1.4	+1.4	24.4	+12.9	0.20	+2.0	7.2	+24.5	3.3**	+1.7	28.2	+18.0
i	-1.5**	+0.5	8.9**	+ 4.3	2.0**	+0.7	20.7**	+ 8.6	0.3	+0.6	4.0	+ 6.5
j	-1.7**	+0.4	15.5**	+ 4.2	2.3**	+0.7	28.0	+ 7.8	-1.4**	+0.5	13.2**	+ 5.8
l	-0.8	+0.9	8.6	+10.4	0.5	+1.42	4.9	+15.9	-1.7	+1.1	8.7	+11.7

generations from three resistant × two susceptible crosses made at ICRISAT, by generation mean analysis, based on the Jinks and Jones (1958) six-parameter model, showed that resistance to rust was predominantly controlled by additive, additive × additive, and additive × dominance gene effects (Table 12). Duplicate epistatis was observed both for rust-disease scores and leaf-area damage. Further studies are required to show conclusively whether rust resistance is governed by two or three major genes or by many genes. Rust resistance in some diploid wild *Arachis* species appears to be partially dominant in nature (Singh et al. 1984), contrary to the observations made in the crosses involving the cultivated groundnut where resistance is recessive. The dominant nature of resistance in the wild species would simplify a backcrossing program.

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Groundnut Rust Disease: Epidemiology and Control

P. Subrahmanyam[1] and D. McDonald[2]

Abstract

Research on rust disease of groundnut at ICRISAT Center from 1976 to 1984 is briefly reviewed. Spread of the disease in India is documented, and the role of continuous cultivation of groundnut in perpetuating the disease emphasized. Data on yield losses from rust are presented. Methods of screening germplasm and breeding lines for resistance to rust are described, and the identified sources of resistance are listed. Components of resistance to rust and their possible use in greenhouse evaluation of rust resistance are discussed. The results of multilocation testing of rust-resistant germplasm lines are considered. The effects of different agronomic systems on epiphytotics of rust are discussed.

Résumé

Rouille de l'arachide—épidémiologie et lutte : *Les auteurs passent en revue les recherches menées sur la rouille de l'arachide au Centre ICRISAT entre 1976 et 1984. L'étude de la progression de la maladie en Inde souligne le rôle de l'exploitation continue de cette culture dans la propagation de la maladie. Les données sur les pertes de rendement dues à la rouille sont présentées. La description des méthodes de criblage des ressources génétiques et des lignées de sélection pour la résistance est suivie d'une liste de sources de résistance repérées. Les caractères intervenant dans le résistance sont examinés ainsi que leur utilisation éventuelle dans les évaluations en serre de la résistance à la rouille. Les résultats des essais multilocaux du matériel génétique résistant sont présentés. Enfin, les effets des différents systèmes agronomiques sur l'épiphytie de la rouille sont étudiés.*

The rust disease of groundnut (*Arachis hypogaea* L.) caused by *Puccinia arachidis* Spegazzini has increased in importance in recent years. Prior to 1969, the disease was largely confined to South and Central America, with occasional outbreaks occurring in the southernmost groundnut producing areas of the USA. The disease was also recorded in the USSR (Jaczewski 1910), Mauritius (Stockdale 1914), and the People's Republic of China (Tai 1937), but did not become permanently established in these countries (Bromfield 1971). In recent years groundnut rust has spread to, and became established in, many countries in Asia, Australasia, Oceania, and Africa (Hammons 1977, Subrahmanyam et al. 1979, and Subrahmanyam and McDonald 1983) (Fig.1). Rust is now of economic importance in almost all groundnut-growing areas of the world. Yield losses from rust are substantial, damage being particularly severe if the crop is also attacked by the two leaf spot fungi (*Cercospora arachidicola* Hori and *Phaeoisariopsis personata* (Berk. & Curt.) v. Arx).

Rust epidemics are regular and severe on susceptible groundnut genotypes at ICRISAT Center. This paper briefly reviews research on the disease carried out in the Groundnut Pathology Subprogram from 1976 to the present time.

Biology of Groundnut Rust

The life cycle and taxonomy of *P. arachidis* are described in detail by Hennen et al. (these Proceedings). Investigations were carried out on the biology

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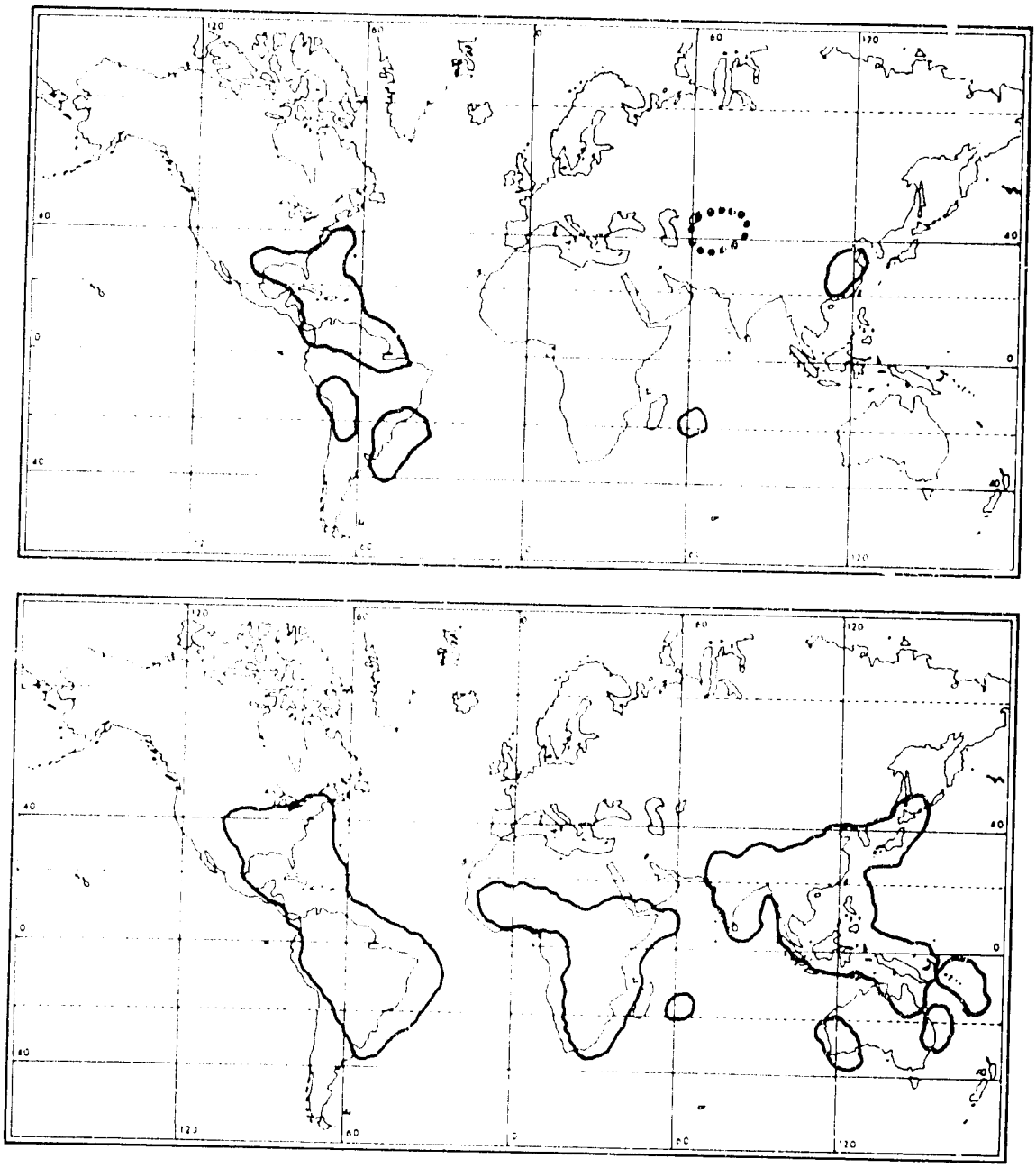

Figure 1. Geographical distribution of *Puccinia arachidis* (top) prior to 1969 (based on Commonwealth Mycological Institute map 16, issued 30 June 1966) and (bottom) in 1983 (based on Commonwealth Mycological Institute map 160, issued 1 Apr 1980).

of *P. arachidis* to determine what factors influenced its perpetuation and spread. Biological data were also needed for the development of resistance-screening methods.

Laboratory experiments showed that urediniospores could be stored for long periods at low temperatures without loss of viability, but that at high temperatures they lost viability within 5 days (Table 1). Temperatures in the range of 20-25° C were optimum for urediniospore germination (Fig.2). Light

Table 1. Effects of storage temperature on viability of urediniospores (from Subrahmanyam and McDonald 1982).

Storage temp (0 C)	Percentage of urediniospores viable after storage (days)										
	5	13	28	40	48	60	70	78	99	110	120
16	88	82	89	90	98	88	92	93	92	94	93
6	84	85	82	38	18	4	0	0			
25	81	88	80	24	0	0	0	0	0		
40	0	0	0	0	0	0	0	0	0		

1 1000 spores per sample Figures to nearest whole number

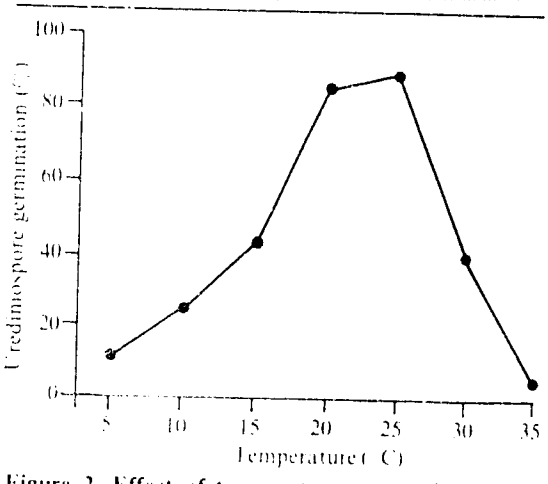

Figure 2. Effect of temperature on urediniospore germination.

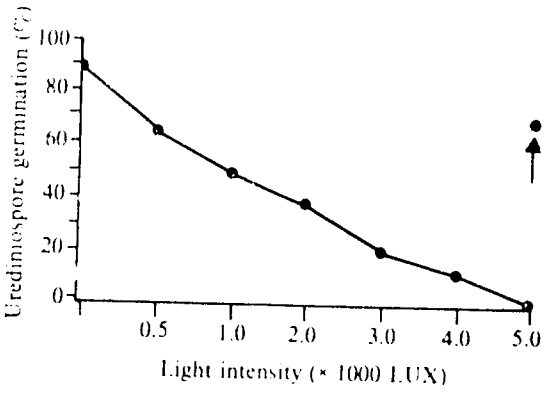

Figure 3. Effect of light intensity on urediniospore germination. Arrow indicates germination percentage of the same spores in dark.

(5000 lux and above) was found to inhibit urediniospore germination (Fig.3). Urediniospores on exposed infected crop debris lost viability within 4 weeks under postharvest conditions at ICRISAT Center (Table 2). Pods and seeds from rust-affected crops are commonly surface contaminated with urediniospores at harvest. Tests on urediniospores taken from surface-contaminated seeds stored at room temperature showed viability to decrease from an initial 95% to zero after 45 days. Inoculation of two-day-old seedlings of a rust-susceptible cultivar grown in petridishes showed that urediniospores

Table 2. Viability of urediniospores after various periods of exposure to weather on infected crop debris (from Subrahmanyam and McDonald 1982).

Period of exposure (days)	Percentage[1] of urediniospores viable			
	Rainy-season crops		Postrainy-season crops	
	1976	1977	1976-77	1977-78
0	65	90	82	89
6	36	74	9	0
14	1	42	1	1
20	0	26	0	0
22	0	10	0	0
26	0	0	0	0
Period of test	13 Dec 1976 to 7 Jan 1977	7 Nov 1977 to 2 Dec 1977	4 May 1977 to 30 May 1977	2 May 1978 to 28 May 1978
RH% 0714 h	80.7	83.5	60.7	60.7
1414 h	26.0	46.6	26.9	23.9
Temp. (°C) Max.	28.3	26.0	37.6	39.7
Min.	13.4	19.5	24.9	25.6

1 1000 spores per sample Figures to nearest whole number

could germinate on the surfaces of hypocotyls and cotyledons but no infection developed. Plants grown in sterilized soil from seeds heavily contaminated with urediniospores, did not become infected with rust disease (Subrahmanyam and McDonald 1982).

There is no record of the occurrence of any collateral hosts of groundnut rust outside the genus *Arachis*. The possible occurrence of other hosts was considered, and various crop and weed plants growing in or near rust affected groundnut crops on the ICRISAT farm and in farmers' fields were examined for rust. Some were also inoculated with urediniospores in the glasshouse. No infection was recorded on any of the plant species examined (Subrahmanyam and McDonald 1982).

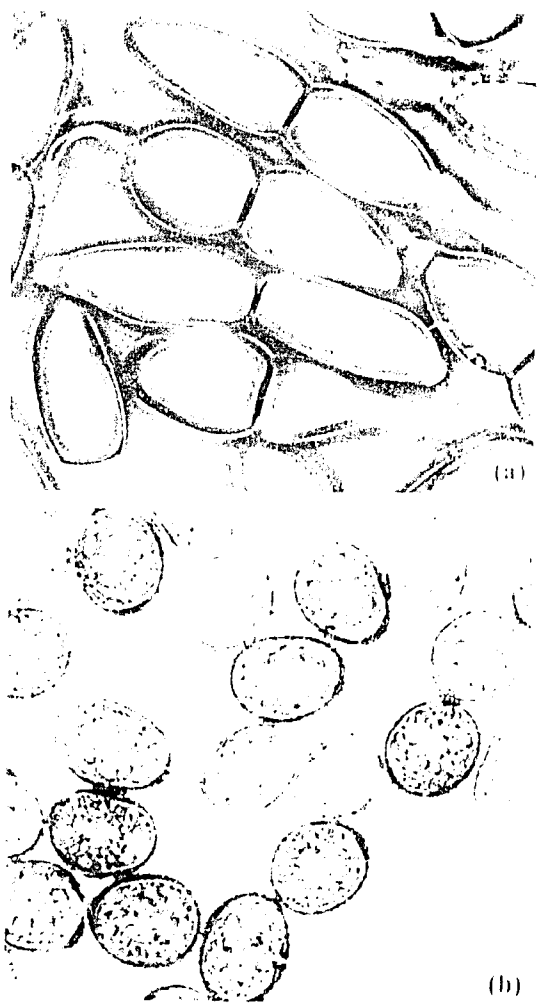

Figure 4. (a) Teliospores (× 800) and (b) Urediniospores (× 800) of *Puccinia arachidis*.

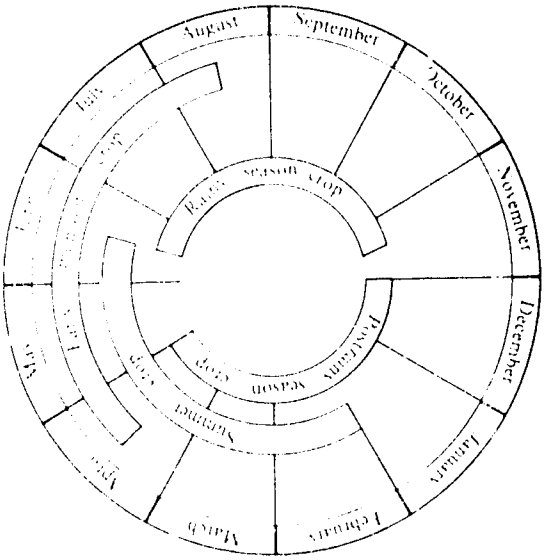

Figure 5. Groundnut cropping seasons in India. Overlapping of these seasons helps to perpetuate rust disease attack.

P. arachidis is known almost exclusively by its uredinial stage. There are a few records of the occurrence of the telial stage on cultivated groundnut (Fig.4(a) and on wild *Arachis* species (Hennen et al. these Proceedings). Only the uredinial stage (Fig.4(b)) of the rust has been found despite constant examination of many groundnut germplasm lines and wild *Arachis* species at ICRISAT and of rust-infected groundnut plants from various parts of India. Attempts to induce telial formation by modification of environmental factors failed. It was concluded that urediniospores were the main, if not the only, means of rust carry-over and dissemination in India. The practice of continuous cultivation of groundnut in southern India (Fig.5) appears to be an important factor in the perpetuation of groundnut rust in the country (Subrahmanyam and McDonald 1982, 1983).

Survey of groundnut rust in India

From 1971 to 1981 surveys were made in all major groundnut-growing states in India to obtain information on rust and other diseases of groundnut, and to assess their relative importance in different regions. Rust and late leaf spot were the most common and severe diseases in all major groundnut-growing areas of India. Rust was particularly serious

in Tamil Nadu, Andhra Pradesh, Karnataka, and Maharashtra States, probably because of extensive and continuous cropping (Subrahmanyam et al. 1979). During the disease survey in Gujarat State in the 1977 rainy season, rust was not observed in the main groundnut-growing tract (Sourashtra region), but a survey in the 1978 rainy season showed rust to be present and causing serious damage to groundnut crops throughout the state. Rust is now a well-established and destructive disease of groundnut in all major groundnut-growing states in India.

Assessment of yield losses

Rust and leaf-spot diseases normally occur together and it is difficult to allocate individual responsibility for the resulting losses in crop yield. During the 1979, 1980, and 1981 rainy seasons, yield losses were estimated by applying selective fungicides on a wide range of susceptible and resistant genotypes; chlorothalonil to control both rust and leaf spots, carbendazim to control only leaf spots, and tridemorph to control only rust. Loss estimates are presented in Table 3. In general, yield losses were less in the resistant than in the susceptible genotypes (Subrahmanyam et al. 1984).

Resistance to groundnut rust

Screening of germplasm

Screening of the world collection of groundnut germplasm for resistance to rust was started at ICRISAT Center in the 1977 rainy season, and a total of 8000 genotypes were screened in the period 1977-83.

Preliminary screening was done on germplasm multiplication material in the rainy seasons. Genotypes were grown in unreplicated, single-row plots. Rows of the cultivars TMV 2, and Robut 33-1, known to be highly susceptible to groundnut rust, were arranged throughout the germplasm fields with 1 to every 10 test genotypes. One week before harvest each genotype was scored for the development of rust using a 9-point scale in which 1 = no disease, and 9 = 50-100% foliage destroyed. Genotypes with scores of 5 or less were selected for advanced screening.

Advanced screening was done in both rainy and postrainy seasons. Genotypes were grown in replicated plots. Test plots were separated by single infector rows of a mixture of the cultivars TMV 2 and Robut 33-1 sown 14 days before the test material. Cultivars TMV 2 and Robut 33-1 were also sown on test plots to monitor disease spread from infector rows. Due to the dry atmosphere, rust development is not usually high during the postrainy season at ICRISAT Center. Therefore, a field-inoculation technique was developed. Infector rows sown as described above were inoculated with a urediniospore suspension at the time of peak flowering. The suspension (50 000–10 000 spores ml^{-1}) was made up in tap water to which a small amount of the wetting agent Tween 80 had been added. Inoculation was done in the evening following furrow irrigation. Potted "spreader plants" heavily infested with rust were placed systematically throughout the field to serve as additional sources of inoculum (Fig. 6). Following inoculation, the fields were irrigated using overhead sprinklers, on alternate days initially, and then as required by climatic conditions until harvest.

The genotypes were scored for rust development just before harvest using the 9-point scale. Genotypes found resistant to rust at ICRISAT Center are listed in Table 4, together with their mean rust scores on the 9-point scale. Some of these genotypes are also resistant to late leaf spot disease (Subrahmanyam et al. 1980 a, 1980 b, 1982, and 1983 a). It is interesting that most of the rust-resistant genotypes listed in Table 4 originated in Peru, which is believed to be one of the secondary "gene centers" of cultivated groundnut (Gregory et al. 1980, Ramanatha Rao these Proceedings).

Pod and haulm yields, and shelling percentages of all resistant genotypes were estimated in almost all the seasons; results of the 1982–83 postrainy and 1983 rainy-season trials are presented in Table 5

Table 3. Yield losses from rust and leaf spots, ICRISAT Center, rainy seasons, 1979, 1980, and 1981.

Genotype	Percentage pod-yield loss[1]		
	Rust	Leaf spots	Rust and leaf spots
Robut 33-1[2]	87	55	68
TMV 2[2]	40	37	58
PI 259747[3]	31	27	29
ICG 7644(292)[3]	12	10	17
NCAc 17090[3]	6	1	26

1. Mean of 1979, 1980, and 1981 rainy-season field trials.
2. Standard susceptible cultivars.
3. Resistant genotypes.

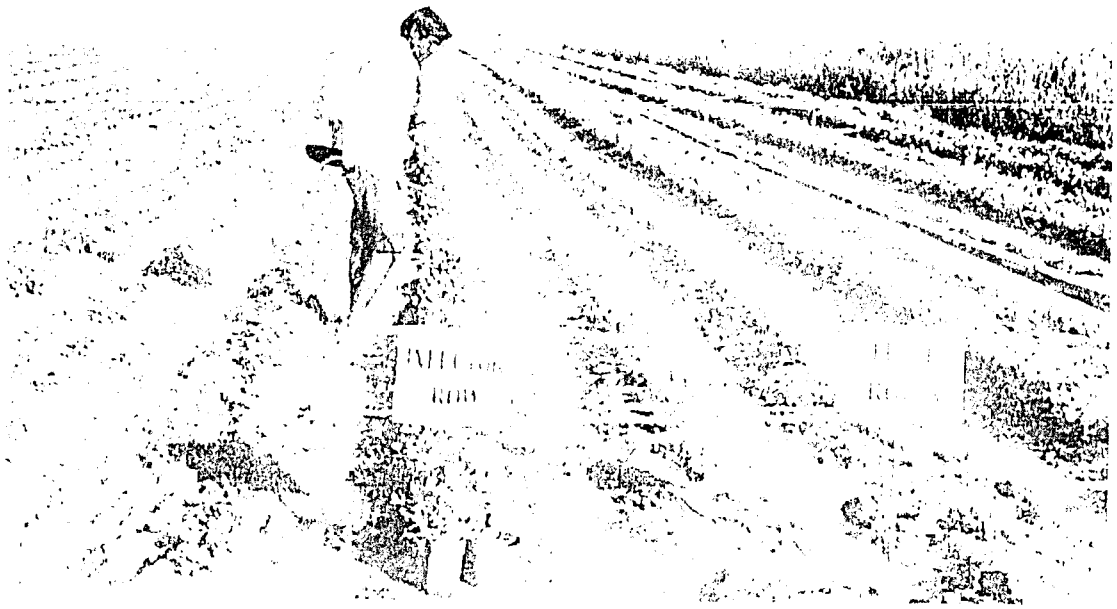

Figure 6. Inoculation of infector rows with urediniospores. Note the potted "Spreader plants" placed in infector rows to serve as additional sources of inoculum.

Table 4. Genotypes resistant to rust at ICRISAT Center.

Genotype	ICG No.[1]	Seed color[2]	Country of origin	Rust score[3]
TMV 2[5]	221	Tan	India	9.0
Robut 33-1[5]	791	Tan	India	9.0
NC Ac 17090	1697	Light tan	Peru	2.2
PI 393646	7896	Purple	Peru	2.5
PI 405142[5]	7897	Purple	Venezuela	2.5
PI 414332	7900	Tan	Honduras	2.5
PI 341879[5]	7884	Purple	Peru	2.6
L4-47-7(LB)	-	Purple	-	2.6
PI 390893	7886	Light tan	Peru	2.7
L4-47-7(MB)	-	Purple	-	2.8
EC 76446(292)[5]	2716	Purple	Uganda	2.9
PI 407484	7898	Tan	Ecuador	2.9
PI 414331	7899	Tan	Honduras	2.9
PI 259747[5]	4747	Purple	Peru	3.0
PI 350686[5]	6340	Purple	Peru	3.0
PI 314817	7882	Light tan	Peru	3.0
PI 315608	7883	Off-white	Israel USA	3.0
PI 381622[5]	7885	Purple	Honduras	3.0
PI 393527-B	7892	Red	Peru	3.0
PI 393643	7895	Light tan	Peru	3.0

Continued.

Table 4. *Continued.*

Genotype	ICG No.[1]	Seed color[2]	Country of origin	Rust score[3]
PI 393517	7889	Off-white	Peru	3.1
USA 63[5]	3527	Purple	USA	3.2
NC Ac 17133-RF[5]	7013	Purple	Peru	3.3
PI 215696[5]	7881	Purple	Peru	3.4
PI 393531	7893	Tan with purple stripes	Peru	3.4
NC Ac 927[5]	6022	Purple	Sudan	3.5
PI 390595[5]	7887	Purple	Peru	3.5
PI 270806[5]	6330	Purple	Zimbabwe	3.7
NC Ac 17132	1707	Purple	Peru	3.9
PI 393641[5]	7894	Light tan with purple stripes	Peru	4.0
NC Ac 17135	1710	Purple	Peru	4.1
PI 393526	7890	Purple	Peru	4.1
NC Ac 17127	1703	Light tan with purple stripes	Peru	4.2
NC Ac 17129	1704	Light tan	Peru	4.2
NC Ac 17130	1705	Tan	Peru	4.2
NC Ac 17124	6280	Tan	Peru	4.2
PI 298115	4746	Off-white	Israel	4.2
PI 393516[5]	7888	White with red blotches	Peru	4.3
Krap.St.16[5]	4790	Purple	Argentina	5.0

1. ICRISAT Groundnut Accession Number.
2. RHS colour chart. The Royal Horticultural Society, London, 1966.
3. Rust scores on a 9-point scale; mean scores of 1977-1983 field trials.
4. Standard susceptible cultivars.
5. Also resistant to late leaf spot (*Phaeoisariopsis personata*) at ICRISAT.

Table 5. Pod and haulm yields and shelling percentages of some groundnut genotypes resistant or susceptible to rust and late leaf spot diseases at ICRISAT Center.

Genotype	1982-83 postrainy season[1]			1983 rainy season[2]		
	Yield (kg ha⁻¹)		Shelling (%)	Yield (kg ha⁻¹)		Shelling (%)
	Pods	Haulms		Pods	Haulms	
TMV 2[3]	4267	5989	71.7	849	914	66.7
J 11[3]	4177	5657	71.5	1098	914	71.3
Robut 33-1[3]	2989	9978	66.2	1012	1062	70.7
JL 24[3]	-	-	-	1117	1012	69.3
M 13[3]	2519	7164	57.8	-	-	-
PI 314817	5610	7104	66.8	1528	1778	69.7
PI 393643	4826	6923	64.0	1547	2049	66.0
PI 393517	4610	7180	61.1	910	1531	65.7
PI 407454	4459	9050	57.8	1547	2074	68.0
PI 393531	4445	6532	58.2	1453	1432	66.7
PI 393527-B	4436	6317	51.3	1242	2074	65.7
PI 390593	4400	7398	56.9	1404	2296	64.3

Continued.

Table 5. *Continued.*

Genotype	1982–83 postrainy season[1]			1983 rainy season[2]		
	Yield (kg ha⁻¹)		Shelling (%)	Yield (kg ha⁻¹)		Shelling (%)
	Pods	Haulms		Pods	Haulms	
NC Ac 17142	4299	7475	64.5	1252	1901	68.3
PI 393646	4225	8614	51.3	1722	1803	62.3
PI 259747	4211	8497	57.2	1333	2543	65.3
NC Ac 17506	4184	8632	56.7	1519	1753	62.3
USA 63	4169	7961	60.4	1610	2099	66.7
PI 403132	4087	7880	57.8	1607	2370	67.7
FC 76446(292)	4037	8510	58.2	1573	2642	69.0
NC Ac 17090	4028	8376	59.6	1668	2000	64.7
NC Ac 17132	3995	7280	55.1	1357	1704	61.0
PI 350686	3953	7913	56.6	1420	2939	66.0
PI 341879	3905	8707	59.6	1437	2469	66.0
C No 45-23	3815	9097	57.1	1116	1358	64.3
NC Ac 17133-RF	3797	8371	55.2	1573	2543	62.7
PI 393526	3777	7916	57.6	607	2296	62.0
PI 393516	3771	8497	56.9	320	2296	53.7
Krap.st 16	3767	9483	55.1	1626	2370	63.7
NC Ac 927	3761	9933	55.5	1778	2469	63.6
RMP 12	3721	8456	61.9	1157	3531	69.7
PI 390595	3712	8329	52.0	1072	1753	62.7
PI 381622	3706	8027	56.0	1746	2840	68.7
RMP 91	3642	7667	61.3	1064	3728	65.7
PI 215696	3542	8825	55.9	1079	2444	65.3
NC Ac 15989	3477	8010	59.7	1382	3210	64.3
PI 414331	3068	10264	57.2	1168	1951	70.4
PI 393641	3054	7084	46.7	1486	1506	63.7
NC Ac 17129	2995	8196	44.3	1364	1333	65.0
NC Ac 17127	2949	7317	43.5	1196	914	64.7
PI 414332	2520	11209	60.0	880	2124	70.3
PI 298115	1982	9120	52.9	1036	1877	65.0
PI 315608	-	-	-	782	1605	66.3
NC Ac 17502	-	-	-	1198	4124	64.7
NC Ac 17135	-	-	-	1888	1975	65.7
PI 270806	-	-	-	1740	2420	64.3
SE	±277.51[4]	±557.20[4]	±1.51[4]	±130.20	±233.12	±1.24
	±279.38[5]		±563.96[5]	±1.54[5]		
CV (%)	9.11[6]	8.50[7]	3.19[8]	17.49	1948	3.26

1. Low disease pressure.
2. High disease pressure.
3. Standard high-yielding check cultivars.
4. Standard error of means for entries appearing in the same block.
5. Standard error of means for entries not appearing in the same block.
6. Efficiency of lattice over RBD is 100.85%.
7. Efficiency of lattice over RBD is 103.53%.
8. Efficiency of lattice over RBD is 112.29%.

Table 6. The FESR (Federal Experiment Research Station Puerto Rico) breeding lines resistant to rust and late leaf spot at ICRISAT Center.

Genotype	Disease scores[1]	
	Rust	Late leaf spot
TMV 2[2]	9.0	9.0
FESR 5-P2-B_1	2.0	3.0
FESR 5-P17-B_1	2.0	3.0
FESR 7-P13-B_1	2.0	3.0
FESR 9-P3-B_1	2.0	3.0
FESR 9-P4-B_1	2.0	4.3
FESR 9-P7-B_1	2.7	3.3
FESR 9-P7-B_2	2.7	4.3
FESR 9-P8-B_1	2.0	3.0
FESR 9-P12-B_1	2.0	2.7
FESR 11-P11-B_1	2.3	2.7
FESR 12-P4-B_1	2.0	2.0
FESR 12-P5-B_1	2.0	2.7
FESR 12-P6-B_1	2.7	3.7
FESR 12-P14-B_1	2.0	3.3
FESR 13-P12-B_1	2.0	2.7

1 On a 9-point scale, where 1 = no disease, and 9 = 50-100% foliage destroyed

2 Standard susceptible cultivar.

together with yields of four disease-susceptible Indian cultivars for comparison. Several of the resistant genotypes outyielded the established Indian cultivars. In addition to the sources of rust resistance listed in Table 4, several other sources of resistance to both rust and late leaf spot diseases have been found in breeding lines from the Federal Experiment Research Station (FESR), Puerto Rico (Table 6). These lines originated from a natural hybrid selected for resistance to rust in Puerto Rico by USDA scientists. Although these lines have low yield potential and poor agronomic characteristics, they are very good sources of resistance to both rust and late leaf spot, and are being used in the breeding program at ICRISAT Center (Nigam et al. 1980).

Screening of breeding populations

Several of the sources of rust resistance listed in Tables 4 and 6 have been extensively used in the breeding program at ICRISAT Center, and crossed with high-yielding but susceptible cultivars (Nigam et al. 1980, Reddy et al. 1984). The F_1 hybrid plants were normally grown in the greenhouse. Subsequent generations were grown in the field and screened for rust resistance using the "infector-row" method. The populations were classified as resistant (2 and 3 on the 9-point scale), moderately resistant (4,5, and 6 on the 9-point scale), and susceptible (7,8 and 9 on the 9-point scale). Selected lines were advanced by pedigree and bulk pedigree methods on the basis of yield and disease reaction (Subrahmanyam et al. 1985, Reddy et al. these Proceedings).

Screening of wild *Arachis* species

Sixty-one accessions of wild species, representing five sections of the genus *Arachis*, were evaluated for reaction to rust during the 1980 and 1981 rainy seasons at ICRISAT Center. They were further tested in the laboratory by inoculation of rooted detached leaves (Fig.7). Most of the species were immune, 6 were highly resistant, and 2 were susceptible (Subrahmanyam et al. 1983 d). The reactions of selected wild *Arachis* species to rust disease are presented in Table 7.

Several diploid wild *Arachis* species resistant to rust and/or late leaf spot were crossed with high-yielding but susceptible groundnut cultivars, and the resulting sterile or fertile tetraploids were treated with colchicine to produce fertile hexaploids. Following field evaluation of hexaploids for disease resistance, promising selections were backcrossed with the cultivated groundnut cultivars to produce

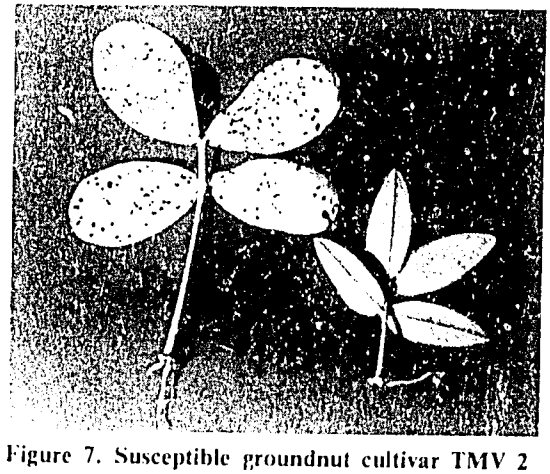

Figure 7. Susceptible groundnut cultivar TMV 2 (left) compared with (right) wild *Arachis* sp with immunity to groundnut rust.

Table 7. Reaction of some wild *Arachis* species to *Puccinia arachidis* (from Subrahmanyam et al. 1983 d).

Section, series and species	USDA plant inventory (PI) number	ICRISAT groundnut accession number (ICG)	Rust reaction
Section: *Arachis*			
Series: *Annuae*			
A. batizocoi	298639	8124	Immune
A. duranensis	219823	8123	Immune
A. spegazzinii	262133	8138	Immune
Series: *Perennes*			
A. correntina	331194	4984	Immune
A. stenosperma	338280	8126	Highly resistant
A. cardenasii	262141	8216	Immune
A. chacoense	276235	4983	Immune
A. villosa	210554	8144	Immune
Section: *Erectoides*			
Series: *Tetrafoliate*			
A. appressipila[1]		8129	Immune
A. paraguariensis[1]		8130	Immune
Section: *Triseminale*			
A. pusilla	338449	8131	Immune
Section: *Extranervosae*			
A. villosulicarpa[1]		8142	Immune
Section: *Rhizomatosae*			
Series: *Eurhizomatosae*			
A. hagenbeckii	338305	8922	Immune
A. glabrata	338261	8149	Immune

1 No PI number allocated because the source was not the USDA.

breeders' lines with 40 chromosomes. These tetraploid, or near-tetraploid, lines were evaluated in field-screening trials for rust and late-leaf spot resistance, using the "infector-row" method, and several lines with rust resistance and high yield were selected (Singh et al. these Proceedings).

Components of rust resistance

In studies of components of resistance to groundnut rust, it was found that neither the size nor the frequency of stomata were correlated with resistance. Urediniospores germinated on leaf surfaces and the fungus entered through stomata irrespective of whether a genotype was immune, resistant or susceptible to rust. However, in immune genotypes the fungus died shortly after entering the substomatal cavity (Subrahmanyam et al. 1980 b). Differences in resistance were associated with differences in rate and extent of mycelial development within the cavity and within leaf tissues. The rust resistance at present available in the cultivated groundnut is of the "slow rusting" type i.e., resistant genotypes have increased incubation period, decreased infection frequency, and reduced pustule size, spore production (Fig.8), and spore germinability (Table 8) (Subrahmanyam et al. 1983 b, 1983 c).

The possible use of the resistance components in greenhouse screening of germplasm has been studied. All the components were significantly correlated with mean field rust scores. Resistant and susceptible genotypes were readily separated on the basis of resistance components measured in the

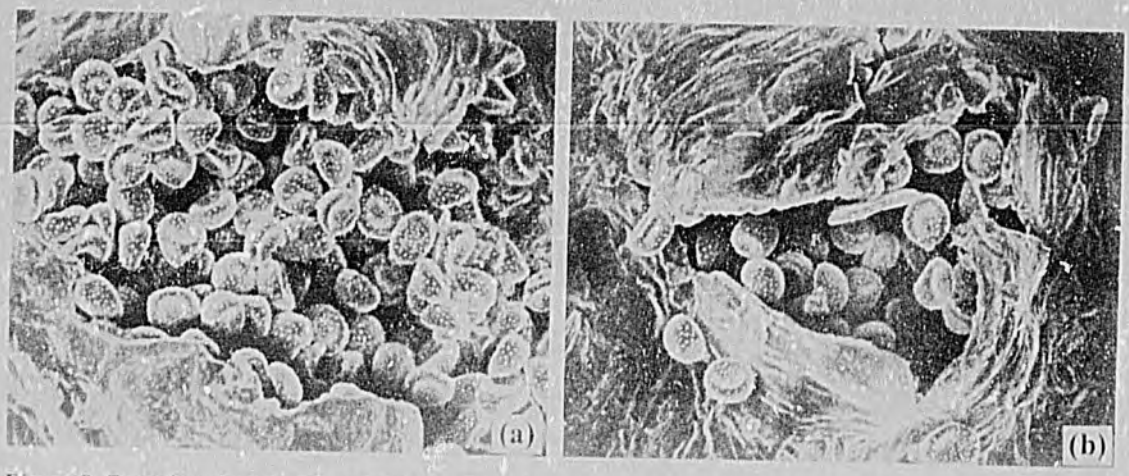

Figure 8. Scanning electron micrographs (× 400) of pustules of *Puccinia arachidis* on (a) the susceptible cultivar TMV 2 and (b) on the resistant genotype NC Ac 17090.

Table 8. Components of resistance to rust in groundnut genotypes (after Subrahmanyam et al. 1983b, 1983c).

Genotype	Rust field score[1]	Incubation period (days)	Infection frequency (lesions cm^{-2})	Pustule diameter (mm)	Pustules ruptured (%)	Spores mm^{-2} pustule area	Urediniospore germination (%)
TMV 2 (Check)	9.0	9.3	13.5	1.12	100.0	855	75.1
NC Ac 17090	2.2	19.3	5.9	0.68	0.5	121	37.2
EC 76446(292)	2.8	17.5	6.2	0.59	13.5	61	48.1
PI 405132	2.4	18.3	8.1	0.63	5.6	127	48.1
PI 407454	2.8	18.5	4.7	0.58	4.7	139	42.6
PI 393643	3.0	14.7	5.5	0.73	9.2	121	43.3

1. Mean rust scores recorded at the ICRISAT Center over the years 1979-82, using a 9-point disease scale, where 1 = no disease, and 9 = 50-100% foliage destroyed.

greenhouse, but classification of moderately resistant genotypes in this way was less effective than by use of field scores (Subrahmanyam et al. 1983b).

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 (Table 9) (Subrahmanyam et al. 1980a).

Stability of rust resistance

The International Groundnut Foliar Diseases Nursery (IGFDN), a cooperative international program, was initiated in 1980. Through the assistance of cooperators in locations throughout the SAT, the

Table 9. Rust reactions of four groundnut genotypes 30 days after inoculation at three physiological stages of development in the greenhouse (after Subrahmanyam et al. 1980).

	Percent leaf area damaged by rust		
	Plant stage at inoculation		
Genotype	Seedling	Peak flowering	Nearing maturity
TMV 2[1]	100.0	85.5	41.1
NC Ac 17090[2]	4.0	6.5	2.8
NC Ac 17129[2]	26.7	38.1	5.9
PI 259747[2]	50.1	30.8	2.9

1. Cultivar susceptible to rust.
2. Cultivar resistant to rust.

IGFDN aims to check under a range of environments the stability of resistance to rust and late leaf-spot diseases of genotypes identified as resistant to these diseases at ICRISAT Center. A collection of 43 resistant and susceptible genotypes identified and/or assembled at ICRISAT was included in the nursery. At present, the nurseries have been located in 8 countries in Asia, 11 in Africa, and 3 in the Americas. In India, nurseries were established at 14 locations through cooperation with the All India Coordinated Research Project on Oilseeds (AICORPO).

The results obtained so far have not been consistent and it is not yet possible to conclude if the rust resistance identified at ICRISAT is stable or not. In many locations the entries were only evaluated under low disease pressure. However, useful data have been obtained from a few locations. It is interesting that the entry NC Ac 17090, which is highly resistant to rust at ICRISAT Center, was found to be only moderately resistant in the People's Republic of China and susceptible in Taiwan. In contrast, the entry PI 298115, which is only moderately resistant to rust at ICRISAT Center, was highly resistant in the People's Republic of China and in Taiwan. Rust isolates from many parts of the world are being tested for pathogenicity to a range of groundnut genotypes by workers in the United Kingdom.

Biological control of groundnut rust

The fungi, *Verticillium lecani* (Zimmerm.) Viegas (Fig.9) *Penicillium islandicum* Sopp., *Eudarluca caricis* (Fr.) O. Ericks, and *Acremonium persicinum* (Nicot) W. Gams have been found growing on *P. arachidis* and their pathogenicity has been confirmed in laboratory inoculation tests. Preliminary investigations on the biological control of rust with *V. lecani* in the laboratory using detached leaves showed considerable reduction in rust development (Table 10).

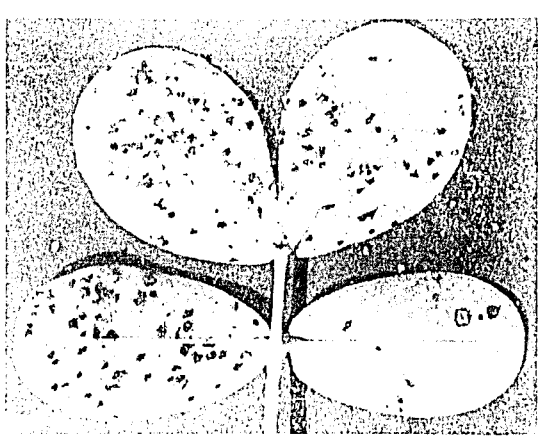

Figure 9. Uredinia of *Puccinia arachidis* parasitized by *Varticillium lecani*.

Table 10. Effect of the hyperparasite *Verticillium lecani* on groundnut rust development on detached leaves.

Inoculation treatment	Rust development assessed by measuring: Infection frequency (lesions cm^{-2})	Leaf area damaged (%)
Rust pathogen alone	12.6	19.9
Rust + hyperparasite (mixture)	7.3	8.6
Premoculation with the hyperparasite	5.3	7.4
SE	±1.27	±1.95
CV (%)	33.7	36.4

Epiphytotics of groundnut rust in different agronomic systems

Many small-scale farmers in the SAT intercrop groundnuts; traditional combinations often involving up to 5 or 6 crops. Although information is available on crop combination, genotype interaction, proportion of each crop in the intercropping system, land equivalent ratio, etc., very little is known of how intercropping affects foliar diseases of groundnut. Trials were carried out at ICRISAT Center during the 1980, 1981, and 1982 rainy seasons to investigate the effect of intercropping groundnut with cereals on the development of rust and leaf-spot diseases. In the 1980 rainy season, there were statistically significant differences in percentage defoliation and percentage leaf area damaged from rust and leaf spots between sole-crop and intercrop systems. Rust and leaf spot severity was higher on groundnut grown as a sole crop than in intercrop situations. Results obtained from the 1981 rainy season were largely in agreement. In the 1982 rainy season there were no significant differences in percentage defolia-

tion or percentage leaf area damaged from leaf spots between sole and intercrop systems, but the percentage leaf area damaged from rust was lower in the intercrop situation.

Investigations on the effects of blending rust and late leaf-spot resistant and susceptible genotypes on the development of these diseases, and on yields were carried out during the 1981-82 postrainy, 1982 rainy, and 1982-83 postrainy seasons. Two trials were conducted in each season, with two sets of resistant and susceptible genotypes physically mixed in different ratios. In general, the resistant genotypes grown in mixed crops showed higher percentage defoliation than those grown as pure crops. There were no significant yield advantages from blending resistant and susceptible genotypes.

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Incorporation of Rust Resistance from Wild *Arachis* Species into the Cultivated Groundnut

A.K. Singh[1], J.P. Moss[2] and B.G. Rao[3]

Abstract

On the basis of genomic relationships in section Arachis *in the genus* Arachis *several cytogenetic manipulations were adopted to aid gene transfer from the diploid wild species (2n = 20) into the cultivated tetraploid* A. hypogaea *(2n = 40). Triploid hybrids were produced between* A. hypogaea *and the eight diploid rust-resistant species of section* Arachis. *Chromosome numbers in these hybrids were doubled to produce hexaploids that were fertile and could be backcrossed with* A. hypogaea. *Some triploids did produce a few seeds and seedlings; these progenies had varying chromosome numbers (2n = 20 to 60) and produced a considerable range of recombinants. Synthetic autotetraploids and amphidiploids were produced from the diploid species. They were then crossed with* A. hypogaea. *This has bridged the ploidy gap between the diploid wild and the tetraploid cultivated species, and increased meiotic recombinations. Backcrossing the resultant hybrids with* A. hypogaea, *with a few intervening selfing generations has produced a large number of* A. hypogaea*-like interspecific derivatives. Screening these derivatives identified segregants incorporating genes from the wild species* A. cardenasii, A. batizocoi, A. duranensis, *and* A. *species GKP 10038 that confer resistance to rust.*

Résumé

Incorporation de la résistance à la rouille dans les arachides cultivées à partir des espèces sauvages d'Arachis : *L'existence de relations génomiques à l'intérieur de la section* Arachis *du genre* Arachis *a permis de faire des manipulations cytogénétiques en vue d'un transfert des gènes à partir des espèces sauvages diploïdes (2n = 20) en tétraploïde cultivé* A. hypogaea *(2n = 40). Des hybrides triploïdes sont obtenus des croisements d'* A. hypogaea *avec les huit espèces résistantes diploïdes de la section* Arachis. *Les nombres chromosomiques chez ces hybrides sont doublés afin d'obtenir des hexaploïdes féconds permettant le rétrocroisement avec* A. hypogaea. *Certains triploïdes ont en effet produit quelques semences et de plantules; ces descendances possèdent des nombres chromosomiques variables (2n = 20 à 60) donnant une large gamme de recombinants. A partir des espèces diploïdes sont obtenus des autotétraploïdes et des amphidiploïdes de synthèse. Leur croisement avec* A. hypogaea *permet de rapprocher, du point de vue génomique, les diploïdes sauvages et les tétraploïdes cultivés tout en augmentant les recombinaisons méiotiques. Le rétrocroisement des hybrides avec* A. hypogaea *en passant par quelques générations autofécondées produit un grand nombre de dérivés interspécifiques d'A. hypogaea. Parmi ces dérivés, on a repéré des ségrégants qui comportent des gènes des espèces sauvages dont* A. cardenasii, A. batizocoi, A. duranensis *et l'espèce GKP 10038 d'*Arachis *responsables de la production de la résistance à la rouille.*

Groundnut (*Arachis hypogaea* L.) rust caused by the fungus *Puccinia arachidis* Speg. often results in yield losses of over 50% (Subrahmanyam et al. 1979). The disease can be controlled with fungicides, but resource-poor groundnut farmers in the semi-arid tropics (SAT) need a groundnut cultivar that has genetic resistance. A wide range of groundnut germplasm, cultivated as well as wild, has been screened

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for resistance to rust and several rust-resistant accessions have been identified (Subrahmanyam et al. 1980, 1982, 1983, 1985).

The cultivated species, *A. hypogaea* (2n=40), has been grouped with a number of cross-compatible wild diploid species (2n=20) in the section *Arachis* (Gregory et al. 1973). All these diploid species have a high degree of resistance to groundnut rust ranging from immunity (no visible symptoms) to hypersensitivity (a few small necrotic non-sporulating pustules or leaflets). These are good sources of rust resistance for use in genetic improvement of *A. hypogaea*.

Ploidy differences between wild and cultivated species in section *Arachis* are barriers to genetic introgression. A basic understanding of genomic structure and interrelationships between the species has helped in the selection of procedures that can overcome these barriers. The present paper reports the progress of work at ICRISAT on the transfer of genes conferring rust resistance from a few diploid wild species into the cultivated tetraploid species using different genomic and ploidy manipulations.

Materials and Methods

The sources and identities of the eight diploid wild species (2n=20) and the cultivars belonging to two subspecies of *A. hypogaea* (2n=40), *A. hypogaea* subspecies *hypogaea* Krap. et Rig. and *A. hypogaea* subspecies *fastigiata* Waldron, all of section *Arachis*, are given in Table 1. Hybridization between the diploid species and cultivars of *A. hypogaea* was done in a screenhouse at ICRISAT Center. The techniques followed for hybridization, cytological analysis, polyploidy induction, and screening against rust in the field and under laboratory conditions have been described earlier (Subrahmanyam et al. 1980, Singh et al. 1983).

Table 1. Sources and taxonomic status of parents used in transfer of rust resistance from wild species.

Species/cultivar	Collector[1]	Coll.No.	ICG No.[2]	Origin
Wild				
A. villosa (Benth)	-	-	8144	Uruguay
A. correntina (Burk.) Krap. et Greg.	GKP	9530	8140	Argentina
A. chacoense Krap. et Greg.	GKP	10602	4983	Argentina
A. cardenasii Krap. et Greg.	GKP	10017	8216	Bolivia
Arachis species	HLK	410	8126	Brazil
Arachis species	GKP	10038	8139	Argentina
A. duranensis Krap. et Greg.	K	7988	8123	Argentina
A. batizocoi Krap. et Greg.	K	9484	8124	Argentina
Cultivated				
A. hypogaea L. ssp *fastigiata* Waldron var *fastigiata* (valencia)				
1. Gangapuri		-	2738	India
A. hypogaea L. ssp *fastigiata* Waldron var vulgaris (spanish)				
2. 99-5		-	1472	Unknown
3. Chico		-	476	USA
4. Tifspan		-	3497	USA
5. 91176		-	4117	India
A. hypogaea L. ssp *hypogaea* Krap. et Rig. var *hypogaea* (virginia)				
6. Robut 33-1		-	799	India
7. M 13		-	156	India
8. Makulu Red		-	6391	Zambia

1. G = Gregory, H = Hammons, K = Krapovickas, L = Langford, P = Pietrarelli.
2. ICG = ICRISAT Groundnut Accession.

Results and Discussion

Transfer of rust resistance

Genome analysis in the section *Arachis* has revealed that *A. hypogaea* is a segmental alloteteraploid with two genomes, "A" and "B", each with base number 10. Among the diploid species there are several species with the "AA" genomic constitution although grouped as "A" genome species, these differ in karyotype and there are genetic differences within "A" genome species (Singh and Moss 1982, 1984a); the "BB" genome is represented by a single species, *A. batizocoi* (Husted, 1936, Smartt et al. 1978, Stalker and Dalmacio 1981, Singh and Moss, 1982). Further studies have revealed that the two genomes "A" and "B" are closely related. *A. hypogaea* forms predominantly bivalents, suppressing A-B intergenomic pairing. However, such a suppression of A-B pairing does not seem to occur at different levels of ploidy in its experimental hybrids with wild species (Smartt and Stalker 1983, Singh and Moss 1984a). Therefore, genetic introgression from wild diploid species of section *Arachis* into *A. hypogaea* is possible provided suitable ploidy and genomic manipulations are adopted.

The cytogenetic manipulations used at ICRISAT to facilitate transfer of rust resistance from wild diploid species into *A. hypogaea* outlined in Figure 1 are discussed below.

Crosses between tetraploid *A. hypogaea* and diploid species

A. hypogaea is freely crossable with these diploid species and direct hybridization between them and *A. hypogaea* for gene transfer is the first logical proposal. Eight rust-resistant wild diploid species were crossed as male parents with cultivars belonging to two subspecies of *A. hypogaea*, and triploid hybrids were established. The hybrids were vigorous, with intermediate leaflet size and a trailing habit, and expressed the dominant morphological features of the wild species; they were also resistant to groundnut rust.

Cytological analysis of these hybrids revealed that the 10 chromosomes contributed by the wild species paired with 10 corresponding chromosomes of the homologous genome of *A. hypogaea* to form 10 bivalents. The 10 chromosomes of the non-homologous genome of *A. hypogaea* predominantly remained unpaired, as univalents. Homoeology of wild species chromosomes with the non-homologous genome of *A. hypogaea* resulted in intergenomic pairing and the formation of more than 10 bivalents, or of multivalents in some pollen mother cells (PMCs) (Singh 1985). Such a pairing behavior indicates that meiotic recombination between wild and cultivated species does occur, but the gametes so formed abort as a result of irregular meiosis caused by high frequency of univalents, thus rendering the triploid hybrids sterile.

Use of amphiploids (hexaploids) of triploid hybrids. Sterile triploids were treated with colchicine to double the chromosome number and restore fertility. This has been the most common method for genetic introgression from wild species and has been adopted by many workers (Smartt and Gregory 1967, Raman 1976, Moss et al. 1981). At Reading University, UK, and at ICRISAT Center, triploid hybrids between all 8 diploid species and *A. hypogaea* were raised to hexaploids. Cytologically, hexaploids formed mostly bivalents (range 19 to 30; mean 21 to 24), but a few multivalent associations (range 0 to 8; mean 1.1 to 2.7) have been observed (Singh 1985) involving the chromosomes of both wild and cultivated species (Spielmann et al. 1979). Consequently, recombinants with desirable traits of wild and cultivated species were formed, though at a very low frequency. They were screened for resistance to foliar diseases under field conditions during the rainy seasons of 1978 and 1979. Segregants resistant to rust and late leaf spot were selected and backcrossed with *A. hypogaea* to reduce their chromosome numbers and regain the agronomic traits of *A. hypogaea*.

Backcrossing of hexaploids with *A. hypogaea* resulted in the production of 32 *A. hypogaea*-like tetraploid derivatives incorporating genes from *A. chacoense*, *A. cardenasii*, and *A.* species HLK 410. These have been screened for resistance to rust under natural field conditions during several rainy seasons, and a large number of resistant segregants have been selected (Table 2).

Use of triploid progenies. Although triploids were reported sterile, they were found to produce some seeds and seedlings (Singh and Moss 1984b). Therefore, useful meiotic recombinations that occur in triploid hybrids are available for utilization. Eighty-two percent of plants in progenies from triploids were hexaploid, 10% aneuploid, and 8% tetraploid. The plants that have either 40, or less than 60, chromosomes are important, because their use redu-

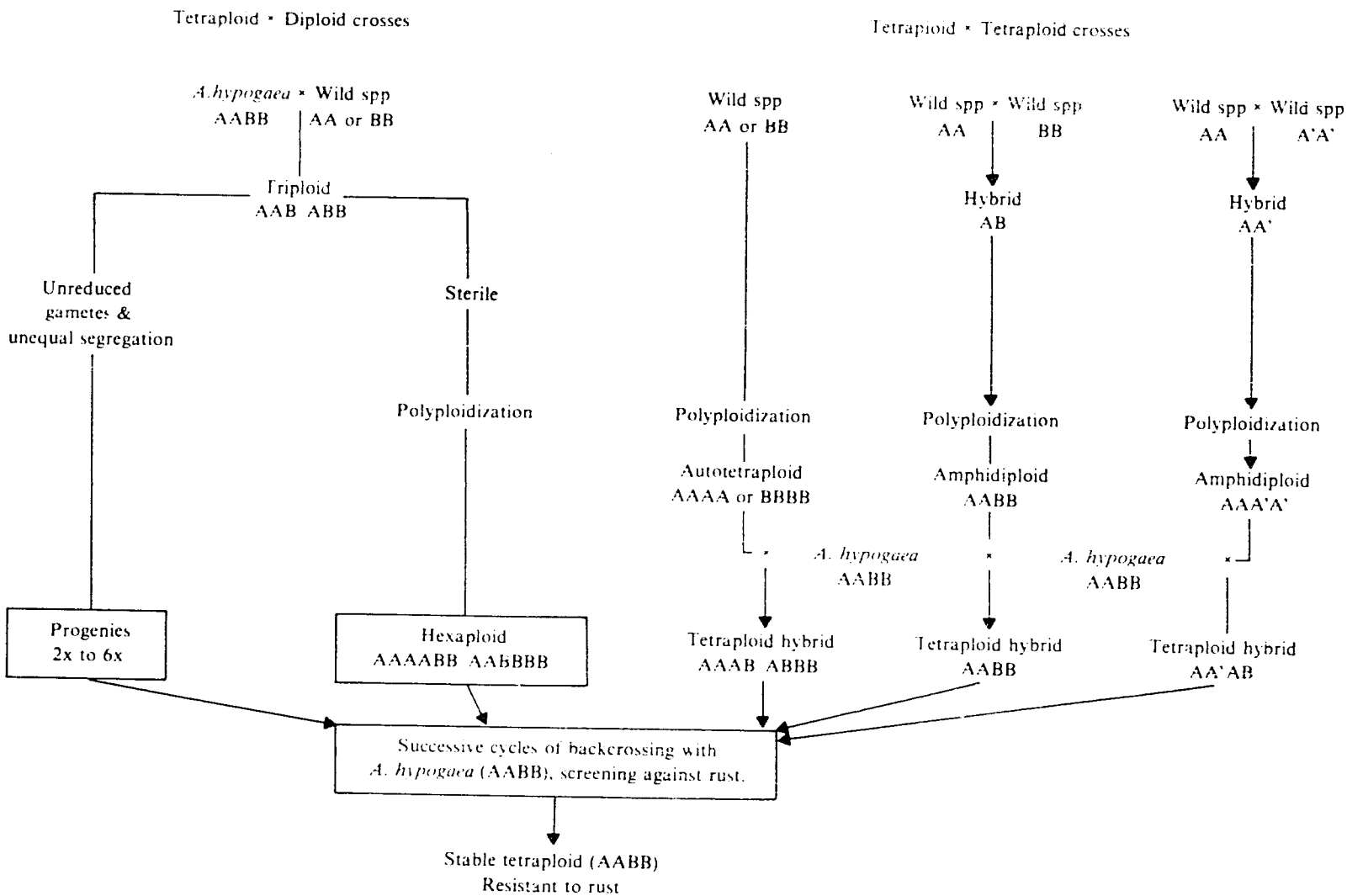

Figure 1. Manipulations for gene transfer in *Arachis*.

Table 2. Number of stable interspecific tetraploid derivatives produced and number of plants selected from their populations for resistance to rust, ICRISAT Center, 1982, 1984.

Route	Species	1982	1983	1984	Total
Self Triploids	*A. cardenasii*	5 (7)[1]	8 (14)	1	14 (21)
	A. chacoense	2		1	3
Hexaploids	*A. cardenasii*	11 (23)	1 (229)	(6)	12 (258)
	A. chacoense	5 (9)	2 (4)	(33)	7 (46)
	A. sp HLK 410	1 (6)	2 (1)	10	13 (7)
Autotetraploids	*A. batizocoi*	2	4 (1)	(2)	6 (3)
	A. correntina		2		2
	A. sp GKP 10038	1			1
	A. sp HLK 410	1			1
	A. villosa	1			1
Amphidiploids	*A. batizocoi* × *A. chacoense*		1		1
	A. batizocoi × *A. correntina*		2		2
	A. batizocoi × *A. duranensis*	1	2 (27)	(484)	3 (511)
	A. correntina × *A. batizocoi*	2	2 (1)	11	15 (1)
	A. correntina × *A. chacoense*		4		4
	A. correntina × (*A. chacoense* × *A. cardenasii*)	1			1
	A. correntina × *A. villosa*	2	2	1	5
	A. duranensis × *A. cardenasii*		1		1
	A. duranensis × *A. chacoense*	1	3 (1)		4 (1)
	A. duranensis × *A.* sp GKP 10038		1		1
	A. villosa × *A. batizocoi*	2	5 (18)	(1)	7 (19)
	A. villosa × *A.* sp HLK 410	2			2
	A. villosa × *A. duranensis*		1	3	4
	A. sp GKP 10038 × *A.* sp HLK 410	1	(1)	16	17 (1)
	A. sp HLK 410 × *A. chacoense*		4		4
	A. sp HLK 410 × *A.* sp GKP 10038		1		1
	Total	41 (45)	48 (297)	43 (526)	132 (868)

1 Figures in parentheses are number of plants selected

ces the number of backcross cycles required for the production of stable *A. hypogaea*-like tetraploid derivatives compared to the number of backcross cycles required from hexaploids.

Backcrossing the progenies from triploids with *A. hypogaea* has resulted in the production of 17 stable *A. hypogaea*-like tetraploids involving *A. chacoense* and *A. cardenasii*. Rust-resistant segregants were selected by field screening of these tetraploid derivatives (Table 2). Certain selections were also found resistant to late leaf spot (*Phaeoisariopsis personata* (Berk. & Curt.) v. Arx.)

The gametic (pollen) fertility of these triploids also indicates that they can be backcrossed with *A. hypogaea* to produce *A. hypogaea*-like tetraploid derivatives, as has been done in wheat (Kerber and Dyck 1973).

Crosses between tetraploid *A. hypogaea* and synthetic tetraploids

The difference in ploidy levels between diploid wild *Arachis* species and tetraploid cultivated *A. hypogaea* restricts sexual genetic introgression, because of the low fertility of the triploid hybrids. Raising the ploidy level of the diploid species to that of *A. hypogaea* and then crossing with *A. hypogaea* at the tetraploid level is a useful option for gene transfer, as in cotton, potato and tobacco (Knight 1953, 1954, Wangenheim 1955, Stavely et al. 1973).

Use of autotetraploids of diploid species. The autotetraploids of diploid species not only facilitate crossing at the same ploidy level as the cultivated species, but also provide an additional dose of the

desired traits and may also permit a forced homoeologous intergenomic (A-B) pairing to effect genetic alteration in the non-homologous genome of *A. hypogaea*.

Autotetraploids of 6 wild diploid species have been crossed with *A. hypogaea*. The F_1 plants were vigorous, and resembled *A. hypogaea*. These hybrids can be either AAAB or ABBB depending on whether an AA or BB species autotetraploid was crossed with *A. hypogaea*. Homology of a genome of *A. hypogaea* with a diploid species can result in the formation of bivalents due to intragenomic (A-A or B-B) pairing. Homoeology with the other genome of *A. hypogaea* results in the formation of more than 10 bivalents (11.2 to 14.1) due to intergenomic (A-B) pairing or multivalents (1.8 to 2.5) due to intra- and intergenomic (A-A-B, A-B-B, A-A-A-B, A-B-B-B) pairing (Singh 1985). The hybrids between *A. hypogaea* and the autotetraploids of section *Arachis* species were resistant to rust (Singh et al. 1984c) and were backcrossed with *A. hypogaea*. Eleven stable *A. hypogaea*-like derivatives have been produced. Of these, six were derived from the hybrids between *A. hypogaea* and autotetraploid *A. batizocoi*. These have been screened during rainy seasons. Several rust-resistant segregants have been selected (Table 2), and are being advanced.

Use of amphidiploids of diploid species. The presence of two homoeologous genomes, "A" and "B", among diploid wild *Arachis* species, and the occurrence of both genomes in *A. hypogaea* suggest that hybridization at the same ploidy level between tetraploid *A. hypogaea* and synthetic amphidiploids of diploid wild species can be a promising approach to provide a high degree of recombination and highly fertile hybrids.

Amphidiploids were produced from sterile or partially sterile interspecific hybrids, representing 34 combinations of the 8 diploid wild species of section *Arachis*. Of these, 22 (AABB and AAAA amphidiploids) have been crossed with *A. hypogaea*. All the F_1 hybrids between *A. hypogaea* and amphidiploids were resistant to rust. The hybrids between *A. hypogaea* and AABB amphidiploids had higher bivalent associations (14.4 to 16.4) and pollen and pod fertility, than the hybrids between *A. hypogaea* and AAAA amphidiploids (10.8 to 15.0). In *A. hypogaea* × AAAA amphidiploid hybrids (AAAB), homoeology between A and B genome results in the formation of more than 10 bivalents and a few multivalents as a result of intra and intergenomic pairing. Subsequent backcrossing with *A. hypogaea*, sometimes with intervening selfing generations, have resulted in the production of 72 stable *A. hypogaea*-like tetraploid progenies. These tetraploid progenies were screened for resistance to rust and late leaf spot during rainy seasons. In derivatives *A. hypogaea* × (*A. batizocoi* × *A. duranensis* amphidiploid) and *A. hypogaea* × (*A. villosa* × *A. batizocoi* amphidiploid) hybrid fertility has enabled the advancement of the progenies into subsequent generations even without backcrossing. Resistant segregants have been selected from these progenies (Table 2).

A large number of *A. hypogaea*-like interspecific derivatives incorporating genes from diploid wild *Arachis* species have been produced that confer a high degree of resistance against rust. The most advanced lines involve a perennial species such as *A. cardenasii*, (resistant to both rust and late leaf spot) and three annual species, *A. batizocoi*, *A.* species GKP 10038, and *A. duranensis* (resistant to rust and some groundnut pests). A number of such lines have been evaluated in replicated trials for agronomic characters and for rust resistance (Table 3). Subsequently several lines resistant to rust and with superior agronomic traits, e.g., ICG(C) 5, ICG(C) 6, ICG(C) 8, and ICG(C) 12, are being tested in India at many locations in the All India Coordinated Research Project for Oil Seeds (AICORPO) trials. In addition, a large number of derivatives involving four other species that are resistant to rust and many other pathogens and pests are being processed.

Genetics of rust resistance

Preliminary investigations on the inheritance of rust resistance derived from diploid wild species have shown that the F_1 hybrids between *A. hypogaea* and diploid species, their autotetraploids, and amphidiploids, are resistant to rust, suggesting that the resistance is governed by a partially dominant factor (Singh et al. 1984c). Identification of the number of loci is in progress. The interspecific stable, tetraploid *A. hypogaea*-like derivatives with resistance from wild species have been crossed with both rust-susceptible and rust-resistant *A. hypogaea* lines. The *A. hypogaea* rust-resistant germplasm lines have also been crossed with susceptible cultivars. These studies should reveal the inheritance pattern of the two resistances and their relationships. These results have generated a great interest in the utilization of wild species as sources of rust resistance and in combining resistance of wild species with that of *A. hypogaea*.

Table 3. Rust resistance (1-9 scale) and other agronomic characters of some of the advanced interspecific derivatives[1] (8 × 8 triple lattice, plot size 10.8 m²), ICRISAT Center, 1984 rainy season.

Code	Pedigree	Rust score	Yield (kg ha⁻¹)	Haulm weight (kg ha⁻¹)	Shelling (%)
CS 36	*A. hypogaea* × *A. cardenasii*	1.4	4470	8690	71
2403	*A. hypogaea* × *A. cardenasii*	1.6	3600	6150	71
2404-4	*A. hypogaea* × *A. cardenasii*	1.6	4770	7150	70
CS 7	*A. hypogaea* × *A. cardenasii*	1.7	4280	8580	75
CS 33	*A. hypogaea* × *A. cardenasii*	1.7	4200	9880	74
2245	*A. hypogaea* × *A. cardenasii*	1.9	4050	7410	69
CS 2	(*A. batizocoi* × *Arachis* sp (GKP 10038) × *A. hypogaea*	1.7	3510	5590	61
CS 19	*A. hypogaea* × (*A. batizocoi* × *Arachis* sp (GKP 10038)	1.7	2730	4840	66
Checks					
Robut 33-1		8.9	2880	7600	54
TMV 2		8.9	2170	4940	40
ICG 76446 (292)		2.8	3620	5840	54
NC Ac 17133-RF		7.2	4410	5000	61
	CV (%)	27	15	18	16
	SE	±0.7	±314.4	±764.7	±2.9

1 All the derivatives are virginia-bunch type

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Physiological Studies on Foliar Diseases: Varietal Differences in Response to Use of Fungicides

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Abstract

*The physiological effects of foliar diseases (*Puccinia arachidis *Speg. causing rust, and* Phaeoisariopsis personata *(Berk. and Curt.) v. Arx., causing late leaf spot) on yield achievement in groundnut have been investigated. The relationship between green leaf area remaining at maturity and yield was linear in most genotypes investigated.*

The yield response to fungicide application (leaf area protection) varied with genotype. Generally, the control of the diseases resulted in small increase in yield in resistant types and larger increases in susceptible types. However, for some resistant genotypes certain fungicides could greatly increase yield without greatly influencing green leaf area. Of the germplasm accessions tested, no line combined resistance to the two diseases with high yield potential. The information so far available points to the existence of a "yield/resistance" barrier.

Résumé

Etudes physiologiques sur les maladies foliaires—différences variétales dans la réponse aux fongicides : *Les effets physiologiques des maladies foliaires, notamment la rouille due à* Puccinia arachidis *Speg. et les taches foliaires dues à* Phaeoisariopsis personata *Berk. et Curt. v. Arx, sont étudiés par rapport aux rendements obtenus chez l'arachide. On constate une relation linéaire entre la superficie foliaire encore verte à maturité et le rendement chez la plupart des génotypes étudiés.*

La réponse en termes de rendement, à l'application de fongicides pour protection de la superficie foliaire, varie selon le génotype. En général, l'augmentation du rendement après traitement de la maladie, est plus importante chez les types sensibles par rapport aux types résistants. Cependant, l'application de certains fongicides entraîne un accroissement considérable du rendement de certains génotypes résistants sans effet significatif sur la superficie foliaire verte. Parmi les accessions sous étude, aucune lignée n'associe une résistance à ces deux maladies à un haut potentiel de rendement. Toutes les données obtenues laissent supposer la présence d'un obstacle "résistance-rendement".

The importance of foliar diseases has long been recognized by groundnut breeders who have also been aware of the existence of resistance to some of them. However, the resistances were apparently associated with low yield potential and little interest was taken in their exploitation. The improved availability of groundnut germplasm and the spread of rust (caused by *Puccinia arachidis* Speg.) to most groundnut-producing areas during the 1970s has led to renewed interest in the utilization of genetic resistances. Many germplasm accessions having appreciable resistance to *P. arachidis* and to the late leaf spot pathogen (*Phaeoisariopsis personata* (Berk. & Curt.) v. Arx), or to both, have now been identified (Subrahmanyam et al. 1980a, 1980b, 1984, Bromfield and Cevario 1970) and utilized in breeding for improved resistance. Aided by pathologists and breeders, the Groundnut Physiology Subprogram at ICRISAT has been investigating the physiology of groundnut genotypes infected with these diseases.

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Relationship Between Remaining Green Leaf and Yield

Using data from fungicide × genotype trials it was found that the relationship between disease severity (1-9 rating) of rust or late leaf spot and the yield achieved was poor. To some extent, this was due to the fact that the research was not dealing with a single disease, so that a genotype resistant to one could be resistant or susceptible to the other. Additionally, the disease scale used to measure the response of a genotype to foliar diseases provided only a visual score of disease on the remaining leaf and is not an accurate measure of the loss of photosynthetic area. The pathologists have shown that defoliation occurs at different severities with different diseases and genotypes.

Leaf area had to be considered if the effects of resistances and foliar fungicides on yield were to be

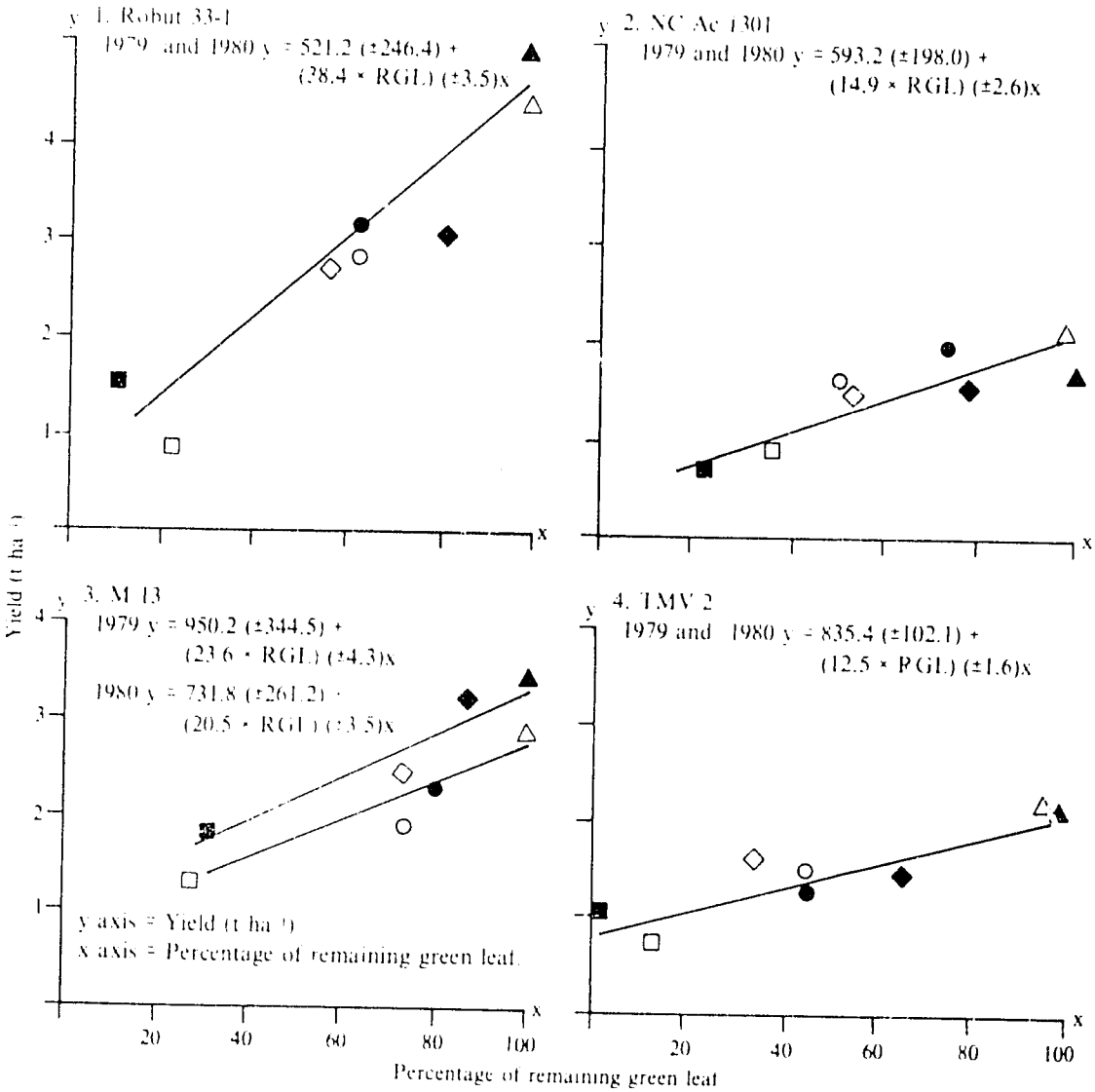

Figure 1. Changes in pod yield and percentage of remaining green leaf in response to sprays with water (1979■; 1980□;), carbendazim (1979●; ;) tridemorph (1979◆; 1980◇;), chlorothalonil (1979▲; 1980△;), for four genotypes with differing disease resistances. Values in parentheses are SEs (Subrahmanyam et al. 1984).

accounted. This was done by combining percentage defoliation (A) and the percentages of leaf area on the remaining leaves damaged by leaf spots (B) and rust (C) at 110 days after sowing. Remaining green leaf (RGL) was estimated by

$$RGL = (100-A)\ [(100-A) + (B+C)\ 100]$$

The yield achieved was linearly related to RGL in most genotypes although the response pattern varied considerably. Four examples are provided in Figure 1.

In the susceptible genotype Robut 33-1 the yield was greatly increased by treatments that increased RGL, but in the equally susceptible genotype TMV 2 the yield response was very much smaller. In resistant lines two types of response were detected. Some genotypes, for example EC 76446 (292), responded only slightly to increased RGL, but the genotype PI 259747 showed a much larger response to fungicides that could not be attributed to changes in RGL since a 15% increase in RGL resulted in a 100% yield increase (Subrahmanyam et al. 1984).

These results show the importance of investigating the response to fungicide applications for individual genotypes. It is clearly erroneous to extrapolate the results of fungicide trials on one genotype to other genotypes.

The results also suggest that the 9-point disease rating system, when used alone, may be a poor indicator of the effect of disease on yield. This occurs because the RGL accounts for a large proportion of the yield variation, and defoliation percentage dominated the RGL. However, RGL also has its limitations because defoliation is not solely attributable to diseases.

Shading in the canopy can also induce defoliation, hence the agronomic environment in which the crop is placed may influence the results. Foliar diseases are more severe, and defoliation greater, in high plant populations than when plants are widely spaced. This must be taken into consideration when assessing foliar diseases. Perhaps the ultimate measurement for relating yield to foliar phenomena will be intercepted radiation and the reflectance of red and green light.

Using these data it was also possible to investigate the association of yield potential (i.e., yield in the absence of stress) with integrated levels of resistance (RGL) to foliar disease. This was done by plotting (for 20 genotypes) the yield in the absence of disease against resistance (RGL) (Fig 2). It was observed

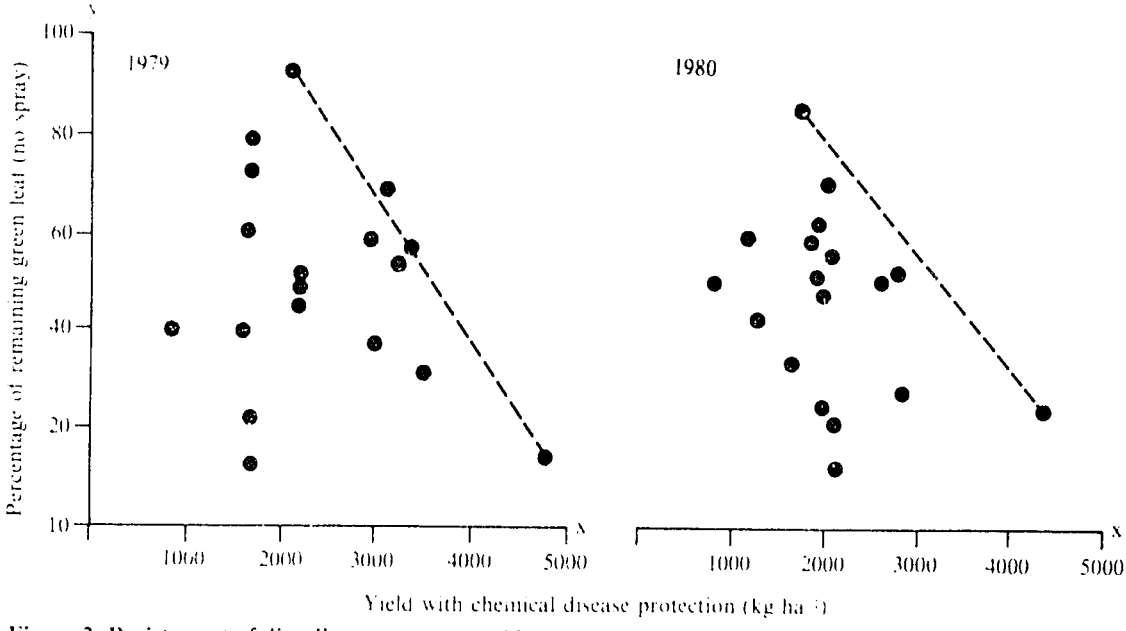

Figure 2. Resistance to foliar disease as measured by percentage of remaining green leaf plotted against yield potential for 20 groundnut cultivars grown at ICRISAT. The most resistant cultivars and the greatest yield potential are joined by the broken line (Subrahmanyam et al. 1984).

that some genotypes had high yield potential but were susceptible to disease (low RGL); others had low yield potentials and were also susceptible. However, those with disease resistance had low yield potentials. None of the genotypes examined combined high yield potential with a high level of resistance.

The physiology of these phenomena is currently being investigated, as is the impact of breeding for foliar disease resistance. In the genotypes initially examined there seems to be a "resistance yield barrier". The implications of this to crop improvement are substantial.

- If selection for resistance is conducted in a disease nursery without simultaneous yield selection, how much of the selected material will have yield potential high enough to increase yield for the farmer?
- If the resistance yield barrier is a physiologically based phenomenon, then the strategies for disease control become complex, since the probability of other yield-limiting factors (such as drought) occurring may determine the emphasis that should be placed on chemical, or genetic control of these diseases. If the resistance yield barrier cannot be overcome, then chemical control would seem to be the best approach where the risk of crop failure from other factors is small and the yield potential of a genotype can be achieved. Where the risk of crop failure is higher it may be more sensible to sacrifice yield potential for the cheaper genetic control of the diseases.

Evidence from other crops and other aspects of groundnut physiology have been assembled to explain the phenomena and speculate on the options that exist if the basic hypothesis is correct. For this, the physiological basis for yield potential and the possible physiological basis for resistance susceptibility needs to be discussed.

Yield Potential in Groundnuts

The yield potential of groundnuts is dependent on three factors: the duration of growth, the amount of energy intercepted, and the distribution of growth between fruit and stems.

The duration of crop growth is a major factor in determining the yield potential of a genotype. The authors' unpublished data, and the findings of Williams et al. (1976) and Duncan et al. (1978), show that, provided energy interception is complete, the crop accumulates between 16 and 22 g m^{-2} day^{-1} of dry matter. This increases total shoot dry matter by between 1 and 1.5 t ha^{-1} week^{-1}. A genotype that matures two weeks later than another can have up to 3 t ha^{-1} more dry matter than the earlier-maturing line. When one considers that groundnut at ICRISAT matures in 80 to 130 days, scope for yield potential to vary with duration of crop growth is very large. However, if adjustments are made for the differences in time to maturity then the relationship between dry matter accumulated and energy intercepted (Fig. 3) is constant for groundnuts (Azam-Ali 1983). This is supported by the observation that crop improvement by selection for yield in Florida has not influenced crop growth rates (Duncan et al. 1978). It has been found that the growth rates of susceptible and resistant genotypes are similar, providing that the interception of radiation is comparable.

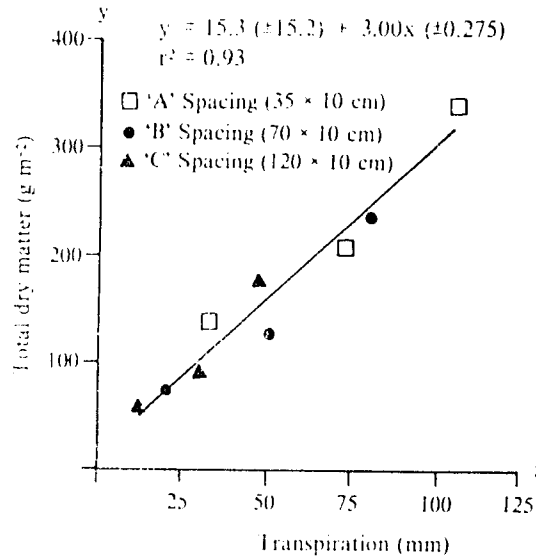

Figure 3. The relationship between transpiration and total dry mass accumulated (including roots) for groundnuts (Cv. TMV 2) at ICRISAT (ICRISAT Annual Report 1985).

The remaining factor that influences yield potential is the distribution of the carbon assimilated between the fruit and shoot the partition factor. This has been found to be a major determinant of differences in yield potential between genotypes (Duncan et al. 1978). Recent research at ICRISAT has shown that up to 95% of the assimilates in high-

yielding genotypes, such as Robut 33-1 and its derivatives, is used for reproductive growth. The resistant genotypes have appreciably lower partitioning.

Phytoalexin Precursors

Phytoalexins having sucrose as a precursor have been associated with resistances to diseases in other legumes (Strange, these Proceedings). If similar compounds are involved in the resistances of groundnut to foliar diseases, the high partitioning necessary for high yield may limit the expression of resistance. For those genotypes where the yield potential is based on a high partitioning factor, the fruit receive most of the carbon assimilated, and it seems reasonable to suggest that the sucrose concentration in the leaves would be less than in those genotypes where the fruit receive less than 50% of the photosynthetic production. If the resistance is based on phytoalexins, which have sucrose as their precursor, it may not be possible to combine resistance with high yield potential. In support of this speculation, is the observation that high yield potential and high RGI were not found together in the genotypes investigated.

Many questions remain unanswered. These RGI estimates were established in the face of a combined rust, late leaf spot disease epidemic and some of the lines have very high levels of resistance to one or other of the diseases. Would RGI have been different if only one of these diseases was present? Does an upper limit to resistance (resistance potential) exist? Are phytoalexins the basis for resistances in all the genotypes found to be resistant? Can resistances based on other mechanisms be identified and exploited to get round the "yield potential RGI barrier"? Many uncertainties exist in this field but it should be emphasized that these physiological aspects are of vital importance in the improvement of the groundnut crop for most crop circumstances.

Another intriguing aspect of these yield resistance interactions is the possible effect that photoperiod may have on the expression of resistance. We are finding that extensions of photoperiod can have major impacts on partitioning. For those genotypes where yield potential and resistance are interacting, the resistance of a genotype to disease may be changed according to latitude. Conventionally, the geneticists would implicate "races" but this may not be correct. So far the evidence for this effect is currently limited to one year's data on the response of the rust-resistant germplasm line NC Ac 17090. It has been found that the yield of this genotype is influenced by photoperiod. Dr. Zheu reports from China (where the day length is longer than at ICRISAT) that NC Ac 17090 is only moderately resistant to rust in Guangdong province although it is highly resistant at ICRISAT Center. Much remains to be investigated in this field but the possibilities are very stimulating.

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Groundnut Rust Disease and Plant Quarantine

B.K. Varma[1] and D. McDonald[2]

Abstract

Plant quarantine legislation and procedures for prevention of spread of groundnut rust in germplasm exchange are discussed. The recent spread of rust in the eastern hemisphere is attributed to long-distance dispersal of urediniospores by winds. There should be little or no risk of rust disease being spread through exchange of germplasm, either as seed or as vegetative material, provided it is conducted through the proper plant quarantine channels.

Résumé

Rouille de l'arachide et la réglementation phytosanitaire : *Les auteurs examinent la réglementation et les mesures phytosanitaires établies pour la prévention de la propagation de la rouille par l'intermédiaire du matériel génétique échangé. La progression récente de la rouille dans l'hémisphère Est est attribuée à la dispersion lointaine des urédospores par le vent. L'échange de matériel génétique, soit en semences soit en matériel végétal, pose peu ou pas de risque à condition de bien respecter les formalités phytosanitaires.*

The international exchange of groundnut (*Arachis hypogaea* L.) germplasm has increased rapidly in recent years. Much of this is associated with germplasm collection and distribution but there has also been an increase in the movement of seed of improved cultivars and breeding lines. The activities of ICRISAT scientists in collecting, evaluating, and distributing groundnut and wild *Arachis* species germplasm, in running international trials and supplying cooperating scientists in many countries with breeders' lines, and segregating populations have already been outlined. In the last 8 years ICRISAT has sent groundnut seed to 73 countries and has received seed from 26 countries. This movement is necessary for the development of improved cultivars worldwide and is essential for the effective functioning of international research programs.

It is essential that the exchanges of germplasm should not result in the spread of diseases and pests. The ICRISAT Plant Quarantine Unit works in close cooperation with the Germplasm Resources Unit and the Groundnut Improvement Program of ICRISAT and the Plant Quarantine Services of the Governments of India and of other countries to ensure that this does not happen. Rust disease of groundnut caused by *Puccinia arachidis* Speg. is recognized as a destructive disease in many countries and is of considerable quarantine importance.

Distribution of Groundnut Rust

The Commonwealth Mycological Institute in 1980 published a map (Fig. 1) of the distribution of groundnut rust and listed 58 countries in which the disease was reported. This number has increased since then (Subrahmanyam and McDonald—these Proceedings). Until the 1960s rust was largely confined to South and Central America with a few isolated outbreaks in the USA, USSR, Mauritius, and the People's Republic of China. In the late 1960s and early 1970s it spread rapidly in Asia, Australasia, and Africa. As plant quarantine legislation for the disease was based on the earlier situation, the

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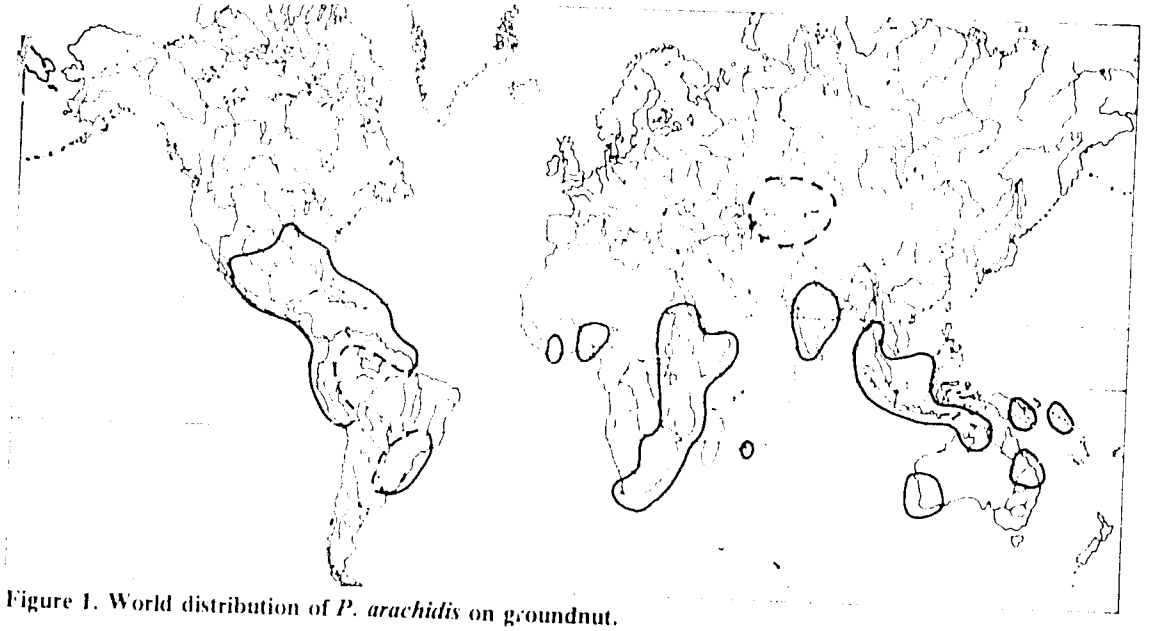

Figure 1. World distribution of *P. arachidis* on groundnut.

raged change in distribution has raised problems for groundnut germplasm exchange.

Plant Quarantine Legislation on Groundnut Rust

According to the Government of India's Destructive Insects and Pests Act of 1914, corrected up to March 1967, the importation of groundnut seeds and seedlings from South and North America, the West Indies, the People's Republic of China, and the USSR is prohibited because of the danger of importing groundnut rust. However, material can be imported for scientific purposes subject to specific conditions. These are that the seeds are treated with an appropriate fungicide prior to export, and that an additional declaration must be given on the official phytosanitary certificate stating that groundnut rust is not prevalent in the exporting country. Israel and Malawi have similar requirements.

Despite this legislation groundnut rust has spread to India and Malawi. In India it appeared in the Punjab in 1969 (Chahal and Chohan 1971), in Madras in 1971 (Bhama 1972), and is now widespread in the country (Subrahmanyam et al. 1979). It is clear that these plant quarantine procedures have not prevented groundnut rust from becoming established in India. Either the procedures were not effective or, as seems more likely, the disease was carried to India by wind and tropical storms. The legislation still stands, but in the interest of research it is permitted to move seed from countries that now have groundnut rust provided that proper precautions are taken. For seed being sent out of India by ICRISAT, a statement is required to the effect that rust is present but the seeds have been fumigated with aluminium phosphide and treated with a mixture of aldrin, Benlate®, and thiram prior to packing and dispatch. Seeds imported into India have also to be treated with appropriate protectant chemicals.

Exchange of vegetative material has been limited. It was necessary to move cuttings from some wild *Arachis* spp that do not readily set seed. These cuttings were first sent from collections in the Americas to Reading University in the UK where they were rooted and grown under plant quarantine supervision. Cuttings were then taken from healthy plants and flown to New Delhi where they were examined by Indian plant quarantine officials. Cuttings judged to be healthy were then flown to Hyderabad and grown under plant quarantine supervision in an isolation screenhouse and plants were eventually released to Groundnut Improvement Program scientists.

This procedure, which was set up mainly to prevent the spread of virus diseases, also precludes the possibility of rust disease being carried into the

country on vegetative material. There is the additional safeguard that almost all the wild *Arachis* species moved as cuttings were of Section *Arachis* and all but one are immune to rust at ICRISAT (Subrahmanyam et al. 1983).

The fact that rust is now widespread does not mean that plant quarantine in respect of this disease should be removed as there are still several groundnut growing countries where it has not yet become established. Furthermore, there is always the possibility that geographically isolated races of *Puccinia arachidis* may occur. However, the possibility of rust being spread by seed exchange should be reviewed in the light of recent studies on the biology of the pathogen, and uniform quarantine regulations and procedures should be agreed internationally.

Implication of Seed Exchange in the Spread of Groundnut Rust

Neergard (1979) and Richardson (1979) list a number of rust diseases that they consider to be seedborne, but so far there is no definite proof that *Puccinia arachidis* is seedborne in groundnut. However, a number of papers on groundnut rust contain references to *Puccinia arachidis* being seedborne and quote other papers as sources of this information. When the source papers are examined it becomes evident that there is no definite proof of the disease being seedborne and that the authors of these papers have been merely presenting their own opinions and suggestions. For instance, West (1931) in Florida, USA, in 1930 found rust on some plants of the cultivated groundnut, two wild *Arachis* species, and a hybrid between one of the wild species and the cultivated groundnut. Seed of the two species had been imported in shell from Brazil in the previous year. The disease had previously been found in Florida in 1918 and 1920 but had not become established there. Because there was no proof of rust having maintained itself in Florida from 1918 to 1930, West assumed that the 1930 outbreak was from the imported material.

More recent studies (Van Arsdel and Harrison 1972) have shown that isolated outbreaks of rust can occur in Texas and can be correlated with air movements from Mexico where rust is endemic. Another commonly quoted paper is that of Peregrine (1971) who reported the occurrence of groundnut rust in Brunei. The rust occurred on a groundnut crop grown from imported shelled seed purchased from a local store. The seeds were treated with an organomercury fungicide prior to sowing. The only other groundnut crop found in the locality was also infected and had been sown some 4-5 weeks later. From this data and from the knowledge that groundnuts imported into Brunei are mainly from China and Thailand, Peregrine makes the entirely unwarranted assumption that "there appears no doubt that the disease has been seed transmitted".

It is difficult to explain the very rapid spread of rust in Asia, Australasia, and Africa that took place in a period of eight years in terms of seedborne urediniospores, but easy to do so in terms of long-distance air dispersal. Indeed O'Brien (1977) quotes Pitkethley's opinion that the rust outbreak in Australia probably originated from wind-blown urediniospores.

Longevity of Rust Urediniospores and their Ability to Infect Plants from Contaminated Seed

Pods from a rust-infected crop commonly carry urediniospores that can be transferred to the seed at shelling (Subrahmanyam and McDonald 1982). Severe rust epidemics occur regularly at ICRISAT Center but uredinia (pustules) have not been observed on pegs or pods. This is not the case in Guangdong Province in the People's Republic of China where Dr. Zhou has found uredinia on pegs and on shells. This latter observation underlines the importance of moving groundnuts as seeds and not as pods.

Research at ICRISAT and in China has shown that urediniospores lose viability rapidly at high temperatures. At ICRISAT spores lost viability after being stored for 45 days at room temperature (25-30°C); in China spores only survived for 16-29 days at summer temperatures, but remained viable for 120-150 days at winter temperatures. Storing seed intended for export at a high temperature should therefore reduce the chance of viable urediniospores being moved between countries.

The question has been posed as to whether or not rust disease can develop from the sowing of seed contaminated with viable urediniospores. In trials at ICRISAT, seed of rust-susceptible cultivars dusted with viable urediniospores were sown in steam-sterilized soil in an isolation plant propagator. None of the seedlings developed rust disease. Emerged seedlings of the same cultivars had their foliage dusted with urediniospores of the same batch and all

developed rust. It would therefore appear that even if viable urediniospores could survive on seed samples through quarantine treatments and transit, they could not initiate rust in plants produced from them. The only prospect of such urediniospores initiating disease in the receiving country would be if they were moved from the imported seeds onto the foliage of susceptible groundnut plants growing in environmental conditions conducive to infection. This is considered to be unlikely to happen.

Conclusions

Most available evidence points to groundnut rust being spread by airborne urediniospores. Urediniospores rapidly lose viability at high temperatures and even at room temperatures of 25-30°C, which are common in the tropics, they will no longer be viable after 45 days. However, if stored at very low temperatures such as those used in germplasm banks, they may retain viability for many months. Most seed dressing fungicides should be effective in killing urediniospores contaminating the surfaces of groundnut seeds.

There is no evidence of rust being internally seed-borne in groundnut. There should be no risk of rust disease being spread through exchange of germplasm conducted through proper plant quarantine channels. A rather more likely route for the spread of groundnut rust, and one that could have implications for plant quarantine authorities, would be through contamination of the clothes and baggage of air travellers. For the present, care should be taken to clean seeds intended for exchange and to follow the recommended quarantine procedures. For those countries that do not already have groundnut rust it may be advisable to insist upon postentry quarantine in isolation greenhouses.

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Discussion

Chairman: R.W. Gibbons

Rapporteurs: P.W. Amin and R.C.N. Rao

R.O. Hammons. Rust disease commonly occurs in the United States Department of Agriculture (USDA) winter peanut disease nursery in Puerto Rico. For 20 years the crop has been harvested, dried, moved as unshelled stock to various parts of the USA, shelled (and debris burnt), dormancy broken, and sown in proximity to plants several weeks old. Over this period of time we have not obtained any evidence of rust spreading from this material.

C.D. Mayee. Groundnut rust is not likely to be spread on infested seed. We took seed from plants severely infested with rust and grew them on 1% water agar in petridishes. No rust developed on the germinating seed or seedlings.

K.J. Middleton. I wonder how important a role travellers play in spreading groundnut rust. We have found that the yellow rust of barley in Australia is the same race as that occurring in Europe and may have been taken to Australia by European travellers.

P. Subrahmanyam. If we walk thorough groundnut fields rust spores become attached to our clothes. We have to determine how long such spores remain viable and how effective is this mode of dissemination.

A.S. Rao. Rust is almost universally present in the groundnut-growing countries of the world, and so it is possible that dissemination by travellers may not be important unless there occur geographically separated races of the fungus.

B.K. Varma. There are still some countries from which groundnut rust has not yet been reported and so the question of dissemination remains important.

D. McDonald. A thorough search for groundnut rust has yet to be made in some countries. The disease has not yet been reported from Burma but on a visit there in early 1984 I found the disease present. In a survey in Nigeria we had to examine many plants and scan leaflets using magnifying glasses before the rust disease could be found on groundnut crops in some areas. Rust has been found in some countries because scientists were working on leaf spot disease and so were carefully examining the groundnut foliage.

K.J. Middleton. The report of rust occurrence in Russia was based on an erroneous identification. Many early reports of groundnut rust should be treated with some scepticism. In most cases, specimens of the rust were not deposited in collections, and host plants may not have been properly identified. We should be careful in reporting new occurrences.

T. Sommartya. What form of benomyl is used for seed treatment by ICRISAT's Plant Quarantine Unit? Several brands are available on the market and some are better than Benlate®.

B.K. Varma. For treatment of groundnut seed we use Benlate® and thiram in a 50:50 mixture, and this gives good control of the surface flora on seed. Benlate® is not effective for the control of rust disease, but application of Calixin® or chlorothalonil gives effective control.

D.L. Cole. You have shown wild *Arachis* species infected with rust; is this the same rust that occurs on *A. hypogaea*?

J.F. Hennen. Rust occurs naturally on many wild *Arachis* species in Brazil. We are not sure if there is only one groundnut rust fungus throughout the world.

V. Ramanatha Rao. In Brazil, rust spores from pustules on *Arachis glabrata* were inoculated onto *A. hypogaea* but no disease developed even after 60-70 days. However, rust did not develop on *A. glabrata* control plants either.

P. Subrahmanyam. At ICRISAT Center we inoculated six accessions of *A. glabrata* with the local isolate of rust but there was no infection although

rust developed on *A. hypogaea* check plants. At present we do not have definite information as to the existence of pathotypes in *P. arachidis*.

R.O. Hammons. *A. glabrata* is polytypic with 6-8 species, so we cannot generalize as to its reaction to rust.

D. McDonald. That is one of the reasons why we always quote accession numbers when reporting on disease-resistance screening of wild *Arachis* species.

J.P. Moss. Do we have any of the *A. glabrata* rust-susceptible accessions at ICRISAT?

V. Ramanatha Rao. No.

J.F. Hennen. We have 27 collections of rust from wild species in Brazil.

E.A. Salako. In Nigeria, in addition to rust, we have the problem of early leaf spot. This is much the more important of the two diseases in our country. Why have you ignored this disease?

P. Subrahmanyam. We take observation on early leaf spot when it occurs on our groundnuts at ICRISAT Center, but the disease is rarely severe enough to permit resistance screening in the field. Our research has been mainly on rust and late leaf spot disease, which occur regularly at severe levels.

D. McDonald. For the present meeting we have concentrated on rust disease. As you will see in the field visit we do have plenty of late leaf spot at ICRISAT Center and we are placing considerable emphasis on research to develop cultivars with resistance to both rust and late leaf spot. Early leaf spot is a major problem in Africa and our unit in Malawi is giving high priority to research on it.

J.E. Parlevliet. You mentioned that some wild *Arachis* species are immune to rust. Can you comment on the inheritance of this immunity? Does the expression of immunity remain similar after transfer?

A.K. Singh. We have screened F_1 hybrids of the immune wild species parent and *A. hypogaea* and found them to be highly resistant but not immune to rust. This probably resulted from partial dominance from increased ploidy level from a different genetic background.

J.F. Hennen. Do you have any evidence from backcrossing?

A.K. Singh. The segregation pattern in hybrids is abnormal, and more work is needed to understand this phenomenon.

R.O. Hammons. Have you sought to obtain diploid *A. hypogaea* and then cross it with diploid wild *Arachis* species?

A.K. Singh. No, we do not have a diploid accession of *A. hypogaea* and so have not been able to study the inheritance of rust resistance at this level.

J.P. Moss. Meiosis is also abnormal in hybrids.

D.L. Cole. Can disease expression on detached leaflets in the laboratory be correlated with that in the field?

P. Subrahmanyam. We have examined this for a large number of genotypes. Resistance screening using detached leaves is good for separation of resistant from susceptible genotypes and this correlates well with field-screening data. The laboratory method is not so good for assessing intermediate levels of resistance to rust.

D.L. Cole. It is the same for greenhouse screening, but this is a greenhouse effect. Do you find that potted plants behave in the same way as detached leaves in reaction to rust?

P. Subrahmanyam. Yes. We also find that greenhouse-grown plants are more susceptible to rust disease than are field-grown plants of the same genotype.

R.N. Strange. Resistance to *P. arachidis* is a post-penetration phenomenon. Is it in any way related to hypersensitivity? Can you differentiate resistance on this basis?

P. Subrahmanyam. Resistance results from failure of rust hyphae to establish contact with host-plant cells of resistant genotypes. In the case of hypersensitivity, as in *A. stenocarpa*, the host cells die immediately after they are invaded by the rust fungus, but in resistant genotypes this does not happen and limited development of disease ensues. The resistance found is of the slow-rusting type.

R.N. Strange. How do you examine the rust fungus in groundnut leaf tissues?

P. Subrahmanyam. We clear the leaves by heating in lactophenol and stain the fungus using the dye cotton-blue in lactophenol. The tissues can then be examined under the microscope.

S. Nagarajan. The 1-9 disease scale (9-point scale) you use at ICRISAT lumps together disease severity and pustule type. These are two quite different things. Why do you not record them separately as is done for cereal rusts? Severity could be shown as a percentage, and reaction type as resistant, moderately resistant, moderately susceptible, or susceptible. Such a system would be both precise and rapid.

P. Subrahmanyam. We did not observe distinct reaction types in groundnut rust as you have in cereal rusts. Hence the lumping together of such factors as infection frequency, lesion size, and sporulation, in our 9-point scale. We have been using this method successfully for evaluating large numbers of germplasm and breeding lines for the past 8 years.

S. Nagarajan. The 9-point scale has certain disadvantages. For example, you can not score 0.2, which is recorded as 1 on your scale. A modified Cobb's scale would be better.

P. Subrahmanyam. We do observe some variation in scores, for example 2 can be scored as 3, but the score is not likely to vary by more than a single unit. A modified Cobb's scale is being used for more accurate evaluation.

S. Nagarajan. This point is particularly important when dealing with slow rusting as the basis of resistance. We must have an accurate system and the 9-point scale may not be suitable.

P. Subrahmanyam. We do not use the 9-point scale in calculating *r* values; we use a modified Cobb's scale for this and other purposes requiring quantitative accuracy.

S. Nagarajan. In wheat-rust studies we use one scale for both the selection and quantification of resistance.

J.E. Parlevliet. For breeding purposes it does not matter which scoring system is used as long as it can identify true genotypic differences in the field in a reliable and reproducible way. The essence of an assessment scale for selection purposes is that it allows scoring to be done rapidly and by relatively untrained people. Its main function is to help decide what material to retain and what to discard. For epidemiological or inheritance studies more scientific data are needed and a different assessment method may have to be used. The modified Cobb's scale has some disadvantages. It is too cumbersome for large-scale evaluation and the epidemic has been developing for some time before it can be used. An even finer scale of disease measurement may therefore be required.

S. Nagarajan. Your 1-9 scale is actually a 1-6 scale, scores of 6-9 being virtually identical.

P. Subrahmanyam. We have evaluated several scales, including that developed for soybean rust, and from consideration of these we have developed the 9-point scale for selection of resistance in germplasm and breeding lines where it was only necessary to differentiate resistant, moderately resistant, and susceptible material.

D.L. Cole. A logarithmic scale has much to recommend it, particularly when analysing the data.

C.D. Mayee. There are basic differences between groundnut and cereal rusts. With groundnut rust you do not get the entire leaf area covered by rust pustules. In fact, when some 37% of the leaf area is covered, the leaflets fall off. This defoliation complicates evaluation of *r* even if the Cobb's scale is used.

P. Subrahmanyam. Defoliation is normally associated with the leaf-spot diseases; rust-affected leaves tend to remain attached to the plant even after they have shrivelled and dried. We use the 9-point scale for field evaluation of resistance and the Cobb's scale for measuring progress of the disease.

A.K. Singh. There has been much discussion on the utility of the 9-point scale. I wonder if the differences in resistance of some *A. hypogaea* genotypes in India and in China could be due to errors in the use of the scale. Perhaps the scale should be shortened.

D. McDonald. The 9-point scale is simple to use and it gives reproducible results.

C.D. Mayee. Hypersensitivity is an extreme sus-

ceptible reaction. Do you have a typical hypersensitivity reaction to rust in *A. hypogaea*?

P. Subrahmanyam. No, but we do find it in some wild *Arachis* species such as *A. stenocarpa*.

R.O. Hammons. What about *A. villosulicarpa*?

P. Subrahmanyam. The *A. villosulicarpa* accessions that we have tested have been shown to be immune to rust.

R.O. Hammons. What is immunity?

P. Subrahmanyam. We consider a genotype to be immune if, following inoculation with viable urediniospores of *P. arachidis* under conditions conducive to infection, there is no development of rust disease as determined by both macroscopic and microscopic examination. Using this definition we have found immunity in several wild *Arachis* species.

S. Nagarajan. The genotypes HLK 408, HLK 409 and HLK 410 show hypersensitive reaction to groundnut rust that is typical of vertical resistance. Some germplasm lines that have disease scores of 2.8 (9-point scale) in the field have small pustules when grown in the greenhouse laboratory. Can this be due to vertical resistance or race specific resistance as happens in other crops?

P. Subrahmanyam. The genotype HLK 410 *A. stenosperma* shows hypersensitivity against *P. arachidis*. We have not observed such a reaction in the cultivated groundnut. A score of 2.8 on the 9-point scale does not represent a hypersensitive reaction. The resistance we have in the cultivated groundnut is similar to horizontal resistance or rate-limiting resistance as reported in other crops.

S. Wongkaew. In Thailand some ICRISAT lines showed a kind of hypersensitive reaction to rust by producing small necrotic spots on the leaflets under heavy disease pressure. Is this a true hypersensitive reaction?

J.E. Parlevliet. The hypersensitive reaction is characterized by host cell collapse. There may or may not be urediniospore formation, so small necrotic spots may not be an indication of hypersensitivity. There must be hyphal invasion of cells resulting in their collapse. Immunity or high resistance should not be confused with hypersensitivity. Why do we not have a hypersensitive reaction in the cultivated groundnut to rust when this reaction is common with other rusts and hosts?

T. Sommartya. In our studies we found that the deposition of urediniospores and penetration of germ tubes into the leaflet involves taking advantage of protruding cuticle islands in *Colocasia* species. Similar studies could well be made on the infection of groundnut leaflets by *P. arachidis*.

P. Subrahmanyam. We intend to carry out such studies when we obtain our scanning electron microscope.

Region and Country Reports

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Groundnut Rust Research in the Americas

R.O. Hammons[1]

Abstract

Groundnut rust was first collected in 1882 in Paraguay by B. Balansa. The disease is now established in the groundnut-growing areas of South and Central America and the West Indies. Outbreaks of rust are known to have occurred in the USA since 1918, but economic damage by the disease has been reported only from southern Texas for the years 1965-71. However, there is cause for concern as all groundnut cultivars at present cultivated in the USA are susceptible, and arrival of rust spores early in the season could result in rust epidemics.

Screening of germplasm for rust resistance started in the Americas in the early 1940s. This work is described and sources of resistance documented. Rust-resistant germplasm is being used in several breeding programs. Immunity and high-level resistance to rust have been found in wild Arachis *species, and there are programs concerned with incorporating the resistance into the cultivated groundnut. It should not be assumed that all accessions of a species will have identical reaction to rust.*

The nature of resistance to rust is considered and reference made to Marion Cook's studies on physiological resistance. There is at present no authenticated evidence of races. The genetics of rust resistance is briefly mentioned as this is covered in detail by D.A. Knauft in these Proceedings.

Résumé

Recherche sur la rouille de l'arachide en Amérique : *Le pathogène de la rouille de l'arachide fut récolté pour la première fois en 1882 au Paraguay par B. Balansa. La maladie s'est ensuite implantée dans les zones arachidicoles de l'Amérique centrale et du Sud ainsi qu'aux Antilles. Aux Etats-Unis, la maladie existe depuis 1918 sans entraîner des dégâts économiques sauf dans le sud du Texas pendant la période 1965-71. Il n'empêche que cela a produit une certaine inquiétude aux Etats-Unis où toutes les variétés cultivées actuellement sont sensibles et l'arrivée des spores de la rouille en début de saison risque de déclencher une épidémie.*

*Le criblage de ressources génétiques pour la résistance à la rouille a commencé en Amérique au début des années 40. Les travaux sont décrits avec rappel des sources de résistance. Le matériel génétique résistant est utilisé dans plusieurs programmes de sélection. Les espèces sauvages d'*Arachis *présentent un haut niveau de résistance et d'immunité. Des programmes en cours tentent d'incorporer cette résistance dans les arachides cultivées. Il faut noter que toutes les accessions appartenant à la même espèce n'ont pas forcément la même réaction au pathogène de la rouille.*

La nature de la résistance à la rouille est élucidée par référence aux études menées par Marion Cook sur la résistance physiologique. Pour le moment il n'existe pas de preuve confirmée de l'existence de différentes races du pathogène. Enfin, les auteurs présentent un bref aperçu sur la génétique de la résistance qui sera approfondi plus loin dans la communication par D.A. Knauft.

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ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) 1987. Groundnut rust disease. Proceedings of a Discussion Group Meeting, 24-28 Sep 1984, ICRISAT Center, India. Patancheru, A.P. 502 324, India: ICRISAT.

Groundnut rust, caused by the fungus *Puccinia arachidis* Speg., has been known to mycologists for a century since Carlos Luigi Spegazzini named and described the disease from *Arachis* material collected by B. Balansa in January 1882 near Caaguazu, Paraguay (Spegazzini 1884). *P. arachidis* is the only rust recorded on the genus.

Within 40 years the disease had become established from Argentina and Peru northward through the groundnut-growing areas of South and Central America and into the West Indies (Bromfield 1971, Hammons 1977).

In South America, rust has been found in Argentina, Brazil, Colombia, Guyana, Paraguay, Peru, Surinam, Uruguay, and Venezuela. In Central America and the Caribbean it has been reported from Antigua, Barbados, Belize, Cuba, Dominican Republic, Grenada, Guadeloupe, Guatemala, Honduras, Jamaica, Montserrat, Nicaragua, Panama, Puerto Rico, and St. Vincent.

The first documented outbreaks in the USA occurred in Florida. Rust was found on 30 Aug 1918 on the farm of the Florida Experiment Station, Gainesville (Sherbakoff 1921). Only four to six plants, all in a close cluster, were affected. Two years later, in November 1920, a "50 percent loss" in the 6 ha field of S.W. Collins on Torry Island in Lake Okeechobee, Florida (Burger 1921) demonstrated the destructive potential of the invader.

Plant pathologists, plant breeders, and growers have observed groundnut rust in southern USA at irregular intervals since 1918. Its sporadic occurrence, often late in the growing season, usually caused relatively little concern outside the affected areas. Rust has been reported from Alabama, Florida, Georgia, Louisiana, New Mexico, North Carolina, Texas, and Virginia (Bromfield 1971, Hammons 1977), and in 1981 from Hawaii (A.P. Martinez, personal communication 1982).

Only the uredinal stage has been found in the USA. Aecia and pycnia (spermogonia) are not known (Higgins 1956). The original description included only teliа and teliospores (Spegazzini 1884). They have been found only rarely since (Hennen et al. 1976). A more detailed account of the life cycle of groundnut rust is presented by J.F. Hennen (these Proceedings).

No authentic host species are known outside the genus *Arachis* (Subrahmanyam and McDonald 1983). Airborne urediniospores disseminate the fungus. As Higgins (1956) reported, the pathogen does not overwinter in the USA, but blows in from subtropical areas (van Arsdel 1973, 1974).

Except in southern Texas, where rust caused economic losses from 1965 to 1971, the disease has not been considered a major limiting factor in groundnut production in the USA (Subrahmanyam et al. 1984). Where preventive applications of fungicides (such as chlorothalonil) are a standard production practice, disease pressure is minimized.

Groundnut rust has been observed in southern Georgia during 22 of the 32 crop years from 1953 to 1984. The first general field epidemic occurred in September 1953, although rust had been observed in breeding plots at the Georgia Experiment Station, Experiment, Georgia, about 20 years earlier (W.K. Bailey, unpubl. ann. report 1953). Rust was not seen in years of severe drought stress, 1954, 1958, 1960, 1963, and 1980. Usually infection was light or late in the season, but either incidence, wider distribution, and crop damage occurred in the years 1953, 1955, 1957, 1961, 1971, 1973, 1976, and 1984.

There is, however, cause for concern. All cultivars presently in cultivation are known to be susceptible. Improved production technology — primarily irrigation and more effective leaf spot control — within the past 15 years has extended the previous growing season by 20 to as much as 50 days in Georgia. Also there is the possibility that inoculum in appreciable quantities will arrive sufficiently early in the season to permit the development of several uredial cycles. If this occurs, a widespread and devastating epiphytotic is distinctly possible, particularly in the absence of resistant cultivars.

American Sources of Resistant Germplasm

Hundreds of primitive or advanced cultivars and breeding lines of *A. hypogaea* have been screened in the Americas for rust sensitivity by exposure to natural or artificial epiphytotics under field or greenhouse environments since the early 1940s (Bromfield 1971, Hammons 1977, Subrahmanyam et al. 1983).

Published evidence shows that Glenn Kenknight (1941) first investigated host-plant susceptibility to groundnut rust. All 50 entries that he exposed to artificial as well as natural inoculation under field conditions in southern Texas became rusted. The apparent greater susceptibility of the runner-type (subsp *hypogaea* var *hypogaea*) entries was attributed to their "greener" foliage when inoculated. (The present writer interprets "greener" to refer to their longer growing season.)

In Venezuela, Mazzani and Hinojosa (1961) observed 254 entries for reaction to natural infections by rust in 1959 and/or in 1961. They developed a 5-point disease scale (0-4) to describe infection intensity. They classified as resistant only one entry, Tarapoto, introduced into Venezuela from Tingo Maria, Peru, in 1955. The nature of this resistance was not defined. They also found Tarapoto most resistant to infection by leaf spot.

Since its inception in 1931, the groundnut breeding program cooperative between the University of Georgia and the Agricultural Research Service, U.S. Department of Agriculture (ARS-USDA), has sought to obtain, evaluate, and incorporate disease resistance into agronomically acceptable cultivars (Higgins 1956). Therefore, we accessioned the bulk of the Venezuelan collection in 1959 as USDA Plant Inventory (PI) numbers 259752-259758. The Tarapoto entry was PI 259747.

Wallace K. Bailey, Leader of Peanut Investigations, ARS-USDA from 1958 to 1972, had worked in Puerto Rico in 1938-41, and he established the USDA winter peanut seed-increase nursery there in the early 1960s. About this time Donald V. McVey, plant pathologist at the USDA Federal Experiment Station, Mayaguez, Puerto Rico, became interested in rust and Bailey furnished germplasm for his investigations.

McVey observed 1500 accessions exposed to natural rust infection in the USDA field nursery in Puerto Rico in 1964. Although there was considerable variability in disease severity among genotypes, McVey concluded that none of the accessions had appreciable resistance except PI 259747 (Tarapoto introduced from Venezuela).

The sporadic outbreaks of rust from 1941 through 1964 in southern Texas were, apparently, of no special concern to growers. In 1965, however, the situation changed. Rust became serious in many fields and, together with the leaf spots, caused severe economic losses.

These losses, together with the constant threat to the southeastern U.S. crop posed by established rust in the Caribbean, prompted further studies. Kenneth R. Bromfield, rust specialist with USDA's Plant Science Laboratories, Fort Detrick, Maryland, initiated a more intensive search for rust resistance in *A. hypogaea* and related species.

Between 1967 and 1969, Bromfield and Cevario (1970) tested 245 recent accessions in the greenhouse for susceptibility to *P. arachidis* cultures from Puerto Rico or Texas (or to both cultures). Resistant PI 259747 (Tarapoto) and two susceptible spanish-type cultivars were used as standards. They identified two additional resistant genotypes, i.e., PI 314817 and PI 315608.

Documentation of these genotypes appears in Hammons (1977), Hammons et al. (1982a, 1982b), and Subrahmanyam et al. (1983).

None of the three resistant genotypes (Tarapoto, i.e., PI 259747, PI 314817, and PI 315608) is acceptable for commercial production. These materials have been disseminated throughout the world from the ARS-USDA and ICRISAT gene banks, and introduced and reintroduced in national and international breeding programs. Hammons (1977) recorded five separate introductions of Tarapoto (PIs 259747, 341879, 350680, 381622, and 405132) into the USA. These and two further acquisitions are documented in Table 1. Also, PI 298115 was an earlier accession of the PI 315608 genotype (Hammons 1977). A natural cross between PI 298115 and an unknown pollen donor gave rise to the first germplasm developed and released with resistance to groundnut rust. The material consisted of 14 F_5 lines representing 7 F. families from the F_1 parent detected in a 1971 seed-increase plot near Isabella, Puerto Rico. The lines, designated FESR 1 through FESR 14, consistently showed levels of resistance equal to that of the resistant parent under field conditions at the Federal Experiment Station in Puerto Rico and under controlled conditions at the ARS Plant Disease Laboratory, Frederick, Maryland (Bailey et al. 1973). Advanced-generation progeny from some of these lines continue to segregate in an inexplicable manner.

Field and greenhouse trials performed in Jamaica by Marion Cook (1972) with 36 accessions from ARS-USDA and 2 local cultivars confirmed the previously reported resistance for PI 259747 and 2 reintroductions of it (PI 341879 and 350680), for PI 314817, and for PI 298115. A later accession, PI 315608, from the same source as PI 298115 had a susceptible reaction in the single greenhouse trial. Cook (1972) suggested that the different reaction could mean that the culture of rust from Jamaica differed physiologically from the Puerto Rico and Texas cultures used by Bromfield, or that plants of this accession were not genetically uniform. In her thesis, Cook (1975) raised the possibility of mislabeling on the seed sample received from the USA. However, PI 315608 was found to be susceptible under repeated attacks by the fungus in Honduras (Hammons 1977).

Cook (1972 and 1975) observed a high level of resistance in the NC 13 breeding line, but that geno-

Table 1. Groundnut germplasm resistant to *Puccinia arachidis*: documentation of introductions and reintroductions of the Tarapoto line (subsp *fastigiata* var *fastigiata*).

Accession		
PI[1]	IC G[2]	Origin and Reference
259747	4747	Introduced to USA in 1989 from Venezuela where it was obtained from Tingo Maria A.E.S., Peru, in 1984 (Mazzani and Hinojosa 1961)
341879	7884	A shorter-podded form selected in Israel from PI 259747 by Z. Frank.
350680	6340	Reintroduced from Honduras; reputed to be from PI 259747 (J. Romero, personal communication).
381622	7885	Received in Honduras from Nicaragua; thought to be from Venezuela (J. Romero, personal communication).
405132	7897	Received from Ecuador as a valencia resistant to both rust and leaf spot (C. Calero H., personal communication)
476306		Campinas (Brazil Inst. Agron (CIA) no. SO 909, ex PI 259747, resistant to *P. arachidis*, *Sphaceloma arachidis*, *Cercosporidium personatum*, and *Meloidogyne arachidis* (Moraes et al. 1978).
476307		CIA No. SO 911, ex PI 350680; resistant to *P. arachidis*, *S. arachidis* and *C. personatum* (Moraes et al. 1978).

1 USDA Plant Inventory Number
2 ICRISAT Groundnut Accession Number

type has been found to be susceptible in Puerto Rico, at ICRISAT Center, and elsewhere.

Two rust-resistant cultivars were developed and released in 1976 in Honduras. Both are derivatives from the cross Florispan Runner × Tarapoto and have moderate tolerance to leaf spot and good resistance to rust in Honduras. Both have the bunch growth habit. Resistente Corto (PI 414331) has smaller pods and seeds and better shelling properties than Resistente Largo (PI 414332), which has slightly higher yield (J. Romero, personal communication). Both cultivars have also exhibited resistance to rust in field trials in Puerto Rico and at ICRISAT (Hammons 1981).

Continued cooperative research on an international scale has led to the identification, documentation, release and dissemination of additional groundnut genotypes with high levels of resistance to rust.

In field trials with a collection of 700 groundnut accessions exposed to a natural epiphytotic at Tifton, Georgia, during 1976, 12 new resistant genotypes were identified. The resistant reaction was confirmed for three seasons (1977-79, in the winter nurseries in Puerto Rico, with careful selection each year to minimize phenotypic variation. Progeny tests in two contrasting environments at ICRISAT Center confirmed their resistance. These entries were named Tifrust-1 through Tifrust-12 and released in 1981 (Hammons et al. 1982 c and 1982d). All but one of the genotypes are derived from collections made in Peru; Tifrust-4 was developed from an accession from Ecuador.

Concurrently, with the above releases, the agencies cooperating in their evaluation named and released the reselected progenies from two accessions evaluated for the past 12 years: Tifrust-13 for PI 315608 and Tifrust-14 for PI 314817 (Hammons et al. 1982 a and 1982 b). Tifrust-1 through Tifrust-14 are briefly documented in Table 2. The stability of these genotypes to rust-disease pressure has also been evaluated at widely separated locations in Asia and Africa as part of the International Groundnut Foliar Disease Nursery coordinated from ICRISAT (Subrahmanyam et al. 1983). These investigations are reported elsewhere in these Proceedings.

Partial documentation is available for another American groundnut accession that has shown resistance to rust and other diseases. The accession NC Ac 17090 (ICG 1675), collected by W.C. Gregory (col. 190) under the name "Mani comun" near Tarapoto on the Huallaga river in Peru, is a var *fastigiata*-type referred to as "A2" or "V2" in genetic studies by Wynne and associates at North Carolina State University (J.C. Wynne, personal communication). Initially the accession was not assigned a PI number, but recently, a reintroduction from Taiwan was given the PI number 478849.

The rather detailed documentation of sources of resistance in *A. hypogaea* (above) was given to facilitate further research. Precise identification, careful labelling, and constant roguing to remove unwanted

Table 2. Rust-resistant germplasm jointly released by the United States Department of Agriculture (USDA), The University of Georgia, and ICRISAT[1].

Germplasm	ICG No.[2]	Selection from PI. No.[3]	Botanical type variety	Seed color[4]	Country of origin
Tifrust 1	7881	215696	*fastigiata*	Purple	Peru
Tifrust 2	7886	390593	"	Light tan	"
Tifrust 3	7887	390596	"	Purple	"
Tifrust 4	7898	407454	"	Tan	Ecuador
Tifrust 5	7894	393841	"	Light tan with purple stripes	Peru
Tifrust 6	7895	393643	"	Light tan	"
Tifrust 7	7896	393646	"	Purple	"
Tifrust 8	7888	393516	"	White with red blotches	"
Tifrust 9	7889	393517	"	Off-white	"
Tifrust 10	7890	393526	"	Purple	"
Tifrust 11	7893	393531	"	Tan with purple stripes	"
Tifrust 12	7891	393527	*hypogaea*	Red	"
Tifrust 13	7883	315608	"	Off-white	USA/Israel/USA
Tifrust 14	7882	314817	*fastigiata*	Light tan	Peru

1 For references to release, see papers by Hammons et al. 1982
2 ICRISAT Groundnut Accession Number
3 Selection to minimize phenotypic variation was practiced for several generations prior to release.
4 RHS colour chart. The Royal Horticultural Society London, 1966

natural hybrids are among the precautions a breeder should use prior to investigations of host susceptibility, differential races, inoculum concentrations, inheritance patterns, and allelism of genes. In the allotetraploid groundnut, success or failure of screening or breeding programs will depend largely upon the integrity and genetic uniformity of the germplasm.

Advanced-generation rust-resistant breeding lines are under evaluation in Georgia, Florida, Texas, and Oklahoma to assess the yield and quality characters needed for acceptance for sophisticated domestic and export markets.

Arachis Species as Sources of Resistance

High levels of resistance and immunity to rust occur in some wild *Arachis* species (Subrahmanyam and McDonald 1983). However, the polyploid nature of species in certain sections of the genus, the occurrence of botanical varieties, and the phenotypic heterogeneity observed in collections of the same species in a common locality or from widely divergent geographical regions suggest that caution should be exercised before categorically associating a rust reaction with all of the variation designated by the specific epithet.

Guarch (1941) reported that *P. arachidis*, in the telial stage only, was collected on *A. marginata* Gardn. in Uruguay on the Brazilian frontier. This author found *A. burkartii* Handro was the dominant wild species in the area specified by Guarch and the material described by him appears to be *A. burkartii*.

McVey (personal communication) observed that *A. glabrata* Benth. in the USDA nursery in Puerto Rico was immune to rust. Bromfield and Cevario (1970) reported that five accessions labeled *A. glabrata* (PIs 118457, 231318, 262141, 262287, and 262801) and one accession of *A. monticola* Krap. et Rig. produced only small, weakly sporulating pustules when tested with their Puerto Rican culture of rust.

In our research *A. monticola* (PI 405933) was killed by a natural outbreak of rust at Tifton, Georgia, in 1976. However, for one accession of *A. villosulicarpa* Hoehne (PI 336985), there were no macroscopic lesions on 66 plants exposed continuously to heavily-sporulating rust from early August until the frost in November (Hammons 1977).

Groundnut rust is known to attack some other wild species in the genus. Germplasm explorers made notes whenever rust occurred on wild *Arachis* materials collected in South America in the multinational work sponsored by the International Board for Plant Genetic Resources and by ICRISAT. C.E. Simpson (personal communication 1984) observed rust on *A. glabrata*, *A. repens* Hoehne, *A. marginata*, and *A. prostrata* Benth. in their native habitat. These species have been reported to be resistant or immune to rust in various publications.

In so far as is known, no breeding program in South America has the specific objective of transfering rust resistance from wild to cultivated groundnut. Work in this area, initiated at the Campinas (Brazil) Institute of Agronomy, is now inactive.

The Nature of the Resistant Reaction

Bromfield and Cevario (1970) reported physiological resistance in PI 259747, PI 314817, and PI 315608 when repeatedly tested in the greenhouse with rust cultures from Puerto Rico and Texas. Reactions of the three accessions (two genotypes) were indistinguishable.

Cook (1972) described this reaction as "resulting in necrotic spots or poorly-sporulating pustules". She demonstrated an association between leaf wettability and the extent of infection: the abaxial surface of leaves of resistant genotypes became appreciably less wettable as the leaf matured (Cook 1972, 1975, and 1980). The rate of change in wettability varied among genotypes, affected spore retention and probably germination and appressorium formation. Physiologic resistance became evident with the failure of chloronemic flecks to become uredia (Cook 1975 and 1980).

From multilocational testing it appears that host-plant resistance is stable over widely-separated geographical locations (Subrahmanyam et al. 1983). At present there is no authenticated report in the American literature for the occurrence of races of differing pathogenicity.

Genetics of Rust Resistance

In a following paper in these Proceedings, D.A. Knauft reviews the studies on inheritance of resistance in groundnut germplasm. I confine my discussion to work that was not available to Dr Knauft.

Cook (1975) experimentally confirmed the bigenic model of inheritance postulated by Bromfield and Bailey (1972). She made reciprocal intraspecific crosses between resistant parents PI 298115 and PI 259747 and two nonresistant cultivars. She subsampled 100 seed each for F_2 populations of the eight resultant two-way crosses. For each cross, individually, for the "male" and "female" sets, and for the 797 total F_2 plants, the observed variations were consistently nonsignificant from the bigenic (15:1) distribution. There were no cytoplasmic effects.

The test cross ratio, 3:1 for duplicate genes, was obtained in each backcross generation (n = 398). Crosses between resistant genotypes showed that the duplicate genes are carried on the same chromosomes for both resistant parents.

Cook (1975) tentatively designated the duplicate genes as *sr1* and *sr2*, with *sr1 sr1 sr2 sr2* signifying either resistant genotype.

Despite these results groundnut breeders are not fully satisfied with the proposed genetic model. The F_2 distributions are sometimes skewed, indicating involvement of fewer genes. Although good fits for 15:1 ratios are obtained using the 9-point scale for scoring progeny plants, ratios could be altered based on the plant age at scoring (S.N. Nigam, personal communication 1984).

Similar concern has been voiced in Australia, where new sets of reciprocal crosses are being screened for possible quantitative resistance parameters (R. Shorter, personal communication 1984).

Many of our own genetic investigations with the allotetraploid groundnut have shown that simple genetic ratios are far less frequent than was formerly thought. Scientists who study this species are cautioned to be certain of the genetic integrity and identity of any accession employed in their research.

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Occurrence and Management of Groundnut Rust in Australia

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Abstract

Areas cultivated and average yields of virginia and spanish-type groundnuts are presented for the period 1977-1982 for the main groundnut-growing regions of Australia. Rust disease was first recorded in the Northern Territory in April 1973 and is now established in the country. The disease is most severe in the warm, wet northern regions of Australia where serious damage can be done in most seasons to unprotected crops. All cultivars grown at present are susceptible. Rust and the leaf-spot diseases are controlled by application of fungicides of which chlorothalonil and bitertanol are most effective. Aircraft and tractor-mounted sprayers are used and controlled-droplet application is becoming popular. Intensive spray regimes are needed more in the north than in the south.

A breeding program has started to incorporate resistance to rust into cultivars suited to the Australian market. Sources of resistance used include PI 259747, PI 314817, PI 298115, and EC 76446(292). The genetics of rust-resistance are being studied using crosses of these cultivars with susceptible high-yielding cultivars. When available, rust-resistant cultivars will be used together with minimum fungicide applications in an integrated foliar-diseases management system.

Résumé

Rouille de l'arachide et sa lutte en Australie : *La superficie cultivée et les rendements moyens des types Virginia et Spanish de l'arachide sont présentés pour les principales régions arachidicoles de l'Australie au cours de la période 1977-82. La maladie de la rouille fut signalée pour la première fois dans le Territoire du Nord en avril 1973, et s'est ensuite implantée dans le reste du pays. La maladie sévit surtout dans les régions chaudes et humides du nord. Les conditions du milieu y étant toujours favorables, les cultures non protégées sont susceptibles d'être attaquées dans la plupart des saisons, d'autant plus que toutes les variétés cultivées actuellement sont sensibles à la maladie. L'application des fongicides, dont les plus efficaces sont chlorothalonil et bitertanol, permet de lutter contre la rouille et les maladies des taches foliaires. La pulvérisation des fongicides est effectuée par avion ou à l'aide de pulvérisateurs portés sur tracteur; l'application par gouttes calibrées commence à se généraliser. L'intensification des rythmes de pulvérisation est à préconiser plutôt dans le nord qu'au sud.*

Un programme de sélection en cours tente d'incorporer la résistance dans les cultivars adaptés aux besoins du marché australien. Les sources de résistance utilisées sont : PI 259747, PI 314817, PI 298115 et EC 76446(292). La génétique de la résistance à la rouille est étudiée à partir des croisements de ces cultivars avec des cultivars sensibles mais à haut rendement. Une fois développés, les cultivars résistants seront utilisés avec application minimale de fongicides selon un système intégré de lutte contre les maladies foliaires.

Production of groundnut in Australia is concentrated in Queensland, with some movement into the most northern parts of Western Australia and the Northern Territory. An upright virginia-type occupies approximately 80% of the area, with the balance being divided between two spanish-type cultivars. The 1983/84 distribution of production and the average yields obtained in the five years 1977/78 to

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Table 1. Distribution of production by region and by type of groundnut grown, and average yields obtained during 1977-1982.

Region	Virginia types		Spanish types	
	Area (ha)	Yield (t ha^{-1})	Area (ha)	Yield (t ha^{-1})
Southern Queensland	24000	1.44	5400	1.04
Northern Queensland	5600	2.16	400	1.71
Queensland (other)	1500	1.63	200	1.71
Northern Western Australia	200	3.5		
Northern Territory	40			

1981/82 are shown in Table 1. All groundnuts grown commercially are susceptible to rust infection. This disease was first recorded in the Northern Territory in early April 1973 following its discovery in Papua New Guinea in December 1972. Rust was observed in northern Queensland a few days after the report from Northern Territory, but was not found in the major production area in southern Queensland until February 1976. At that time the distribution indicated that low levels of infection had overwintered in southern Queensland since the previous crop. Significant damage is now caused (up to 100% yield loss) to any unprotected crop in northern Australia in every season. In southern Queensland, disease incidence varies from season to season but some fields suffer yield losses each year. Groundnuts are grown in Australia during the November-April summer season, and the earliest reports of rust are usually from southern Queensland due to the earlier planting date in that area. However, warmer and wetter conditions in northern Australia cause a more rapid increase in the epidemic in that area than in southern Queensland.

Use of Fungicides

Producers currently rely on frequent applications of fungicide to minimize damage to their crops. In southern Queensland, 3 or 4 applications may be made per year, whereas in northern Australia 10 to 12 applications per season are usual. This represents over 40% of the preharvest costs in that area, although fungicides are also necessary for the control of leaf spot (principally *Cercosporidium personatum* — late leaf spot).

The fungicide most widely used is chlorothalonil but bitertanol is finding a place in the industry because of its capacity to eradicate as well as prevent infection.

Due to the different intensity of epidemic in southern and northern Australia, a different approach to the use of fungicides is recommended in the two areas. In northern Australia, the application of fungicide commences when the disease is first observed (usually 4-6 weeks after planting) and is continued at 10-14 day intervals until 2 weeks before harvest. In southern Queensland, fungicides are applied when the disease incidence has reached a low level, and are reapplied at 14-day intervals while conditions are suitable for infection (i.e. periods of rainfall or heavy dew). Regular use of fungicides in southern Queensland will not only be in excess of that necessary to maximize yield, but the fully-protected crop canopy appears to deplete soil-moisture reserves, compounding the late season droughts, which commonly occur.

Application equipment

The fungicides are applied either by air, usually using Micronair equipment applying a total volume of 22-25 l ha^{-1}, or by grower-operated, tractor-mounted boom sprays, which apply 150-250 l ha^{-1} through hollow-cone jets. There has been significant adoption of rotary atomizers (CDA = controlled droplet application) on booms. Most are using spinning-disc atomizers but at least one unit operates hydraulically-driven Micronair atomizers on a boom. Most operators of CDA equipment choose to apply the same rate of fungicide as would be applied through a conventional boom, using any gain in efficiency due to CDA principles to improve disease control.

Resistance Breeding Program

A program has commenced to incorporate resistance to rust into groundnuts of an acceptable type

for the Australian market. The resistant parents PI 259747, PI 314817, and PI 298115 were used initially in crosses with local and introduced virginia-type cultivars and local spanish-type cultivars. Early generation (F_3 and F_4) mass selection among and within crosses was conducted in the field for rust and leaf spot resistance and for kernel traits following harvest. Subsequently, F_5 derived lines from these populations were selected for resistance to these diseases and evaluated for yield under disease-free conditions. On a 1 (no disease or hypersensitive reaction) to 9 (severe disease) scale, commercial cultivars rated 9 and the selections 1-2 for both diseases. All selected progeny were derived from the PI 259747 resistant parent. Kernel yields of some selections approached those of commercial cultivars. The most promising progenies are being used in a second cycle of crossing with recent high-yielding introductions.

The resistant parent EC 76446 (292) has also been used in crosses with high-yielding cultivars. However, F_3 populations from these crosses showed much less rust resistance in the field than progeny derived from PI 259747.

Genetics Studies

Three resistant parents (PI 259747, PI 314817, and EC 76446(292)), and two susceptible parents (Shulamit and Virginia Bunch) are being used to study the genetics of rust resistance. Parents and progeny were assessed in terms of components of resistance (infection efficiency, generation time, lesion size, etc.) identified elsewhere. F_1s from susceptible × resistant crosses and their reciprocals generally were similar to the resistant parent or were intermediate between the resistant and susceptible parents. These preliminary results suggest dominant or partially dominant additive gene action for resistance. They contrast with Bromfield and Bailey's (1972) report that resistance is recessive to susceptibility. Differences among reciprocal crosses were evident in some of the crosses.

Disease Management

While genetic resistance to rust is an important aim of the peanut program of the Queensland Department of Primary Industries, the sources of resistance currently available do not confer immunity to the disease. In fact, immunity may not be desirable if durable resistance is to be achieved. The result is that disease management will become more important in future.

In northern Australia where foliage-disease epidemics are predictable and severe, the cost-benefit squeeze will ensure that growers do not make more applications of fungicide than necessary for maximum returns. While rust-susceptible cultivars are being grown, an understanding of economic injury levels of the disease on these cultivars will enable growers to save unnecessary applications. When rust resistance is introduced, the economic injury level of leaf spot will dictate the timing of fungicide applications. When resistance to both diseases is incorporated into commercial cultivars, fungicide applications will be reduced to a supportive role during periods of weather conditions highly conducive to infection. The requirement for these applications will be indicated by disease incidence as determined by monitoring, and a knowledge of the effects of diseases on yield in these cultivars.

In southern Queensland where disease epidemics are less predictable or less severe, thorough scouting of susceptible crops has always been necessary to enable accurate decisions about fungicide use, based on economic injury levels for that cultivar. Introduction of genetic resistances to rust (and leaf spot) would enable growers to significantly reduce the costs of fungicidal protection for the crop. However, it would then become more important for growers to regularly scout their crops for the presence of disease as their crops would be normally unprotected by fungicides against epidemics that could lead to damage.

Thus genetic resistance to rust (and leaf spot) will reduce both the dependence on fungicides and the costs of production, but will not reduce the growers' management decisions about use of fungicides. Precise knowledge of the method of action and the disease control spectrum offered by fungicides becomes more important to enable selection of appropriate fungicides when chemical support for genetic resistance is warranted.

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The Groundnut Rust Disease Problem in Burkina Faso

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Abstract

Groundnut rust caused by Puccinia arachidis *Speg. was first recorded in Burkina Faso in 1977. Disease surveys have shown that the rust causes serious damage to farmers' groundnuts in the high rainfall, southern region of the country. A resistance breeding program was started and local cultivars, IRHO (Institut de Recherche pour les Huiles et Oleagineux) lines, and ICRISAT germplasm lines are being screened for rust resistance under field and laboratory conditions. Techniques have been developed for rust inoculum production and laboratory screening of detached leaves. Some IRHO lines reported resistant to rust have been found susceptible in Burkina Faso. Pustule types on susceptible and resistant genotypes varied. It was suspected that disease reaction could be influenced by environmental conditions and the nutritional status of the host plants.*

Résumé

Rouille de l'arachide au Burkina Faso : *La rouille de l'arachide due à* Puccinia arachidis *Speg. fut signalée pour la première fois au Burkina Faso en 1977. Des études sur la maladie révèlent que les dégâts sont plus graves aux champs situés dans la région sud à forte pluviosité. Le programme de sélection étudie les cultivars locaux ainsi que les lignées provenant de l'Institut de recherche pour les huiles et oléagineux (IRHO) et le matériel génétique fourni par l'ICRISAT. Les essais sont menés au laboratoire et au champ. On a mis au point des techniques de production de l'inoculum et de criblage au laboratoire des folioles detachées du matériel sous étude. Certaines lignées de l'IRHO considérées comme résistantes se sont montrées sensibles au Burkina Faso. Les types de soores (pustules) varient sur les génotypes sensibles et résistants. Il se peut que la réaction à la maladie soit influencée par les conditions du milieu ainsi que l'état nutritionnel des plantes-hôtes.*

Burkina Faso is a country of the semi-arid tropics of West Africa. It has an annual rainfall that ranges from 500 mm in the north to over 1200 mm in the southwest. The economy is based on agriculture, and groundnuts are grown in most parts of the country by small-scale farmers who grow many other crops. Groundnut rust caused by the fungus *Puccinia arachidis* Speg. was first recorded in Burkina Faso in 1977, and it was found that the cultivars that IRHO (Institut de Recherche pour les Huiles et Oleagineux) had been working with since 1949 were all susceptible to the disease. This paper considers data from rust disease surveys and describes resistance screening of local and introduced cultivars and germplasm lines.

Rust Disease Surveys in Burkina Faso

The groundnut rust disease situation is summarized in Figure 1, which indicates the severity of the disease in different regions of the country. Rust is most severe, and causes economic damage to the crop in the southwest where the annual rainfall is 1000-1100 mm, minimum temperature is 19-25°C, and relative humidity averages 80%. These are environmental conditions highly favorable for infection and build-up of rust disease. Towards the north and east of the country rust is less severe, and in the far north it does not occur.

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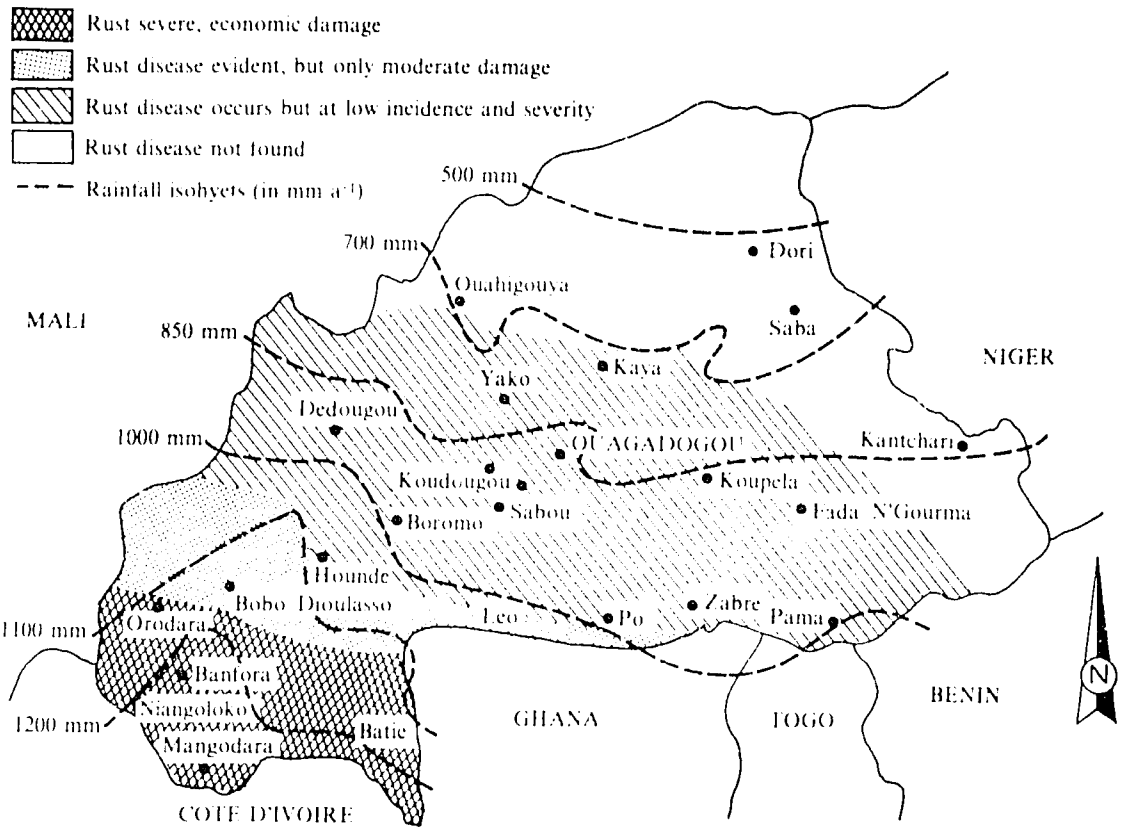

Figure 1. The occurrence and severity of rust disease of groundnut in Burkina Faso.

Breeding for Resistance to Groundnut Rust

Field screening

Following the discovery of rust in 1977, the IRHO started a resistance-breeding program at Niangoloko Research Station in the southwest (Figure 1). Commonly-grown cultivars were crossed with rust-resistant germplasm lines and their progenies screened for resistance in the field under natural disease pressure. Advanced, rust-resistant selections are now almost uniform and will be fully evaluated in field trials in 1985.

Forty cultivars germplasm lines from ICRISAT were field-screened for resistance to rust in the 1983 rainy season. Seeds were sown on 2 Jun and rust pustules appeared on susceptible genotypes by 1 Aug. Scoring for rust disease was done on 24 Aug and on 15 Sep using the ICRISAT 9-point disease-asessment scale (Subrahmanyam et al. 1982). Rust attack was very light on 24 Aug but the disease was present on all genotypes by 15 Sep (Table 1). The cultivars TMV 2, and Robut 33-1, used as susceptible checks at ICRISAT Center, were also highly susceptible to rust at Niangoloko, as were FC 76446, RMP 12, RMP 91, and NC Ac 3033. However, many of the genotypes had very low disease scores.

Rainfall was 350 mm below average in 1983 and the screening of ICRISAT material should be repeated in more normal seasons before definite conclusions can be drawn as to the resistance of the test genotypes to rust in Burkina Faso.

Laboratory screening

At a cost of approximately $400 an incubator was constructed. This was basically a wooden box lined with aluminium foil. It was cooled by an air conditioner and illuminated by 3 fluorescent tubes (30

Table 1. Mean rust disease scores for ICRISAT groundnut accessions in field and laboratory screening at Niangoloko Research Station, Burkina Faso, 1983.

Genotype	Rust disease field scores[1] on the 9-point scale on 24 Aug	15 Sep	Rust disease score[2] in detached-leaf laboratory screening
TMV 2[3]	3	9	8
Robut 33-1[3]	2	8.6	8
NC Ac 1301	2	5.5	8
NC Ac 17090	1	2	1
NC Ac 17127	1	2.6	2
NC Ac 17129	1	4	4
NC Ac 17132	1	2.5	2
NC Ac 17135	1	2	1
NC Ac 17142	1	3.1	2.5
FC 76446 (292)	1	2.1	1
CN 45-23	1	7.3	7
FC 76446	6.2	8.5	6.8
PI 298115	2	3	2
PI 259747	1	2.2	1
Krap Str No 16	2	2.1	1.6
NC Ac 927	2	3.3	6.5
RMP 12	2.4	8.3	8
RMP 91	2	9.5	4.8
PI 270806	1	2	5
PI 350680	1	2.3	3.3
NC Ac 3033	2	8.3	4.8
NC Ac 17133(RF)	1	3.2	3
PI 215696	1	4.2	6
PI 314817	2	2.3	0.3
PI 341879	1	2.1	0.1
PI 381622	2	2	2.6
PI 390593	1	2	0.3
PI 390595	1	2	2
PI 393516	2.1	4	3.8
PI 393517	1	2	0.3
PI 393526	1	2.1	1.6
PI 393527-B	1	2	6.5
PI 393531	1	2	1.3
PI 393641	2.1	2.3	7.5
PI 393643	1	2	0.1
PI 393646	1	2	1.8
PI 405132	1	2	6.8
PI 407454	1	2	0.6
PI 414331	1	2	1
PI 414332	2	3.3	7.8

1. Rust disease scored on a 1-9 scale, where 1 = no disease, and 9 = 50-100% foliage destroyed.
2. Rust disease scored on an arbitrary 1-9 scale.
3. Standard susceptible cultivars.

watts). Temperature was maintained at 20°C and relative humidity at 40%. These conditions were chosen to facilitate incubation of groundnut leaves with *P. arachidis* and to ensure good rust-disease development. The incubator was used both for multiplication of inoculum and resistance screening, the procedures being essentially the same, and using detached groundnut leaflets.

Detached, healthy groundnut leaves rooted in sterile sand were inoculated with a suspension of rust spores in water (10^5 urediniospores mL^{-1}) as described by Subrahmanyam et al. (1983). After incubation in the dark for 12 h, the leaf cuttings were subjected to a 12 h light/12 h dark regime. Rust pustules appeared some 10 days after inoculation on susceptible genotypes. Inoculum was harvested, or genotypes scored for resistance as required. The 40 ICRISAT germplasm accessions field-screened for rust resistance in 1983 were also screened using the detached-leaf technique in the incubator. Disease severity was scored on an arbitrary 1-9 scale, and rust resistance rankings were in overall agreement with those obtained by the field screening (Table 1). However, further trials will have to be carried out to determine the stability of resistance.

The nature of resistance

Rust-resistant germplasm lines introduced by IRHO were found to be susceptible in Burkino Faso and this raised the possibility of there being different pathogenic races of *P. arachidis*. Accordingly, 8 cultivars were tested for resistance to 8 isolates of *P. arachidis* collected from different parts of the country. The detached-leaf method was used and the disease scores are shown in Table 2. There was no evidence of races.

In the course of general observations it was noted that rust pustules on a 110-day old local cultivar were small and did not rupture, whereas on the susceptible cultivar 4710 pustules were large and ruptured readily. Spores were collected from both types of pustule and inoculated independently onto 10 cultivars. With both isolates small, nonrupturing pustules appeared on cultivars local, PI 341879, and PI 259747 whereas pustules on the other 7 cultivars were of the susceptible type, large and readily rupturing.

It is thought that the differences in pustule type are due to genetic differences in the defence reaction in the genotypes tested. The defence reaction may be influenced by the nutritional status of the plants and

Table 2. Mean rust disease scores for 8 groundnut genotypes in detached leaf inoculation tests using 8 different isolates of *P. arachidis*.

	Mean rust score[1] after inoculation with *P. arachidis*							
Genotype	Niangoloko	Yendore	Timperba	Banfora	Toussiana	Bobo	Sabou	Po
47-10	9	8	7	7	9	6	9	8
1S 32	7	8	6	8	8	7	6	7
TMV 2	8	8	7	7	6	7	6	8
Robut 33-1	8	8	6	7	7	8	6	7
RMP 12	7	8	6	7	6	7	7	6
RMP 91	7	8	6	7	6	7	8	6
PI 341879	1	2	2	2	2	2	2	2
PI 259747	2	2	1	2	1	2	2	2

1 Rust disease scored on an arbitrary 1-9 scale

by environmental conditions. Further studies are under way to obtain more information on the nature of resistance.

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Rust Disease of Groundnut in Maharashtra State of India

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Abstract

Rust disease of groundnut caused by Puccinia arachidis *Speg. was first recorded in Maharashtra State of India in 1973/74. It has since become a serious problem, causing yield losses of over 50%. Groundnut production in Maharashtra has declined over the past 10 years and rust disease could be an important factor in this problem. No alternate or alternative hosts of* P. arachidis *have been found and the fungus occurs only in the uredinial state. However, perpetuation of the disease has been shown to be effective. Continuous cropping of groundnut is probably important in the carry-over of the disease from year to year. The biology and epidemiology of the disease have been extensively studied. Cultural and chemical control measures have been evaluated and management practices evolved that will incorporate use of resistant cultivars as these become available. Future research priorities are indicated.*

Résumé

Rouille de l'arachide dans l'Etat de Maharashtra en Inde : *La rouille de l'arachide due à* Puccinia arachidis *Speg. fut signalée pour la première fois dans l'Etat de Maharashtra en 1973-74. Cette maladie est ensuite devenue un problème inquiétant avec des pertes de rendement dépassant 50% de la production. La production de l'arachide au Maharashtra a diminué au cours des dix dernières années; cette baisse serait attribuée dans une grande mesure à la rouille. On n'a pas encore trouvé un hôte alternant ou d'autres plantes-hôtes de* P. arachidis. *Ce champignon ne se trouve qu'à l'état urédinal. Pourtant la maladie se propage facilement. Sa transmission d'une année à l'autre est favorisée par la culture continue de l'arachide. La biologie de la rouille et son épidémiologie ont fait l'objet d'études approfondies. Les mesures culturales et chimiques de lutte ont été évaluées. Les systèmes de lutte vont intégrer des cultivars résistants dès leur production. Les recherches prioritaires à entreprendre dans l'avenir sont proposées.*

Rust of groundnut induced by *Puccinia arachidis* Speg. was first recorded in Maharashtra State of India almost simultaneously from four locations during 1973/74 (Patil and Kalakar 1974, Shukla et al. 1974, Shinde and More 1975, Garud et al. 1976a). Rust disease assumed epidemic proportions in 1976/77 (Garud et al. 1976b) and since then has been economically important in all groundnut-growing areas of the State (Mayee et al. 1977a, Mayee 1982). During this period the production of groundnut in Maharashtra declined by 35% from 639 000 t in 1975/76 to 419 000 t in 1982/83. Nearly 25% of the reduction in production appears to be due to a decrease in area under groundnut from 855 000 ha to 640 000 ha, the remaining 10% reduction being attributed to unreliable rainfall, pests, and diseases.

It is thought that rust disease has limited groundnut production in the state by lowering yields of the rainy-season crop and by promoting the process of reduction of area cropped to groundnut in the main season.

As a result, summer cultivation of groundnut, little known prior to 1976, has gained momentum and now accounts for 19% of the total area and 40% of the total production of the crop in the State. High yields of summer-season groundnut (ca. 1200-1400 kg ha^{-1}) have compensated for the yield reductions in the rainy-season crop to keep the productivity level around 600-650 kg ha^{-1}. The scope for further increase in production through expansion of area under summer cultivation is limited. Hence any production improvement program in Maharashtra

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should concentrate on increasing and stabilizing production of the rainy-season crop. In this context it is imperative that disease-management strategies should be evolved to control rust.

Losses in Yield

Pod-yield losses from rust disease commonly exceed 50% and the damage is particularly severe when the disease occurs together with early leaf spot caused by *Cercospora arachidicola* Hori and/or late leaf spot caused by *Cercosporidium personatum* (Berk. & Curt.) Deighton. The two leaf spots are often referred to in India as "tikka" leaf spot disease. Losses due to rust and leaf spots were estimated in two field experiments. It was discovered that rust could be selectively inhibited by the fungicide tridemorph (N-tridecyl-2, 6-dimethylmorpholine), and the two leaf spots could be exclusively checked by carbendazim (2-methoxy carbonylbenzimidazole) (Mayee et al. 1978 a, Mayee et al. 1979c, Ghuge et al. 1980).

In the locally-recommended bunch cultivar SB XI, rust caused losses in pod yield of 49% and reduced the kernel weight by 19% (Ghuge et al. 1981). During 1982-83, various levels of rust disease were achieved by applying different numbers of tridemorph sprays at various intervals. It was found that artificially-induced rust epidemics could cause up to 79% reduction in pod yield. When initial rust incidence and further development were manipulated by chemical spray schedules, the losses in pod yield ranged from 4.8 to 71.9%, while the kernel-weight reduction was from 1.6 to 34.1% (Mayee 1983, Mayee and Baheti in press).

Biology

Perpetuation of rust

P. arachidis produces only the uredinial stage on the host, and attempts to induce other stages, specially telia, were unsuccessful. No alternate, alternative, or collateral host could be found. *Zornia diphylla*, a leguminous weed commonly found in drier areas of Maharashtra, was extensively surveyed for rust as it has been reported as a host of a closely related rust (Hennen et al. 1976). However, no rust was found on this species and it could not be infected artificially by *P. arachidis*.

Urediniospores are short-lived under the environmental conditions prevailing after harvest in Maharashtra. They remained viable for 20 days on field debris, and for slightly longer when the harvested, dried plants were stored in bags. At low temperatures (-6° C) urediniospores survived beyond 52 days (Mayee and Ekbote 1983). Pods and seeds from rust-affected crops are commonly surface-contaminated with urediniospores, but surface-contaminated seeds failed to produce rust-diseased seedlings. The pattern of cropping in Maharashtra is such that groundnut crops are available throughout the year, thus ensuring perpetuation of rust in the uredinial stage. Groundnuts are sown from January to August depending on the availability of water. Season length of adopted cultivars varies from 90 to 150 days. On June-July sown crops the pathogen completes 6-9 cycles, while on February-April sown groundnuts, when temperatures are high, it has 1-4 cycles.

Liberation and dissemination

Wind-propelled spore traps set at 0.5 m above ground were operated continuously during 1979 and 1980. Urediniospores were caught throughout the year at Parbhani, but at low frequency from January to April. High spore-counts were recorded in September and October. Depositions were greater in the daytime than at night (Mayee and Ekbote 1983). Mayee and Ekbote (1983) demonstrated the development of elliptical infection centres governed by wind direction prior to the large-scale spread of rust. Rust is very effectively wind disseminated.

Numerical threshold

Munde and Mayee (1980) studied the factors influencing development of rust on detached leaves, and determined the optimum conditions. When inoculated leaves were incubated at 27° C and 100% relative humidity for 120 h and subjected to fluorescent light for 12 h alternating with 12 h of darkness, there was excellent development of rust. Even under these favorable conditions, no rust developed on the leaves when inoculum concentrations of less than 700 spores mL^{-1} were used. However, using the agar leaf disc technique of inoculation (Mayee and Munde 1979), single, viable urediniospores were found capable of initiating rust disease.

Variability

Cook (1972) stated that *P. arachidis* probably exists in more than one racial form. Mayee et al. (1979a) observed differential susceptibility of some groundnut genotypes over a period of two years. The pathogenic variability in rust of groundnut has neither been unequivocally confirmed nor completely ruled out. However, the present results indicate that the pathogen population has become well adapted to certain host populations under diverse environmental conditions. Thermosensitivity of three isolates collected from different agroecological regions of India differed when inoculated on detached leaves of SB XI groundnut (Munde and Mayee 1979). A set of 16 groundnut genotypes comprising resistant, moderately resistant, and susceptible reactions were planted at four locations in Maharashtra. Although no major differences in the level of resistance were noted, the area under the disease curve varied for genotypes, indicating the possibility of ecotypes in the rust population.

Epidemiology

Groundnut rust is known to infect several other members of the genus *Arachis*, but they can hardly be involved in the perepetuation of groundnut rust outside their native South America (Subrahmanyam and McDonald 1983). The urediniospores are short-lived and any break between crop seasons would be unfavorable for their carry-over. However, with the availability of irrigation, groundnut cultivation practices are so modified that the crop is available throughout the year in Maharashtra. The rainy-season crop is sown at the onset of the monsoon, which varies from June to July. Long-duration cultivars K 4-11, T 33, M 13, and local types are grown in many areas. In command areas the summer planting commences in January and continues into early May. Therefore, the continuous cultivation of groundnut appears to be the single most important factor in the perpetuation of rust in Maharashtra. Moreover, this practice of continuous cultivation of groundnuts is common in the adjoining southern states (Subrahmanyam and McDonald 1982), and inoculum from these areas could be important in the epidemiology of the rust disease in Maharastra.

In an experiment conducted for 5 years, the groundnut cultivar SB XI was sown in small plots on the 5th day of each month from Jun 1978 until Sep 1983. Rust development was recorded on the crops at intervals of 10 days. Rust developed in plots sown in every month, but the development was slow in the January- and February-sown plots. The disease development was rapid on rainy-season crops as compared to postrainy season and summer crops. The incubation period was prolonged under the high temperatures condition of the summer months. When field samples of apparently healthy leaves collected during April and May from plots sown in January and February were incubated at 27°C and 90% relative humidity, rust pustules soon erupted on the leaves, indicating the possibility of rust infection of the summer crop quite early in the season. The present trend of groundnut cultivation from January to May therefore helps in effective carry-over of the rust. Epiphytotics of rust on the rainy-season crop build up early and thus cause heavy losses.

Apparent infection rates (r) of rust ranged from 0.278 to 0.366 units per day for the crops sown in June to August, while very low infection rates were recorded for the crops sown from December to April (Mayee and Ekbote 1983). A critical analysis of periodical infection rates over a period of 5 years is presented in Figure 1. Early infection rates (i.e. up to 60 days after planting) are often high. However, during June to September high "r" values are observed until crop maturity, indicating enhanced spread of the epidemic because of favorable weather conditions during the rainy season.

The rust epidemic is dependent on many biotic factors such as infection of the host plant by other pathogens, hyperparasitization of uredosori, etc. In an experiment to study the interaction between peanut mottle virus and rust, it was found that infection with the virus prior to rust inoculation reduced rust severity (Mayee et al. 1979b, Mali et al. 1980). The uredosori are often parasitized by such fungi as *Darluca filum* (Biv.) Cast. and *Tuberculina costaricana* Syd. During 1983, a very wet year, rust development was substantially interrupted by mycoparasites. Rust alone does not induce high defoliation, but when leaf spots accompany rust, heavy leaf fall occurs. It is obvious, therefore, that biotic factors have definite roles in the epidemic buildup of rust.

Forecasting

During the last 8 years, it has been noted that rust infection occurred regularly on the rainy-season crop but the development of rust was substantially

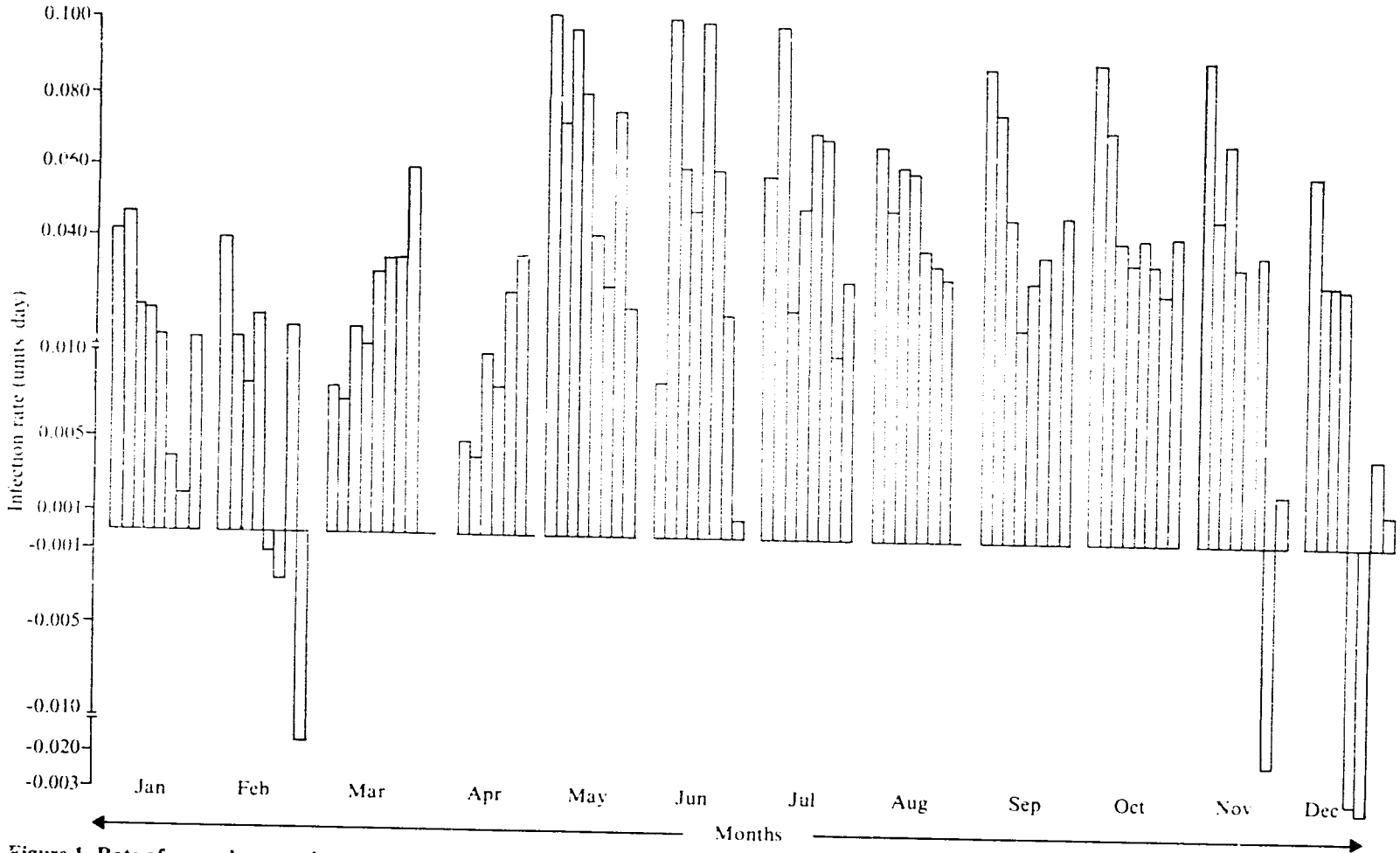

Figure 1. Rate of groundnut rust increase (apparent infection rate) during eight intervals between 40 and 120 days after planting in plots sown every month. Each bar represents infection rate for one time interval averaged over five years.

Table 1. Correlation coefficients of latent period and apparent infection rate (after 1 month) of *P. arachidis* in SB XI groundnut and environmental factors.

Environmental factors	Correlation coefficients (r) Latent period	Infection rate
Temperature		
Maximum	0.787**	0.623**
Minimum	0.259**	0.293
Mean	0.603**	0.496**
Number of days with less than 20°C	0.004	0.046
Number of days with more than 20°C	0.956**	0.046
Relative Humidity		
Maximum	0.707**	0.621**
Minimum	0.607**	0.525**
Mean	0.682**	0.592**
Number of days with less than 80%	0.901**	0.418*
Number of days with more than 80%	0.333*	0.418*
Rainfall		
Total	0.205	0.457**
Number of rainy days	0.297	0.410*
Evaporation rate	0.786**	0.692**
Sunshine hours	0.305	0.115

* Significant at 5%
** Significant at 1%

influenced by the prevailing weather conditions. Attempts were therefore made to develop a workable forecasting model based on the weather parameters. Rust progress is positively correlated with minimum temperature, relative humidity, and rainfall. Average temperatures of 20-22°C, relative humidity above 85% and 3 rainy days in a week, if continued for 2 weeks, favors outbreak of rust (Mayee 1983).

A critical study was undertaken at Parbhani on the influence of 5 temperature parameters, 5 relative humidity parameters, rainfall, number of rainy days, evaporation rate, and sunshine hours, on the latent period and early infection cycles of rust disease. All variables except rainfall, sunshine hours, and number of days with temperature below 20°C showed significant correlation with the latent period of *P. arachidis*. Temperature and evaporation rates were positively correlated with latent period while relative humidity, excepting number of days with relative humidity below 80%, were negatively correlated (Table 1). The multiple regression analysis of six combinations of environmental parameters explained more than 96% of the variation in the latent period (Table 2). The partial regression coefficients for number of days with temperature above 20°C and mean temperature, were significant, indicating high functional relationship of these parameters with the latent period of rust.

A reverse trend of relationship was observed between apparent infection rate of *P. arachidis* and

Table 2. Regression coefficients of latent period and apparent infection rates.

Independent variable	Latent period (dependent) bi	SE	Apparent infection rates (dependent) bi	SE
	(b_0 = 11.8930)		(b_0 = 0.4060)	
X1 Mean temperature (0°C)	0.2940*	±0.1290	0.0100	±0.0056
X2 Days with temperature above 20°C	1.3360*	±0.0720	0.0050*	±0.0010
X3 Mean relative (%) humidity	0.0310	±0.0380	0.0010	±0.0010
X4 Days with RH above 80%	0.3370	±0.2970	0.0002	±0.0020
X5 Total rainfall (mm)	0.0010	±0.0060	0.0002	±0.0010
X6 Evaporation rate (mm/day)	0.3430	±0.2820	0.0070	±0.0070
R^2	0.9590		0.6540	

Where $Y = b_0 + b_1 \cdot 1 + b_2 \cdot 2 + b_3 \cdot 3 + b_4 \cdot 4 + b_5 \cdot 5 + b_6 \cdot 6$
Y = Latent period or apparent infection rate.
bi = Partial regression coefficients of xi and bo = intercept
i = (1-6 variables), R^2 = Coefficient of determination
SE = Standard error

the environmental parameters. With rise in temperature the infection rate declined, whereas increase in relative humidity enhanced the rate of infection. However, the multiple regression with combinations of the six environmental factors gave a fit of only 66%, indicating that the nearly 34% variation in the infection rate observed was dependent on factors other than those considered. Temperature, however, appears to be a major factor in the development of groundnut rust.

Mechanisms of Resistance

The early stages of pathogenesis of susceptible groundnut cultivars by *P. arachidis* involved the formation of germtubes, and appresoria on the epidermis, followed by either direct penetration of the epidermis (when detached leaves were used), or entry through stomata. A comparative morphological and histological study of the susceptible and resistant cultivars indicated that minute chlorotic dots observed on the susceptible cultivars 5 days after inoculation were due to the formation of intercellular hyphae (Tables 3 and 4) after cellular contact was developed. The time taken after penetration for formation of intercellular mycelium, and aggregation of mycelia for sorus formation increased in the resistant cultivar, resulting in delayed appearance of pustules. In conjunction with the histological studies, the sequence of physiological and biochemical alterations were followed at intervals of 24 h until 19 days after inoculation when the resistant cultivar EC 76446(292) exhibited definite, dark brown, erupted uredosori. Rust disease induced changes in photosynthesis, respiration, total amino acids, sugars, phenols, nucleic acids, ascorbic acid, oxidative enzymes, and mineral contents during early stages of pathogenesis in the susceptible cultivar. Relatively minor alterations were noted in the resistant cultivar (Table 5). From the mass of changes in the physiological and biochemical processes of groundnut as a response to infection by *P. arachidis* it is inferred that alterations in respiration, oxidative enzymes, phenol, ascorbic acid, amino acid contents, and nucleic acids are primarily important in resistance as they reflect the changes in metabolism that provide for a chemical and physiological environment that is either inhibitory or conducive to the growth of *P. arachidis*. The deficiencies and excesses in mineral elements indirectly contribute to the altered physiology of the plant for causing the diseased condition (Ekbote and Mayee 1983, Ekbote and Mayee—in press).

Table 3. Time sequence of early visible symptom development of rust of groundnut.

Symptom	Time (days after inoculation) SB XI	EC 76446(292)
Minute chlorotic dots	5	11
Chlorotic flecks on upper surface	6	12
Yellow minute pustule heads	7	14
Brownish pustules (5%)	8	15
Brownish pustules (50%)	9	17
Dark brown developed pustules	9	18

Table 4. Time sequence of infection of groundnut leaves by *P. arachidis*.

Subphase	Time (h) SB XI	EC 76446(292)
Uredospore budding (through germpore)	3-4	3-4
Germination (50%)	8-9	8-9
Appresorial formation	20-24	20-24
Penetration pegs visible	24-48	24-48
Penetration occurred	40-64	40-84
Formation of intercellular hyphae	64-108	84-160
Aggregation of mycelial structures below epidermis	108-132	160-200
Appearance of pustular heads below epidermis	132-156	200-260
Subepidermal uredosori and cracks in epidermis	156-180	260-304

Management

Cultural

The influence of cultural practices such as time of planting, addition of fertilizers, and intercropping on the development of rust of groundnut have been critically examined at Parbhani with a view to utilizing the information in field-disease management. Except for the addition of phosphatic fertilizers, other practices appear to have limited scope for management of the disease. Rust progressed more slowly in treatments where 60 and 75 kg P_2O_5 ha^{-1} were applied than in those where low levels of phosphorus or no phosphorus were given (Mayee 1983).

Table 5. Physiological and biochemical changes induced by rust in SB XI and EC 76446(292) groundnuts.[1]

Parameter	%(+) (-) Over noninoculated		Parameter	%(+) (-) Over noninoculated	
	SB XI	EC 76446(292)		SB XI	EC 76446(292)
Photosynthesis	12.8	1.6	Peroxidases	+176.6	+65.9
Total chlorophyll	27.6	23.3	Catalases	+ 26.6	+16.4
Respiration	+ 49.5	+16.5	AA oxidases	+152.6	+42.8
Sugars	+ 43.0	+17.4	PP oxidases	+ 45.9	+10.3
Red. sugars	23.2	20.5	Nitrogen	24.9	5.3
Amino acids	6.3	+ 2.1	Phosphorus	10.9	12.3
Ascorbic acids	20.5	+ 7.1	Potassium	13.7	9.7
Phenols	+103.1	+72.3	Calcium	+ 22.7	+10.3
RNA	+ 11.0	+ 3.2	Magnesium	15.5	16.5
DNA	19.4	-22.4	Sulphur	31.1	16.1

1. Observations recorded at intervals of 24 h after inoculation. Data averaged over a period of 19 days after inoculation.

Chemical

Foliar applications of fungicides have been reported to markedly reduce rust spread (Smith and Littrell 1980, Mayee 1982). Inorganic sulphur fungicides applied either as dusts or wettable powders were initially recommended for control of rust and leaf spots (Patil and Kalekar 1974). Subsequently, the organosulphurs such as mancozeb and maneb were found superior in reducing rust and increasing the pod yield of the recommended cultivar SB XI (Mayee et al. 1977b, Patil et al. 1979, Wangikar et al. 1981).

In a series of trials conducted over 3 years, it was found that the systemic fungicide tridemorph was highly selective for controlling rust, and carbendazim for controlling leaf spots of groundnut (Mayee et al. 1978a, 1979c, Ghuge et al. 1980). The efficacy of these chemicals against rust and leaf spots was also proved in the multiseason experiment at another location in Maharashtra on four cultivars of groundnut. The cost benefit ratio of the combined application was 1:2 (Patil et al. 1984). However, the cost of these chemicals is high for groundnut farmers, and it is essential to work out the conditional profit function based on the number of sprays. Mayee and Baheti (1983) found that early applications of tridemorph were more effective in reducing the rust epidemic than applications later in the season. Four or more applications of the chemical gave significant additional increases in yield. Under resource constraint conditions where funds are limiting, it is necessary to apply the sprays so as to obtain maximum profits. In the case of rust management, it was found that when funds were sufficient for applying only 2 sprays, then to derive maximum profit the first spray should be given at 30 days after planting and the second at 54 days after planting (Mayee et al. 1985).

These decisions, however, could be different for leaf-spot management and therefore a complete foliar-disease management strategy needs to be established for each agroclimatic zone depending upon the relative importance of the diseases. Wankhede and Mayee (1980) examined the possibility of reducing initial inoculum of rust by use of systemic fungicides as seed dressings, but it was clear that after 1 month the chemicals applied as seed dressings could not give adequate protection.

Smith and Littrell (1980), pointed out that though breeding for resistance to foliar diseases of groundnut was under way at several locations, release of agronomically acceptable, disease-resistant cultivars was still awaited. Therefore attention should be given to refining chemical and non-chemical control strategies.

Host resistance

None of the groundnut germplasm lines available at the Oilseed Research Station, Latur, was found resistant to rust. From the elite material received from ICRISAT, several sources of resistance were identified. Accessions PI 259747, PI 350680, PI 407454, EC 76446 (292), NC Ac 17090, NC Ac 17135, and NC Ac 17142 were rust-resistant. These lines are being used in the breeding programs at all the groundnut research centres in Maharashtra. Deokar et al. (1983) studied the inheritance of rust resistance and found that resistance in PI 259767 is governed by a recessive gene.

Future Research Priorities

Because of the increasing costs of purchasing and applying fungicides for management of foliar diseases, there is a need to develop new cultivars with disease resistance. Additional information on cultural management for reducing rust disease will be useful in formulating integrated management. Similarly, spraying technology, and scheduled applications based on precise predictions would go a long way in combating the disease economically. The long-distance movement of rust needs to be understood before a perfect system is devised to predict rust occurrence in different parts of the country.

There is a wide gap in the present knowledge of pathogen variability. It is necessary to make an in-depth study of the race situation so that the breeding programs can be undertaken on a sound footing.

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Groundnut Rust Research in Thailand

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Abstract

Groundnut rust caused by Puccinia arachidis *Speg. was first seen in Thailand in 1970. The disease soon spread to all groundnut-growing areas and is now endemic. Rust occurs on groundnut crops in all three growing seasons but is serious only on the early rainy-season crop where, in conjunction with the leaf spot diseases, it has been shown to cause losses in pod yield of 27-85%.*

Only the uredinial stage has been found and the rust occurs only on groundnut. There is no indication of occurrence of different pathogenic races of P. arachidis *in Thailand. A mycoparasite,* Darluca *sp, occurs and may reduce rust attack when groundnuts are cropped successively on the same field. Plants can be infected at any age.*

For management of rust disease, attention has been given to cultural, chemical, and resistance-breeding approaches. In Thailand the use of cultural methods is limited. Several fungicides have been tested for control of rust and the leaf spots. Dithiocarbamate, chlorothalonil, and a combination of benomyl and oxycarboxin were all effective. ICRISAT field disease screening and scoring techniques were introduced and proved effective in identifying rust-resistant genotypes that are now being used in the rust-resistance breeding program.

Résumé

Recherche sur la rouille de l'arachide en Thaïlande : *Dès son apparition en 1970 en Thaïlande, la rouille de l'arachide (*Puccinia arachidis*) s'est propagée dans toutes les zones arachidicoles du pays. La maladie devenue endémique, attaque les cultures de toutes les trois campagnes agricoles. Cependant, seule la culture pluviale précoce subit des pertes élevées allant de 27 à 85% du rendement en gousses; celles-ci sont dues aussi bien aux maladies des taches foliaires qu'à la rouille.*

Le pathogène n'est connu qu'au stade urédinal et la rouille n'atteint que l'arachide. Il n'y a aucune indication de l'existence de différentes races pathogènes de P. arachidis *en Thaïlande. Le mycoparasite* Darluca *sp. serait utile à réduire l'incidence de la rouille en cas de cultures successives de l'arachide sur le même champ. Les plantes sont attaquées à n'importe quelle époque de leur vie. Dans la lutte contre la rouille, l'accent est mis sur les méthodes culturales, chimiques et de sélection de la résistance. En Thaïlande, les méthodes culturales de lutte ne sont pas très répandues. Parmi les fongicides mis à l'essai contre la rouille et les taches foliaires, le dithiocarbamate, le chlorothalonil et une combinaison de bénomyl et d'oxycarboxine se sont tous révélés efficaces. Les techniques de criblage au champ et de notation mises au point par l'ICRISAT se sont avérées utiles dans l'identification de génotypes résistants. Ces génotypes sont actuellement utilisés dans le programme de sélection pour la résistance à la rouille.*

Groundnut rust caused by *Puccinia arachidis* Speg. was first observed in the northeastern region of Thailand in 1970 (Kanlong et al. 1971). Two years later, it had spread into the northern region causing considerable yield losses (Schiller and Indraphun 1978). The disease is now endemic to all groundnut-growing areas of the country. Rust can be found on groundnut in any growing season, but the highest incidence and severity is observed on the rainy-season crop where conditions are most favorable for

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its development. Combined loss from rust and leaf spots was estimated in 1978 at 27-85% (Schiller and Indraphun 1978).

Prior to 1982, the main research activities were screening for resistance to rust and investigations on chemical control. At present, more attention is being given to the biology of *P. arachidis* and to epidemiological studies. Information concerning these two aspects is still largely lacking for the agroecosystems of Thailand.

Biology of *Puccinia arachidis*

Only the uredinial stage of the pathogen was found in the rust disease samples collected from the different regions of Thailand. There has been no report of the telial stage in the country. The urediniospores were similar in both size and appearance to those described by Cummins (1978). The lesions induced by the pathogen were either of multipustule or unipustule type, depending on the host cultivar. A mycoparasite, *Darluca* sp, was usually found associated with the rust pathogen in disease samples collected from the northern and northeastern regions (Wongkaew and Surin 1983). At present, there is no indication of race variation among the isolates collected from the different groundnut-growing regions (Wongkaew and Surin 1984). There have been no reports of any alternate host for groundnut rusts.

Epidemiology of Rust Disease

Although the disease can be found throughout the country in all three growing seasons, in farmers' fields its peak incidence is in the early rainy-season crop (sown in mid-April to early March). Both the incidence and severity are minor in the late rainy-season crop (sown in mid-July to early August) and the dry-season crop (sown in mid-January). There is variation in disease incidence and severity depending on the location rather than the geographical region. By monitoring the epidemic pattern of the disease in experimental fields at Khon Kaen (northeastern region) it was found that plants could be infected at any age, but most often at the flowering stage. The infection rate was fastest in crops sown in mid- or late June and in late August (Wongkaew and Larppanya 1983). In the 2nd year of monitoring, groundnut plants grown successively in the same plots were observed to be less affected by rust than plants grown after another crop. It was speculated that the buildup of a population of the rust parasite *Darluca* sp may be linked to this reduction.

Management of Rust Disease

Although such cultural practices as sowing groundnut at a specific date or in a specific season have proved to be effective in reducing rust damage, their applications have in practice been rather limited, due to the diversity of cropping cycles in the country. Therefore, research has been concentrated on chemical control and breeding rust-resistant cultivars.

Chemical control of rust

There have been two types of experiments conducted on chemical control of rust disease. In a disease nursery where screening for leaf-spot resistance was being performed, there was need only for fungicides that are specific for control of the rust pathogen. For this purpose, oxycarboxin (0.05% a.i.) applied at 14-day intervals was effective in controlling rust but did not give any control of *Cercospora* leaf spot diseases. A larger dose, as recommended for other crops, was tested and found to be very phytotoxic to groundnut (Wongkaew et al. 1985). Pyracarbolid and carboxin were not effective against rust. The former also caused injury to groundnuts (Wongkaew et al. 1983). Since leaf spots caused by *Cercosporidium personatum* and *Cercospora arachidicola* are also found to be destructive to groundnuts, the other investigation in the experiment was to find chemicals effective against all three foliar diseases. It was found that the combination of benomyl and oxycarboxin (Chompoonutprapa and Sripoley 1973), and dithiocarbamate (Kitisin et al. 1976) were effective and economical for control of the foliar diseases if sprayed five times at 2-week intervals in each crop. Chlorothalonil alone, or mixed with oxycarboxin, was equally effective (Chompoonutprapa and Sripoley 1973). The yield increases from chemical control ranged from 47% to 300% (Kitisin et al. 1976).

Screening for rust resistance

Prior to 1982, screening cultivars for rust resistance was conducted almost entirely under natural conditions using only the natural inoculum source

Table 1. Rust scores of certain groundnut lines tested in the rust-disease nursery at Khon Kaen University, Thailand.

Pedigree	Rust score (at 83 days after sowing)[1]	Comments[2]
(GAUG 1 × PI 279747)-5-1-1-F5	2	Hypersensitive reaction
(GAUG 1 × PI 259747)-10-1-1	2	"
PI 296115	2	"
(Chico × PI 259747)-1-1-1	3	"
(Chico × PI 259747)-1-1-2	3	"
(NC Ac 2564 × NC Ac 17090)F2-P28-B1-B1-B	3	"
ICG 2337 NC Ac 2569	4.5	
JH 60 × FC 76446	4.5	C.R.
M 13 × Dht 200	4.5	C.R.
KUP 080	4.5	
KUP 362	4.5	C.R.
KUP 083	4.5	C.R.
(OB 69-6-1 × NC Ac 17090)F2-12-1-1	4.5	
ICG 5053 SB NC Ac 2433	5	
ICG 1697 NC Ac 17090	5	C.R
ICG 2956 SM 5	5	C.R
(C 148 × PI 259747)-7-2-1-1-F5	5	
FC 76446 (292)	5	C.R.
Singh	5	
PI 309839	5	C.R.
A2 Rust Res. ICRISAT 7	5	
(NC Ac 17135 × Robut 33-1)F2-B1-B1	5	C.R.
(75 24 × NC Ac 17090)F2-P1-B1-B1-B	5	
(JH 89 × NC Ac 17090)F2-B1-B1-B1-B1	5	
ICG 4991 SBNC Ac 2903	5	
ICG 2376 SBNC Ac 2944	5	
ICG 2309 SBNC Ac 2155	5	
(NC Ac 17142 × TMV 2)	5	C.R.
(FC 76446 (292) × Robut 33-1)	5	C.R.
Robut 33-1 × Dht 200	5	
Argentine × NC Ac 17090	5	
M 145 × NC Ac 17090	5	C.R.
KUP 009	5	
KUP 084	5	C.R.
KUP 370	5	
KUP 497	5	
KUP 248	5	
(Punjab × PI 259747)-7-1-10	5	
(RS 114 × FC 76446)F2-2-2-1-1	5	
(NC 17 × NC Ac 17090)F2-P2-1-1-1-1	5	C.R.
PI 314817	5	C.R.
PI 259747	5	C.R.
(Gadjah × PI 314817)-13-1-30	5	C.R.
(CES 103 × PI 314817)-3-1-5	5	
(JH 171 × NC Ac 17090)F2-B1-B1-B1	5	
ICG 1703 SB NC Ac 17127	5	C.R.
(JH 89 × PI 407454)F2-B3-B2	5	

Continued.

Table 1. *Continued.*

Pedigree	Rust score (at 83 days after sowing)[1]	Comments[2]
(NC-Fla 14 × FC 76446 (292))F2-1-1-1-1	5	C.R.
ICG 2254 SB NC Ac 60	5	C.R.
ICG 2400 SB NC Ac 1672	5	
(Taiwan 2 × PI 314817)21-1-46	5	
Tainan 9 (susceptible check)	8.5	

1 Mean of scores from two seasons except for those of KUP code number, using the 9-point disease scale where 1 = no disease, and 9 = 50-100% of foliage destroyed

2 C.R. = resistant to leaf spots

(Chompoonutprapa et al. 1974, Kitisin et al. 1982-1984). As a consequence, results were inconsistent and unreliable. The methods of screening and scoring for disease severity were also not standardized, hence the results obtained from different sources could not be compared. In 1982, the infector-row technique developed at ICRISAT was tested and found to be very effective (Wongkaew et al. 1983). This technique and the associated disease-scoring method (9-point scale) are now widely adopted and are currently used at Khon Kaen where the central rust disease nursey is located. In this nursery the native Tainan 9 cultivar is used as a susceptible check and as an inoculum spreader. The infector row to test rows ratio is 1:4.

Screening under greenhouse conditions has also been performed regularly by the Department of Agriculture and the results compared with those obtained from the field (Boothanu et al. 1983). In each season, about 200-300 genotypes or cultivars received from domestic agricultural institutes and from abroad are screened in the central rust nursery at Khon Kaen University. ICRISAT and the North Carolina State University are the major contributors of resistant sources from outside the country. Table 1 shows some of the lines that have been found to be highly or moderately resistant to *Puccinia arachidis*. A breeding program for rust-disease resistance has been initiated using local cultivars and identified resistant sources as parent materials. In 1983, an experiment was conducted to determine suitable criteria for use in evaluating rust resistance of test genotypes using a detached-leaf technique. It was found that lesion size and incubation period were two assessed criteria that correlated well with field resistance. Cultivars that produced small lesions when infected with the rust pathogen were evaluated as highly resistant in the field. The pathogen had longer incubation periods on these cultivars (Wongkaew and Tangthumniyom 1984).

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Groundnut Rust in Central Thailand

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Abstract

Groundnut rust is an important disease in central Thailand causing epidemics on the rainy season crop. Symptoms of rust, and the morphology of the pathogen are described. High rainfall, high atmospheric humidity, and air temperatures around 29-30°C favor rust attack. When the ICRISAT rust-disease nursery was grown at Kampaengsaen Research Station, only the genotype ICG 4740 showed marked resistance. Several fungicides were tested but none gave good control of rust at the concentration and application rate used. Future research will examine the biology and epidemiology of groundnut rust. Management of the disease will be attempted using resistant cultivars and fungicide applications.

Résumé

Rouille de l'arachide dans le centre de Thaïlande : *La rouille de l'arachide est une maladie importante dans le centre de Thaïlande où elle est responsable des épidémies chez les cultures pluviales. Les symptômes de la rouille et la morphologie du pathogène sont décrits. La forte pluviosité ainsi que l'humidité et les températures (environ 30°C) élevées créent des conditions favorables aux attaques de la rouille. A la Station de recherches de Kampaengsaen, seul le génotype ICG 4740 s'est montré résistant parmi le matériel expédié par l'ICRISAT pour les essais de résistance à la rouille. Plusieurs fongicides sous étude ne se sont pas manifestés efficaces au dosage utilisé. Les recherches ultérieures porteront sur la biologie et l'épidémiologie de la maladie. La lutte contre la rouille reposera sur l'emploi des cultivars résistants et des fongicides.*

Groundnut rust disease (*Puccinia arachidis* Speg.) is one of the two most important diseases of groundnut in central Thailand and throughout the country. The rust epidemic generally occurs at the same time as that caused by leaf spot (*Cercosporidium personatum* (Berk. & Curt.) Deighton), during the heavy rainfall months of Jul to Sep. Research on groundnut rust is being carried out in Thailand by the Department of Agriculture, Khon Kaen University, and Kasetsart University. Research by Kasetsart University is conducted at the Suwan and Kampaengsaen stations where the major objective is to assist the breeder to produce a groundnut cultivar suitable for the Central Plain.

Rust Disease Symptoms

The first obvious symptom of groundnut rust is the appearance of yellow-orange pustules on the lower surfaces of leaflets. The pustules enlarge and rupture exposing brown urediniospores. As the disease develops the affected leaflets become chlorotic, then necrotic, and finally they wither and may fall off.

Morphology

The rust-susceptible cultivar Tainan-9 was used in laboratory studies of pustule development. Inoculated leaves were incubated at 20°C in petridishes at high humidity. The incubation period was 5-6 days. Pustules developed from pale yellow lesions, which increased in size and eventually ruptured to release the brown urediniospores. Mature urediniospores are binucleate and measure 21.9 × 25.63μ. In the presence of water and at 20°C in the dark they germinate within about 3 hours.

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Epidemiology

It is not yet known how the rust survives from season to season in the Thailand agroecosystem, but significant outbreaks occur during the rainy season. To better understand the rust epidemic, records were collected in Jul-Aug 1984 of rainfall, relative humidity, and air and soil temperatures, and were then correlated with rust disease development on groundnuts as measured on the 9-point scale at weekly intervals. High relative humidity and air-temperatures of 29-30 °C favored buildup of groundnut rust. It may eventually be possible to develop a rust forecasting program, based on climatic data, that can be used to assist in rust-disease management.

The International Groundnut Foliar Diseases Nursery

The ICRISAT International Groundnut Foliar Diseases Nursery (IGFDN) was sown on Kampaengsaen Research Station farm on 16 May 1984. The test accessions were surrounded by border rows of a rust-susceptible cultivar, Taiman-9, sown 2 weeks earlier. Rust disease developed early on the border rows and spread to the infector rows and test accessions. Rust disease scores on the ICRISAT 9-point scale indicated that only the entry ICG 4746 showed any marked resistance to the disease. Further studies are required to confirm the rust reactions of these genotypes. The rust disease levels were high and Kampaengsaen is obviously a very suitable location for screening germplasm for rust-disease resistance.

Screening Fungicides for Control of Rust Disease

The commercially available fungicides Difolatan® (captafol), Brestan® (FPTA), Delsein MX® (mixture of carbendazim and mancozeb), Carbenzin® (carbindazim) and Benlate 75C® (carbendazim) were selected for test. Dosage response curves were determined for each fungicide for inhibition of urediniospore germination. The ED 50 values were 10 ppm for Brestan®, Delsein M® and Benlate 75C®, and 50 ppm for Difolatan® and Carbenzin®. Based on these results, the fungicides were applied to rust-susceptible groundnuts in a field trial. All five fungicides were applied at a concentration of 2000 ppm. None gave satisfactory control of groundnut rust (Table 1).

Table 1. Efficiency of five fungicides for control of groundnut rust at Kampaengsaen, Thailand.

Fungicide applied	Mean rust score from 4 replications (ICRISAT 9-point scale)[1]
Brestan® (FPTA)	6.07
Delsein MX® (MBC + mancozeb)	6.12
Carbenzin 60® (MBC)	6.33
Benlate 75 C® (MBC)	6.52
Difolatan® (captafol)	6.82
Control	7.58

1 Field disease scale where 1 = no disease, and 9 = 50 to 100% of foliage destroyed

Future Research on Rust Disease

It is proposed to conduct research on the following:

- Biology and epidemiology of groundnut rust
- The life cycle of the pathogen
- Rust-disease management through the use of fungicides and resistant cultivars.

Occurrence and Importance of Rust Disease of Groundnut in Nigeria

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Abstract

Rust is one of the major foliar diseases of groundnut in Nigeria. Yield loss estimates in 1982 indicated that it was responsible for 0.7-1.4 t ha⁻¹ loss in pod yield of cultivar F 152-4. In drier years, yield losses due to rust are usually much lower.

The occurrence of the disease is highly dependent on the amount and spread of rainfall. In the wetter parts of Nigeria where rainfall is spread over 7 to 9 or more months, the disease occurs regularly at high intensity. In the drier groundnut-growing areas however, its occurrence is normally mild to insignificant.

Control of the disease has been achieved by foliar application of mancozeb and tridemorph fungicide formulations. More recently, resistant cultivars with widespread ecological adaptation (e.g., cv RRB) are being evaluated for eventual distribution to farmers.

Résumé

Rouille de l'arachide au Nigéria : *Au Nigéria, la rouille est une maladie foliaire importante de l'arachide; par exemple, en 1982, les pertes de rendement en gousses du cultivar F 152. l'étaient estimées à 0,7-1,4 tonnes hectare. Les pertes sont moins élevées aux années plus sèches.*

L'apparition de la maladie dépend largement de la pluviométrie et de sa distribution. Dans les régions plus humides du pays où la saison des pluies dure 7 à 9 mois, parfois plus, les attaques sont intenses et régulières, tandis que dans les régions plus sèches elles sont modérées à négligeables.

L'application des fongicides mancozèbe et tridémorphe sur les feuilles de la plante permet de lutter contre la rouille. Des cultivars résistants à bonne adaptabilité (ex. cultivar RRB) sont en cours d'évaluation avant d'être vulgarisés auprès des paysans.

The major foliar diseases of groundnut (*Arachis hypogaea* L.) in Nigeria are early leaf spot (*Mycosphaerella arachidis* Deighton, conid: stat: *Cercospora arachidicola* Hori), late leaf spot (*Mycosphaerella berkleyi* W.A. Jenkins, conid: stat: *Cercosporidium personatum* (Berk. & Curt.) Deighton), rust (*Puccinia arachidis* Speg.) and groundnut rosette (Salako, 1981, 1982, 1985). Leaf scorch (*Leptosphaerulina* sp) occurs with some regularity, especially in the wetter years, but does not seem to constitute a threat to the crop as the maximum level of occurrence has never been above 10%.

Occurrence of Rust of Groundnut

Based on the Commonwealth Mycological Institute maps, numbers 16 and 160, rust of groundnut was apparently unknown in Africa prior to 1969. By 1983 the distribution of the disease had covered 75% of the continent. The first record of the disease in Nigeria was in 1976 (Arokoyo et al. 1977) from the northeast part of the country from where it rapidly spread to all major groundnut-producing areas. By 1980, rust was well established in the areas south of latitude 11°30'N where widespread damage occurred each year. In the drier areas north of 11°30'N latitude the occurrence of rust and damage due to the disease has not been significant.

In the Northern and Southern Guinea Savanna zones of Nigeria, it is possible to conduct field screening for rust resistance with considerable success, with or without artificial inoculation. But in drought years, (e.g., 1983) success could be attained

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only in the Southern Guinea Savanna zone. Screening trials are, therefore, always replicated in these two zones to ensure success.

Occurrence of rust is highly dependent on the amount and spread of rainfall. Figure 1 shows the scores for rust at various periods during the growing seasons of 1981 and 1983 at Mokwa and Samaru. The cultivar 1452-4, which is highly susceptible to the disease, was used as the disease indicator. Mokwa is located in the Southern Guinea Savanna while Samaru is in the Northern Guinea Savanna. In 1981 there was adequate rainfall at both sites, 1058.2 mm at Mokwa and 1019.1 mm at Samaru. Mokwa, as usual, had the slightly higher rainfall. Rainfall at Mokwa is normally spread over 7-8 months, while in Samaru the spread is over 5 to 6 months. Scores for leaf spots and rust were the maximum attainable in 1981 at Mokwa, while scores were near maximum at Samaru. In 1983, there was drought at both sites, annual rainfall being 653.2 mm at Mokwa and 610.0 mm at Samaru. The Mokwa crop however, established earlier than the Samaru crop thereby providing higher humidity in the crop microenvironment. This enhanced the establishment of rust and was responsible for its greater development at Mokwa. At Samaru the crop established rather late, resulting in a relatively scanty canopy. This was not optimum for rust establishment and development. At both sites leaf spots developed well as shown by the near-maximum scores recorded.

Groundnut cultivation is gradually increasing in the southern part of the country (south of latitude 9° N) (Harkness and Salako, 1982) due to increasing home consumption and continuous appreciation of the market values of the haulms and the seeds. The southern production area is regarded as a secondary production area. The bottleneck in production there has been the devastating effect of the major foliar diseases (leaf spots and rust). The rainy season in some of the areas spans from March/April to October/November, making postharvest drying difficult. In addition, the environment favors volunteer crops that serve as sources of primary inoculum. When the late-maturing cultivars resistant to these diseases

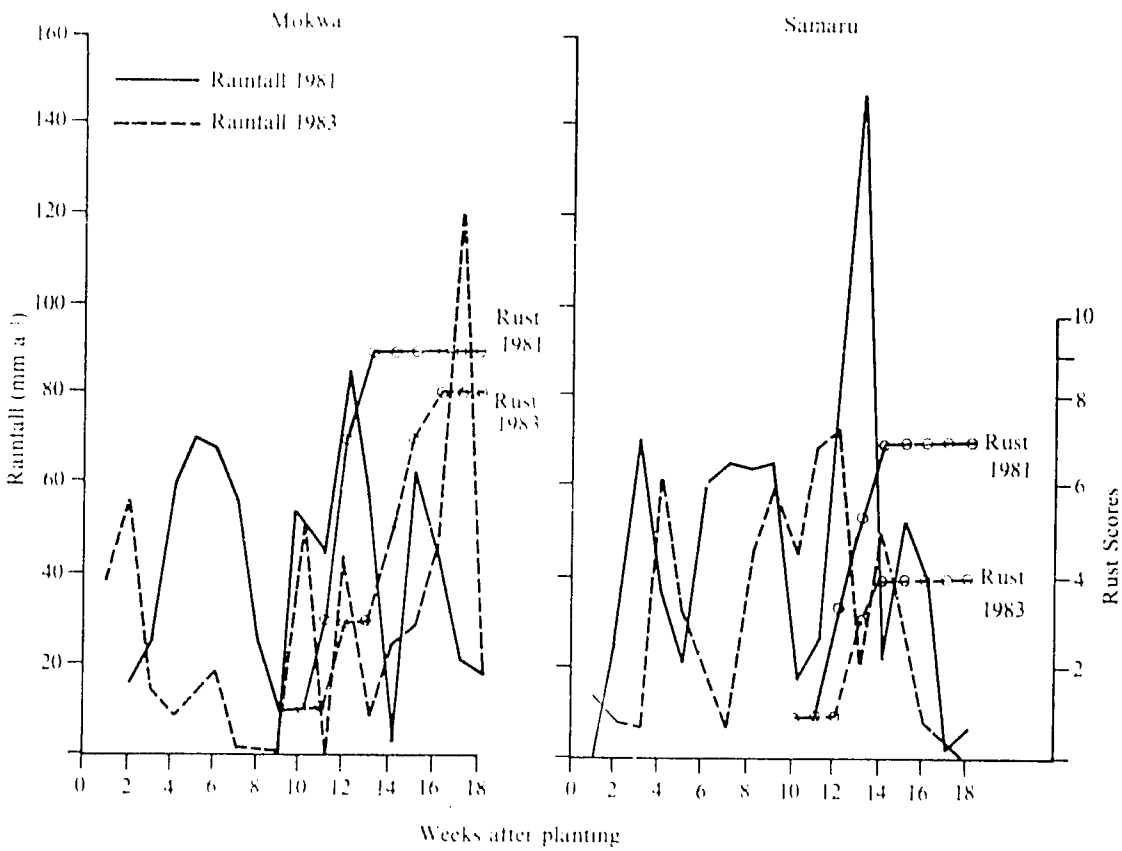

Figure 1. Rainfall and groundnut rust incidence at Mokwa and Samaru.

now being bred at the Institute for Agricultural Research are released, it is expected that groundnut cultivation in the southern areas will receive a great boost.

Importance of Rust

Wherever it occurs, rust disease significantly reduces the yield of the crop. In conjuction with the leaf spots, the yield is drastically reduced. The foliage rapidly withers (giving rise to "hot spots" of "charred" plants). This reduces photosynthetic activity and the translocation of photosynthesates to the developing seeds (Salako 1981). Table 1 shows typical results obtained from field trials with fungicides for control of rust and leaf spots on cultivar F452.4. Estimated pod yield losses from rust alone ranged from 0.7 to 1.4 t ha^{-1}, while rust and leaf spots could jointly cause 1.5-2.0 t ha^{-1} pod yield losses. It is clearly desirable to control all the three foliar diseases, especially as they almost always occur together. Foliar application of fungicides and genetic resistance are the major control measures for the diseases.

Control of Rust by Fungicide Application

Mancozeb (ULV and WP formulations) and tridemorph + maneb (systemic, ULV and medium volume applications), are quite effective in controlling rust and leaf spots (Salako 1982, 1984).

Another dimension to fungicidal control is the possible interaction between fungicides and the level of applied phosphorus. Plants that did not receive any fertilizer (single superphosphate), but were sprayed with tridemorph formulations were either scorched or stressed, which resulted in reduced yields.

Preliminary results from trials at Mokwa in 1983 in respect of S0 (no single superphosphate) and S4 (200 kg ha^{-1} of single superphosphate) had the following highlights:-

- Pod-yield differences between tridemorph + maneb and BAS 350 treated plots were S0 = 325 kg ha^{-1} and S4 = 188 kg ha^{-1}.
- Pod-yield difference between tridemorph + maneb and mancozeb treated plots were S0 = 421 kg ha^{-1} and S4 = 46 kg ha^{-1}.

Evidently, an adequate level of superphosphate fertilization is required for effective utilization of fungicides. Farmers who may not be in a position to provide the optimum level of fertilizer should be able to choose between fungicides. This option is what this project was designed to provide.

Table 1. Fungicidal control of groundnut rust and leaf spots in the field trials at Samaru and Mokwa, 1982.

Fungicide treatment	Mean[1] pod yield (kg ha^{-1}) Samaru	Mokwa
Rust and leaf spots controlled	3021	3111
Rust only controlled	1986	1296
Leaf spots only controlled	2323	1556
No disease control	1567	1024
SEM	±177.3	±197.1
CV (%)	15	23

1. Mean of four replications.

Breeding for Resistance

The increase in frequency of rust outbreaks in several groundnut-growing areas, and the acquisition of rust-resistant germplasm from researchers and institutions in several parts of the world, facilitated the initiation of a rust-resistance breeding program. The parent lines used in the program had varying levels of leaf-spot resistance.

The objectives of the Institute's groundnut breeding program (Harkness and Salako 1982) are to develop:

- Drought, rosette, and leaf spots resistant, early maturing, high-yielding lines for the Northern Guinea Savanna zone.
- Rosette, leaf spots, and rust-resistant, early- to medium-maturing, high-yielding lines for the Southern Guinea Savanna zone.
- Rosette, leaf spots, and rust-resistant, late-maturing, high-yielding lines for the more southern, "secondary" groundnut production zone.

From a set of crosses made in 1977, initial selections were made in the F_2 generations in 1979.

Further single-plant selections were made in 1980 and 1981. Selections were based on reaction to rust and leaf spots, yield potential, and other agronomic traits. Infector indicator rows of cultivar F452.4 were sown systematically between the entries and around the whole trial, and the young plants were inoculated with rust. Plants having at least 40 (usually about 50-60) pods were selected if they possessed the other desired traits. In 1982, further selections were made. The selected entries and their reactions to rust and leaf spots are shown in Tables 2 and 3. The early- to medium-maturing selections mature in 95-105 days. They tend to mature early in the drier zone. Entries 2-10 originated from the cross KH 149 × 2424.74. The cultivar KH 149 is a rosette-resistant Senegalese crossbreed that is also early, while 2424.74 had the rust-resistant *A. monticola* as one of its parents. The best single plants from these entries were bulked. This early-maturing bulk, now known as Red Resistant Bulk (RRB) is performing well, giving pod yields of 3000-3500 kg ha⁻¹, and is adapted to a wide range of ecological zones. The other entries shown in Table 2 have demonstrated similar high-yield potentials.

The late-maturing selections shown in Table 3 are also potentially high yielding. Parents were mainly rosette-resistant females and rust-resistant males. Entry K 2990.80 is particularly noteworthy for its high level of resistance to rust and late leaf spot.

Newer crosses have been made using more recently available rust-resistant accessions. The progenies of these crosses are now in the F_3 stage, and selection will commence in the 1984 growing season. Apart from the Red Resistant Bulk made from the earlier crosses, a few more cultivars will hopefully emerge. In addition, selections from both the earlier and the recent crosses will be incorporated in the Institute's multiple-disease resistance project.

Table 2. Reactions of early- to medium-maturing selections to early and late leaf spots and rust, 1982.

	Mean disease score (1-9 scale)[1]		
Selection	Early leaf spot	Late leaf spot	Rust
M 362.81H	2.5	4.5	2.8
M 654.81H	3.5	3.5	3.8
M 656.81H	3.0	3.5	4.0
M 668.81H	3.8	4.0	3.0
M 673.81H	3.5	3.5	3.8
M 675.81H	3.0	4.0	3.0
M 695.81H	3.3	4.8	3.0
520.81H	3.8	3.5	2.0
548.81H	2.5	4.0	3.5
549.81H	3.0	3.0	4.0
K 2896.81H	2.5	5.5	3.0
K 3007.80	2.0	4.3	1.0
K 3140.79	2.3	4.8	2.0
586.81H	2.0	4.5	2.5
615.81H	2.0	5.0	1.0

1. Disease scoring scale where 1 = no disease, and 9 = 50% or more foliage destroyed.

Table 3. Reactions of late-maturing selections to early and late leaf spots and rust, 1982.

	Mean disease score (1-9 scale)[1]		
Selection	Early leaf spot	Late leaf spot	Rust
343.81H	3.0	1.5	4.0
590.81H	3.0	1.8	4.5
K 2964.80	2.8	4.5	2.5
K 2970.80	2.0	4.0	4.0
K 2990.80	3.3	1.0	1.0
K 3041.80	2.0	5.0	3.8
M 354.81H	2.5	3.0	5.0
M 304.81H	3.8	1.5	5.0

1. Disease scoring scale where 1 = no disease, and 9 = 50% or more of foliage destroyed.

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The Groundnut Rust Situation in the People's Republic of China

Zhou Liang-gao[1]

Abstract

Rust disease of groundnut was first found in the People's Republic of China in 1934; it appeared in southern China in 1956 and caused sporadic outbreaks over the next 13 years. In 1969 the disease damaged the autumn crop in Guangdong Province, and has been a serious problem in the region ever since. Rust symptoms, biology of the fungus, the infection process, disease cycle, and epidemiology are described. Cultural and chemical control measures are described. Crop hygiene and adjustment of sowing dates are important. Several fungicides are effective for control of rust but time of spray application is most important. Screening of exotic groundnut germplasm has been successful and several rust-resistance sources are being used in a breeding program. Some rust-resistant genotypes show different degrees of resistance when screened in Guangzhou as compared with ICRISAT Center in India; this may indicate a race occurrence in Puccinia arachidis.

Résumé

Rouille de l'arachide en République populaire de Chine : *La rouille de l'arachide fut signalée pour la première fois en République populaire de Chine en 1934. Elle fit son apparition dans le sud du pays en 1956 où elle était sporadique pendant les 13 prochaines années. Depuis 1969, lorsqu'elle a attaqué la culture d'automne, la rouille pose un problème grave dans la province de Guangdong. L'auteur décrit les symptômes, la biologie du champignon, le processus d'infection, le cycle de la maladie et son épidémiologie. Les mesures de lutte culturale et chimique sont présentées. L'hygiène des plantes et l'adaptation des dates de semis sont des éléments importants. Plusieurs fongicides sont efficaces, cependant l'époque de leur application est d'importance primordiale. Le criblage de matériel génétique exotique a fourni plusieurs sources de résistance déjà intégrées aux programmes de sélection. La variation dans le degré de résistance de nombreux génotypes au Guangzhou et au Centre ICRISAT en Inde, laisse supposer l'existence de races au sein de* Puccinia arachidis.

Distribution and Importance of Groundnut Rust

Groundnut rust disease caused by *Puccinia arachidis* Speg. is one of the more serious foliar fungal diseases of groundnut (*Arachis hypogaea* L.) in the People's Republic of China. The disease was first recorded in Hebei Province in 1934 (Tai 1937), but no more was heard of it until 1956 when it was found at Xinhu Agricultural Experiment Station in Guangdong Province. Thereafter, sporadic outbreaks were noted over the next 13 years in Guangdong, Guangxi, Fujian, Jiangxi, Hunan, Hubei, Hebai, Jiangsu, Shandong, Sichuan, and Liaoning Provinces. In 1969 there was an outbreak of rust on the autumn crop in Guangdong Province and the disease spread rapidly during 1970-1973 causing severe damage in 1973. Rust is now a regular and important limiting factor for groundnut production in Guangdong, Guangxi, and Fujian Provinces. In recent years the disease has become more severe in the central and northern regions of Shandong.

In southern mainland China, two main groundnut crops are grown each year. The spring crop is sown

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in February-March and harvested in June-July; the autumn crop is sown in August and harvested in December. Rust is generally more severe on the larger spring crop than on the autumn crop, which is the main source of seed for sowing. However, rust can be serious on the autumn crop in some seasons, and it regularly causes significant damage to this crop in Fujian and Jiangxi Provinces.

Yield losses from rust range from 15-59% depending upon the severity of the disease attack and on the stage of development of the crop when the attack begins. Experiments using artificial inoculation have shown that rust attack at flowering results in a pod-yield loss of 49%, while attack at pegging, at pod initiation, and at the middle of pod formation, causes losses of 41%, 31%, and 18%, respectively. In addition to reducing numbers of mature pods available at harvest, rust attack reduces mean weights and oil content of seeds.

The Infection Process

Whole leaflets were examined by the method described by McBryde (1936) to study the infection process in groundnut rust. Germination of urediniospores started about 2 h after inoculation and appressoria formed at the tips of the germtubes in 6 h. Infection pegs were then formed from the appressoria and the mycelium entered the leaflet through the stomata. Penetration directly through the epidermis was also seen; this took place between epidermal cells, and was not common.

Once within the leaflet, the rust mycelium increased in length, attaining 8.7, 12.5, and 22.5μ, within 6.5, 14, and 20 h, respectively. After 77 h, the mycelium had produced branches and formed haustoria, and its total length was around 80μ. After 120 h, the mycelium had increased in size and a few uredinia had been initiated. After 168 h, it was possible to discern minute, white pustules (uredinia) that contained urediniospores that had achieved their maximum dimensions. The mycelium was extensive and amply provided with haustoria. By 192 h (8 days), typical uredinia had developed and ruptured to expose the reddish-brown, mature urediniospores.

Symptoms of Rust

Rust disease symptoms have been well described by Garren and Jackson (1973). The rust fungus can infect and produce uredinia upon all above-ground parts of the groundnut plant except the flowers; uredinia have also been found on pods. On the foliage the uredinia are circular, or roughly circular, in shape, and are often surrounded by narrow, yellow halos. Leaflets with many uredinia rapidly become chlorotic and then necrotic, they dry up, shrivel, and eventually fall off. Plants attacked early in development are stunted and may mature some 2-3 weeks earlier than healthy plants. Pods often become detached and are left in the ground at harvest.

The uredinia formed on stipules are similar in shape but rather larger than those on leaflets. Uredinia on petioles and stems are elliptic and up to 2 mm in length. Uredinia formed on shells are circular to irregular in shape and up to 2 mm in diameter.

Biology of Rust Fungus

Only the uredinial stage of *Puccinia arachidis* has been found in China. Under favorable conditions the mature urediniospore begins to germinate within 1 h. Although there are two germpores, the spore usually produces only one germtube. With optimal moisture and temperature the development is rapid and infection takes place within 9 h.

The optimum temperature range for urediniospore germination is 24.5-28°C. Thermal death point is 50°C for 10 min. No germination occurs below 8°C and very little above 31°C. Viability declines rapidly when urediniospores are kept at high temperatures. At summer season room temperatures at Guangzhou, spores retained viability for 16-29 days. When they were stored at 40°C they remained viable for 9-11 days, and when stored at 45°C they were viable for only 7-9 days. However, at winter and spring temperatures spores retained viability for 120-150 days. When stored at 5°C spores could remain viable for over a year.

Light has an adverse effect upon urediniospore germination. Direct, intense sunlight inhibits germination, but some spore germination can take place on shaded leaflets in the daytime. In the laboratory it was found that light of over 8000 lux completely inhibited germination, some germination occurred at 3000 lux, and spores germinated well at below 100 lux (Zhou et al. 1980).

Urediniospore germination was also inhibited under anaerobic conditions and also by high concentrations of spores, the latter effect probably being due to production of a self-inhibitor.

Disease Cycle and Epidemiology

Research at Guangzhou (Anon. 1974, Zhou et al. 1980) has shown that rust inoculum can come from various sources.

1. Rust-infected crops: Urediniospores from the rust-infected spring crop may infect the summer crop that is sometimes grown in southern China and spores from the summer crop can then infect the autumn crop. Spores from the autumn crop could then infect the winter crop in Hainan from which spores could infect the next spring crop.
2. Rust-infected volunteer plants: Volunteer plants from the autumn crop can safely overwinter and urediniospores produced on them can infect the spring crop. Similarly, rust-infected volunteer plants from the spring crop can co-exist with the autumn crop and serve as inoculum.
3. Infected crop debris: Urediniospores on infected crop debris from the autumn crop can retain their viability through the winter months and give rise to infections in the spring crop in the following year.
4. Rust-infected pods: It was found that urediniospores on infected pods, or dusted onto healthy pods, could retain viability for 132 days at temperatures of 18-20°C, indicating another possible carry-over mechanism.

As no host of rust other than the groundnut has been found in China, the above inoculum sources are considered to be responsible for the carry-over of rust in southern China. Rust-infected volunteer plants are probably the most important sources of inoculum.

No detailed studies have been made of primary rust inoculum sources in central and northern China, but the main source may well be wind-borne urediniospores from southern China.

Optimal temperatures for spore germination and for infection have already been described. Another effect of high temperature is that it speeds up evaporation of water from the leaflet surface, thus decreasing the rate of infection. Incubation period is also affected by temperature, being increased when it is below 21°C or above 29°C. Typical incubation periods at different temperatures are as follows: 18 days at 18°C, 10-14 days at 24°C, 6-8 days at 24.5-26°C, and 9 days at 29°C.

Plants inoculated at the 2-leaf, 4-leaf, and early-flowering stages all developed rust and there were no differences in infection success or in incubation periods.

Humidity after inoculation was important for successful infection. In an experiment, inoculated plants were kept at 25.5-26°C in moist chambers for 4, 6, 8, and 23 h. Even after only 4 h in the moist environment, infection occurred but at low severity; after 6 h at high humidity infection was 100%, but rust severity increased with longer periods of incubation at high humidity. Climatic conditions in southern China in the spring and summer are highly conducive to rust infection and to rapid build-up of the disease. Severe rust is often found after typhoons.

Rust development is also affected by soil type, sowing date, fertilizers used, and irrigation practices, with sowing date being the single most important factor.

Disease Management

Cultural measures

Removal of crop debris and eradication of volunteer plants can greatly reduce carry-over of rust inoculum between crops. Early sowing of the spring crop and late sowing of the autumn crop increases the time gap between them for survival of urediniospores, it also helps to avoid environmental conditions favorable to rapid establishment and build-up of rust epidemics.

Chemical control

Many chemicals have been tested for control of rust disease. Highly effective fungicides were: Baycor 300EC® (1:1000), 0.5% of Bordeaux mixture, chlorothalonil (75% Daconil® 1:600), experimental fungicide F 849 (1:500), 97% sodium P-aminobenzene sulfonate (1:600), and experimental fungicide BAS 3170 (1:1000). Moderately effective fungicides were: colloidal sulphur (1:150), 45% Ambam (1:800), 50% Fermate® (1:300), 50% Monzet® (1:800), 50% Zerlate® (1:300), 50% captan (1:300), experimental fungicide 25% 3050 F (1:500), and experimental fungicide 3191 (1:500). Salts of fluosilicate, RH 124, caused phytotoxicity (Anon. 1975 and 1977). Non-effective chemicals were: experimental fungicide CW 524, 50% Bavistin®, and Validamycin®. The unsectioned leaf method (McBryde, 1936) demonstrated that application of Bavistin® increased the

amount of *P. arachidis* mycelium in the leaf by 10 times compared with an untreated control leaf measured 5 days after infection, so it is not advisable to apply this fungicide on its own to control leaf spots when rust is also present.

Time of spraying is the key to good control of rust. Even a moderately effective fungicide can give good rust control if applied at the right times. Delay in starting spray applications from when 45% of plants were infected to when all were infected reduced gains from fungicide application from 64 to 31%. In Guangdong Province it is best to start spraying when 50% of plants are infected, 5% of leaves are infected, or when the disease index is less than 2.

Disease resistance

Screening of local cultivars was carried out in several Provinces, and during 1974-1976 over 1000 accessions were evaluated in Guangdong Province but none was resistant to rust. Following consideration of the literature on rust resistance (Bromfield 1971, 1974; Bromfield and Cevario 1974; Hammons 1980; Subrahmanyam et al. 1982), rust-resistant genotypes were obtained from the USA and from ICRISAT. Screening of this material showed that the Tarapoto lines (PIs 259747, 250680, 381622), Israel line 136 (PIs 298115, 315608), and FC 76446(292) were highly resistant to rust. Lines DHT 200 (PI 200 314817) and PI 393518 showed moderate resistance to rust. In Guangdong, PI 298115 and PI 315608 showed an immune reaction to rust in early stages of growth, and had only a few uredinia on the lower leaves at harvest, but at ICRISAT they were rated as only moderately resistant; NC Ac 17090 showed high resistance to rust at ICRISAT but was only moderately resistant in Guangdong, Guangxi, and Hubei Provinces. This variation in reaction of specific genotypes to rust in southern China and India suggests that pathogenic races of *P. arachidis* occur.

Tifrust lines 1-12 were moderately susceptible to rust apart from lines, 7, 8, and 12, which showed moderate resistance. The wild species (*Arachis glabrata*), PI 231318, and PI 262801 were immune to rust.

Components of resistance included longer incubation period, reduced size of uredinia, failure of uredinia to rupture, reduced spore production, and low infection frequency.

Rust-resistant genotypes have been crossed with local high-yielding cultivars and some promising lines obtained. Breeding for rust resistance is described in more detail by Zheng Guangrou (these Proceedings).

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Breeding for Resistance to Groundnut Rust in the People's Republic of China

Zheng Guangrou[1]

Abstract

Rust disease regularly causes groundnut pod yield losses of 20-50% in southern China. Rust-resistant genotypes from ICRISAT were crossed with local high-yielding cultivars. Yui-10 116 × EC 76446 (292) proved to be a good combination. Some promising rust-resistant selections have been made in the F_6-F_9 generations. Experiments were conducted to study the inheritance of rust-resistance and involved half and full-diallel crosses. More than two genes were involved, and this agrees with other reports.

Résumé

Sélection pour la résistance à la rouille de l'arachide en République populaire de Chine : *Dans le sud de la Chine, la rouille est responsable des pertes régulières allant de 20 à 50% du rendement en gousses. Parmi les croisements des génotypes résistants de l'ICRISAT avec des cultivars locaux à haut rendement, le croisement Yui-10 116 × EC 76446 (292) a donné de bons résultats. On a repéré quelques descendances intéressantes aux générations F_6 à F_9. L'étude de l'hérédité de la résistance faite à partir de croisements diallèles complet et partiel (50%), met en évidence le rôle de plus de deux gènes, ce qui corrobore les résultats obtenus ailleurs.*

Groundnut breeding started in the People's Republic of China in 1954 at the Guangdong Economic Crops Research Institute (GECRI). The main objectives of the program are to breed high-yielding cultivars with resistance to rust (caused by *Puccinia arachidis* Speg.) and bacterial wilt (caused by *Pseudomonas solanacearum* E.F. Smith). These are regarded as the most serious diseases of groundnut in southern China. It has been estimated that in this region rust regularly causes yield losses of 20-50%. If rust resistance could be incorporated into a high-yielding adapted cultivar, then groundnut production in southern China would be greatly increased.

Screening for Resistance to Rust

Forty-two groundnut genotypes including 38 rust-resistant germplasm lines, and 2 rust-susceptible check cultivars (TMV 2 and Robut 33-1) from ICRISAT, and 2 local check cultivars, i.e., Baisar Aiyon (very susceptible to rust in southern China) and Yui-io 116 (tolerant to rust in southern China), were screened in two spring seasons and one autumn season (1981-82) at the GECRI. Disease scores were fairly constant across seasons. With the exception of the four check cultivars and the genotypes NC Ac 1307, EC 76446, MRP12, and MRP91, all the entries showed resistance to rust disease. The Israel line 136 (PI 298115, PI 315608) was highly resistant to rust but susceptible to late leaf spot. Seventeen of the rust-resistant genotypes were resistant to late leaf spot, and of these 11 were also resistant to early leaf spot.

The yields of the rust-resistant genotypes were all significantly lower than that of the local check Yui-io 116, and had quality defects that precluded their direct use. However, they could be used as parents in a rust-resistance breeding program.

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Breeding for High Yield and Rust Resistance

Rust-resistant genotypes were crossed with high-yielding but rust-susceptible local cultivars. Back-crossing and multiple crossing was also done. Some mutation breeding was conducted using ethyl methansulfonate and Co seed treatments. Progenies were used as parents in crossing. All materials were field screened for resistance to rust, leaf spots, and bacterial wilt.

Some promising lines were selected from the F_6-F_9 generations. They showed high resistance to rust and had good yield potential. Yui-io 116 × EC 76446 (292) proved to be a an excellent combination and many lines have been selected from it that have moderate rust resistance, large numbers of pods per plant, large seeds, and high shelling percentages. Yindu Huapi is also a good source of resistance to rust and bacterial wilt. The line Yui-io 39 was selected from the cross Yui-io 116 × Yindu Huapi, and the F_9 is highly resistant to rust and is high yielding; it is now being tested in yield trials.

The Inheritance of Rust Resistance

Two experiments were conducted at GECRI in 1981-83, one involving a half-diallel cross, and the other a full-diallel cross, to study the inheritance of rust resistance. Resistance to rust was found to be recessive and preliminary results indicated that more than two genes were involved, agreeing with other published reports.

Acknowledgement

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Rust Disease of Groundnut in Southern Africa: Present Situation and Possible Interactions with Other Groundnut Foliar Diseases

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Abstract

Groundnut rust was first reported from southern Africa in 1974. It spread rapidly, and is now endemic in the region. Serious outbreaks of rust appear to be confined to specific groundnut-growing areas, and the disease is of sporadic occurrence elsewhere in the region. Rust-prone areas are at low altitudes where temperatures and humidity are high. Spread of rust disease in southern Africa may be limited by the problem of carry-over of inoculum from crop season to crop season over long dry seasons. Breeding for rust-resistance has had low priority in the region but resistant germplasm and breeding lines from ICRISAT are under test in several countries. Mycoparasites may play a part in reducing the rust inoculum late in the season. Rust may have to compete with other foliar diseases that are common in southern Africa.

Résumé

Rouille de l'arachide en Afrique australe—situation actuelle et interaction eventuelle avec d'autres maladies foliaires de l'arachide : *La rouille de l'arachide fut signalée pour la première fois en Afrique australe en 1974. La maladie est devenue endémique sauf à sa propagation rapide dans la région. Ses attaques n'atteignent un niveau grave que dans certaines régions arachidicoles; elles sont sporadiques ailleurs. Les zones favorables à l'attaque sont situées aux altitudes inférieures, la température et l'humidité y étant élevées. La progression de la maladie en Afrique australe serait limitée par les longues saisons sèches qui entravent la transmission de l'inoculum d'une campagne agricole à l'autre. La sélection pour la résistance n'était pas jusqu'ici prioritaire; mais on entreprend actuellement des essais de matériel résistant de l'ICRISAT dans plusieurs pays de l'Afrique australe. Les mycoparasites seraient également utiles à réduire l'inoculum vers la fin de la campagne. La concurrence eventuelle de la rouille avec d'autres maladies foliaires répandues en Afrique australe est à noter.*

It is 10 years since the first report of rust (*Puccinia arachidis* Speg.) on the African continent came from Zimbabwe in March, 1974 (Rothwell 1975). Reports from other southern African countries followed in quick succession. It was observed in Zambia and Malawi in 1975 (Raemakers and Preston 1977) and also in the Transvaal region of South Africa that same year (Young, Blamey, and Chapman 1980). It is also present in Mozambique and Tanzania. Its sudden appearance and the speed with which it spread through southern Africa gave cause for concern, but although it is now endemic in the region, serious rust outbreaks are confined to specific groundnut-growing areas and in the remainder of the production areas, its presence is somewhat sporadic. Partly because of this, very little work on rust has been done here.

Location of Rust

It appears that conditions in many groundnut-producing areas of the region are not optimal for widespread rust outbreaks. There are two factors

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likely to limit rust. One of these may be high altitude, and consequently, low humidity. Where groundnuts are grown below an altitude of 750 m, rust can be a major constraint to production, e.g., in the lakeshore area of Central Malawi and the Northern and Southern regions (Subrahmanyam 1983), which all lie below 500 m (Fig. 1). Rust was reported as one of the most important diseases of groundnut in the Nampala district (altitude 0-1000 m) of Mozambique in 1980-81 (Malithano 1981), although in the latest annual report rust is given no special mention as a constraint to groundnut production (Malithano 1985) (Fig. 2).

The Naliendele district of southern Tanzania lies between 500-1000 m and is one of the major groundnut-producing areas of Tanzania. Simons (1985) considers that rust is now one of the major diseases on groundnuts in the district, though as late

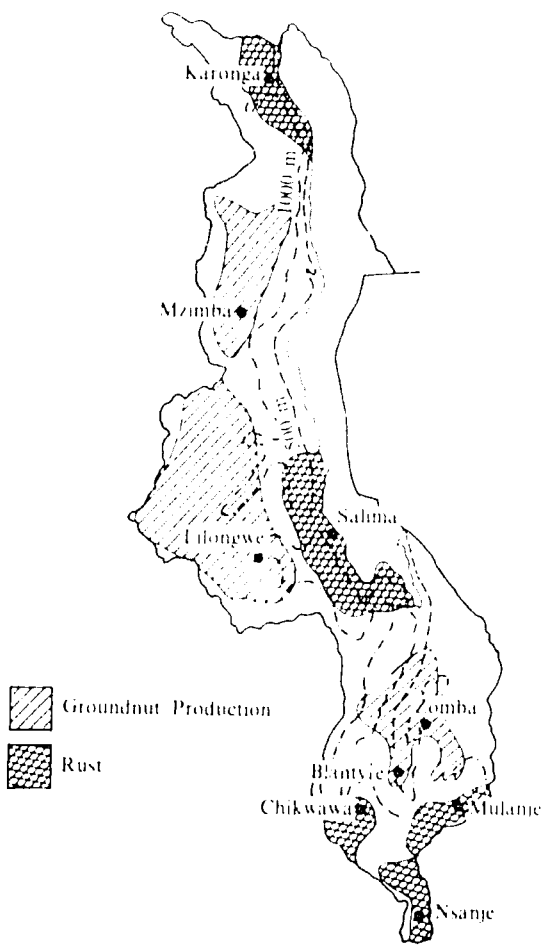

Figure 1. Main groundnut-producing areas in Malawi.

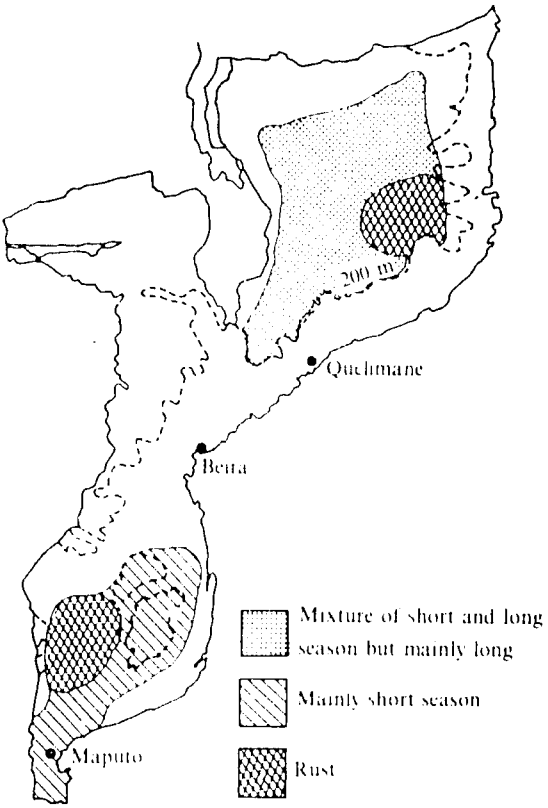

Figure 2. Main groundnut-producing areas in Mozambique.

as 1980, Bolton (1980) made no mention of it in his report. All other groundnut-growing areas of Tanzania are at higher altitudes, but little information on the importance of rust is available (Fig. 3).

Like Tanzania, much of the groundnut production in southern Africa occurs at elevated levels between 900-1500 m. At these elevations the humidity is generally low, and although day temperatures are comparatively high, about 27-30°C, night temperatures drop below 20°C during the growing season. Under these conditions, urediniospore reproduction and buildup is probably much slower, so that it is only towards the end of the season that sufficient inoculum is present to cause measurable visible infection.

In Zimbabwe where most groundnuts are grown in the middle (900-1200 m) to high veld (over 1200 m), rust is not a problem, and in some years it is not observed though more usually it appears shortly before lifting. It seems fortuitous then that the first report of rust should come from Zimbabwe, but this was on an experimental crop in the lowveld (altitude

Figure 3. Main groundnut-producing areas in Tanzania.

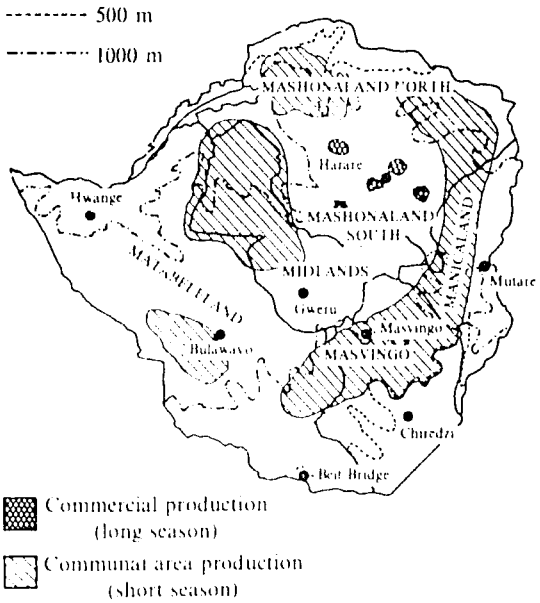

Figure 4. Main groundnut-producing areas in Zimbabwe.

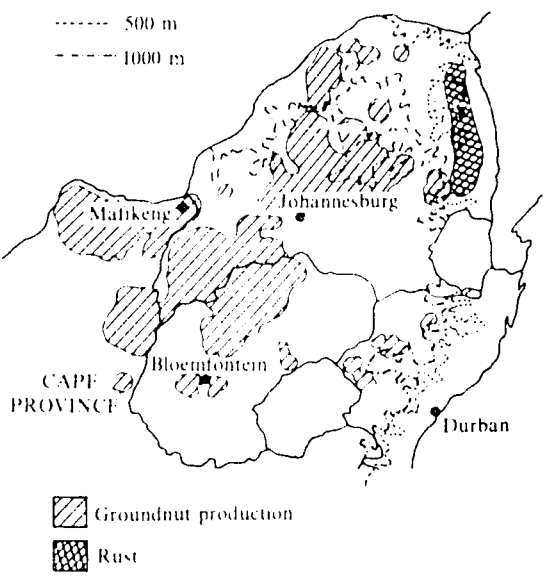

Figure 5. Main groundnut-producing areas in South Africa.

430 m), which is not traditionally a groundnut-growing area. The following year however, it was recorded from all areas (Fig. 4).

The main groundnut-growing areas of South Africa are situated at altitudes of over 1000 m and rust is occasionally recorded, but there are small areas of groundnut in the Eastern Transvaal grown below 900 m where rust is present every year, although serious yield losses because of rust have not yet been reported (Swanevelder, personal communication) (Fig. 5). Yet at similar altitudes in the Western Transvaal and in adjacent areas in Botswana, rust is not of any consequence (Mayeux, personal communication) (Fig. 6). In Zambia, rust was initially recorded in all groundnut-growing areas (Raemakers and Preston 1977) but serious outbreaks seem to be confined to the Eastern Province (Sandhu, Kelly, and Kannaiyan 1985) where much of the groundnut-growing area is below 1000 m. (Fig. 7).

A second factor that limits rust spread is likely to be urediniospore overwintering. Continuous cropping is thought to be important in rust carry-over as the urediniospores, which are the only spores produced by *P. arachidis* in southern Africa, do not survive long in crop debris (Subrahmanyam and McDonald 1982). With the exception of southern Mozambique where the first crop is planted from July to October and the second crop in December-January, (Malithano 1981) all other areas grow a single crop per season. The main constraint to double cropping is the short duration of the rainy sea-

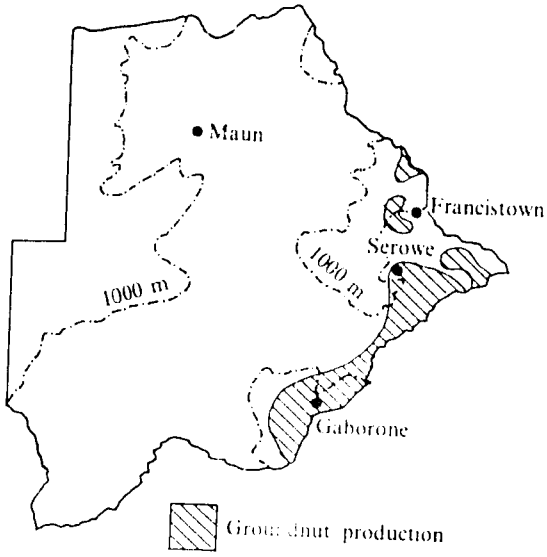

Figure 6. Main groundnut-producing areas in Botswana.

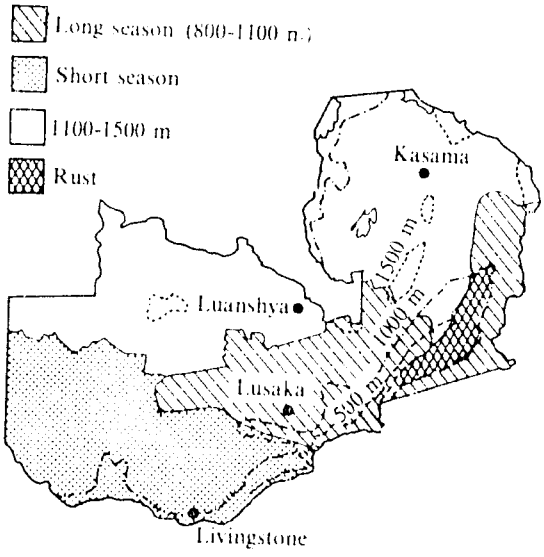

Figure 7. Main groundnut-producing areas in Zambia.

son, which starts in October-November and tails off in March, except in some parts of Tanzania where it continues raining until May-June (Mwenda 1985).

Rust urediniospores have somehow to overwinter for 6 dry months. Volunteer groundnuts are not responsible to any extent for carrying urediniospores over the winter because the dry conditions do

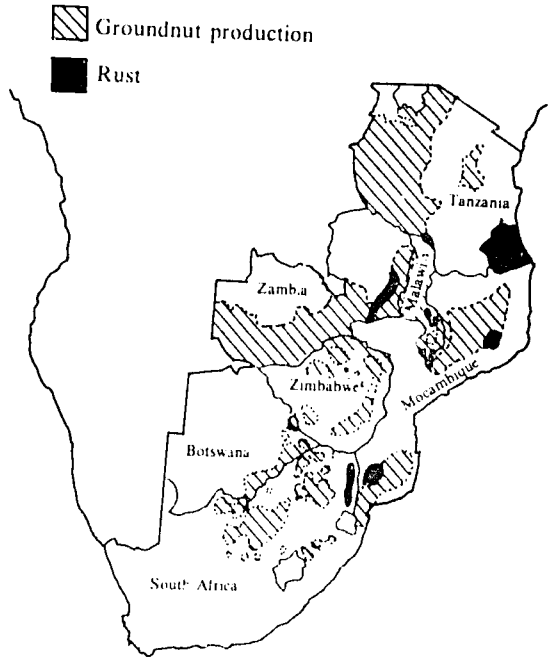

Figure 8. Main groundnut-producing areas in southern Africa.

not allow many plants to survive. It is more likely that the spores are transported from an area where they are always present, e.g., southern Mozambique, (although rust has not been reported as a major problem in this area) to the inland areas (Fig. 8). If this was so, it could account for the very late appearance of rust in the interior even at susceptible sites like the rust-prone areas of Malawi, where it appears comparatively late in the season although it spreads rapidly and may cause "substantial losses" (Subrahmanyam 1983). In Zimbabwe rust appears 15-30 days before harvest and is often confined to isolated plants in the field. Even if it does spread beyond this initial focus, the levels of infection are still low (Table 1).

Table 1. The percentage incidence of rust on the long-season groundnut cultivar Egret at Henderson Research Station (alt. 1300 m), Zimbabwe, in late February 1982, 3 weeks before harvest.

Fungicide treatment	Incidence of rust disease (%)
No fungicide	9.2
Chlorothalonil sprays	3.1
Mancozeb + benomyl sprays	7.5
Bitertanol sprays	4.4

Rust Management

Breeding for resistance

Breeding for resistance has had a relatively low priority in much of the region. From 1977-81 (Anon. 1977-78 to 1980-81) the FESR rust-resistant lines obtained from the United States Department of Agriculture (USDA) were screened for rust resistance in Zimbabwe. Their resistance to rust was satisfactory, but their yield potential was low. Many of the lines had undesirable marketing qualities such as poor shelling percentage, purple seeds, and a high percentage of shrivelled kernels. Because of this and the low incidence of rust, and other more pressing breeding priorities, the program was suspended.

Rust-resistant lines are being screened in Mozambique (Malithano 1985) and Tanzania (Mwenda 1985) where selections are being made, especially from ICRISAT segregating material. With the establishment of the ICRISAT Regional Center in Malawi, rust-resistant lines will be more readily available for testing in the countries of the region.

Biological control

The mycoparasite, *Eudarluca caricis* (Fr.) O. Eriks has been regularly observed in rust pustules in Zambia (Raemakers and Preston 1977) and in Zimbabwe (Rothwell 1975; Cole, personal observation). Another mycoparasite belonging to the genus *Darluca* has been reported from Malawi (Subrahmanyam 1983). These fungi would have little effect in slowing down rust epidemics but may be important in reducing the number of urediniospores produced towards the end of the season because in many parasitized pustules, no urediniospores are visible (Cole, personal observation).

Interactions with Other Groundnut Diseases

This has not been studied in Zimbabwe because of the late occurrence of rust. It is quite possible that earlier colonizers such as the leaf spots would deplete the leaves of essential nutrients and make them a less suitable substrate for rust germination and infection. *Cercosporidium personatum* also colonizes the abaxial surface of leaves under the same conditions as rust and these pathogens may compete for sites. The possibilities of pathogens producing fungitoxic compounds that inhibit one another, needs to be studied, but preferably in an area where leaf spots, both early and late, and rust are economically important.

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Discussion

Chairmen: D. McDonald, J.A. Wightman

Rapporteurs : P. Subrahmanyam, A. B. Mohammad, and L.J. Reddy

L.J. Reddy. The two breeding lines PI 414331 and PI 414332 from Honduras have no flowers on the main stem and have an alternate branching habit. Also, they have fresh seed dormancy. Hence we consider them to be virginia (*hypogaea*) type.

R.O. Hammons. These are cultivars (rather than breeding lines) and have rather complex pedigrees. The Florispan Runner parent is the product of a four-way cross involving spanish and runner genotypes. Resistente Corto and Resistente Largo have some characteristics similar to those of each ancestral parent group. Hence it is not strictly accurate to place them in a botanical category such as *hypogaea* or *vulgaris*. Unfortunately, terms have yet to be coined for accurately defining the botanical affinities of germplasm with a background of *hypogaea*, *fastigiata*, and *vulgaris* ancestry.

J.E. Parlevliet. In your presentation, you stated that most lines were susceptible to rust disease and only a few resistant. Does this suggest a discontinuous distribution of this characteristic?

R.O. Hammons. Whether or not the distribution is (was) discontinuous is a good question. We do not have an answer. By choosing to evaluate all possible accessions from Peru and those of *fastigiata-fastigiata* type, we undoubtedly obtained a higher return of resistant genotypes than would have been possible with a random sample. A similar and classic case is that of resistance to bacterial wilt in groundnut. Schwarz found only a few surviving plants in a badly diseased area. Subsequent evaluation in the same field led to the development and release of the Schwarz 21 cultivar, which "saved" the groundnut industry in Java 60 years ago.

V. Ramanatha Rao. I would like to emphasize the importance of documentation in keeping track of material with its right number (identity), origin, etc., so that no further confusion will be caused in the germplasm collection or in the literature. This must be taken care of while screening and reporting.

R.O. Hammons. Of the 24 accessions of rust-resistant *hypogaea* from Peru, 8 have been released. We are way behind other crops as far as utilization of resistance is concerned.

R.W. Gibbons. Many of the South American germplasm lines are in fact market samples and are mixtures. Initially when some of these collections were screened we found a mixture of rust reactions and we separated resistant and susceptible lines, e.g., resistant lines from NC Ac 17133 were called NC Ac 17133-RF because the resistant plants were red-flowered (RF). It is, therefore, important to quote the full numbers/names of the resistant sources in the literature to avoid confusion.

R.O. Hammons. The Plant Inventory (PI) system in the USDA-ARS encourages scientists to document such separate phenotypes with a new P.I. number. Did you assign different ICG numbers for NC Ac 17133-RF and NC Ac 17133?

V. Ramanatha Rao. Yes. NC Ac 17133 is ICG 1708, and the rust resistant selection NC Ac 17133-RF is ICG 7013.

J.F. Hennen. What is the explanation for rust resistance centering in Peru?

R.O. Hammons. This is an interesting question since Peru is definitely not the place of origin of groundnut. However, Peruvian farmers grew peanuts in a fairly "modern" agricultural venue long ago. It is possible to guess that 90% of the resistant lines accessioned thus far could be descended from some ancestral type. A more concentrated effort has recently been made to obtain and screen Peruvian material. Tarapoto and DHT 200 (Tifrust-14) both came from Peru, causing us to postulate that location as being a good prospect for a more intensive search.

C.D. Mayee. How much are the wild species of *Arachis* being used in Latin America for resistance breeding?

R.O. Hammons. Work in this area was undertaken by Dr. A S. Pompeu at Campinas (S.P.) Institute of Agronomy, but has received a setback because of his illness. As far as I can ascertain in talking with recent *Arachis* germplasm explorers, there is no such work being done at present.

R.N. Strange. Is the association of wettability of leaves with susceptibility to rust diseases related to the leaching of a self-inhibitor from the rust spores?

D.L. Cole. An inhibitor is known.

E.A. Salako. Your disease scores were based on numbers of lesions 10 cm^{-2} of leaf area. Why then did your scores increase and differ from time to time with increase in days after inoculation?

K.J. Middleton. This could be because of poor identification of early phases of lesion development.

L.J. Reddy. By "juvenile" leaves and "mature" leaves do you mean just young and old leaves collected at the same plant age, or were they collected at two different plant ages?

The pattern of resistance in the reciprocal crosses seems to follow the pattern of the female parents. How sure are you that the hybrids were genuine? They could possibly be selfs.

K.J. Middleton. The leaves were taken from different node positions on plants of the same age. The data shown are the means of several plants.

J.E. Parlevliet. This is a remark in relation to the susceptibility of young versus mature leaves. Not only the age of the leaf, but also the age of the plant and the position of the leaf on the plant may affect its susceptibility.

K.J. Middleton. Acknowledged, but all plants used in this study were of the same age. The important thing to note is the reversal of trend between two susceptibles plus one resistant parent; and the other two resistant parents.

P. Subrahmanyam. We studied effects of plant age (30, 60, and 90 days) and leaf age on rust development and components of rust resistance and found strong effects of plant and leaf age. Young leaves were more susceptible than older leaves. We did not find any differences between juvenile and mature leaves in leaf wettability and we believe that something beyond leaf wettability is involved in our observed differences in susceptibility of juvenile and older leaves.

K.J. Middleton. All the plants were of the same age when we compared juvenile and old leaves.

J.E. Parlevliet. Differences in cultivars could also be important; those with sinks may be more susceptible.

K.J. Middleton. All the plants were in the vegetative stage when tested.

R.O. Hammons. Did you choose the leaves from the same location?

K.J. Middleton. Yes, they were of the same age.

R.W. Gibbons. Spanish types are more susceptible than virginia types of the same age because spanish types do have sinks earlier during their growth and appear more susceptible. There is much in the literature about this. There are also morphological differences between spanish and virginia types. Why do you have more rust in Burkina Faso than in Nigeria and Niger? Can it be explained purely by climatic conditions?

P. Sankara. We have rust in the southwest of Burkina Faso because there we have a good rainfall with low temperatures (19-20°C). With these climatic conditions, the rust develops very quickly and susceptible cultivars can be completely destroyed.

P. Subrahmanyam. Climatic conditions can be important for rust development. Epidemics of rust do not occur in northern Senegal.

R.W. Gibbons. Do you grow two crops a year in Burkina Faso?

P. Sankara. No, we grow only one crop.

R.O. Hammons. Is wind movement a factor in the rapid buildup of rust in Burkina Faso?

P. Sankara. Yes, there is much air movement in the production fields. Rust was first observed in the Ivory Coast.

D. McDonald. When rust was first found in Nigeria in 1975 it appeared to have come from the north-

east. In subseqeent years the rust disease spread from the southwest on the monsoon winds. In Nigeria the rust probably survives in the wet southern areas of the country where groundnuts are grown as backyard crops.

J.F. Hennen. Did you study the developmental morphology of sori from initiation to spore formation, sporogenous cells and number of spores produced per sporogenous cell?

P. Sankara. During our observations we did not study the developmental morphology of sori. We did not observe differences in the morphology of rust spores.

A.S. Rao. We are interested in studying the histopathology of pustule development from the time of entry of the pathogen up to sporulation, in susceptible and resistant cultivars. There has not been any published information on that. Moreover, the rate of pustule development is very much dependent on temperature. Pustules do not open above 35°C. That is why we are interested in knowing the rate of development.

C.D. Mayee. Rate of development of pustule has important epidemiological implications.

R.W. Gibbons. What is the name of the cultivar that shows very small rust pustules?

P. Sankara. It has the local name Moaga and is a very old cultivar.

R.W. Gibbons. Have you looked at its reaction to leaf spot?

P. Sankara. No, but it will be tested again

R.N. Strange. To what stage did infection develop in leaves incubated in darkness?

C.D. Mayee. This is difficult to state because leaves kept in the dark after inoculation became spoiled after 72 hours.

A.S. Rao. In your detached leaf test there was no infection because of leaf deterioration. However, it would be worth trying to germinate urediniospores on detached leaves floated on nutrient solution, or on leaves implanted on agar.

C.D. Mayee. I agree that this could be attempted.

P.W. Amin. The amount of work you have done on rust disease is commendable. In the light of your opinion that the summer crop supplies inoculum to infect the rainy-season crop, can we consider controlling rust on the summer crop in order to reduce rust in the rainy-season crop? This should be a possibility as the area under summer crop is much smaller than that under rainy-season cultivation and only a few fungicide sprays would be necessary to control late-season rust infection. Secondly, the major constraint in adopting a spray schedule is scarcity of clean water in the quantity required for high-volume spraying and the difficulties involved in carrying and storing it. Can you in future concentrate on research on appliances, particularly to reduce spray volume? Low-volume spinning-disc type applicators would be immensely useful.

C.D. Mayee. Thank you for commending our work. Yes, this is very important and can be done. The only problem is that in Maharashtra there is no uniform practice for summer groundnut cultivation, sowing being done at any time from late January to early May according to the cropping systems used. The infector crop planted in summer is thus available at any time from June to September. The situation is more complex when farmers plant cultivars of different durations, especially in irrigation command areas. Spraying summer groundnut at critical stages of disease development holds promise, provided it could be done on a massive scale. I agree that we should work on low-volume sprays.

E.A. Salako. Your yields from fungicide-treated plots were low, at approximately 1 t ha^{-1}. Why was this so? Also, have you considered the cost-benefit of fungicide application, especially with respect to calixin application?

C.D. Mayee. The yield potential of the cultivar SBXI, grown in the heavy soils of Maharashtra, is not very high. A yield of 1200-1400 kg ha^{-1} of SBXI in the rainy season is considered quite high. Concerning the cost-benefit ratio of Bavistin® + Calixin® for total management of foliar diseases, this works out at around 1:5.5 while that of Bavistin ® + Dithane M45 ® is around 1:5. This is because in spite of the high cost of Calixin ®, only 2 sprays are required to get a good level of disease control compared with 4 sprays of Dithane M45 ®.

V. Arunachalam. I was surprised by the observation that phosphorus fertilization results in lower incidence of rust. Is it an experimental result or incidental observation in a few trials? Insofar as the basic available soil phosphorus is a major factor, would you think one can suggest an optimum level of P for reducing rust incidence in soils of Maharashtra?

C.D. Mayee. This was no incidental observation. We conducted trials subsequently for two years and also built up disease levels artificially. I think we could determine an optimum P level once we have multilocational trials taking into account the basic available P.

S. Nagarajan. Do you believe that ecological races exist? How do you explain anti-epidemic in the *r* values of your field data? How is it that >80% RH is negatively correlated?

C.D. Mayee. Ecological races in *P. arachidis* do exist. One needs to have suitable experimentation to prove it. On negative *r* values, I do not consider these to be anti-epidemic provided they are obtained at the end of disease development.

P. Subrahmanyam. How did you measure the latent period?

C.D. Mayee. We used the definition of Zadoks and Schein (1979), *in toto*, i.e., it is the time period (in days) between the day of inoculation and day on which the first open pustule is observed. In epidemiology, I consider that the first appearance of an open pustule is very important because it is going to contribute immediately to subsequent infection cycles.

J.E. Parlevliet. Dr Mayee used the first ruptured sorus as an indicator whereas Dr. Subrahmanyam used the 50% ruptured sori. Both measure the latent period, but the latter carries a smaller error than the former, which is important. Dr. Mayee remarked that the first appearance of pustules is the most important from an epidemiological point of view.

P. Subrahmanyam. Did you test the pathogenic fitness of your thermosensitive isolates on a differential series? What is the basis for your assumption that ecotypes of groundnut rust exist in India?

C.D. Mayee. No. The isolates were pathogenic to cultivar SBX1 and all produced the same type of pustule on this cultivar.

The assumption about ecotypes is based on the observation that the susceptible cultivars do show a differential progress of rust when sown at different locations. Probably, we need to examine the disease development on a set of known susceptible lines at many locations.

P. Subrahmanyam. Did you measure the yields of some of the resistant breeding lines supplied by ICRISAT?

S. Wongkaew. Yes, we did grow some of the breeding lines but the evaluation was done by the agronomist and we reported the results in the agronomy section. I am sorry that I did not include the results in my presentation, but they can be obtained from the report sent to ICRISAT.

J.F. Hennen. Does direct penetration of the urediniospore germ tube into the epidermal cell occur?

P. Sommartya. Observation under the scanning electron microscope revealed that germinating urediniospores could penetrate either directly or indirectly into host tissues. This occurs 20-24 h after inoculation in leaves incubated in a moist chamber at 25°C.

C.D. Mayee. The leaf penetration in groundnut rust can be direct or through stomata. Direct penetration through the epidermis is more common when detached leaves are inoculated.

E.A. Salako. You mentioned that farmers in Thailand do not apply fungicides or fertilizer, but you feel that the future of rust control lies in the use of *Darluca* for biological control. Do you believe that your farmers would accept this?

S. Wongkaew. What I meant was that biological control could be used in such a way that the farmers would not have to participate in the treatment. The bio-control could be done by letting nature take its course without much interference from man. By refraining from spraying the crop with broad-spectrum fungicides, or by not applying any fungicides at all, the hyperparasitic fungus could build up its own population and be able to keep the rust population in check, perhaps at below the economic threshold. I do not see why the farmers should not accept the idea when they do not have to do anything other than be more selective in using fungi-

cides, or not use them at all, which is usually the case.

D.L. Cole. Is *Darluca* easy to culture and have you applied spores to rusted plants?

S. Wongkaew. Yes, but I have not yet applied spores to rusted plants. It is my intention to do so.

D. McDonald. You mentioned that rust and leaf spots are important yield reducers in the southern or riverain groundnut-growing area of Nigeria, and have quoted large increases in yield from fungicide applications. However, if you hope to use resistant cultivars you will have the problem that you will need resistance to rust and to early and late leaf spots. Available foliar-diseases-resistant genotypes have resistance to rust alone or to rust and late leaf spot, but are not resistant to early leaf spot. Are you checking on the proportional importance of the two leaf spots in the Mokwa, Samaru, and Kano areas?

E.A. Salako. In order of importance and of potential to cause yield losses, late leaf spot is followed by early leaf spot, and rust ranks third. However, all three diseases are being studied and resistance to them is being bred for simultaneously. We now have lines that show appreciable levels of resistance to the three diseases, e.g., the red resistant bulk (RRB), K 2990, and M 362 among others.

Once we can get a suitable level of resistance to all these diseases, the proportional importance of each of them will not be that important anymore.

R.W. Gibbons. Some of the late-maturing, stable, interspecific hybrids from ICRISAT, with rust and leaf-spot resistance, may be suitable for your southern zones where there is a long growing season. They, however, will not have resistance to rosette.

E.A. Salako. We would very much like to have some of these promising interspecific hybrids for use in our program.

P. Subrahmanyam. How do you evaluate your germplasm or breeding material under multiple-disease situations? Do you evaluate your material for all diseases in the same field?

E.A. Salako. Our interest is in developing multiple disease-resistant cultivars. Our germplasm and our segregating generations, as well as lines that have reached advanced stages of testing, are usually sown in fields that are often exposed to the major groundnut foliar diseases. This helps in the rapid elimination of susceptible material. We still get lines that hold up even in the presence of all the diseases.

D.A. Knauft. While screening for resistance to early and late leaf spots, do you face the problem of the occurrence of one disease masking the expression of susceptibility for another disease?

E.A. Salako. Our screening is done over several years at several locations. The lines we retain are those that are not susceptible to the diseases of interest except when they are just being considered as sources of particular resistance gene(s). A line that has at least moderate resistance to each disease is less likely to be significantly affected by the masking effect of one disease on the other. Since our field trials are multilocational, it is difficult for the same disease development type to operate at all locations to give a similar masking effect. By and large, we are still able to sort out the lines according to their true resistance patterns.

P. Subrahmanyam. Is it not possible to identify hot-spot locations for various diseases and evaluate the material for each disease separately? It would be a much more reliable system.

E.A. Salako. In the Northern Guinea Savanna Zone rust is usually unimportant, and it is more important to screen for drought resistance. In the Southern Guinea Savanna Zone, rust and the leaf spots usually occur yearly. In the Mokwa area, they occur with great intensity almost every year, while in Samaru, rust may not be serious in some drought years. By replicating our screening trials in these areas, it is usually possible to determine resistance to the three major fungal foliar diseases.

C.D. Mayee. Do the variations in resistance to rust observed in some genotypes between ICRISAT Center in India and Guangdong Province in the People's Republic of China indicate race-level differences?

D. McDonald. The ICRISAT Groundnut Program has been cooperating for several years with scientists in Guangdong Province in evaluating germplasm for resistance to rust disease. The screening and scoring methods used are compatible. Most genotypes gave similar rust-disease scores in India and in the People's Republic of China, but some differed. Perhaps Dr Subrahmanyam would comment further on this.

P. Subrahmanyam. The majority of the genotypes found resistant to rust at ICRISAT Center showed similar levels of resistance when tested in Guangdong Province. However, the genotype NC Ac 17090 was classed as highly resistant in ICRISAT Center but only moderately resistant in Guangdong Province, while the reverse was the case for genotype PI 298115. Host × pathogen × environment interactions may be responsible for some of the differences noted but the possible occurrence of pathotypes cannot be ruled out. Further research is required to clarify the situation.

D. McDonald. Dr Cole has done an excellent job in putting together a regional picture of the distribution and importance of groundnut rust in southern Africa. Similar work should be done for other important groundnut-growing regions of the world.

D.L. Cole. Some of the data presented for the region are taken from Dr. Subrahmanyam's recent report on disease surveys in Malawi. Can he give any additional comments on this?

P. Subrahmanyam. Rust is an important disease in the low-altitude southern areas of Malawi and in the Lake Shore areas. In the main groundnut-growing areas of central Malawi rust normally appears late in the growing season and does not cause any appreciable damage.

Distribution and Spread of Groundnut Rust

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The Epidemiology of Wheat Stem Rust and Implications for Study of Groundnut Rust Perpetuation and Spread in India

S. Nagarajan[1]

Abstract

Urediniospores of Puccinia graminis *f. sp* tritici *rapidly lose viability during the hot, dry, summer months in the plains of India, but survive in large numbers throughout the year in the Nilgiri and Palney Hills of south India. Their survival in these areas is also favored by the year-round presence of wheat and other collateral hosts. In India, barberry, the alternate host, does not play any role. During November, when there is a month-old wheat crop in central India, tropical cyclones that cross Tamil Nadu or Andhra Pradesh and dissipate over central India transport large quantities of* Puccinia graminis *f. sp* tritici *urediniospores. These spores carried from the southern source are rain scrubbed over central India and, conditions being congenial, disease epidemics develop before mid-March. Detailed climatic rules, forecasting procedures, and methodology have been repeatedly tested and validated. The pathogen spreads northward through a fixed geographical track called the "*Puccinia *path". This system also seems to hold good for* P. arachidis *though usage of the path occurs during June-July. Similarities between these different pathogens are explained.*

Résumé

Epidémiologie de la rouille des tiges du blé et son influence sur l'étude de la propagation de la rouille de l'arachide en Inde : *Les urédospores de* Puccinia graminis *F. sp tritici perdent rapidement leur viabilité au cours de la saison chaude et sèche dans les plaines de l'Inde, tandis qu'elles abondent pendant toute l'année dans les collines de Nilgiri et de Palney dans le sud du pays. Leur survivance dans ces régions est favorisée par la présence permanente des plantes-hôtes alternantes dont le blé. En Inde, les épines-vinettes (berbéris) ne jouent aucun rôle d'hôte alternant. En novembre lorsque la culture de blé dans le centre du pays est âgée d'un mois, de grande quantités d'urédospores de P. graminis f. sp tritici sont disséminées par les cyclones tropicaux qui traversent le Tamil Nadu ou l'Andhra Pradesh pour s'affaiblir dans le centre. Ces spores provenant du sud sont touchées par les pluies dans le centre où elles provoquent des épidémies avant mi-mars, les conditions y étant favorables. Les conditions climatiques spécifiques, les processus de prévision météorologique ainsi que la méthodologie d'échantillonnage ont été étudiés et confirmés à plusieurs reprises. Le pathogène suit un chemin géographique fixe allant vers le nord appelé le "chemin de* Puccinia" *(*Puccinia *path). Ce système est également valable pour* Puccinia arachidis *qui prend ce chemin plus tard en juin-juillet. Les points de similitude entre ces deux pathogènes sont expliqués.*

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Early Work on Wheat Stem Rust in India

Wheat stem rust incited by *Puccinia graminis* f. sp *tritici* is one of the few diseases that has been studied in great detail in various parts of the world. The long-distance dispersal of the urediniospores and the recurrence of the disease has therefore been well documented (Hogg et al. 1965).

Butler, who initiated systematic work on plant diseases in India, showed that all the three wheat rust pathogens, namely *P. graminis* f. sp *tritici*, *P. recondita* f. sp *tritici* and *P. striiformis* f. sp *striiformis*, that cause stem, leaf, and stripe rusts, respectively, occur in India. Subsequently, Mehta (1940) clearly demonstrated that *Berberis* spp. the alternate hosts of *P. graminis* f. sp *tritici*, were non-functional, the pathogen perpetuating and causing epidemics through repeated urediniul cycles. In the absence of the main wheat crop the pathogen survives on grasses that act as collateral hosts and on self-sown or volunteer wheat plants. On the basis of the aerobiology of urediniospore dispersal, field observations, and inferences drawn for the spore shower, Mehta (1952) concluded that *P. graminis* f. sp *tritici* urediniospores survive in the cooler Nilgiri and Palney Hills of southern India and all through the Himalayas, particularly in central Nepal. According to Mehta (1952) these are the primary centers of survival from where the stem rust pathogen spreads to cause fresh infections.

Recent Work on Wheat Rust in India

When the high-yielding dwarf wheats were introduced for large-scale cultivation, a systematic wheat-diseases survey program was organized by the Indian Agricultural Research Institute (IARI), New Delhi. Qualified plant pathologists conducted routine scouting of wheat fields through a fixed route and recorded for various diseases such observations as severity, reaction type, prevalence, soil type, and crop growth stage, on standardized reporting forms. When years of information from repeated surveys were condensed and analyzed, the directional movement of the wheat rusts became very clear (Joshi 1976). The stem rust pathogen was observed to spread yearly from the Nilgiri and Palney Hills of southern India. It is now clear that severe stem rust epidemics are not initiated from stray inoculum that may survive all along the Himalayas, and that spread of primary inoculum is unidirectional, being from south to north.

The spread of urediniospores of the stem rust pathogen from southern Indian foci, to central India and northwards implies long-distance dispersal. Such a spread across more than 800 km at a stretch cannot be achieved through ground level wind currents alone. It was therefore speculated that, as in the USA, primary inoculum of *P. graminis* f. sp *tritici* in India can also be rain deposited (Roweli and Romig 1966). Rain samplers were fabricated locally and installed at many locations within plots of susceptible wheat. A glass rod impaction-aerobiology wind vane was placed in the same plot, to sample the airborne inoculum. A large number of rain samples were analyzed following the procedure of Roelfs et al. (1970); spores in air were monitored daily through glass-rod impactors and the date of appearance of the disease on susceptible wheat lines was also recorded. When statistically tested, it was clear that the urediniospores arrive with rain, cause primary infection, and the rust is subsequently spread by ground-level winds. Based on this, a set of three upper air synoptic conditions called "The Indian stem rust rules" (ISR) were proposed, to explain the recurrence of the disease (Nagarajan and Singh 1975). The following conditions constitute the rules.

1. A storm depression should be formed either in the Bay of Bengal or in the Arabian Sea between 65-85° E and 10-15° N, and should end over central India.
2. A persistent high-pressure cell must be present over south-central India (not far from the Nilgiris).
3. A deep trough, extending up to southern India and caused by the onward movement of the easterly disturbance, should occur.

If one or a combination of these conditions are satisfied, stem rust appears in central India. So far, in the last 13 years of forecasting, the disease appearance satisfies these weather rules. When the first section of ISR is satisfied, the disease appears exactly below where the tropical cyclone dissipates. If weather conditions during Jan-Mar are favorable, a disease epidemic occurs; if unfavorable, isolated pockets of disease occur.

The distribution and extent of disease damage depends upon the amount of viable primary inoculum deposited and the prevalence of subsequent favorable weather conditions. The amount of spores

that take-off from the Nilgiris seems to depend upon the track of the cyclones. It has been found that when urediniospores are transported at altitudes providing around 700 (mb), after 120 h of travel in upper air they cannot cause infections. Based on this outline, a procedure to forecast the probable appearance of stem rust has been developed (Nagarajan and Singh 1976).

1. Check if there have been rains during November in central India, coupled with southerly winds.
2. Check the urediniospore content of the rain.
3. Check if a section of the Indian stem-rust rule is satisfied.
4. Check the satellite television cloud photographs for the weather over central India.
5. Check the viability of transported urediniospores by finding the hours taken for transporting them from the source to the target.
6. Check that a susceptible host is available.
7. Check that the ground-level conditions following the deposition of the urediniospores by rain are favorable for infection.

Following this procedure, occurrence of stem rust has been predicted 30 days in advance since 1973 (Nagarajan and Singh 1976, Nagarajan and Joshi 1980). The forecasts were exact and highly successful. In order to predict disease severity, a linear model was developed, based on data collected through artificial field epiphytotics (Nagarajan and Joshi 1978), and its utility was subsequently validated through multilocation tests.

A large number of backward trajectories drawn for various case studies revealed that the wind-borne urediniospores spread through a particular geographical tract. This defined zone from the Nilgiris and Palney Hills to central India could be called the "*Puccinia* path". This single epidemiological zone of the Indian subcontinent where spread of *P. graminis* f. sp *tritici* and *P. recondita* f. sp *tritici* urediniospores is identical can be further divided into subzones based on the mode of arrival of the spores (Nagarajan and Joshi 1980).

This has opened up new and exciting possibilities of disease management by diversifying host resistance genes all along the "*Puccinia* path". Gene development, gene cycling, multilineal varieties, and multilines, are possible means by which the desired level of genetic barrier can be achieved. The efficiency of the different resistance genes varies between zones due to the prevalence of different pathotypes. Therefore, different gene combinations have been recommended for usage and incorporation in the wheat improvement approaches (Nagarajan et al. 1984).

Comparision of *P. graminis* f. sp *tritici* and *P. arachidis* Epidemiology

Groundnut (*Arachis hypogaea* L.) can be grown almost all round the year in southern India, particularly in the states of Andhra Pradesh, Tamil Nadu, and Karnataka. This availability of the host in all seasons permits survival of *P. arachidis* inoculum on the main host itself. The telial stage is not common and alternate hosts are unknown. Groundnut rust is known to attack several other members of the genus *Arachis*, but they can hardly be involved in the perpetuation of *P. arachidis* outside South America (Subrahmanyam and McDonald 1982). The population of the pathogen, its multiplication and sporulating capacity are severely curtailed during the warm and dry summer months of Apr-Jun. Groundnut-rust severity is very high in the rainy-season crop in central India when the relative humidity is over 90% and leaf wetness persists for several hours. Temperatures around 20-24 °C are ideal for urediniospore germination and infection. But both development and symptom expression are poor when the temperature exceeds 30 °C, and this partly explains why hot summer (Apr-Jun) weather is not favorable for disease development.

With the onset of the southwest monsoon over southern India in early June, the pathogen is provided with a congenial environment for multiplication. Subsequently, the monsoon advances towards central and eastern India. In this tract, land is prepared for groundnut sowing after the early showers. During this period the wind pattern is southwesterly, and by Jul-Aug abundant inoculum from the southern states is carried to and deposited over central India. From there the disease can spread northwards. So far as the pattern of spread of this disease is concerned, it follows the *Puccinia* path defined earlier for wheat stem rust. Many other *Puccinia* spp are thought also to spread from south to north during Jul-Aug when the southwest monsoon is fairly active. During this period crops such as jowar (*Sorghum vulgare*), bajra (*Pennisetum typhoides*), and groundnut, are grown in central India, whereas, in the southern states of Tamil Nadu and Andhra Pradesh they are grown throughout the year. The pathogens that initiate the various rust diseases on

these crops (*Puccinia purpurea*, *P. substriata* var *penicillariae*, and *P. arachidis*) survive around the year, and possibly spread to central India during Jul-Aug, by means of the weather conditions generated by the southwest monsoon. The concept of the "*Puccinia* path" of India (Nagarajan and Joshi 1980) therefore has a wider application than was visualized at the time of its proposal.

In the northwest state of Gujarat two crops of groundnut are generally grown, and there is a break in cultivation during summer. But self-sown groundnut plants may survive here and there, and a few irrigated, summer groundnut fields help ensure survival of rust inoculum around the year. With the onset of the southwest monsoon in July the weather becomes favorable for rust development and the rainy-season crop is soon infested. Uredinospores of the rust pathogen may spread from this west Indian focus to Rajasthan, Haryana, and even to the Punjab. Spread to central India may also occur. It is tempting to speculate that rust can spread to central India from both southern and western inoculum, and that in years when they both arrive early in the season, severe epidemics of groundnut rust occur. This indicates the possible existence of three sub-zones.

In conclusion, it can be said that the study of comparative epidemiology of both wheat and groundnut rusts reveals certain striking similarities in their nature and recurrence. The deviations that occur do not detract from the relevance of these observations.

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Aerobiology of Groundnut Rust

K.V. Mallaiah and A.S. Rao[1]

Abstract

Important airborne fungal diseases of groundnut are briefly mentioned and the literature on aerial spread of groundnut rust reviewed. Aerobiological studies on groundnut rust in southern India are reported and data given on daily and seasonal fluctuations in urediniospore concentrations in the air above groundnut crops. Groundnut rust urediniospores are very efficiently dispersed by air. Airborne concentrations follow the pattern of field disease incidence and can be used to assess severity. High concentrations occur when temperatures are in the range of 29-31° C, relative humidity in the range of 75-85%, and wind speed ranges from 4-10 km h^{-1}. Mechanical disturbance of the crop results in a sharp but temporary increase in urediniospore concentrations in the air over the crop. Spore deposition was observed over 100 m downwind of a rust-infected groundnut crop.

Résumé

Aérobiologie de la rouille de l'arachide : *Les auteurs présentent les principales maladies fongiques véhiculées par le vent et récapitulent la documentation sur ce moyen de propagation de la rouille de l'arachide. Les études aérobiologiques de la rouille effectuées dans le sud de l'Inde sont présentées avec les données sur les fluctuations journalières et saisonnières de la concentration d'urédospores dans l'atmosphère au-dessus des cultures d'arachide. La dissémination d'urédospores de la rouille de l'arachide par le vent est très efficace. La concentration dans l'air correspond à l'incidence de la maladie et permet donc d'évaluer son intensité. Les conditions favorables à de fortes concentrations sont : température de 29-31° C, humidité relative de 75-85%, et vitesse de vent de 4-10 km/heure. Il y a une augmentation brusque mais temporaire dans la concentration des spores en cas de perturbation mécanique des plantes. On a observé la déposition des spores sur une distance de 100 m sous le vent d'une culture d'arachide contaminée par la rouille.*

More than 40 fungal diseases have been reported on groundnut (*Arachis hypogaea* L.) (Jackson and Bell 1969). These can be broadly divided into airborne diseases and soilborne diseases. Although a large number of fungal diseases of the crop are soilborne, the airborne diseases are of greater concern worldwide on account of their widespread occurrence and the losses they cause. The airborne diseases are mainly foliar and hence are conveniently placed for take-off, which is an important step in effective dispersal (Hirst 1959). Feakin (1973) classified rust (*Puccinia arachidis* Speg.), leaf spots (*Cercospora arachidicola* Hori, and *Cercosporidium personatum* (Berk. & Curt.) Deighton), and scab (*Sphaceloma arachidis* Bitancourt & Jenkins) as airborne diseases of groundnut. Our aerobiological studies in India (Mallaiah and Sreeramulu 1976; Mallaiah and Rao 1976) and those of Smith and Crosby (1973) in the USA clearly show that pepper spot and leaf scorch, caused by *Leptosphaerulina crassiasca* (Sechet) Jackson & Bell is also an airborne disease.

Aerial Dispersal of Pathogen

Aerial dissemination is of paramount importance for groundnut rust as the uredinial stage is the only stage of *P. arachidis* found in most parts of the world. The rapid spread of rust through Asian and African countries in the recent past implies effective

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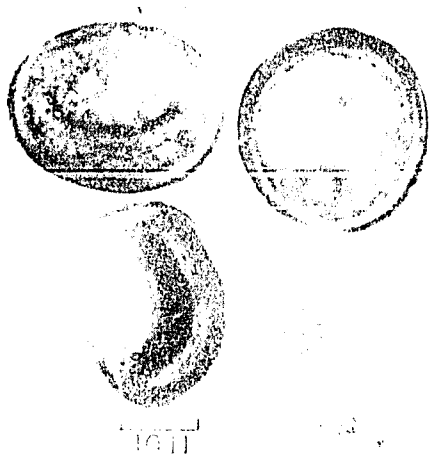

Figure 1a. Urediniospores of *Puccinia arachidis*.

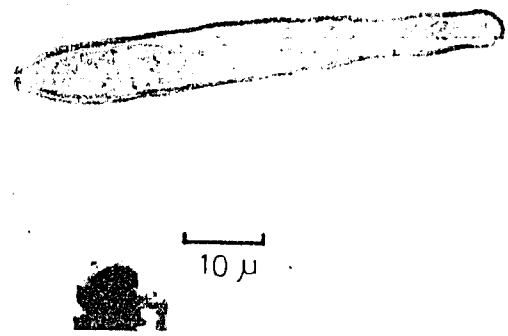

Figure 1b. Conidium of *Cercosporidium personatum*.

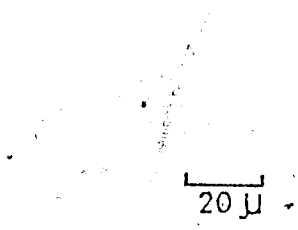

Figure 1c. Conidium of *Cercospora arachidicola*.

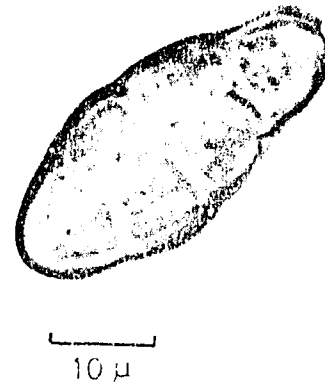

Figure 1d. Ascospore of *Leptosphaerulina crassiasca*.

aerial spread. By analogy with the spread of wheat rusts, long-distance dispersal of urediniospores of groundnut rust has also been assumed. Higgins (1956) stated that the fungus did not apparently overwinter in the United States, but was blown in from neighbouring subtropical regions. Van Arsdel and Harrison (1972) reported that initial infections in groundnut fields in Texas arose from urediniospores orginating from Mexico. They trapped spores in rain water during Jul-Aug 1970, and observed rust in the fields 10-15 days later. At that time rust was prevalent in a region of Mexico 1290 km distant. Mallaiah and Rao (1982) reported aerial dissemination of urediniospores under field conditions. Apart from these studies, the aerobiology of groundnut rust has not received the attention it deserves.

Since its first report by Spegazzini in 1884, rust was almost confined to the Western hemisphere for ninety years (CMI map 160, issued in 1966) with widespread occurrence in Central and South Ameri-

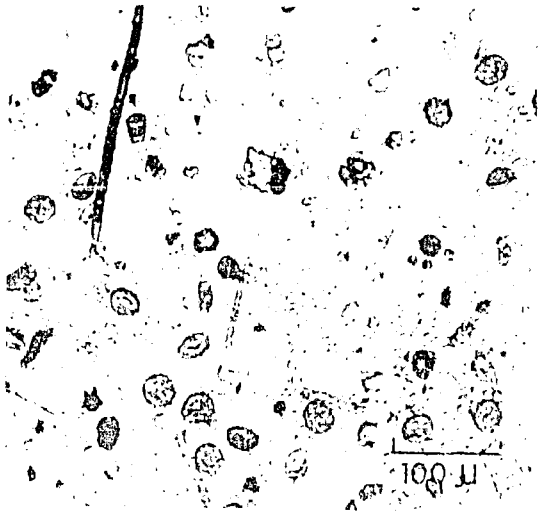

Figure 1e. A microscopic field of sporetrap slide showing heavy concentration of urediniospores of *P. arachidis*.

can countries from Cuba to Argentina, and occasional occurrence in the States of Albama, Georgia, North Carolina, and Texas in the USA. Outside America it was reported from Russia in 1910 (Jaczewski 1910), Mauritius in 1913 (Stockdale 1913) and in China in 1937 (Tai 1937). The rust disease was considered to be of only minor importance at that time, except in the West Indies. However, the situation changed completely in the late 1960s and early 1970s, when rust spread rapidly through most East Asian countries, Australia, and Africa, and became the most destructive disease of the crop.

The rapid spread of rust suggests aerial dispersal of the pathogen from the East Asian region as center, to India and on to Africa towards the west and to Australasia to the south. The summer cyclone in 1969 that occurred over the east coast of India due to a severe depression in the Bay of Bengal could have helped in introducing the rust inoculum into the country, since the uredinial stage of the disease in India was first observed along the east coast in 1971. The time gap might represent the period required for increase of the disease to recognizable proportions. Earlier studies by Sreeramulu (1970) in India and Smith and Crosby (1973) in the USA on aerial dissemination of groundnut pathogens did not indicate the presence of rust. Because of the paucity of aerobiological information on this important disease, we started a study in 1974.

For our aerobiological studies the crops were raised in three seasons in each year, i.e., in the rainy season (Jul-Oct), in winter (Dec-Mar), and in summer (Apr-Jul); the cultivar used was TMV 2. For spore trapping we used the Casella model of Hirst's Automatic Volumetric spore trap (Hirst 1952), an efficient, robust, power-operated spore trap, and also the much less expensive "vertical cylinder traps" (Gregory 1973) and "rotorod samplers" (Perkins 1957). The traps were placed in the centres of square field plots (0.5 ha) with their trapping surfaces 0.5 m above ground level, i.e., just above the foliage. The slides in the Hirst trap and the adhesive-coated cellophane strips in vertical cylinders were changed regularly between 0700 and 0800 h daily and were exposed for 24-h periods.

During the study urediniospores of *P. arachidis*, conidia of *Cercosporidium personatum* and *Cercospora arachidicola*, and ascospores of *Leptosphaerulina crassiasca* were observed (Fig.1 a-d). A heavy concentration of urediniospores at the peak hour of occurrence on a single microscopic field under low power is shown in Figure 1e.

Seasonal periodicity

Day-to-day changes in urediniospore concentrations in the air over groundnut fields were studied for a period of 3 years (1974-76) covering 9 crop seasons: 3 each of rainy, winter and summer seasons. The urediniospores were present in the air over crops in all but 2 summer crop seasons.

In the rainy-season crops, the pattern of urediniospore incidence in the air and the occurrence of rust in the field showed much variation.

During 1974 (Fig. 2a), the urediniospores were present in the airspora in high numbers during September and early October. The amount and periods of rainfall were normal but the rust incidence in the field and the concentrations of airborne urediniospores were lower than in 1975 and 1976. The airborne-spore concentrations were higher on dry days between periods of rainfall than on rainy days.

Rainfall was normal in 1975 (Fig. 2b) and rust appeared in the field in the middle of August. In the early part of September there were heavy rains and rust disease became severe soon afterwards. The urediniospore concentrations were highest during this season. The seasonal peak occurred in the last week of September.

During 1976 (Fig. 2c), there was a very long dry spell of over four weeks from the end of the first

week of September. The rust disease and airborne urediniospores appeared in the middle of August, but unlike in 1975, the disease and airborne-spore concentrations increased gradually, reaching a peak only towards the end of October.

In contrast to the pattern of incidence of airborne urediniospores in the rainy season, the pattern during the three winter seasons was remarkably similar. The rust appeared in the field when the crop was 30-35 days old and increased gradually. The spores were trapped in very low numbers in January but concentrations increased gradually in February,

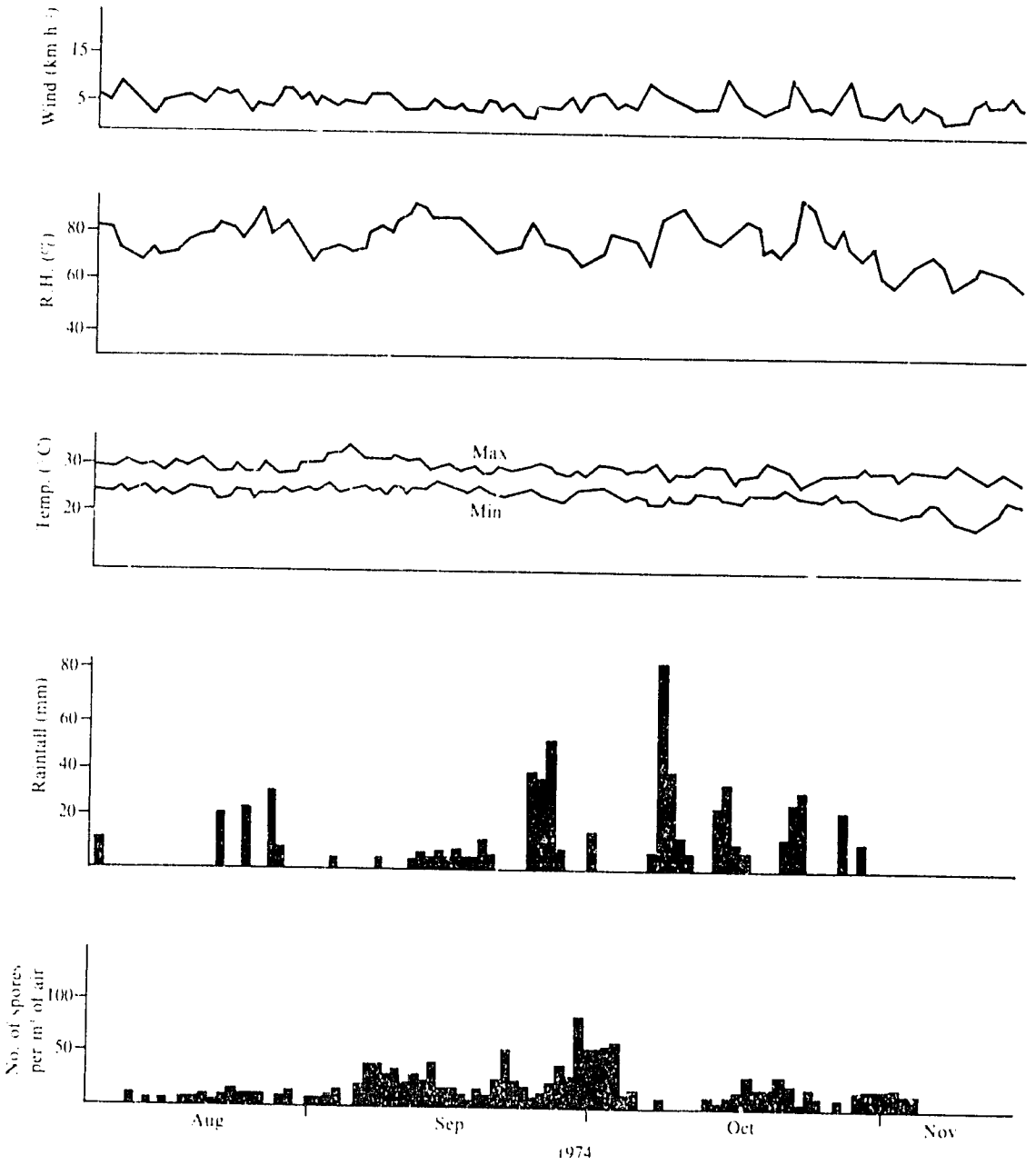

Figure 2a. Periodicity exhibited by the airborne urediniospores of *P. arachidis* during the 1974 rainy-season crop period.

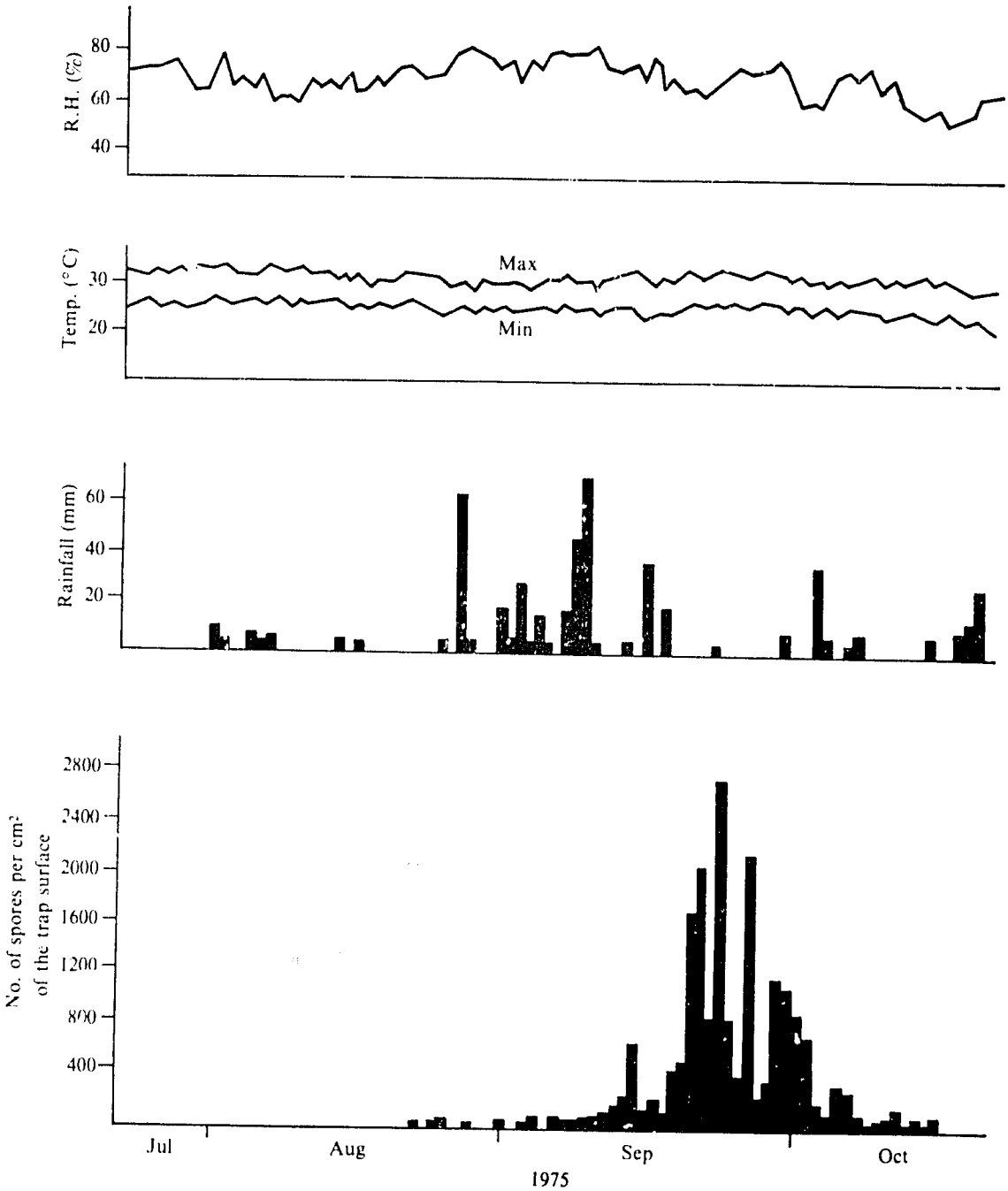

Figure 2b. Periodicity exhibited by the airborne urediniospores of *P. arachidis* during the 1975 rainy-season crop period.

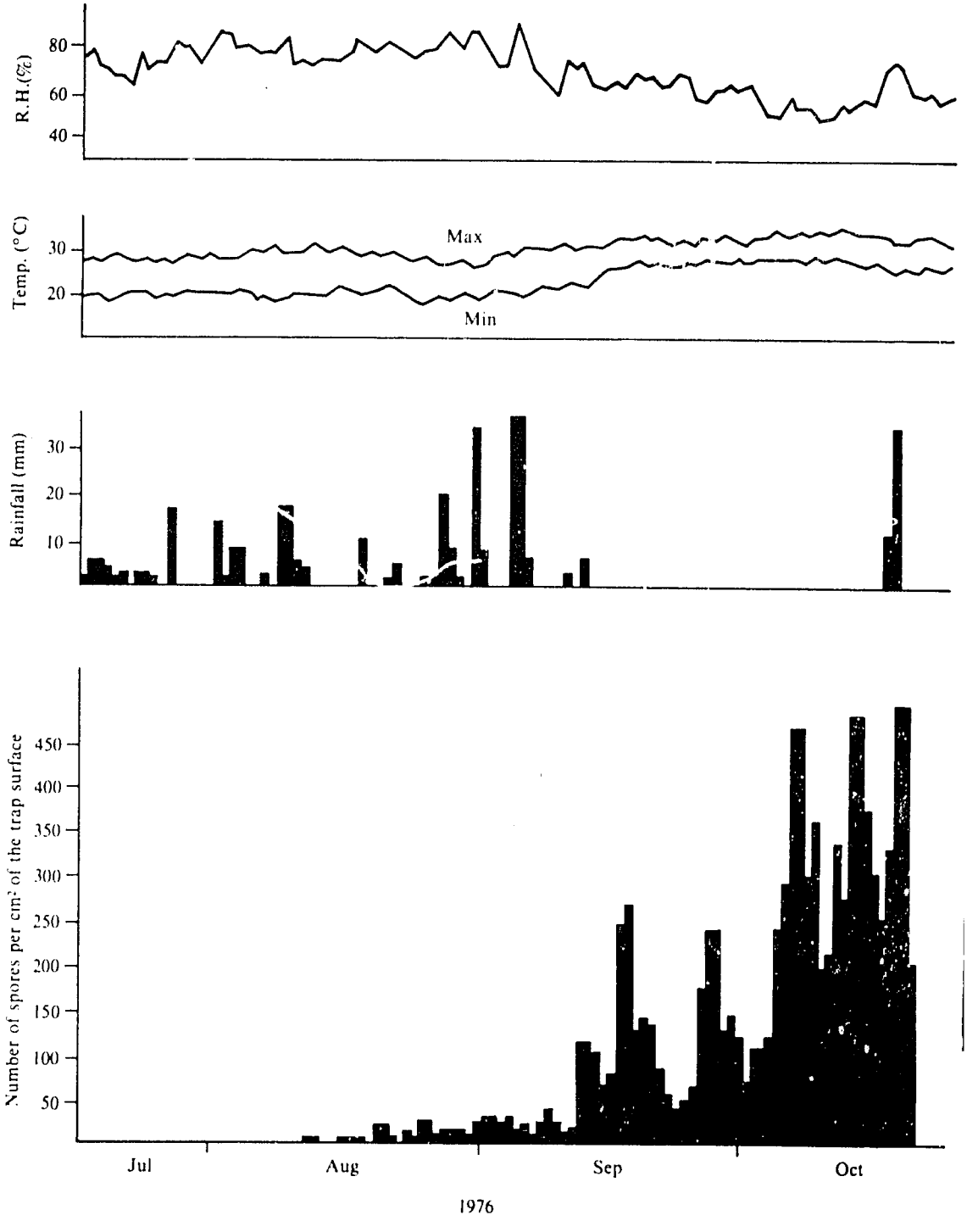

Figure 2c. Periodicity exhibited by the airborne urediniospores of *P. arachidis* during the 1976 rainy-season crop period.

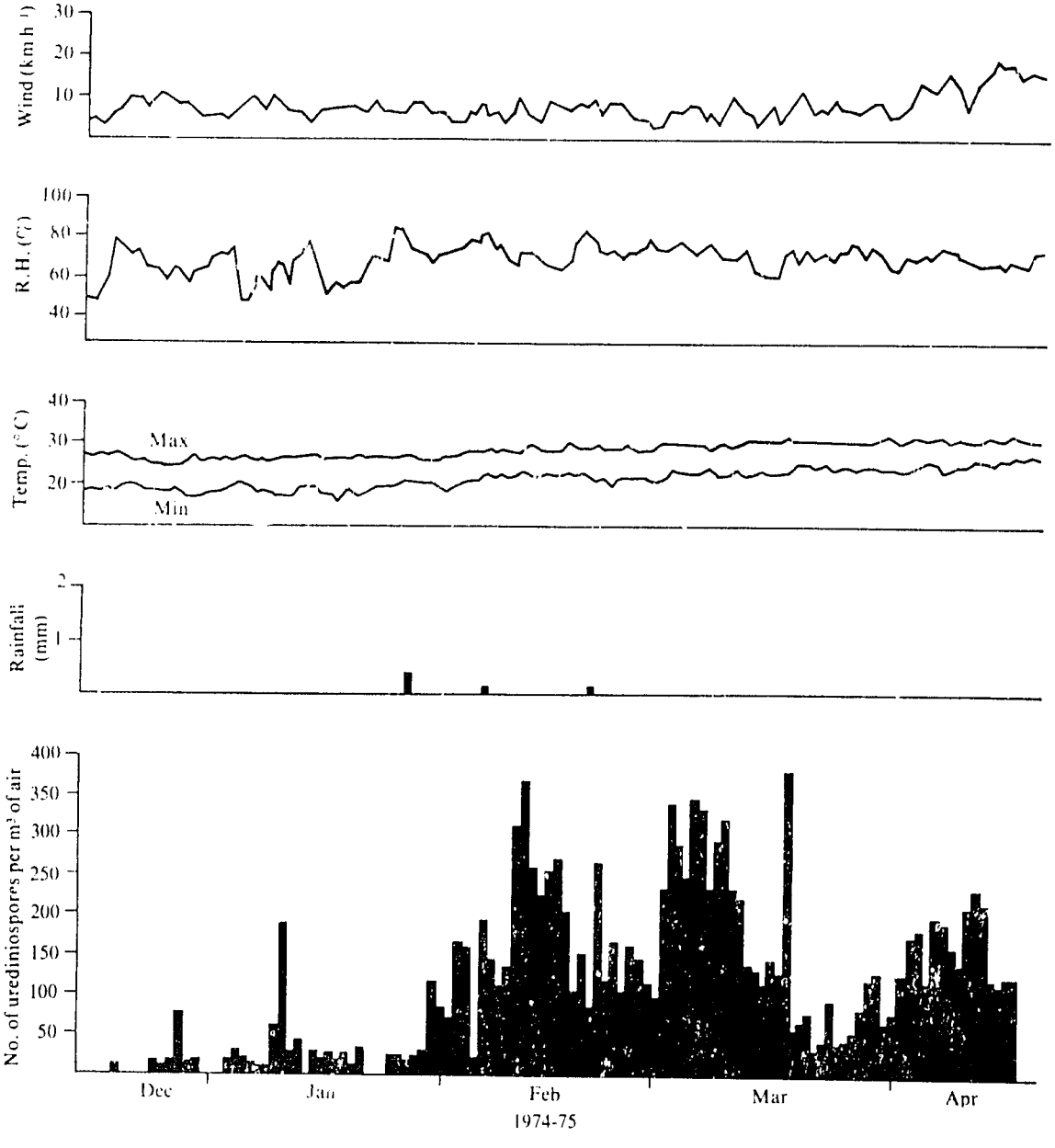

Figure 2d. Periodicity exhibited by the airborne urediniospores of *P. arachidis* during the 1974-75 winter- season crop period.

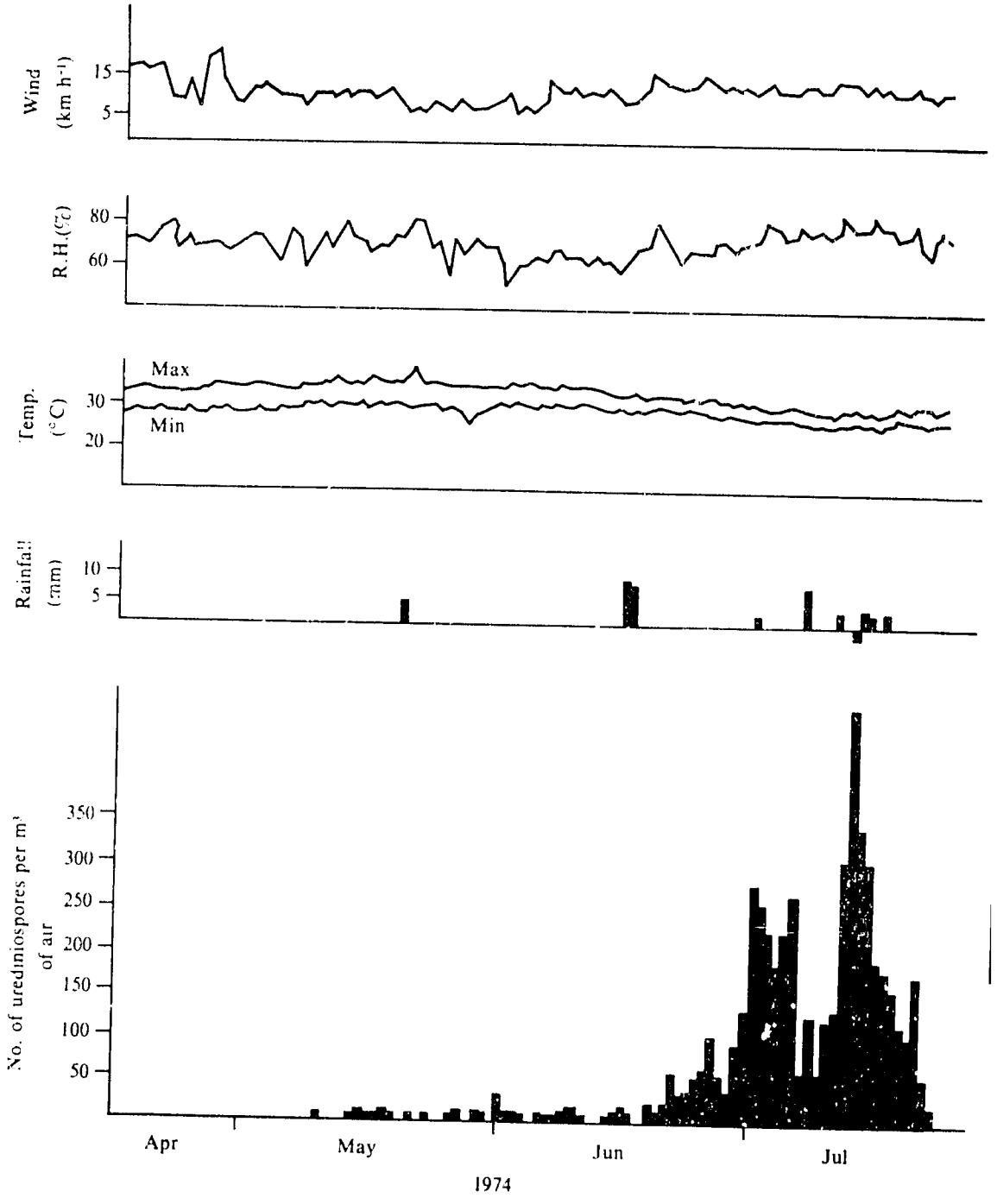

Figure 2e. Periodicity exhibited by the airborne urediniospores of *P. arachidis* during the 1974 summer-season crop period.

reaching a peak towards the end of the month (Fig. 2d) in 1974 and 1975 and in early March in 1976. They were trapped till the end of the crop season in all three years.

In the summer crop of 1974 (Fig. 2e), concentrations of airborne urediniospores were very low until Jun 20. But rust was prevalent after the first monsoon rains on Jun 16 and 17, and within 5 to 6 days after the rains urediniospore concentrations increased (over 50 m^{-3} of air) reaching a peak during mid July. In 1975 there was no rust in the field till the end of June, and no spores were trapped during this period. However rust did appear in the field prior to harvest after heavy rains in July. In the summer crop of 1976 rust did not appear and urediniospores were not observed in air spora.

Circadian periodicity

Using a Hirst spore trap the circadian periodicity in airborne urediniospores was recorded continuously by scanning the slides at 2-h intervals throughout the season.

The urediniospores formed part of the day-spora, with a peak occurring between 1000 and 1400 h. However, they were caught on the trap slides throughout the 24-hours (Fig. 3). The day to night catch ratio was 5:1.

In the rainy season, the spores showed a double-peak pattern of circadian rythm, with a minor peak at 1000 h and the main peak at 1400 h. The rise and fall of concentrations were gradual except for a small slump at noon and the minima were recorded at 0400 h and 1800 h.

In winter, the peak was observed at noon. The rise of concentrations before the peak was steep while the fall was quite gradual, with minima occurring at 0400 h.

In summer, a single peak at noon was observed as in winter, but there was a gradual increase in concentrations reaching the peak at noon but the fall was steep, with lowest concentrations recorded at 1800 h.

Highest daily mean

The highest daily mean concentrations observed in different crop seasons together with the age of the crop are given in Table 1. The highest daily mean of 2755 cm^{-2} of the trap surface was observed during the rainy-season crop of 1975. The peak occurred when the crop was 80-90 days old, except in the summer crop of 1974 and the rainy-season crop of 1976 when it occurred at a later stage (105 days), perhaps due to a slow buildup of rust disease in these seasons.

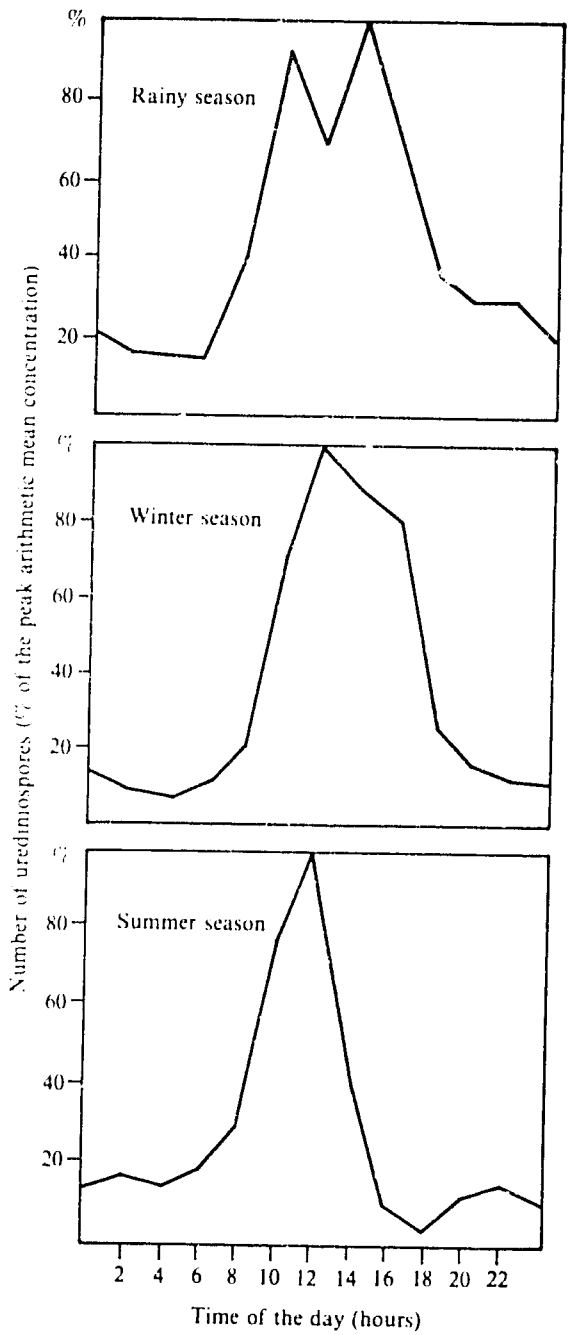

Figure 3. Circadian periodicity exhibited by the airborne urediniospores of *P. arachidis* during three different crop seasons.

Table 1. Highest daily mean concentrations of airborne urediniospores of *P. arachidis* in different crop seasons.

Year	Crop season	Spore trap used	Spores estimated	Highest daily mean	Date	Age of the crop in days
1974	Winter	Vertical cylinders	cm^{-2} of slide	208	27 Feb 74	89
1974	Summer	Hirst trap	m^{-3} of air	1786	14 Jul 74	105
1974	Rainy	Hirst trap	m^{-3} of air	87	30 Sep 74	87
1974-75	Winter	Hirst trap	m^{-3} of air	370	12 Feb 75	85
1975	Rainy	Vertical cylinders	cm^{-2} of slide	2755	23 Sep 75	85
1975-76	Winter	Vertical cylinders	cm^{-2} of slide	1350	5 Mar 76	82
1976	Rainy	Vertical cylinders	cm^{-2} of slide	501	19 Oct 76	106

Seasonal mean

Seasonal mean concentrations of the airborne urediniospores during different crop seasons together with mean temperatures, relative humidity, and total rainfall recorded are presented in Table 2, to demonstrate the general effect of weather factors on aerial spread. The seasonal means directly reflect the amount of disease present in the field. Airborne urediniospores were caught in considerable numbers over a broad range of temperatures, relative humidity and wind speeds.

At the temperature range of 28-34°C (maximum) and 21-26°C (minimum), urediniospore concentrations of more than 10 m^{-3} of air were observed when the rust was present in the field.

Table 2. Seasonal mean concentrations of airborne urediniospores of *P. arachidis*.

Year	Crop season	Seasonal mean	Spores estimated
1974	Winter	38.72	cm^{-2} of slide
1974	Summer	113.00	m^{-3} of air
1974	Rainy	9.00	m^{-3} of air
1974-75	Winter	110.00	m^{-3} of air
1975	Rainy	258.00	cm^{-2} of slide
1976	Winter	127.00	cm^{-2} of slide
1976	Rainy	96.0	cm^{-2} of slide

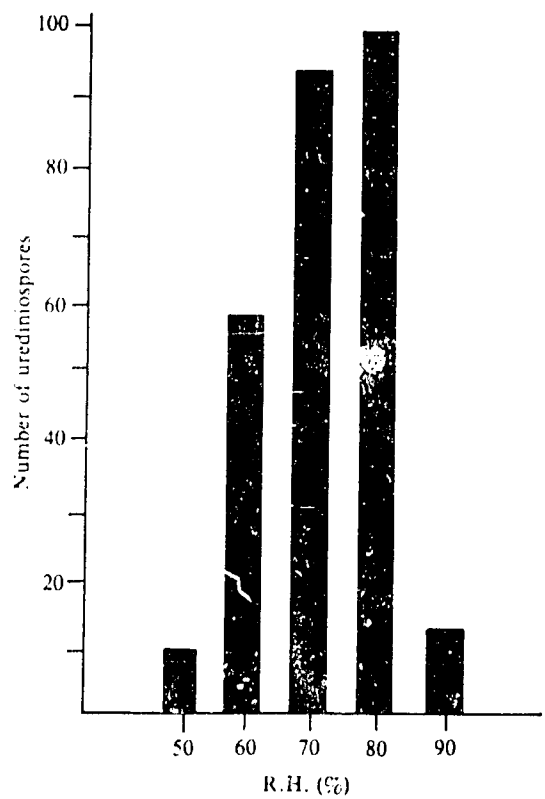

Figure 4. Effect of temperature on the incidence of airborne urediniospores of *P. arachidis* presented as percentages to the maximum recorded at a point in the range observed.

Effect of temperature

Levels of airborne spore concentrations were analyzed in relation to temperature and are presented in Figure 4 as percentages of the highest numbers recorded at a point in the range. The optimum range was 29-31°C and spore concentrations above 32°C and below 26°C were very low.

Relative humidity

Urediniospores were trapped over the relative humidity range of 45-95% but highest concentrations were recorded when relative humidities were between 75 and 85%. Fairly high concentrations were recorded in the range of 65-75% RH and to a lesser extent in the range of 55-65% RH. They were very low below 55% RH and above 90% RH (Fig. 5).

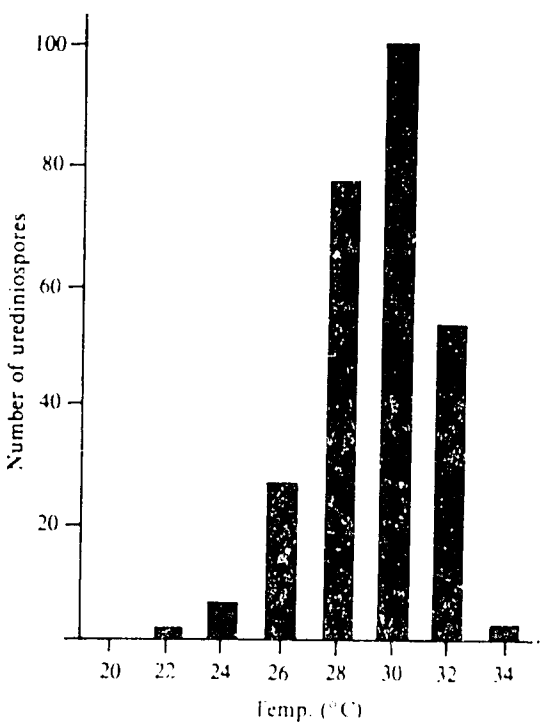

Figure 5. Effect of relative humidity on the incidence of airborne urediniospores of *P. arachidis*, presented as percentages to the maximum recorded at a point in the range observed.

Effect of mechanical disturbances

During the study it was observed that concentrations of the pathogenic spore types in the air were unusually high on certain days or during certain times of the day, which could not be explained by changes in weather conditions but coincided with such field operations as weeding and watering. Hence, the effect of mechanical disturbance on the spore load in the air was determined in the rainy-season crop of 1976, using rotorod samplers, which were operated continuously for 70 min, changing the rotating units at 10 min intervals. The plants around the trap were shaken gently for 1 min after the first 10-min interval of trap operation. The urediniospore concentrations were very high immediately after the plants were shaken, but the concentrations fell rapidly and predisturbance levels were recorded during the third 10-min trapping period. The increase in concentrations due to shaking was more pronounced for the urediniosores of rust than for conidia of *C. personatum* (Table 3).

Vertical profiles

Changes in concentrations of pathogens in the air over the crop fields were observed by exposing glass rods with sticky cellophane strips at different heights up to 3 m above ground level for 24 h duration. The urediniospore concentrations at plant heights of 1 m and 3 m were 43.5% and 4.2% respectively, of that at 0.5 m (Figure 6), clearly showing that peak concentrations occur at foliage level and decrease above the crop with a steep fall above 2 m.

The observed spore concentrations showed that though the proportional decrease in conidia of *C. personatum* and urediniospores of rust were similar,

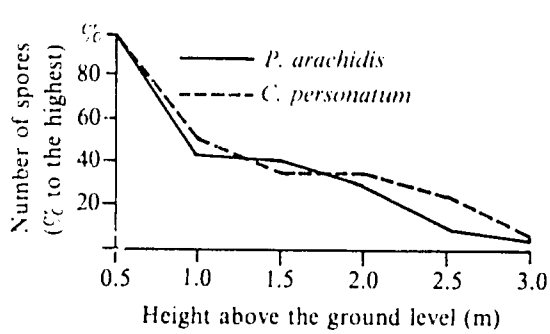

Figure 6. Vertical profiles of groundnut pathogens.

Table 3. Changes in the concentration of pathogenic spore types in the air caused by mechanical disturbance of infected plants.

Spore type	Concentrations of different pathogenic spore types at consecutive 10-min trapping periods (m^{-3} of air)[1]						
	I	II[2]	III	IV	V	VI	VII
Urediniospores of *P. arachidis*	294	7933	384	294	271	294	316
Conidia of *C. personatum*	158	3005	203	181	158	226	181
Conidia of *C. arachidicola*	0	226	0	0	0	0	0

1 Concentrations expressed as average of four observations
2 Infected plants were shaken at the start of this trapping period

the urediniospore concentrations were almost 10 times greater than those of the conidia of *C. personatum* at foliage level and 5 times greater at the 3-m level (Table 4).

Horizontal gradients

The deposition of pathogenic-spore types at different distances from the field was observed by exposing gravity slides for 24-h periods for 10 days from one edge of a 90-100 days-old crop field in a windward direction for up to 100 m. Urediniospore concentrations decreased gradually with distance, but were present at all distances checked (Fig. 7). At all distances the numbers of urediniospores were always higher than those of conidia of *C. personatum*.

Table 4. Concentrations of pathogenic spore types at different heights above the crop field[1].

Spore type	Spore concentrations cm^{-3} at height above ground level (m) of					
	0.5	1.0	1.5	2.0	2.5	3.0
Urediniospores of *P. arachidis*	236	102	83	73	24	10
Conidia of *C. personatum*	25	12	9	9	6	2

1 Averages of five observations.

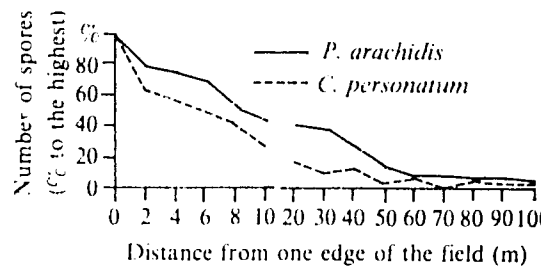

Figure 7. Horizontal deposition of groundnut pathogens.

Deposition on leaflet surfaces

The deposition of airborne urediniospores on upper and lower host leaf surfaces and its relation to airborne concentrations was studied using the sticky-cellotape method. The numbers of spores deposited on the upper surfaces of the leaflets were slightly higher than those deposited on the lower surfaces on each occasion. The number of spores deposited showed a positive correlation with the number of spores trapped on the particular day of study. The ratio of number of urediniospores deposited on upper to number deposited on lower surfaces ranged from 1:0.656 to 1:1.142 with an average of 1:0.795. The ratio between the number of spores estimated from the vertical cylinder traps on the particular day to that deposited on leaflet surfaces was in the range of 1:0.084 to 1:0.351, with an average of 1:0.199 (Table 5).

Table 5. Deposition of urediniospores of *P. arachidis* on leaflet surfaces.

Date	Spores deposited on[1] Upper surface (cm⁻²)	Lower surface (cm⁻²)	Ratio of upper to lower[2]	Average no. of spores deposited cm⁻² area	No. of spores on trap surface on the day	Ratio of airborne spores to deposited spores[3]
2 Mar 76	67	57	1:0.850	62	321	1:0.130
8 Mar 76	139	100	1:0.719	120	476	1:0.251
12 Mar 76	172	119	1:0.691	146	632	1:0.232
27 Sep 76	13	9	1:0.691	11	131	1:0.084
29 Sep 76	21	24	1:1.142	23	176	1:0.131
5 Oct 76	64	42	1:0.656	53	248	1:0.214
8 Oct 76	121	95	1:0.691	108	307	1:0.351
10 Oct 76	69	43	1:0.623	56	283	1:0.197

1. Each number is average of 10 observations.
2. Correlation coefficient between spores deposited on upper to lower leaflet surface is 0.98.
3. Correlation coefficient between spores deposited on leaflets to airborne spores is 0.93.

Effect of Leaching

The urediniospores of groundnut rust contain a germination inhibitor, methyl cis-3, 4-dimethoxy cinnamate, which is water soluble (Foudin and Macko 1974). During the washing down of airborne spores by rain water, the spores will be subjected to leaching. Hence the effect of leaching of urediniospores on their subsequent germination was studied by subjecting them to successive centrifugations in water at 5000 rpm for 10 min. There was a steep increase in the percentage of germination after the first leaching but germination did not increase appreciably when the spores were subjected to further leaching (Table 6). This indicates that the washing down by rain water of airborne spores has a positive effect on their subsequent germinability, which is the most important initial step in the initiation of successful infection.

Table 6. Effect of leaching (by centrifugation in water 5000 rpm for 10 minutes) on germination of *P. arachidis* urediniospores.

Leaching treatment	No. of spores counted[1]	No. of spores germinated[1]	Percent of germination
Control: no leaching	500	321	64.2
1 leaching	500	412	82.4
2 leaching	500	420	84.0
3 leaching	500	424	84.8
4 leaching	500	425	85.0

1. Average of three observations.

Conclusions

1. The urediniospores of groundnut rust are efficiently dispersed by air currents.
2. Airborne concentrations follow the pattern of disease incidence in the field and can be used for disease assessment.
3. During the rainy season, the airborne concentrations vary greatly depending on the rainfall and weather conditions.
4. During the winter season, urediniospore concentrations increase gradually.
5. Higher urediniospore concentrations occur in the air when temperatures are in the range of 29-31°C., relative humidity in the range of 75-85%, and windspeeds in the range of 4-10 km h^{-1}.
6. A clear circadian rythm with peaks between 1000 and 1400 h is exhibited by airborne urediniospores.
7. Spore concentrations decrease with increasing height above ground level, with a sharp reduction above 2 m.
8. Spore deposition occurs for more than 100 m in a windward direction from the edge of a field containing an infected crop.

9. Mechanical disturbances greatly increase airborne spore concentrations over an infected crop but the effect soon disappears.
10. The ratio of airborne spores to those deposited on leaflet surfaces is around 1:0.199.

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Discussion

Chairman: J.A. Wightman

Rapporteurs: P. Subrahmanyam, V.M. Ramraj

P.W. Amin. The rust spores are dispersed by wind currents to considerable heights in the atmosphere and it is known that at such heights temperatures are very low. Is it possible that the low temperatures spores encountered at high altitudes could preserve their viability beyond the 120 h quoted by Dr Nagarajan?

S. Nagarajan. At high elevations there are high levels of ionising radiations and this is the cause of spores being killed.

J.E. Parlevliet. Stem-rust spores do seem to be able to survive for longer periods. There is good circumstantial evidence that on very rare occasions stem-rust spores derived from southern Africa can reach Australia. Spore spread from Australia to New Zealand (1500 km) occurs yearly.

S. Nagarajan. Yes. Dr Watson has recently reached the same conclusion through biochemical testing of spores. The weather pattern aids spread of stem rust, probably from Mozambique or South Africa. However, this is not of regular occurrence because of the great distances involved.

E.A. Salako. Since the Nilgiri Hills in southern India have been identified as the only source of wheat rust inoculum for other parts of the country, would it be possible to eliminate the pathogen from there by use of resistant cultivars and fungicide application?

S. Nagarajan. In the 1940s Dr Mehta recommended breeding resistant cultivars for use in the Nilgiri Hills. In 1953 the Government banned wheat cultivation in the Nilgiris, but this was not effective. The pathogen survives on grasses as alternative hosts. Because of the topography and difficult weather conditions, chemical control is not practicable. Resistance breeding is the only practical approach and the wheat-breeding station at Wellington is responsible for introducing resistant cultivars. The pathogen is dynamic and resistance breaks down in a matter of 2 to 3 years. CIMMYT considers the Nilgiris to be the graveyard of wheat cultivars. It is probably better to allow the pathogen to remain in a state of ecological equilibrium rather than to induce it to produce new pathogenic races by frequent introduction of resistant hosts.

K.J. Middleton. Is the wheat rust movement in India only a one-way transfer from south to north?

S. Nagarajan. Yes. The movement of rust is unidirectional. Because of different harvest times the chance of the rust feeding back to the source is minimal. This situation is advantageous for gene deployment

P. Subrahmanyam. What is the distribution of collateral hosts, and what is their contribution to the perpetuation of wheat rust?

S. Nagarajan. *Brachipodium* sp and *Bromus* sp are the collateral hosts. These grasses are very common in the Nilgiris and the pathogen survives well on them. In northern India on the plains the chances of the pathogen surviving on these grasses are slim because of the high temperatures in the summer months.

C.D. Mayee. I feel that the *Puccinia* path for wheat stem rust may not be valid for groundnut rust as the groundnut crop is grown throughout the year and several foci of infection are present in southern India.

S. Nagarajan. In view of the paucity of information, the *Puccinia* path's relevance for groundnut rust can neither be accepted nor rejected. I agree that there can be two or three foci. Depending upon where the cyclonic systems operate, over the Arabian Sea or over the Bay of Bengal, the focus could shift. Groundnut rust could survive in southern India because of the overlapping cropping patterns, particularly south of the Narmada.

A.S. Rao. There is a good possibility that groundnut rust can survive in a dormant state in the host in the summer months when temperatures are high. We have found that the fungus does not produce pus-

tules when the ambient temperature is above 35°C. However, when the monsoon rains arrive and temperatures fall, pustules appear on summer-crop groundnut plants within 4 to 5 days. We therefore consider that the summer crop is a latent carrier of rust and that with the overlapping cropping pattern there is a multifocus system.

C.D. Mayee. I agree with Dr Rao. Leaves can be detached from plants that show no symptoms of rust and if they are placed under conditions conducive to rust development, pustules then appear in a very short time.

B.K. Varma. What was the wind speed when horizontal displacement of groundnut rust urediniospores was observed at 3 m height by Drs Mallaiah and Rao? Wind speeds are very important in dispersal of spores over distances in excess of 100 m.

K.V. Malliah. Wind speeds were not measured. However, we feel that the observed 4% concentration of spores was very high, certainly much higher than the minimum required for effective dispersal irrespective of wind speed.

A.S. Rao. We were actually studying dispersal over short distances. I agree that for long-distance dispersal, wind speeds and turbulence in the upper atmosphere play important roles.

P. Ramachar. The photomicrograph of urediniospores showed only one kind of spore present on the slide. Can it be inferred that the air spora contained only one kind of spore?

K.V. Malliah. Different kinds of spores were trapped. Identification of groundnut-rust spores was based on their morphological characters using slides of rust spores from authentic *Puccinia arachidis* sources.

J.F. Hennen. What is the theoretical possibility for the airborne introduction of groundnut rust into paleotropica from neotropica considering the length of time that spores remain viable under the prevalent weather conditions?

S. Nagarajan. In the case of wheat rust there is the evidence already quoted, but for groundnut rust there is no systematically collected information to permit any definite conclusions being made on this point.

C.D. Mayee. Obviously the concentration of urediniospores in the air over a crop is greatest when rust disease is most severe. Is it possible to use such aerobiological data to measure the amount of rust disease present?

K.V. Malliah. The concentration of rust spores in the air can be correlated with weather factors and with the amount of disease present in a crop. It may well be easier to measure the amount of disease present in a crop by measuring the air spora than by counting pustules on plants but it would be necessary to standardize methods.

S. Wongkaew. Can the methodology employed for studying the epidemiology of wheat rust be used to obtain an understanding of the spread of groundnut rust?

S. Nagarajan. Yes. I feel that methods used in the study of wheat rust and some of the data obtained can be of considerable benefit to research workers concerned with groundnut rust.

The Taxonomy of *Puccinia Arachidis* Speg. and Possible Occurrence of Races

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The Taxonomy, Life History, and Evolution of *Puccinia arachidis* Speg.

J.F. Hennen[1], P. Subrahmanyam[2], and M.B. Figueiredo[3]

Abstract

The early history and nomenclature of the groundnut rust fungus is critically reviewed. Information on the occurrence of teliospores on the cultivated groundnut and wild Arachis *species is summarized. The basic features of rust life-cycles are presented, and the current status of the taxonomic position of groundnut rust is discussed. The authors believe that the inclusion of groundnut rust in the genus* Puccinia *is suspect. 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 tentative. Several areas of research required for a better understanding of the taxonomic position of groundnut rust are suggested.*

Résumé

Taxonomie, cycle de vie et évolution de Puccinia arachidis : *Les auteurs récapitulent avec commentaires l'historique et la nomenclature du champignon de la rouille de l'arachide. Suit une synthèse des connaissances sur la présence de teleutospores chez l'arachide cultivée et les espèces sauvages d'* Arachis. *Les éléments fondamentaux du cycle de vie du pathogène ainsi que l'état actuel de sa taxonomie sont présentés. D'après les auteurs, l'intégration de la rouille de l'arachide dans le genre* Puccinia *est douteuse, étant donné qu'il manque des connaissances sur les spermogonies, les écidies, les hôtes des basidiospores et le cycle de vie complet du pathogène. La position taxonomique du champignon reste imprécise et provisoire. Plusieurs domaines de la recherche permettant de mieux comprendre la position taxonomique de la rouille de l'arachide, sont proposés.*

The rust disease of groundnut (*Arachis hypogaea* L.) caused by *Puccinia arachidis* Speg. is hypothesized to have originated in South America along with the domestication of the groundnut, in prehistoric time (Leppik 1971). Commercial production of groundnuts in South America seems not to be severely affected by the rust now but the disease restricts groundnut production in the Caribbean islands and Central America (Hammons 1977). The time of movement of the disease from South America northward is unknown. Occasional outbreaks occur in the southern-most groundnut producing areas of the United States by windblown spores from the south (Bromfield 1971). The disease has been reported as far north as Virginia (Smart 1962). Hammons (1977) concluded that although in general, groundnut rust is not regarded as a serious problem in the USA, the disease causes serious economic losses on a few farms nearly every year in southern Texas. The disease has the potential to become epiphytotic causing widespread damage to the groundnut crop in Texas.

Before 1970 groundnut rust was also recorded from Mauritius (Stockdale 1914) and China (Tai 1937) but we know of no voucher specimens for these records. A record from the USSR (Jaczewski 1910) is erroneous according to Tranzschel (1939);

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3. Pathologist, Instituto Biologico, Sao Paulo, S.P., Brazil

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1987. Groundnut rust disease. Proceedings of a Discussion Group Meeting, 24-28 Sep 1984, ICRISAT Center, India. Patancheru, A.P. 502 324, India: ICRISAT. (CP 409)

no voucher specimens were saved and there are no further reports of the rust from the USSR.

Since 1970 groundnut rust has spread to groundnut-growing areas of Africa, Asia, Australasia, and Oceania where, in many countries, it is reported as one of the most important production constraints for groundnuts (Jackson and Okezie 1981). The source or sources of inoculum and means of spread responsible for the movement of the rust into these areas have not been determined.

There are only a few records of the occurrence of teliospores on cultivated groundnuts, the pathogen being known almost exclusively by its uredinial (conidial) stage. Recently telia have been found on many new collections of wild *Arachis* species from South America. Because there is no knowledge of spermogonia, aecia, and hosts that basidiospores will infect, the full life cycle is unknown and the taxonomic position of the pathogen is obscure and tentative.

This paper reviews the history of the discovery and naming of *Puccinia arachidis*, presents results from examining specimens for the occurrence of teliospores, reviews what is known about the host and geographic range on wild species of *Arachis*, presents information on developmental morphology of the fungus, speculates about the life cycle, taxonomy, and evolution, and suggests areas of research needed to clarify some of the questions raised.

Early History and Nomenclature

The first record of groundnut rust is a collection made in Surinam in 1827 or 1828 by chr. Weigelt, who was sent to Surinam by the Government of Saxony to make botanical collections. He died early in 1828, soon after his arrival (Stevenson 1971). Among his specimens was a small collection of fungi, which was taken by his companion, a Dr Hering, to the famous mycologist Lewis David von Schweinitz, of Bethlehem, Pennsylvania, who had studied in Saxony before he went to Pennsylvania. Schweinitz worked over the collection, assigning tentative names and preparing brief diagnoses, which he never published. To the groundnut rust he assigned the name *Uredo arachidis* Schweinitz but did not write a description for it. The host was identified, presumably by Weigelt, as *Arachis hypogaea* L. Records in the Arthur Herbarium (PUR, herbarium abbreviations follow Holmgren and Keuken 1974) show that the host identification was confirmed in 1915 by the botanist Percy Wilson at the New York Botanical Garden. Probably before Schweinitz died in 1834, the Weigelt specimens were divided into sets. One set was sent to Elias Magnus Fries in Sweden and one to Gustav Kunzein Leipzig, Germany. Both Fries and Kunze received pieces of the rusted groundnut leaves. After Schweinitz died his herbarium was placed in the Philadelphia Academy of Sciences. From Philadelphia the Weigelt Surinam specimens were sent to Miles Joseph Berkeley in England for study. After completing his study Berkeley kept parts of the specimens for which there was sufficient material and returned the remainder to Philadelphia. Thus, parts of the original Weigelt groundnut rust collection came to be located in four different collections i.e., Kunze's, Fries', Berkeley's, and the Philadelphia Academy.

Although Kunze sent out some of the Surinam collections in what has become known as "Weigelt's exsiccati", the date, number, and distribution are unknown (Stevenson 1971). The groundnut rust, however, was not among them. Kunze entered the groundnut rust into his herbarium under the name of *Uredo apiculata* Strauss var *arachidis* Kunze but he never published this name. Unpublished herbarium names, such as these of Schweinitz and Kunze, although of historical interest, have no scientific standing according to the International Code of Botanical Nomenclature.

Berkeley and Curtis (1853) were the first to report on this Surinam fungus collection. They mistakenly identified and published the groundnut rust as *Uredo fabae* Persoon. They noted that the specimen was in bad condition. The portion of Weigelt's collection that was sent to Fries was studied later by Nils Gustav Lagerheim who recognized it as a new species and published it as *Uredo arachidis* Lagerheim in 1894. This is now the correct binomial for the anamorphic uredinial state of the groundnut rust, the stage most often encountered. The part of the Weigelt collection in the Stockholm Museum is the nomenclatural type for this species and any parts or duplicates of the original collections from Surinam found in other herbaria are isotypes.

Kunze's part of the Weigelt collection finally ended up in the Reichenbach herbarium in the Berlin Museum and was eventually studied by Paul Hennings. Apparently unaware of Lagerheim's work, Hennings published the groundnut rust as a new species (Hennings 1896). He described the fungus as a species of *Uromyces* as follows:

"*U. Arachidis* P. Henn. (n. sp.)

Maculis subflavis vel nullis; soris amphigenis gregariis vel sparsis, minutis, ochraceis, primo epider-

mide inflata tectis dein liberis; teleutosporis subglobosis, ellipsoideis vel ovoideis, laete brunneis, 22-28 × 20-26μm episporio cinnnamomeo, tenui sublevi vel minute verrucoso, pedicello fragili, hyalino, brevi.

Surinam, auf Blattern von *Arachis hypogaea*. Weigelt in Herb. Reichenbachiano."

Hennings mistook the urediniospores for teliospores of *Uromyces*, but Henning's type material is reported by Sydow (1910) to have only urediniospores. Therefore, Hennings' binominal is a synonym of *Uredo arachidis* Lagerheim.

The second record of groundnut rust was made by the French botanist Benedict Balansa, who collected the rust in Caa-guazu, Paraguay in 1882, collection number 3449. He sent his specimen, along with many other fungi, to Carlos Spegazzini in Buenos Aires, Argentina. Spegazzini published it as a new species, *Puccinia arachidis* Spegazzini in 1884. The rust specimen consisted almost entirely of teliospores, the only stage that Spegazzini described. This teleomorphic name is the current correct name for the groundnut rust holomorph. He described the fungus as follows:

"*Puccinia arachidis* Speg. (n. sp.)

diag. Maculae nullae v. vix manifestae, parvulae, indeterminata, fuscescentes; acervuli hypo-rarissime epiphylli, nanuti (200-350 μm diam.), plus minusve dense gregarii v. sparsi, hemisphaerico-prominuli, primo epidermide tenuissima velati, dein nudi, laxe granulosi, ferruginei; teleutosporae ellipticae v. obovatae (38-42 × 14-16 μm), sursum obtuse rotundatae v. acutatae, ibique crassiuscule tunicatae, medio 1-septate, parce constrictae, deorsum leniter attenuato-truncatae, fulvellae, episporio laevissimo, protoplasmate nubiloso; stipes longiusculus, gracilis (50-60 × 1-5 μm), hyalinus.

Hab. Ad folia viva *Arachidis hypogaea* prope sylva subvirginea Caa-guazu, Jan. 1882 (sub num. 3449)."

Spegazzini did not mention urediniospores in his description. Notes in the Arthur Herbarium (PUR) show that J.C. Arthur examined the type material supplied by Spegazzini on 3 Feb 1921 and found some urediniospores that measure 23 × 25 μm. G.B. Cummins further examined Spegazzini's type material on 6 Jun 1931 and found some 3-4 celled teliospores, in addition to the commonly present 2-celled teliospores. We reexamined Spegazzini's isotype material at PUR 13 Jul 1980 and confirm the above observations but we question the identification of the host as *A. hypogaea*. We believe that it is a wild species of *Arachis*, and not the cultivated *A. hypogaea*. Independently, Lindquist (1983) came to the same conclusion.

When Lagerheim published *Uredo arachidis* he also reported that *Puccinia arachidis* Spegazzini occurred in South America. He did not, however, make the connection of the *Uredo* to the *Puccinia*, probably because he had none of Spegazzini's material for comparison. Lagerheim also suggested that the rust data supported the hypothesis that South America was the original home of the groundnut rather than Africa.

In an attempt to bring the nomenclature of numerous plants into accordance with his revisions of the 1867 "Paris Code of Botanical Nomenclature" and his insistence on using 1737 as the starting date for generic names of plants, Otto Kuntze changed nearly 30 000 plant names (Zanoni 1980), among these changes was the transfer of numerous species of *Puccinia*, including *P. arachidis*, to the genus *Dicaeoma* S.F. Gray 1821, thus *D. arachidis* (Spegazzini) O. Kuntze, 1893. According to the Paris Code, Kuntze reasoned, the genus name *Puccinia* applied to the original 1729 concept of Micheli and later validated in 1763 by Adanson. According to this concept the name *Puccinia* applied to the current genus *Gymnosporangium*, the "cedar-apple" rusts. As *Puccinia* was not available, Kuntze found that the first valid name published that was available for our current concept of *Puccinia* was S.F. Gray's *Dicaeoma* of 1821. However, more recent codes of botanical nomenclature specify 1801 as the starting date, which is the date of publication of Persoon's Synopsis Methodica Fungorum. It is this work that validates usage of *Puccinia* in its modern form with *Puccinia graminis* Pers. as the nomenclatural type species.

The putative connection of the uredinial anamorph to the telial teleomorph was first published by J.C. Arthur and E.B. Mains (1922). Records in PUR show that they studied both the Surinam and the Paraguay specimens, the types of *Uredo arachidis* and *Puccinia arachidis* respectively, and found a few urediniospores in the Paraguay specimen that matched the urediniospores from Surinam. They, however, transferred *P. arachidis* to *Bullaria arachidis* (Spegazzini) Arthur and Mains (1922). They based the generic concept of *Bullaria* on the number and kinds of stages in the life cycle rather than strict morphological relationships. This life cycle concept for rust genera has not been supported by uredinologists and was later abandoned by Arthur (1934).

The first experimental proof of the connection of *U. arachidis* and *P. arachidis* was reported by

Hennen et al. (1976). Thus, *Puccinia arachidis* Spegazzini is the currently accepted teleomorphic and holomorphic binomial for the groundnut rust fungus. However, as discussed later, new evidence indicates that the groundnut rust is not a *Puccinia*. The proper genus must probably await the determination of spermogonial and aecial characteristics, phases of the life cycle that currently are unknown.

Teliospores on *Arachis hypogaea*

The occurrence of teliospores on cultivated *A. hypogaea* seems to be rare. The following summarizes the reports in the literature and our own observations.

1. Although Spegazzini (1884) reported that the host of his new species *P. arachidis* was *Arachis hypogaea* L., we conclude that it is an undetermined wild species of *Arachis*. Independently, Lindquist (1983) came to the same conclusion.
2. Jaczewski (1910) reported that N.V. Spishnev observed *P. arachidis* causing rust on groundnut in 1903 in Lenkoran, Yerevan (near the Turkey-Iran borders, between the Black and Caspian Seas) and Karayazakh of the Transcaucasian region of USSR. Only teliospores were reported. This is the first report of groundnut rust outside the Western Hemisphere. Jaczewski believed it possible that *Uromyces arachidis* P. Hennings, which proved not to be a *Uromyces* but a urediniial stage, was another stage of *P. arachidis*. Unfortunately, no information was given about the morphology of the fungus or host and no voucher specimens were reported to have been preserved. Tranzschel (1939) believed that Jaczewski's report was in error. We also do not accept the report because there are no subsequent records from the USSR and there are no voucher specimens to confirm it.
3. In July 1921 J.A. Faris collected rust on *A. hypogaea* near Haina, Santo Domingo in Central America and the specimens were deposited in the Brooklyn Botanical Garden Herbarium. A portion of the material has urediniospores and teliospores of the groundnut rust pathogen. The teliospores are 2-celled and 64 × 21 μm.
4. Another collection of rust on *A.hypogaea* from near Gainesville, Florida collected by Hull and West on 4 Oct 1930 in BPI also has both urediniospores and teliospores. The teliospores are 2-celled and 53 × 17.5 μm. This is the first record of the occurrence of teliospores of groundnut rust in the United States.
5. On 2 Sep 1936 (BPI), W.A. Archer (and A. Gehrt?) collected rust on *Arachis hypogaea* L. sub sp. *rasteiro* Chev. (No. 23) near the city of Campo Grande, now in the state of Mato Grosso du Sul, Brazil. A portion of this material was also sent to Arthur at Purdue University (PUR-F6251), either directly from Archer or through the National Fungus Collections. We believe that the identity of the host is not correct. It is probably a wild *Arachis* species. The material deposited in both herbaria has urediniospores and teliospores. Teliospores were predominantly 2-celled but sometime 3-celled.
6. Chahal and Chohan (1971) reported the occurrence of teliospores of groundnut rust from Ludhiana, Punjab State, India on plants growing in a greenhouse. As the authors did not give details of spore morphology and we know of no voucher specimens, this report cannot be confirmed.
7. Bromfield determined the occurrence of both urediniospores and teliospores of groundnut rust from *Arachis hypogaea* (cultivar Chibahanda) collected by H.S. Chung in Suwon, Korea on 30 Aug 1972 (BPI). We examined this material but found only urediniospores and in some cases conidia of *Alternaria* spp.
8. Hennen et al. (1976) reported the occurrence of teliospores of groundnut rust (Fig. 1) developing within uredinia on *Arachis hypogaea* (Cultivar Tatu) after artificial inoculation in a greenhouse at Campinas, Sao Paulo, Brazil. A portion of this material has been preserved in the Arthur Herbarium (PUR-F19745) and in the plant pathological herbarium of Instituto Biologico, Sao Paulo, Brazil.

In summary, only three confirmed records of teliospores of *P. arachidis* on *A. hypogaea* exist: one from Santo Domingo, one from Florida, and one from Sao Paulo state, Brazil.

Teliospores on Wild Species of *Arachis*

Six records of telia on wild species of *Arachis* are known.

1. We know now that Spegazzini's type from Paraguay reported to be on *A. hypogaea* was on a wild species of *Arachis*.
2. Archer made several collections of telia on wild species of *Arachis* in South America in 1936.

Figure 1. Teliospores of *Puccinia arachidis* on *Arachis hypogaea* (cv Tatu) in Brazil.

They include the collection cited above that was erroneously identified as *A. hypogaea* L. var *vasteiro* from Campo Grande, Mato Grasso do sul, Brazil. Two other collections by Archer from Campo Grande, whose hosts were identified as *A. glabrata* (BBI-US46495, BPI-US46491, PUR-F6251) were reported by Bromfield (1971).

3. Archer's collection from Tupeceretan, Rio Grande do Sul, No. 11, 1936 (BPI-US46526, PBI-US46527) has teliospores. The host is probably *A. burkartii* and not *A. marginata* as originally identified.
4. Guarch (1941) reported teliospores on a collection of *A. marginata* from Uruguay but we have not seen voucher specimens.

During the past few years we have collected groundnut rust on phanerogamic herbarium specimens and in the field in Brazil in 1983-84. Specimens of *Arachis* species were examined at the following herbaria: Instituto Botanica de Sao Paulo, Sao Paulo Brazil; CENARGEN, Brasilia, D.F. Brazil; the Missouri Botanical Garden, St. Louis, Missouri, USA; the Field Museum, Chicago, Illinois, USA; the US National Museum, Washington, D.C., USA.; and the collection of C. Simpson, Stephenville, Texas, USA. From this work we now have 66 new collections of rust on wild species of *Arachis* of which 33 have telia or teliospores. We conclude that telia are regularly produced on wild species of *Arachis* in South America.

What is the Best Taxonomy for the Groundnut Rust Pathogen?

Ideally, to determine the best taxonomic position for a rust, comparative morphological studies should be made for all of the stages in its life cycle to determine its overall similarity to other rusts. Unfortunately, for the many pleomorphic rusts whose life cycles are unknown, this is not possible and only preliminary taxonomic approximations can be made.

Rust life cycles

The basic features of rust life cycles are summarized below. See Cummins and Hiratsuka (1983), and Peterson (1974) for other details.

A rust species may have up to five spore forms (rarely six) and two taxonomically unrelated hosts while completing its life cycle. Several life cycle patterns for these spore forms are known, the commonest of which are modifications of the long and short cycles. A single life-cycle pattern is not always constant within a species. The different spore forms of a species are often separated from each other not only on different hosts but also they may occur at different times during the growing season. Within a species some spore forms may be produced only rarely, some spore forms may be more widespread geographically than others of the same species, and some spore forms may have a much wider or narrower host range than others of the same species. Thus, frequently, it is not apparent from a rust collection that usually has only one or two spore forms, what other kinds of spore forms occur in that rust's life cycle. Because of this highly developed pleomorphism, the taxonomy of rusts has developed by necessity mostly through comparative studies of structures that represent only part of the complete organism. Life cycles of rusts are usually inferred a piece at a time from stages that are associated in herbarium collections. Proof of a life cycle requires experimental verification but this has not been carried out for most subtropical and tropical rusts. The taxonomic positions of these species must therefore be regarded as tentative or approximate.

Stages in rust life cycles

The different sori produced by the different stages in rust life cycles have been defined as follows (Cummins and Hiratsuka, 1983).

1. Spermogonia, which are always produced from infections made by basidiospores, produce gametes and are symbolized by 0.
2. Aecia, which are also produced from infections made by basidiospores, result from a sexual fusion, produce aeciospores that are analagous to zygotes. The aeciospores germinate with an infective germ tube, not a metabasidium, and are symbolized by I.
3. From either aeciospore or urediniospore infections, uredinia result that produce conidia known as urediniospores; these are symbolized by II.
4. Telia may develop from infections made by basidiospores, aeciospores, or urediniospores, depending on the kind of life cycle. They produce teliospores that germinate to produce metabasidia and basidiospores; teliospores are symbolized by III.
5. Basidiospores are meiospores and are symbolized by IV.
6. Thus according to our usage, these life-cycle stages are defined by their function and position in the life cycle, not by their morphology.

Recently the terms anamorph, teleomorph, and holomorph have come into use. In the rusts, spermogonia, aecia, and uredinia are anamorphs; telia are teleomorphs, and all of the stages of the life cycle of a species is the holomorph. For nomenclature, each anamorph may have a separate binomial but the correct name for the holomorph is the binomial applied to the teleomorph.

Taxonomy of groundnut rust

Currently the groundnut-rust pathogen is identified as being in the genus *Puccinia* because the teliospores are laterally free, pedicellate, usually 2-celled, and each cell has one germination pore. But this identification is suspect. Morphology, host relationships, and evolutionary theory support this doubt. The doubt is raised on morphological grounds because the uredinia of *P. arachidis* produce a membranous net-like peridium, a characteristic unknown in any other species of *Puccinia* (see later). In addition the rust fungi are well known for their host specificity at various levels. The family Leguminosae, to which *Arachis* belongs, contains hosts of numerous rust taxa but probably no true species of *Puccinia* produce uredinia and telia on legumes (Cummins 1978, Leppik 1972, Savile 1971). Several rusts occurring on Leguminosae, originally placed in *Puccinia*, have been transferred to the genus *Soratea* (Savile 1971, Eboh and Cummins 1980). There are indications that many taxa of the Leguminosae coevolved with various kinds of rusts, excluding true *Puccinia* (Savile 1971). If *P. arachidis* is not a true *Puccinia*, then its behavior need not necessarily be similar to that of other species of *Puccinia*, such as *P. graminis*.

Description of *Puccinia arachidis* Spegazzini

The description here is modified from Cummins (1978).

0. Spermogonia not known
I. Aecia not known
II. The uredinial stage, *Uredo arachidis* Lagerheim, is the predominant and most commonly observed. Uredinial sori are pustular and mostly hypophyllous (on abaxial leaf surfaces), but can develop on petioles, stipules, and stems. They are scattered or irregularly grouped, elliptical, round, or oblong, subepidermal in origin, covered by a thin, membranous, net-like peridium and are blister-like when immature. They become erumpent, powdery, and dark cinnamon brown when mature. Individual pustules are 0.2-0.8 mm (mostly 0.5) in diameter, ruptured epidermis conspicuous; urediniospores are broadly ellipsoid or obovoid, (21-)23-29 × (16-)18-22(-24) μm, wall brown, 1-2 μm thick, finely echinulate, echinulae 2-3 μm apart, with mostly 2 occasionally 3 or 4, nearly equatorial germpores, often in flattened areas, teliospores may be intermixed with urediniospores.
III. Telia chiefly hypophyllous, 0.2-0.3 mm in diameter, scattered, prominent, soon naked, pulvinate, chestnut brown or about cinnamon brown, becoming grayish from germination of spores, ruptured epidermis prominent; teliospores oblong, obovate, or ellipsoid, with rounded to acute and thickened apex, slightly or not constricted at the septum, somewhat or gradually attenuate at the base or more or less rounded attenuate at both ends, predominantly 2-celled, sometimes with 1, 3, or 4 cells (33-)38-56(-60) × (12-)14-16(-18) μm, wall smooth, light or golden yellow, or chestnut brown, 0.7-0.8

(-1.0) μm thick at sides, 2.5-4.0(-5.0) μm thick at top, apical thickening almost hyaline, pedicel thin walled, usually collapsing laterally, hyaline, up to 35-65 μm long but usually broken, shorter or detached at spore base, spores germinating at maturity without dormancy.

The life cycle of groundnut rust

To understand the life cycle of *P. arachidis* and its relationship to other rusts, it is essential to know which hosts basidiospores infect and what kind of rust structures (spermogonia and aecia, if they are produced) these infections produce. The geographical region most likely to yield this information is Central South America (Hennen et al. 1976), where the pathogen, *P. arachidis* and its wild hosts, *Arachis* species, are believed to have coevolved over geological time. The original homeland of a host-parasite relationship is the region where the parasite most likely goes through its sexual life cycle with at least some regularity.

Rust Species Closely Related to Groundnut Rust

The relationship of *P. arachidis* to other, apparently closely-related rusts, requires further study to determine if they can also infect groundnuts. They are *P. zorniae* McAlpine (Fig. 2) and *P. offuscata* Arthur (Fig. 3) on *Zornia* species and *P. stylosanthis* Viegas (Fig. 4) on *Stylosanthes* species. The rust *P. offuscata* was made a variety of *P. arachidis* by Cummins (1978) because of morphological similarity; *P. stylosanthis* is only known from four Brazilian collections, the type collection from Campinas, Sao Paulo, Brazil, and three others (Fig. 4). It is morphologically very similar to *P. zorniae*. Certain species of *Stylosanthes* are planted widely in tropical regions as forage legumes but their susceptibility to rust is not known. Therefore, it would be useful to know the relationship of *P. stylosanthis* and *P. zorniae* to *P. arachidis*. The rust *P. zorniae* occurs in Africa and Australia (Fig. 2) on wild species of *Zornia* but the susceptibility of *Arachis* to this rust is unknown.

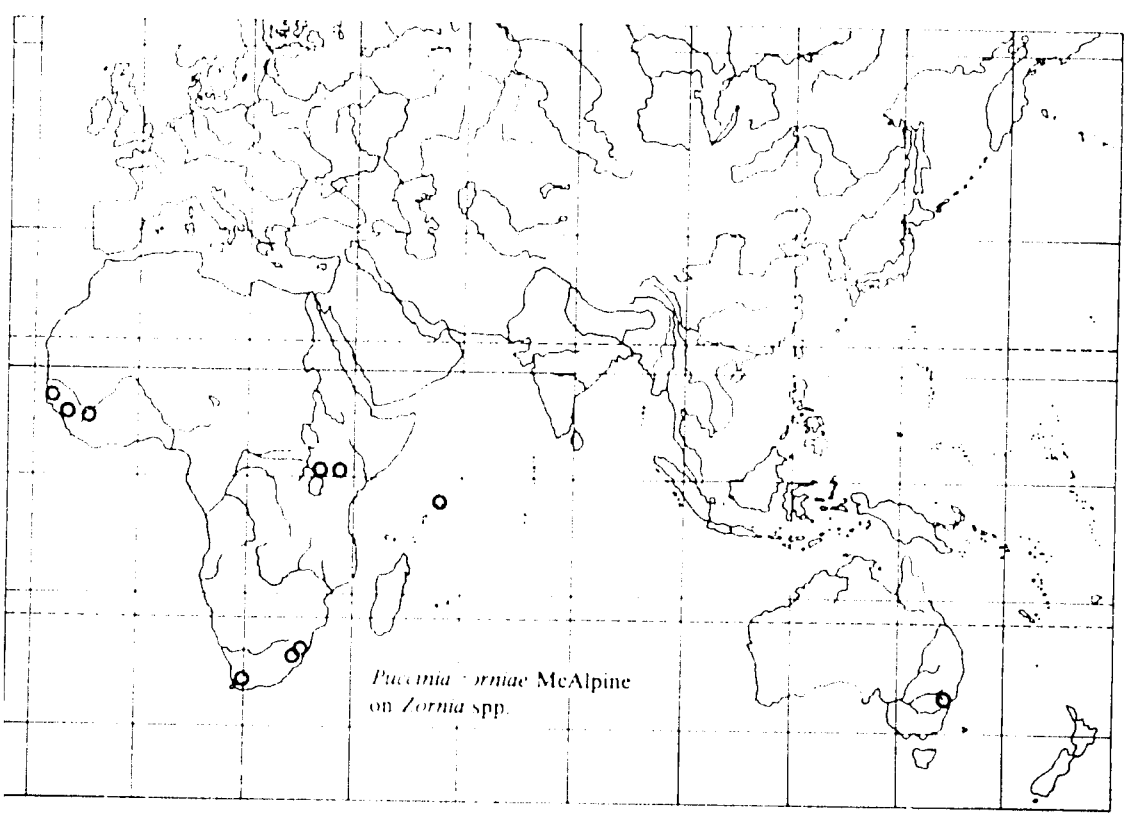


Figure 2. Geographical distribution of *Puccinia zorniae* on *Zornia* spp.

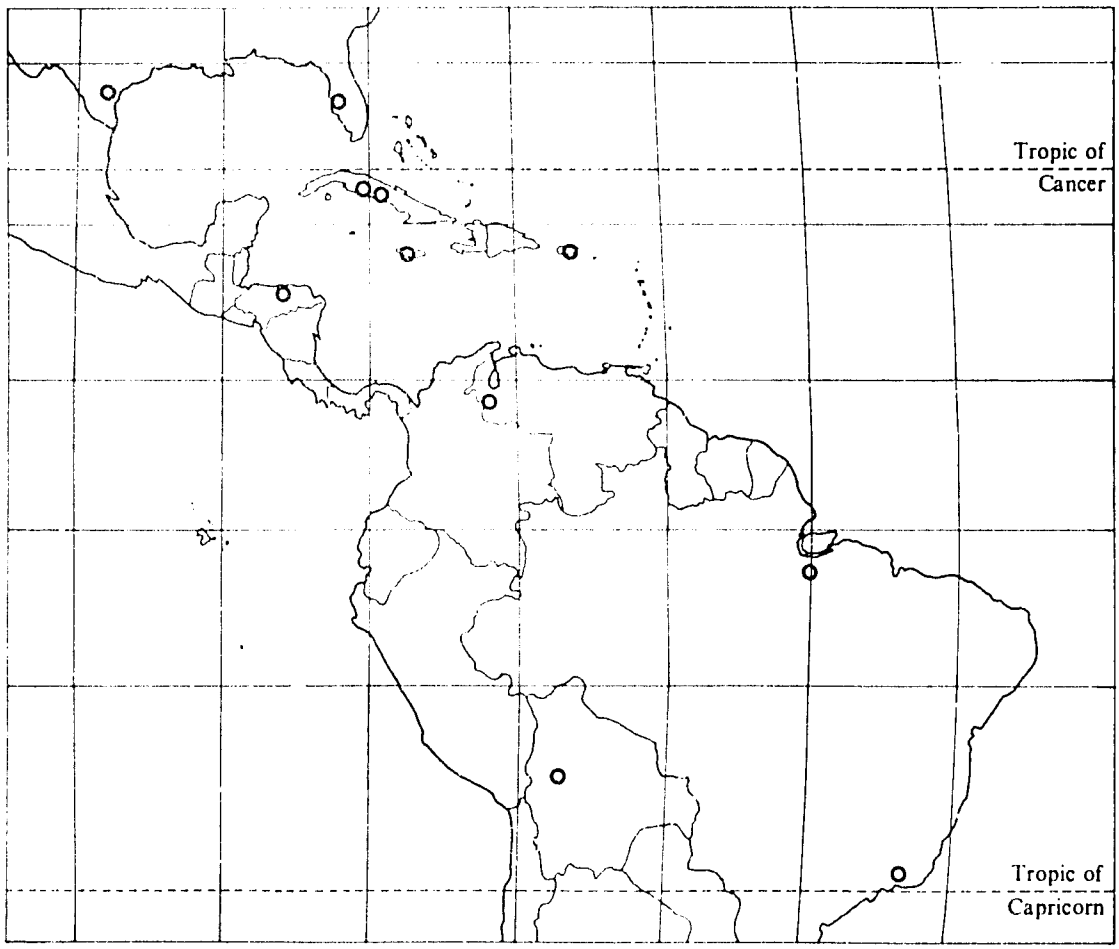


Figure 3. Geographical distribution of *Puccinia offuscata* on *Zornia* spp.

The early report of groundnut rust from Mauritius (Stockdale 1914) is of interest because the first collection of *P. zorniae* is also from there. We do not know of any voucher specimens.

Structure and development of uredinia

For the study of the structure and development of uredinia whole mounts and free-hand transverse sections of small pieces of leaves with rust infections were cleared and mounted in saturated chloral hydrate solution on standard glass microscope slides, covered with a cover glass, and observed with bright light, dark-phase, and interference-phase microscopy.

An urediniumbegins as a small mass of irregularly intertwined hyphae usually in an abaxial substomatal chamber. Intercellular hyphae extend into this mass from surrounding mesophyll tissue. The hyphal mass increases radially, especially just below the epidermis, but it does not cross the larger leaf veins. Increase in diameter occurs by the addition of new hyphal cells around the margin of the young sorus. These new hyphal cells originate from beneath the developing sorus and their tips terminate just beneath the epidermis. As growth continues, these hyphal tip cells differentiate into a region of catenulate cells, 2-3 cells deep (Fig. 5a).

The upper layer of these catenulate cells adjacent to the epidermis develops into a thin-walled, reticulate-like peridium. The cells next in the chains eventually rupture. This separates the peridium layer from the remainder of the sorus. The peridium usually remains attached to the epidermis when the sorus breaks through the epidermis. The mycelial

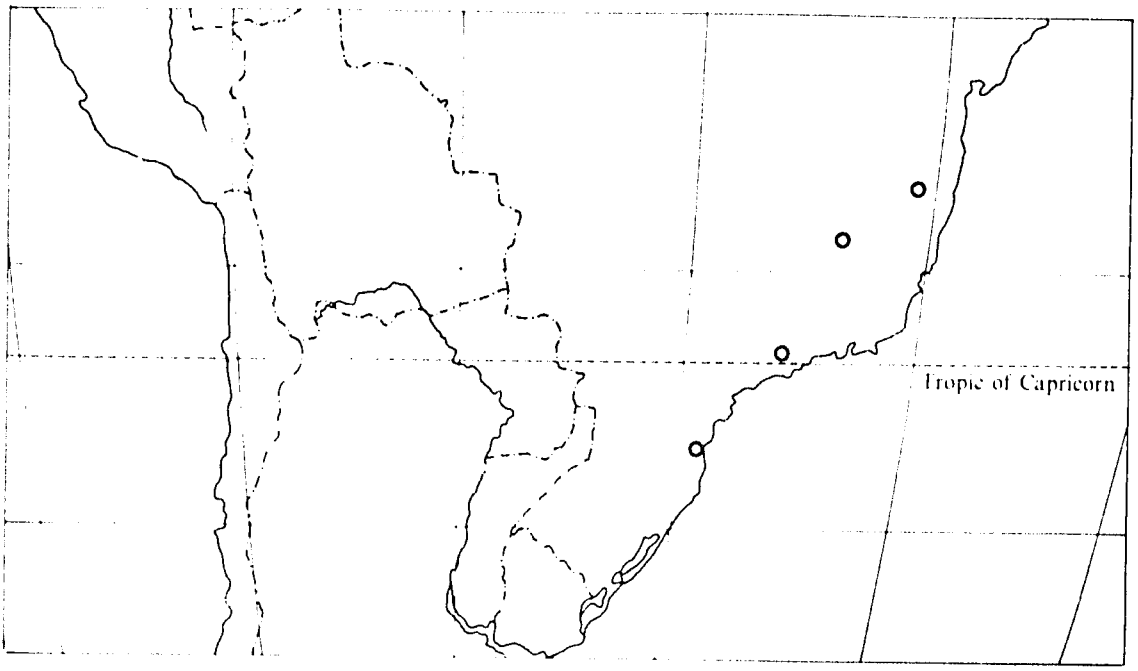
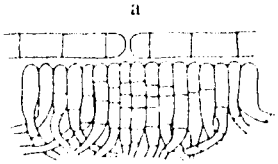


Figure 4. Geographical distribution of *Puccinia stylosanthis* on *Stylosanthes* spp.

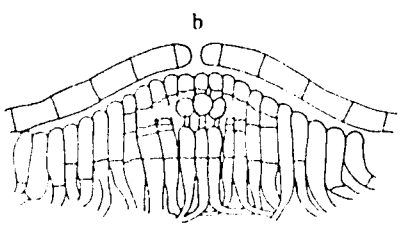
cells below those that rupture become spore-producing cells. They divide to form spore initials, which in turn undergo a division to form young urediniospores distally and pedicel cells proximally (Fig. 5b).

As the urediniospores mature, they enlarge, their walls become thicker, pigmented, and echinulate, and germination pores are differentiated. Pedicel cells elongate during maturation. At magnifications of about × 15, immature uredinia appear as minute, hyaline or yellow-orange, blister-like areas. As an uredinium matures, the epidermis and peridium break open irregularly (Fig. 5c).

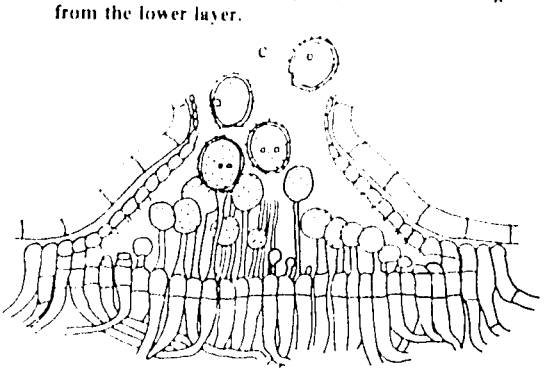
Remnants of the epidermis and peridium may remain loosely attached. Mature spores are loosely attached to the pedicels. They are easily detached by



a. Protosorus developing in a substomatal cavity showing palisade of protosoral cells. Central cells divided into three layers.



b. Early development of sorus showing peridium coming from the upper layer, disjunctor cells coming from the middle layer, and sporogenous cells coming from the lower layer.



c. Young sorus showing development of urediniospores, breaking open of the epidermis, and indeterminate radial growth of the sorus by new hyphae at the margin.

Figure 5. Developmental stages of uredinia of *Puccinia arachidis*, schematic interpretation.

the development of younger spores, by plant movements, or wind. The first-formed spores are irregular, angular, and broadly ellipsoid because of the surrounding pressure under which they are formed. Additional spores are apparently formed by the spore mother cells by a similar method although the details were not observed clearly. They push between the old pedicels, eventually reaching the exterior surface of the sorus. The later-formed spores are broadly ellipsoid and more regular in shape than the first-formed spores.

At maturity, an uredinium is composed of an hymenial layer of sporogenous cells subtended by a pseudoparenchymatous region, from which numerous intercellular hyphae extend into the surrounding mesophyll. The intercellular hyphae are irregular in shape and branch irregularly. Arising from the hymenial layer are numerous older pedicels, whose spores have become detached, pedicels with mature spores still attached, and pedicels of varying shorter lengths, with various stages of spore maturity, pushing their way up between the other pedicels and spores. Because the peridium continues its development radially, as the sorus matures, the youngest part of the peridium remains around the circumference of the sorus, while the older part is attached to the broken and recurved epidermis (Fig. 5c).

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On the Likelihood of Pathogenic Forms or Virulences, in *Puccinia arachidis* Speg., that Cause Groundnut Rust in *Arachis* Species.

S. Nagarajan[1]

Abstract

Concepts of vertical and horizontal resistance as applied to rust diseases are discussed and published data on reactions of groundnut genotypes to Puccinia arachidis *are critically examined. Additional points are brought to light. Better methods of evaluating the host-pathogen interaction in groundnut rust disease are suggested.*

Résumé

Note sur l'existence éventuelle de formes pathogènes ou de virulence chez Puccinia arachidis Speg., responsables de la rouille de l'arachide chez les espèces d'Arachis : *Les principes de la résistance horizontale et verticale sont abordés par rapport aux maladies de la rouille. Les données documentées sur les réactions des génotypes d'arachide à* Puccinia arachidis *sont commentées. D'autres faits sont mis en lumière. L'auteur propose des méthodes permettant de mieux évaluer les interactions entre la plante-hôte et le pathogène de cette maladie.*

The Origins of the Cultivated Groundnut and of Groundnut Rust

The cultivated groundnut or peanut (*Arachis hypogaea* L.) is native to South America and is said to have evolved in the region south of the Amazon river and east of the Andes mountains. The genus *Arachis*, which includes the groundnut and its many wild relatives, has great genetic diversity. The cultivated groundnut is a tetraploid, annual species that contains genotypes with a wide range of growth habits, season length, pod and seed types, and adaptation to many different environments and stresses including diseases. The diversity in the mainly diploid wild *Arachis* species is even greater. Groundnut rust incited by *Puccinia arachidis* Speg., is also believed to be native to South America, from where it has spread to Central and North America and, more recently, to most groundnut-growing countries of the world (Subrahmanyam et al. 1980).

Variability in the Pathogen

Every organism has to adapt its evolution to others. This interdependence is especially pronounced between a host and its parasite. The host defence against infection is matched a by counteraction of added virulence by the pathogen (MacKey 1981). If the rust-resistance genes in groundnut have exerted a selection pressure on the pathogen, then variability as pathogenic forms must occur. But current literature does not substantiate the existence of physiologic forms in *P. arachidis* (Bromfield and Cevario 1970, Lin 1981, Subrahmanyam et al. 1983a, 1983b).

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Present Knowledge of the Host-Pathogen Interaction

Subrahmanyam et al. (1982), evaluating the world collection of groundnut germplasm at ICRISAT, described differences between genotypes on the basis of a 9-point scale they had developed for the field assessment of foliar diseases. Their scale for rust evaluation is given in Table 1. This scale covers two parameters, i.e., (1) disease severity, and (2) pustule type. The 9-point scale is very good for quick evaluation of genotypes, but does not fully meet the requirements for critical evaluation of the host-pathogen interaction. Table 2 has been reproduced from Subrahmanyam et al. (1983b) wherein the field disease scores of 30 genotypes selected to represent a range of rust resistance are given together with data on incubation period ("p"), pustule diameter in mm, and percentages of pustules that had ruptured by the 20th day after inoculation. Their data show that "p" is dependent on the level of susceptibility. Even in cereal rusts the susceptible pustules take about 25% less time than resistant ones to rupture the epidermis and sporulate profusely. A critical look at Table 2 shows that genotypes in botanical variety *hypogaea* have "p" values about 10% lower than those in botanical variety *fastigiata* producing similar-sized pustules. The differences between botanical varieties for these characters have gone unnoticed (Table 2).

Table 1. The 9-point ICRISAT field scale[1] for foliar-disease (rust) assessment.

Score	Description
1	No disease.
2	A few small pustules on older leaves.
3	A few pustules (mainly on older leaves) some ruptured, poor sporulation.
4	Pustules small or large, mostly on lower or middle leaves, disease evident.
5	Many pustules, mostly on lower and middle leaves yellow halo develops, moderate sporulation
6	Same as 5, but heavy sporulation.
7	Pustules all over the foliage, lower and middle leaves withering
8	As rating 7 but withering is more severe.
9	Plants severely affected, 50-100% leaves withered

1 Based on Subrahmanyam et al. (1982)

Vertical resistance

Van der Plank (1963) broadly grouped resistance in the host-pathogen interaction into vertical (VR) and horizontal (HR) resistance. He further stated that VR involves differential host-pathogen interaction, and is race specific. Situations as monitored by Subrahmanyam et al. (1983b) (Table 2), where some

Table 2. Variation between botanical varieties of *Arachis hypogaea* that has gone unnoticed.

Description of genotypes		Rust field score (mean)	Components of resistance			
Identity	Botanical variety		Incubation period (days)	Infection frequency (lesions cm^{-2})	Pustule diameter (mm)	Ruptured pustules (%) 20 days after inoculation
PI 414332	*hypogaea*	2.4	14.7	4.1	0.86	1.4
PI 405132	*fastigiata*	2.4	18.3	8.1	0.63	1.3
PI 393646	*fastigiata*	2.4	18.1	6.7	0.57	0.6
PI 414331	*hypogaea*	2.8	11.9	1.4	0.57	3.8
PI 407454	*fastigiata*	2.8	18.5	4.7	0.57	1.1
EC 76446(292)	*fastigiata*	2.8	17.5	6.2	0.59	5.1
PI 393527 B	*hypogaea*	3.0	15.9	4.2	0.51	14.4
PI 314817	*fastigiata*	3.0	15.2	3.2	0.49	2.4
PI 393643	*fastigiata*	3.0	14.7	5.5	0.73	3.0
PI 218115	*hypogaea*	4.0	9.2	11.3	1.16	90.5
NC Ac 17142	*fastigiata*	3.8	9.9	12.3	1.12	96.0
NC Ac 17130	*fastigiata*	4.2	10.1	10.2	1.29	97.1

Data in table are reproduced from Subrahmanyam et al. (1983)

genotypes have large, heavily-sporulating pustules and others have small, poorly-sporulating pustules, indicate the existence of differential host-pathogen interaction. As per Van der Plank (1963) such differential host-pathogen interaction is due to VR, and it is improper to conclude it to be due to HR.

Various attempts have been made to exploit the resistance genes present in wild relatives of the cultivated groundnut. The F_1 hybrids between two rust-susceptible cultivars and diploids, tetraploids, and amphidiploids involving *Arachis* species closely-related to *A. hypogaea* were evaluated for their resistance to *P. arachidis*. The genes that condition resistance were found to be partially dominant (Singh et al. 1984), indicating that VR genes are probably operating against groundnut rust in these *Arachis* species.

Horizontal resistance

When resistance is evenly spread against all races of a pathogen, it is horizontal or lateral, and is clearly reflected by "r" the apparent rate of infection. For measuring HR it is necessary to measure accurately "X", the level of disease severity (Van der Plank 1963). In their experiment, Subrahmanyam et al. (1983b) observed that highly resistant genotypes had much smaller uredosori, than had moderately resistant and susceptible genotypes. As these reaction types varied for "p", amount of spores produced, pustule size, etc., they concluded that resistance was of the horizontal type. In fact, they had compared resistant and susceptible genotypes. When the level of susceptibility is not identical as required for evaluating HR (Van der Plank 1963), such differences are bound to occur. They have even observed that in immune genotypes (found only in some wild *Arachis species*), the germ tube died without further development, and in others, differences occurred in the level of proliferation of mycelium in substomatal cavities.

Measuring horizontal resistance

Reduction in the apparent rate of infection is the major epidemiological effect of horizontal resistance, and can be measured only by using matching races of the pathogen (Kulkarni and Chopra 1983). For purposes of characterizing slow-rusting behavior, the susceptible spring wheats, Pictic 62 and Ponjame 62 were taken and compared with the slow-rusting cultivar Banza 55 for their "r" value (MacKenzie 1976). Explanations such as slow spore production and shorter incubation period, are parameters that contribute to HR.

To start with, HR should be quantified in the absence of major VR genes. Groundnut varieties TMV 2, J 11, NC 30333 and Robut 33-1 differ little for "p," pustule size, and for percentage of pustules ruptured, etc. (Table 3). All these genotypes are uniformly susceptible and if they differ for their "r" value, then only the presence of HR can be inferred. Following the 9-point scale of ICRISAT, if "r" is to be calculated, there will be some error because it has lumped both severity and pustule type together. It is therefore necessary to record disease severity as a percentage, and a new scale will have to be developed for this purpose. Either of the two internationally accepted approaches can be followed, i.e., (1) taking total green leaf area as 100% against which area occupied by the disease lesions is scored as a percentage (James 1971), and (2) taking the maxi-

Table 3. Uniformly susceptible genotypes lack variation for parameters that contribute towards horizontal resistance.[1]

Description of genotypes		Rust field score (mean)	Components of resistance			
Identity	Botanical variety		Incubation period (days)	Infection frequency (lesions cm^{-2})	Pustule diameter (mm)	Ruptured pustules (%) 20 days after inoculation
J 11	*vulgaris*	9.0	9.7	16.4	1.15	100.00
TMV 2	*vulgaris*	9.0	9.3	13.5	1.12	100.00
NC 3033	*hypogaea*	9.0	9.1	10.8	1.01	100.00
EC 76446	*vulgaris*	9.0	9.0	14.9	1.26	99.60
Robut 33-1	*hypogaea*	9.0	9.0	15.5	1.08	99.80

1. Data reproduced from Subrahmanyam et al. (1983).

mum attainable disease severity as 100%, current severity level can also be evaluated as a percentage (Peterson et al. 1948). Unless a scale permitting interpolation and accurate recording of disease severity is developed, measuring "r" and characterizing HR is difficult. In the case of cereal rusts wherein we record say 40S, to denote 40% severity with susceptible "4" type pustules or 5R for 5% severity with resistant (0 to 2) pustules, this is both precise and fit for mathematical scrutiny. In groundnut rust also, separating both the parameters and recording them would enable better analysis than that being done at present.

A Proposed System to Identify Physiologic Forms — If Indeed They Exist

Bromfield and Cevario (1970), using two North American isolates of *P. arachidis*, evaluated a large number of accessions and noted that PI 314817 and PI 315608 possessed physiological resistance, whereas, with the Jamaican isolate PI 315608 was susceptible. This is indicative of the existence of physiologic forms (Cook 1972). Their evidence cannot be taken as final proof as the seed lot used was genetically heterogeneous. Fourteen isolates of the pathogen when tested on 3 accessions showed no evidence for the physiologic forms (Lim 1981); this could be due to the lack of genetic variation in the host. Vertical resistance, according to Van der Plank (1963), creates a time delay in the onset of the epidemic (Δt), and is comparable to sanitation. In a field evaluation of 695 entries, 3 were highly resistant and none immune. Yet, resistance was observed to be closely related to the time of disease occurrence (Chen et al. 1981). These findings neither prove nor disprove the possibility of physiologic forms occurring in *P. arachidis*.

Based on the information available on the host-pathogen interaction (Subrahmanyam et al. 1980, 1982, 1983a, 1983b, Bromfield and Cevario 1970), a procedure to score the reaction type caused by *P. arachidis* is suggested in Table 4. There are several wild *Arachis* species that are immune to rust, with no visual symptoms being produced on inoculation. Necrotic lesions or hypersensitive reaction of the "0" type without any pustulation are produced by some

Table 4. Host-pathogen interaction grouping for purposes of greenhouse evaluation of groundnut genotypes.[1]

Tentatively-assigned reaction value	Host-pathogen interaction characteristics	Probable types (host)	Ranking as per 1-9 ICRISAT scale
0	Immune		
0	Small necrotic lesions, no pustulation.	HLK 410, GK 30031 GK 30035, etc.	1
1	Small (< 0.60 mm diameter) pustules few pustules, poor rupturing, delayed, poor sporulation.	PI 405132 NC Ac 17090	2
2	Medium-sized pustules (< 1.0 mm) poor rupture and sporulation. Chlorotic necrotic area may form.	PI 381622	3
3	Pustules, large (< 1.2 mm) rupture with good sporulation. Chlorosis may occur around pustule. Upper surface of leaf may not rupture.	NC Ac 17130 NC Ac 17142	4,2 5,4
4	Large pustules (> 1.2 mm) profuse sporulation, upper leaf epidermis may also rupture, secondary pustules.	PI 270806 TMV 2 J 11	7 9 9

1 To be tested at 25°C mean temperature. Reactions to be recorded 20 days after inoculation, on a standardized leaf. Add + or − to reaction value if needed to show higher or lower reaction type within that class. Data of Subrahmanyam et al. (1983b), rearranged.

taxa such as *Arachis* species HLK 408, HLK 409, and other *Arachis* species (Subrahmanyam et al. 1983b). A number of lines produce pustules 0.6 mm in diameter or 0.28 mm^2 in area (accepting that the pustule is circular). Occasionally they produce a necrotic area around the pustule, have poor sporulation and delayed epidermal rupture. This reaction can be rated as 1. Genotypes such as PI 381622 produce pustules 0.6 mm and 1.00 mm in diameter but with poor sporulation and delayed epidermal rupture, and this can be rated as reaction type 2. In the third type, pustules are large, 1.2 mm in diameter with good sporulation and 90% of them rupture the epidermis. Area of the pustules is 0.77 mm^2 i.e., three times larger than those on the resistant genotypes. Reaction 4 type has almost 100% epidermal rupture and pustules also develop on the upper surface of the leaf. Occasionally, secondary pustules also develop. The susceptible pustule covers an area of 1.1 mm^2, i.e., nearly four times the size of a resistant pustule.

Table 4 lists the genotypes that produce these distinctive reaction types against the ICRISAT isolate of the pathogen. To start with, the 12 groundnut genotypes listed in Table 4 should be evaluated against pathogen isolates from geographically diverse areas. Evaluation after 20 days incubation at 25 °C using rooted, detached groundnut leaves or intact plants should help to either substantiate or reject the utility of these differentials in identifying pathogenic forms.

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Discussion

Chairman: D. McDonald

Rapporteurs: S.L. Dwivedi, K.V. Mallaiah

D.L. Cole. In *Puccinia psidii* where aecia look like uredinia, and develop from basidiospore infection, how would the urediniospores become dicaryotic?

J.F. Hennen. I do not know.

J.E. Parlevliet. Possibly due to anastomosis during basidiospore infection.

J.F. Hennen. Whether anastomosis occurs or not, is not known to me.

D.L. Cole. You have shown a slide of teliospores of *P. arachidis*. Are they from a herbarium sheet or from fresh material?

J.F. Hennen. The only specimen that I can confirm over and over again as teliospores on *Arachis hypogaea* is a specimen that I have from Brazil from a plant grown in the greenhouse and inoculated there.

D.L. Cole. Did you get basidiospores from it?

J.F. Hennen. No, I did not attempt that.

C.D. Mayee. In *Puccinia psidii* the sori that developed from basidiospore infection look like uredinia, but why do you call them aecia?

J.F. Hennen. Because of their position in the life cycle. According to definition, the sori that are produced immediately after basidiospore infection, if not telia, are aecia.

J.E. Parlevliet. Dicaryotic basidiospores occur in some other rusts, how often do these occur in *Puccinia* species?

J.F. Hennen. In short-cycle *Puccinia* species it is not at all uncommon to find dicaryotic basidiospores, but I have the impression that this is not common in long-cycle *Puccinia* species.

E.A. Salako. You mention that the peridium seen in *Puccinia arachidis* resembles that of the Melampsoraceae. Are the telia also connected and sessile as in Melampsoraceae?

J.F. Hennen. No, in the new system of Cummins' classification, there are 12 families in the Urediniales. This breaks up mainly the old Melampsoraceae. Probably, *Puccinia arachidis* belongs to the Ravenaliaceae in which there are 5-6 other genera. Most of them occur on Leguminosae. All produced pedicellate teliospores and not sessile ones as in the old concept of Melampsoraceae. This character of pedicellate teliospores is not necessarily important in classification. Spermagonia are the most important structures according to the Cummins system of classification.

A.S. Rao. Do you also have a peridium on teliosori?

J.F. Hennen. I must study that.

A.S. Rao. They occur in Brazil and the research must be done there.

J.F. Hennen. A good point, we need to go there.

C.D. Mayee. Do you consider the size of the pustule and its appearance on the lower or on the upper leaflet surface, as host-parasite interaction?

S. Nagarajan. The very consistency of pustule size (0.6 mm) shows clearly that it is the host-parasite interaction.

A.S. Rao. In the susceptible cultivar TMV 2, even if inoculation is made on the upper surface of the leaves, pustules first appear on the lower surface.

P. Subrahmanyam. Eruption of pustules on the upper surface is a typical susceptible reaction. Most of the lesions in resistant cultivars are on the lower leaves, the middle and top leaves are relatively free, while in susceptible cultivars the lesions are found on all leaves and disease development is much faster.

C.D. Mayee. I agree, but could this be considered as infection type?

J.E. Parlevliet. They call it reaction type but it is not the same reaction type as seen in cereal rusts.

C.D. Mayee. But if you inoculate the plants at the seedling stage, you have to wait in such a case for a very long time for differentials.

S. Nagarajan. To record host-pathogen interaction and pustule types, you can clip off the first two leaves of the groundnut, inoculate it and keep it for 20 days at 25° C to get the pustule reaction. If you are able to differentiate the reactions of a Peruvian isolate and isolates from India and China then we would consider that there is differential reaction. If there is no difference of reaction at all, irrespective of the source of isolates, then they are similar. This is only a proposition and it has to be verified.

The Physiology of Rust Diseases

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The Possible Role of Phytoalexins in the Resistance of Groundnuts to *Puccinia arachidis* Speg.

R.N. Strange[1]

Abstract

Chemotherapy and immunization have been very effective in human medicine but little attention has been given to increasing the resistance of plants to diseases by enhancing their defence mechanisms. The author describes one defence mechanism, production of phytoalexins, that is thought to make a major contribution to the disease resistance of many plants, and suggests how it may be exploited to increase resistance in groundnut to important foliar pathogens including Puccinia arachidis.

Résumé

Rôle éventuel des phytoalexines dans la résistance des arachides à Puccinia arachidis : *La chimiothérapie et l'immunisation se sont avérées très efficaces dans la médecine humaine; cependant peu d'études ont été consacrées sur l'augmentation de la résistance des plantes par une amélioration de leurs propres mécanismes. L'auteur décrit un mécanisme de défense, à savoir, la production de phytoalexines, qui serait un élément important de la résistance aux maladies chez nombreuses espèces végétales. Il explique comment ce phénomène peut être exploité pour renforcer la résistance de l'arachide aux principaux pathogènes foliaires dont* Puccinia arachidis.

During the last 100 years there has been spectacular progress in the control of some of mankind's most acute diseases which, in the past, have left many people disfigured, disabled, or dead. An understanding of the microbial nature of disease and the resulting improvements in sanitation and hygiene have played vital roles in this success but two other factors have perhaps been even more important, these are chemotherapy and immunization. Millions have been spared long periods of illness, if not death, by the timely administration of antibiotics while the eradication of smallpox by a concerted program of immunization is a triumph of medical science and an outstanding example of control through the enhancement of a natural host-defence mechanism.

Of course, these successes have meant that there are more people to feed and this in turn has led to an increased awareness of the vulnerability of man's food supplies. One reason for this vulnerability is that crop plants are themselves susceptible to disease, which in some circumstances, exact enormous tolls in terms of yield losses. For example, losses in groundnuts to foliar diseases, including *Puccinia arachidis*, may exceed 50% (Gibbons 1980).

Traditionally, man has attempted to curb crop losses caused by disease by selecting and breeding resistant cultivars, originally unconsciously but more recently consciously. Also, chemical control has become widely available and there is an ever-lengthening list of pesticides on the market. These two factors, coupled with the wide range of plant species with which the crop scientist has to work has meant that scant attention has been paid to increasing the resistance of plants by enhancing their defence mechanisms. In other words, there has been no sustained effort in plant pathology analogous to the highly successful immunization program in human pathology.

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This paper describes one defence mechanism that is thought to make a major contribution to the resistance of many plants and puts forward some suggestions as to how it might be exploited to increase the resistance of groundnuts to some of its more important parasites, including *P. arachidis*.

The Phytoalexin Response and Evidence for its Role in Resistance

Phytoalexins are low molecular weight, antimicrobial compounds that are synthesized by and accumulate in plants after exposure to microorganisms (Paxton 1981). There are now in the region of 300 such compounds that have been chemically defined and there is little doubt that many more await discovery. The importance of their role in defence, although disputed by some, is becoming steadily better established. Mansfield (1982) for example, describes in detail 8 cases in which there is strong evidence for phytoalexin involvement in resistance and cites 18 more in which such a role has been suggested. The evidence for a causal role of phytoalexins in resistance is generally based on five principles:

1. Phytoalexins accumulate in response to infection.
2. They are inhibitory to parasites *in vitro*.
3. They accumulate to inhibitory concentrations in the infected plant at the time the parasite ceases to grow.
4. Varying the rate of phytoalexin accumulation causes variation in the degree of resistance.
5. Varying the tolerance of the parasite to the phytoalexin causes variation in virulence.

The first four of these points may be illustrated by one example, that of the rust *Puccinia coronata* f. sp. *avenae* and oats (Mayama 1983). Three nitrogen-containing phytoalexins, the avenalumins, accumulated in incompatible associations of the rust with the plant. These compounds inhibited germination and germ-tube growth of the fungus at concentrations of 50-300 g mL^{-1}. In a survey of 21 cultivars of the host inoculated with two races of the fungus a variety of reactions were obtained from highly resistant to susceptible. The phytoalexins accumulated to inhibitory concentrations within 36 h of inoculation in resistant reactions but such concentrations were never attained in susceptible reactions. Elevated temperatures and treatment of leaves of the plant with α-aminooxyacetate (a competitive inhibitor of the enzyme phenylalanine ammonia lyase, which is associated with avenalumin synthesis) both reduced avenalumin accumulation and enhanced the growth of the parasite in interactions that were normally incompatible.

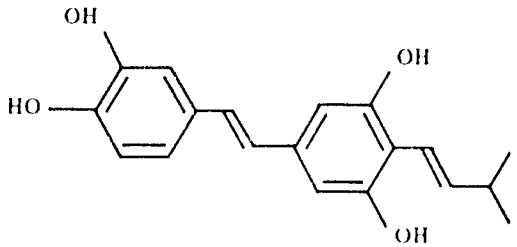
The fifth point is illustrated by a different study: Tegtmeier and Van Etten (1982) surveyed isolates of *Nectria haematococca* for virulence on peas and tolerance of the pea phytoalexin, pisatin. Only tolerant isolates were virulent; sensitive isolates were less virulent. Genetic analysis of crosses segregating for virulence and pisatin sensitivity confirmed that pisatin tolerance was necessary for virulence.

Evidence for Phytoalexin Involvement in the Resistance of Groundnuts to Fungal Parasites

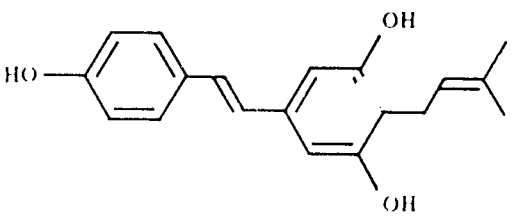
In 1981 we reported the isolation and identification of three phytoalexins from kernels of groundnuts (Aguamah et al. 1981). One of these had been described previously, but the other two were novel (Fig. 1). Accumulation of the compounds to which we have given the trivial names arachidins I, II, and III occurred when imbibed kernels were sliced and exposed to their native microflora. Subsequently, it was found that the microflora was not required and high yields (up to 6 mg g^{-1} fresh weight) could be obtained by slicing surface-sterilized kernels under aseptic conditions and incubating them for 96-120 h at 25°C. Very recently, in cooperation with Dr D.L. Cole of Zimbabwe, we have analyzed leaf samples of groundnut plants infected with *Phoma arachidicola* or *Cercospora arachidicola*. We have also received samples of leaves infected with *P. arachidis* from Dr D. McDonald of ICRISAT Center. Infected leaf samples generally accumulated medicarpin (Fig. 2), a phytoalexin that has been found in over 20 other species of legume. Some cultivars synthesized other antifungal compounds, which remain to be identified. There is good evidence therefore that both kernels and leaves of groundnuts accumulate phytoalexins and the chemical structures of some of these compounds have been established.

We have tested the antifungal activity of the arachidins (Wotton and Strange 1985). *Aspergillus flavus* was inhibited in the low μg mL^{-1} range as was *Cladosporium cucumerinum*, but *C. arachidicola*

Arachidin I



Arachidin II



Arachidin III

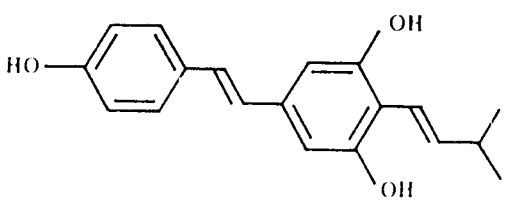


Figure 1. Structures of the arachidins, three phytoalexins synthesized by groundnut kernels.

(-)- Medicarpin
(demethylhomopterocarpin)

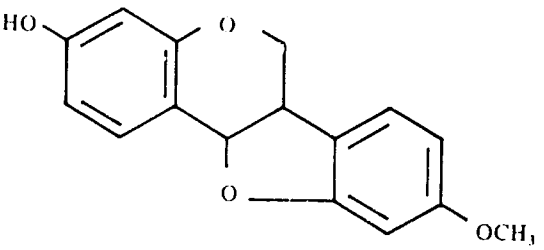


Figure 2. Structure of medicarpin, a phytoalexin synthesized by groundnut leaves in response to infection with leaf spot fungi.

was less sensitive (Table 1). We have not tested the antifungal activity of medicarpin, but other workers have reported ED_{50} values around 100 g mL^{-1} for mycelia of *Phytophthora megasperma* f.sp *medicaginis* (Vaziri et al. 1981), *Fusarium oxysporum* and *Helminthosporium carbonum* (Ibrahim et al. 1982). When groundnut kernels were hydrated to 20% moisture and inoculated with spores of *A. flavus*, fungal growth occurred but was halted when the concentration of the arachidins reached values that have been shown to be inhibitory *in vitro* (Fig.3).

Cultivars of groundnut vary widely in their resistance to infection by *A. flavus* and we have found that this variation correlated with their ability to accumulate the arachidins as a response to wounding (Fig. 4). Elevated temperatures and drought stress have both been reported to increase the susceptibility of groundnut to infection by *A. flavus* (Sanders et al. 1984). Both also reduce the capacity of kernels to accumulate phytoalexins. When imbibed kernels were sliced and incubated at 37°C, maximum phytoalexin concentrations attained were only one third to one half those of kernels similarly

Table 1. Antifungal activity of the Arachidins.

	ED Values (μg mL^{-1})					
	Arachidin I		Arachidin II		Arachidin III	
Test Fungus	Germination	Hyphal extension	Germination	Hyphal extension	Germination	Hyphal extension
Cladosporium cucumerinum	3.6	4.3	7.6	22.1	4.9	13.0
Cercospora arachidicola	11.5	21.0	25.1	63.0	17.0	36.3
Aspergillus flavus	12.8	4.9	12.7	6.8	8.9	9.7

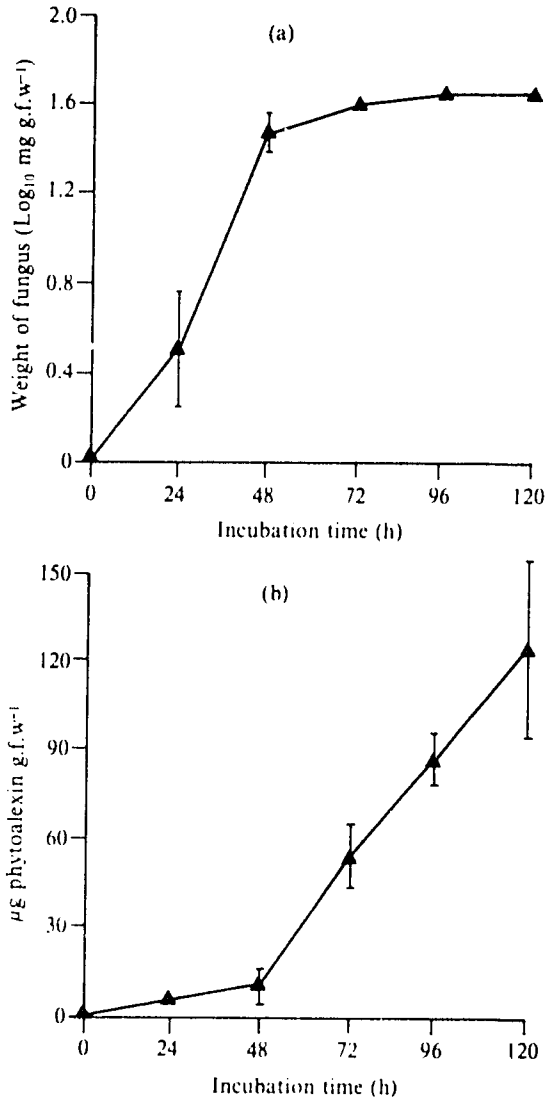


Figure 3. (a) Invasion of groundnut kernels by *Aspergillus flavus*, (b) phytoalexin accumulation. Fungal growth measured by chitin assay and phytoalexins by HPLC, bars represent ±SE.

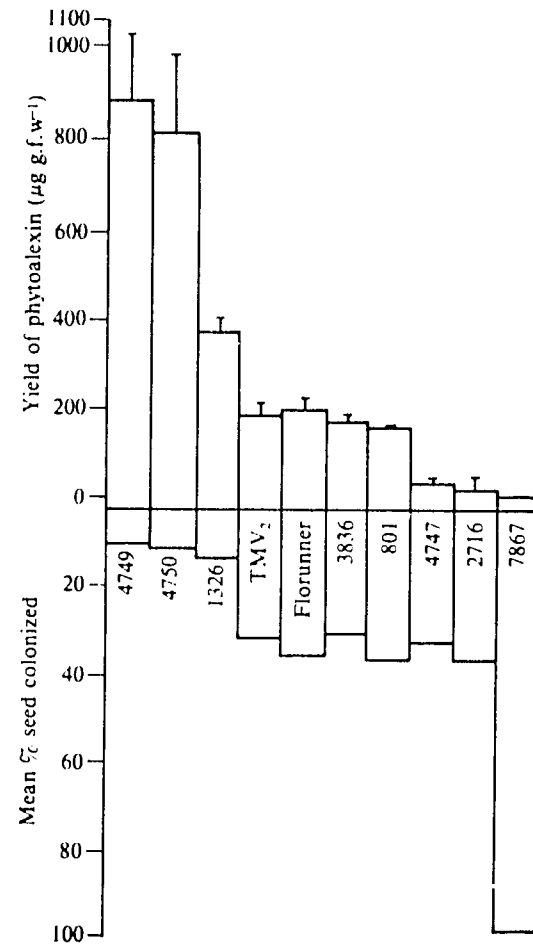


Figure 4. A comparison of phytoalexin accumulation 24 h after wounding and dry seed resistance. Phytoalexins were assayed by HPLC.

treated but incubated at 25 °C and even low levels of drought stress markedly reduced phytoalexin accumulation in response to inoculation with *A. flavus* (Fig.5). Phytoalexin accumulation was negatively correlated with fungal invasion (Fig. 6).

Thus the potential to accumulate only low concentrations of phytoalexins, whether this is caused by genetic or environmental factors, is correlated with increased invasion by *A. flavus*. We have not yet approached the question of variation in tolerance of strains of *A. flavus* to the arachidins and whether the more tolerant strains are also the more invasive, but we have initiated a program of chemical synthesis for these compounds. It is hoped that this will lead to bulk production of the phytoalexins, which may then be used for screening isolates and possibly mutants for variation in sensitivity.

The role of medicarpin in limiting leaf-spot fungi of groundnut, including *P. arachidis*, is unknown, but the finding at ICRISAT that urediniospores from more resistant plants germinated less well than those from susceptible ones is intriguing (Subrahmanyam et al. 1983). Could medicarpin or other phytoalexins be responsible for this phenomenon?

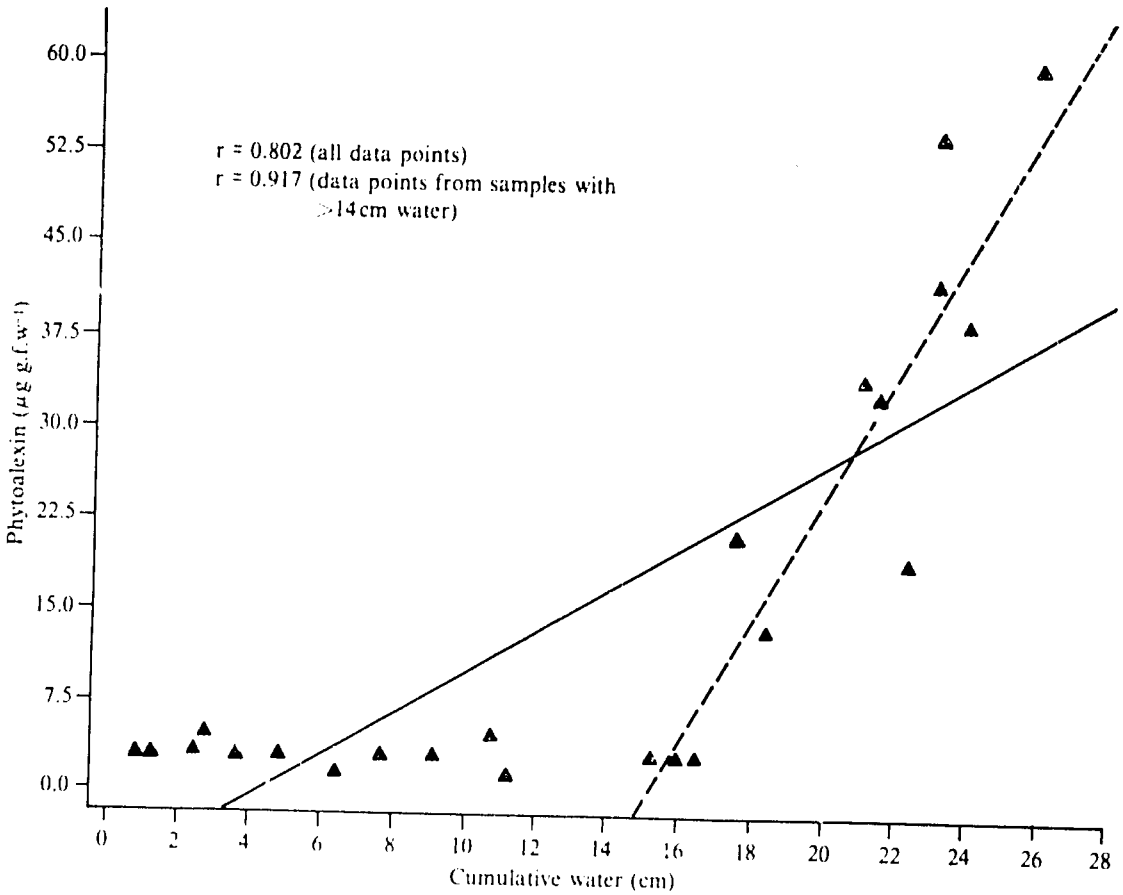


Figure 5. The relation between drought stress and phytoalexin accumulation 72 h after inoculation with *Aspergillus flavus*. Kernels from groundnut plants (cv ICG 221) that had received varying cumulative amounts of water from 82-118 days after sowing were inoculated, and accumulated phytoalexins assayed by HPLC.

Further Evidence Required Before Ascribing a Role to Phytoalexins in the Resistance of Groundnut to *Puccinia arachidis*

Preliminary experiments have shown that in some cultivars more than one inhibitory compound (medicarpin) is produced by groundnut leaves in response to infection by *Phoma arachidicola* and *Cercospora arachidicola*. It is possible that *P. arachidis*, too, will be found to elicit other phytoalexins. These will require isolation and identification. The effect of the phytoalexins on spore germination and hyphal extension of *P. arachidis in vitro* should give some idea of the activity of the compounds against the fungus. However, caution must be exercised here as only limited development of this obligate parasite occurs outside the host, and differences in its physiology when growing biotropically may be reflected in differences in sensitivity to the phytoalexins.

Once the phytoalexins that accumulate in response to *P. arachidis* infections are known it should be possible to quantify them, probably by means of HPLC (high-performance liquid chromatography). Quantitative data on phytoalexin accumulation may then be related to the growth of the fungus within the leaf. A good correlation between the time at which the fungus ceases to grow and the accumulation of phytoalexins to concentrations that are inhibitory *in vitro* would provide circumstantial evidence for phytoalexin involvement in resistance. The evidence would be strengthened by an analysis

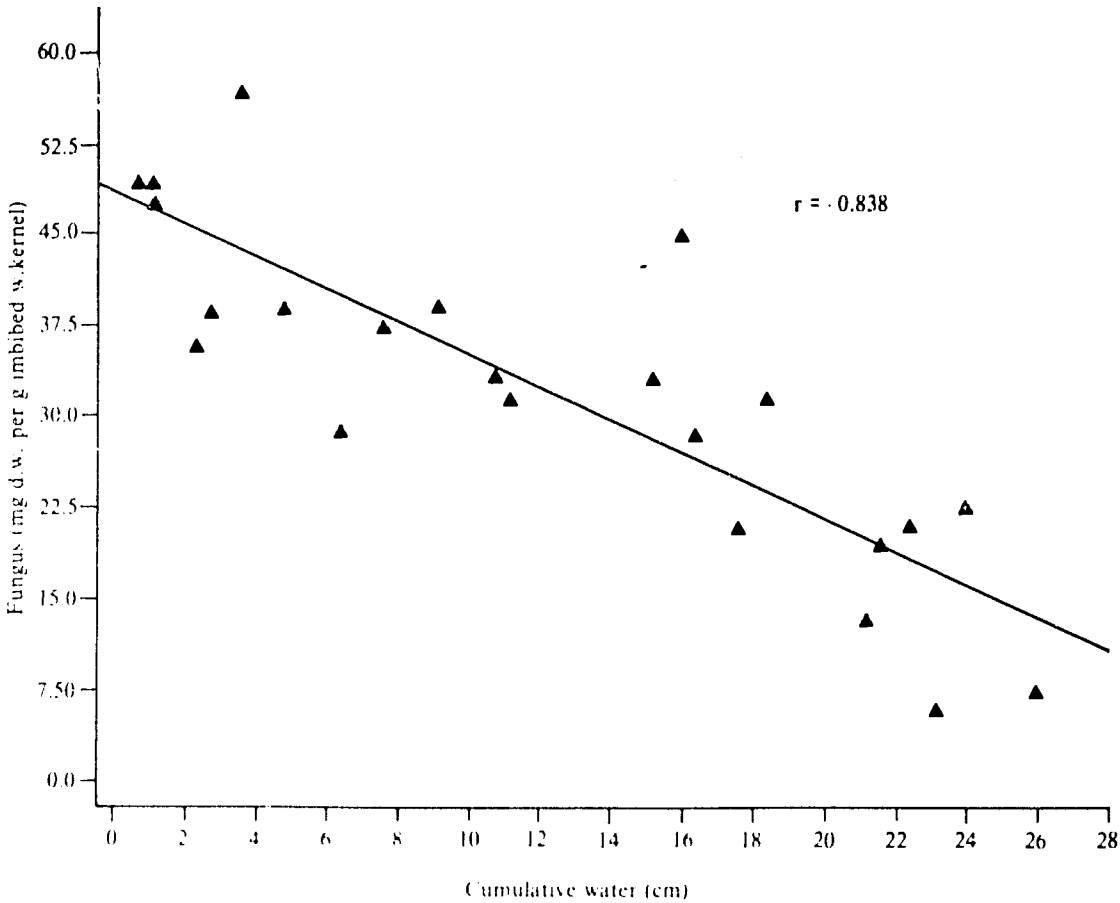


Figure 6. The relation between drought stress and fungal colonization by *Aspergillus flavus*. Kernels from groundnut plants (cv TC G 221) that had received varying cumulative amounts of water from 82-118 days after sowing were inoculated and fungal growth assessed by a chitin assay.

of many combinations of host and parasite differing in their degree of compatibility as well as experiments in which the amount of phytoalexin accumulating were altered by, for example, inhibitors such as α-aminooxyacetate or by environmental conditions. The effect of elevated temperatures would be of particular interest here in view of the tropical nature of the host plant.

It is probable that agricultural scientists would be disinclined to produce mutants of *P. arachidis* with decreased sensitivity to phytoalexins as such mutants might well prove to be more virulent in the wild! The alternative might be to select wild isolates that vary in their tolerance to the compounds. The absolute requirements of phytoalexin tolerance for a high degree of virulence would be indicative of a role for phytoalexins in resistance.

Prospects for Improving the Resistance of Groundnuts to Parasites by Exploiting the Phytoalexin Response

The data reported in this paper are consistent with the view that phytoalexin accumulation may be an important resistance mechanism in groundnuts (see Figs. 3,4,5 and 6). If further work proves that this is so then selection of cultivars capable of an adequate phytoalexin response under normal conditions of cultivation could provide a starting point from which plants with high levels of resistance may be developed. Since phytoalexin accumulation is an active response this means that some reproducible way of triggering (or, to use the jargon, eliciting) the

response must be found. Phytoalexin elicitation is still something of a mystery. Most evidence points to the necessity of the juxtaposition of dead or dying cells and apparently healthy cells. We have found, for example, that groundnut kernels and peas respond to mechanical injury but soybean seeds do not. They, however, produce phytoalexins in response to solutions of the salts of heavy metals, $AgNO_3$ being the most effective one found to date (Stossel 1982). Microorganisms should not be used as elicitors as they may either suppress phytoalexin synthesis (Doke and Tomiyama 1980, Ride and Drysdale 1972) or degrade the phytoalexin once it has been synthesized (Weltring et al. 1981). After finding a suitable elicitor it would be necessary to test its effects under conditions likely to be encountered by the plant, e.g., a range of temperatures, water regimes, lighting, and soil.

The possibility of phytoalexin suppression or degradation by parasites is a matter for concern. Little is known about phytoalexin suppression (Shiraishi et al. 1980) in any host-parasite interaction but phytoalexin degradation may be studied *in vitro* with facultative parasites and to a limited extent with the sporelings of obligate parasites. It is hoped that neither phenomenon will prove to be of significance in the interaction of groundnut with its parasites.

The results of experiments in which groundnut genotypes selected for high phytoalexin potential are challenged by parasites are awaited with interest. In the meantime it may be instructive to learn what phytoalexin potential resides in wild species of *Arachis*.

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Discussion

Chairman: R.W. Gibbons

Rapporteurs: V.K. Mehan, A.K. Singh

R.W. Gibbons. What is the role of sucrose in phytoalexin production? If it stimulates production, could this explain the increased damage caused by rust and the leaf spots late in the plant's development when assimilates are being diverted to the fruits?

R.N. Strange. Sucrose appears to be the "endogenous elicitor" of phytoalexin synthesis in pigeonpea leaves. It is also effective in peas. There are no firm data yet on groundnut. If sucrose is also the "endogenous elicitor" in this species, it would be interesting to know if the sucrose content of groundnut leaves decreases late in the season to a level at which its effectiveness as an elicitor is impaired.

S. Wongkaew. Under field conditions rust-resistant cultivars show some pustules on the lower leaves but there is no development of pustules on the upper leaves after the primary infection. Could this be the result of a translocatable product inducing phytoalexins?

R.N. Strange. I do not know. Perhaps there is a translocatable product that potentiates the phytoalexin response so that it occurs more rapidly on challenge.

S.L. Dwivedi. Could phytoalexins be common inhibitors to more than one disease?

R.N. Strange. Yes. Phytoalexins are effective against many parasites.

A.K. Singh. A pathogen causing initial injury can result in phytoalexin production in the host, which then becomes more resistant to other pathogens. This has been referred to as induced resistance.

P. Subrahmanyam. Are phytoalexins specific to pathogens?

R.N. Strange. Phytoalexins are not specific to the invading parasite, they are specific to the plant that produces them. However, since they are relatively simple compounds it is not surprising to find the same compound being produced by several plant species. For instance, over a dozen legume species, including the cultivated groundnut, synthesize medicarpin

H. Sudhakar Rao. If phytoalexins are only effective against specific pathogens, how do you screen for multiple disease resistance?

R.N. Strange. The method for screening for multiple disease resistance depends upon the particular parasites involved. In breeding programs we need to ensure that we do not impair the basic defence mechanisms but should seek to enhance them. If they should still prove ineffective the elucidation of the reason for this might suggest a novel procedure for selection. For example, the parasite might produce a toxin that inhibits the defence response; selection for tolerance to the toxin might allow expression of the normal defence mechanism.

T. Somartya. I understand that interferon is the substance that is initiated by infection with a virus, and this is then spread throughout the plant. Are phytoalexins produced and translocated in a similar fashion?

R.N. Strange. Phytoalexins are thought to be synthesized and to accumulate locally. Systemic acquired resistance is a human phenomenon. In the case of cucurbits lignification seems to be the defence mechanism that is promoted, but the signal that travels through the plant and potentiates this response is unknown.

Breeding for Resistance to Groundnut Rust

Modern Concepts in Breeding for Resistance to Rust Diseases

J.E. Parlevliet[1]

Abstract

From the viewpoint of a host, organisms with a pathogenic way of life can be classified roughly into three groups; the non-pathogens, the non-specialized pathogens, and the specialized pathogens, wherein specialization refers to the width of the host range. Mechanisms responsible for the non-host/non-pathogen condition are broad or general mechanisms and/or absence of pathogenicity for that host. The resistance mechanisms responsible for the quantitative type of resistance found against non-specialized pathogens are of a race-nonspecific and/or pathogen-nonspecific nature.

Resistance to the specialized pathogen is of a pathogen-specific nature; the resistance genes are effective against one pathogen only, whether they are race-specific or by and large race-nonspecific. The resistance to these pathogens seems to be of two types. A major-gene type of resistance is often of the hypersensitive type and race-specific, and a polygenic type of resistance, partial resistance. This partial resistance, although polygenic in nature, also shows race-specific effects. These effects, however, are too small to identify races with them. Therefore this type of resistance appears by and large race-nonspecific. Contrary to the major gene type, partial resistance seems durable.

Selection for partial resistance is not difficult in the absence of major genes. But when both types of resistance are present it is difficult to recognize partial resistance, especially when a mixture of races is used.

Résumé

Concepts modernes pour la sélection de la résistance à la rouille : *Les organismes à tendance pathogène sont classés en trois groupes par rapport à l'organisme hôte : organismes non pathogènes, pathogènes non spécialisés, pathogènes spécialisés, où la spécialisation se réfère à l'ampleur de la gamme des hôtes. La condition d'être non hôte ou non pathogène est déterminée par les mécanismes généraux de résistance ou l'absence de pathogénéité vis-à-vis l'hôte donné, ou les deux phénomènes. Les mécanismes responsables du type de résistance quantitatif au pathogène non spécialisé sont non spécifiques à la race ou au pathogène, ou les deux.*

La résistance au pathogène spécialisé est spécifique au pathogène et les gènes de résistance y sont efficaces contre un seul pathogène, sans égard à leur spécificité aux races du pathogène. La résistance à ces pathogènes serait de deux types : résistance à gène majeur souvent de type hypersensible et spécifique à la race; et résistance polygène ou résistance partielle. Cette résistance partielle, quoique polygène, manifeste une spécificité à la race. Cependant les effets de cette spécificité sont trop infimes pour y associer les races. En général, ce type de résistance serait donc non spécifique à la race. A la différence de la résistance à gène majeur, la résistance partielle serait durable.

La sélection visant la résistance partielle n'est pas difficile compte tenu de l'absence des gènes majeurs. Cependant, il est difficile de distinguer la résistance partielle de la résistance à gène majeur, surtout lorsque les deux types de résistance sont en présence d'un mélange de races.

In modern agriculture, the dynamic nature of the host-pathogen relationship is evident through the frequency by which pathogens neutralize the effects of resistance genes introduced with newly bred cultivars. Loss of resistance was already known some 70 years ago (Kommedahl et al. 1970), but it took a long time before the seriousness of this phenomenon was fully realized. Van der Plank (1968) developed a

1. Professor, Institute of Plant Breeding, Agricultural University, Wageningen, The Netherlands.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1987. Groundnut rust disease. Proceedings of a Discussion Group Meeting 24-28 Sep 1984, ICRISAT Center, India. Patancheru, A.P. 502 324, India: ICRISAT.

general hypothesis to explain the dynamics of the host-pathogen relationship. He classified host-plant resistances as horizontal or vertical. According to Van der Plank vertical resistance (VR) is characterized by interactions between host genotypes and pathogen genotypes; the resistance of the host depends on the race of the pathogen present, i.e., VR is identical with race-specific resistance. Horizontal resistance (HR), he stated, is characterized by the absence of such host genotype-pathogen genotype interactions; it is equivalent to race-nonspecific resistance.

Van der Plank also concluded that VR is major-genically inherited, operating on a gene-for-gene basis and is non-durable. In contrast HR is expected to be polygenically inherited, not operating on a gene-for-gene basis, and is durable.

This hypothesis, though attractive because of its simplicity, does not explain all the data collected and reported by a growing number of scientists. In nature all living organisms are exposed to parasites and the defence mechanisms they employ are likely to be of a bewildering variety. This enormous variety of defences cannot be grouped into two sharply defined and distinct classes as Van der Plank did. Nevertheless some classification seems possible as long as one realizes that not all defence mechanisms fit into such a classification.

Defence of host plants against parasites may be due to either avoidance or resistance mechanisms (Parlevliet 1981). Avoidance reduces the chance of contact between the prospective host tissue and the parasite, whereas resistance operates, after contact has been made, by reducing the growth and development of the parasite. Tolerance is not really a defence mechanism; it is a mechanism that helps the host to cope with the parasite, which it can neither avoid nor resist.

Against pathogens, avoidance and tolerance seem of restricted importance for breeders as the genetic variation for them is often small, while their recognition, if present, is far from easy. Resistance on the other hand is generally not difficult to find and is fairly easy to recognize. Because of this, the following discussion is centered around resistance to pathogens.

Classification of Host-pathogen Systems

Each host species is exposed to numerous potential pathogens, but only a few of these actually attack it. Each pathogen on the other hand is surrounded by a wide range of potential hosts of which it appears to parasitize only a restricted number. This restricted number, though, varies widely. Some pathogens have become "specialists" (in terms of host range). They parasitize only host species belonging to one genus or a few related genera (*Puccinia hordei*, barley leaf rust on some *Hordeum* species only). Others have learned to exploit a wide host range; these are "generalists" such as *Sclerotinia sclerotiorum*, affecting hundreds of plant species belonging to 64 families. The two examples represent the extremes of a more or less continuous distribution. *Erysiphe graminis*, the powdery mildew of grasses, parasitizes many species of the very large family of the Gramineae. Other pathogens may affect species belonging to a few families.

For a given host the organisms with a pathogenic way of life can be grouped into three categories:

1. Non-pathogens

All pathogens that do not infect a given host are non-pathogens for that host. The stem rust of wheat is a non-pathogen for groundnut, and the wheat is a non-host for the groundnut rust. The mechanisms underlying the non-host non-pathogen situation can be of two kinds: the host has one or more resistance mechanisms that are effective against these non-pathogens and or the non-pathogens lack the pathogenicity to attack the non-hosts. Hosts do have resistance mechanisms that are effective against a wide range of pathogens. This is "general resistance" (Parlevliet 1981). The phytoalexins for instance, produced by many plants following cell damage, are effective against most but not all fungi. Some fungi have learned to cope with the phytoalexins of a certain host by tolerating or neutralizing the produced phytoalexins or by preventing their production. These fungi became pathogens of that host and breeders want resistance to such pathogens. General resistance, therefore, is not likely to be of great importance for resistance breeding.

2. Non-specialized pathogens

Also termed generalists, these include several *Pythium* species causing seedling blight and root rot in many crops, *Rhizoctonia solani* and *Sclerotinia sclerotiorum*, which have wide host ranges. Resistance to these pathogens is nearly always of an

incomplete nature. Cultivars within a host species vary in degree of resistance, from low to moderate. This resistance is of a non-specific type in the sense that the resistance is conferred by genes that are involved in governing other characteristics; resistance is a more or less incidental side-effect. Increasing the level of resistance to such non-specialized pathogens is, therefore, very difficult as other characteristics are involved at the same time (Bruehl 1983). This resistance seems to be of a race-nonspecific nature. Some of the resistance to non-specialized pathogens may also be derived from general resistance mechanisms. Resistance to the grain mold of sorghum, a complex of different species of fungi, operates against all of them.

3. Specialized pathogens

The general resistance mechanisms (see non-pathogens) do not operate against specialists such as many rust, bunt, smut, powdery and downy mildew species. The host employs resistance genes effective against one pathogen species only, and the pathogen carries pathogenicity and virulence specific for a narrow range of host species. Much resistance breeding deals with host-pathogen systems that can be classified in this category. The remainder of the discussion is devoted to this category.

Pathogen-Specific Resistance

This resistance operates against one pathogen species only. The resistance of wheat to wheat stem rust, *Puccinia graminis* f.sp *tritici*, is governed by a series of Sr-genes. Each of the more than 40 Sr-genes is effective against wheat stem rust races that do not carry the corresponding virulence genes. It is a typical race-specific resistance. These genes are not effective against wheat leaf rust, P *recondita* f.sp. *tritici*, irrespective of the virulence genes of that pathogen. Race-specific resistance to wheat leaf rust is caused by more than 30 Lr-genes. Wheat also carries such pathogen-specific and race-specific genes for yellow rust, *P. striiformis* (Yr-genes), for powdery mildew, *Erysiphe graminis* f.sp *tritici* (Pm-genes), and for loose smut, *Ustilago nuda* f.sp *tritici* (Un-genes). And also the Dm-genes in lettuce to downy mildew, *Bremia lactucae*, the V-genes in apple to scab, *Venturia inaequalis*, the Cf-genes in tomato to leaf mould, *Fulvia fulva*, and the Xa-genes in rice to bacterial leaf blight, *Xanthomonas campestris* pv *oryzae* are examples of this race-specific and pathogen-specific resistance, of which there are so many.

Selection for this type of resistance is generally straightforward. Often effective screening methods have been developed that can discriminate efficiently between plants or lines carrying such a race-specific major gene and plants or lines not carrying such genes.

In the same host-pathogen systems one can often, if not always, find another form of resistance variously indicated as partial resistance, residual resistance, field resistance or with rusts, slow rusting. This resistance is of a quantitative and incomplete nature and is possibly governed by polygenes. Van der Plank (1968) and others assume that this type of resistance is race-non-specific and durable. According to Parlevliet (1979), small race-specific effects occur in this type of resistance. About the durability of this resistance he agrees with the former. The fact is that this type of resistance is also highly pathogen-specific (Parlevliet 1981). Partial resistance to the related rusts *Puccinia hordei* and *P. striiformis* occurs independently of each other in the various barley cultivars and slow rusting of wheat to *Puccinia recondita* does not operate for the other two wheat rusts, *P. graminis* and *P. striiformis*.

Because of its assumed durability, partial resistance has received most attention in recent years.

Partial Resistance

The presence of partial resistance can be demonstrated in two ways.

1. If one studies accurately the so-called susceptible cultivars, a range in susceptibility can often be observed as in the case of barley against barley leaf rust, *Puccinia hordei*.
2. When new cultivars with monogenic resistance are introduced they are initially quite resistant, but due to the appearance of new corresponding races the effects of these resistance genes are soon neutralized (Table 1). The resistance against yellow rust and powdery mildew decreased and the level of resistance ultimately reached varied from scores of 3 to 6; most cultivars fell back to 4 or 5. It is not difficult to find among exotic cultivars far more susceptible genotypes that would score a 1 on this scale. After the major race-specific resistance gene is broken, apparently a certain level of residual resistance shows up. This residual resis-

Table 1. Change in resistance levels (10 = extremely resistant, 1 = extremely susceptible) of 4 wheat cultivars for 2 pathogens according to the Dutch lists of recommended cultivars after introduction (first cipher) and some years later (second cipher).

Cultivars	Yellow rust[1]		Powdery mildew[2]	
Clement	8	3	8	3
Manella	8	6	6	5
Caribo	6	5	6	4
Norda	8	4	7	4

1. *Puccinia striiformis*
2. *Erysiphe graminis* f sp *tritici*

tance is the same as the resistance causing variation among the so-called susceptible cultivars mentioned in item 1 above. Partial resistance against rusts is characterized by a reduced rate of epidemic buildup. The individual uredinia are smaller and there are fewer of them. Necrosis or marked chlorosis surrounding the small pustules, so characteristic of the race-specific major genic resistance (hypersensitivity), is lacking. To describe partial resistance in some detail the data collected with barley against barley leaf rust, *Puccinia hordei* are discussed.

Partial resistance in barley to barley leaf rust

If large numbers of barley cultivars are screened for resistance to barley leaf rust by inoculating seedlings one notices a few cultivars with a hypersensitive type of resistance. All other cultivars show the normal susceptible reaction of well-formed uredinia. Looking more closely one can observe small differences in number and size of the pustules. If one grows these cultivars in the field in plots well isolated from each other to prevent interplot interference, large differences in the amount of rust appear. The cultivars vary greatly in partial resistance. Table 2 shows the results of 4 cultivars grown in 3 different test-plot situations. In plots isolated from each other by wheat (to prevent interplot interference) the true partial resistance is measured. In adjacent plots, the way lines and cultivars are normally compared, the partial resistance is underestimated considerably. The level of barley leaf rust in adjacent plots four rows wide was only 36 × lower on Vada than on L94 compared with the 4500 × difference in the isolated plots. This is because the more resistant cultivars receive most of their inoculum from the neighbouring susceptible cultivars. But the ranking order of the cultivars remains the same. A breeder, therefore, can select very well in small adjacent plots. He should, however, realize that the resistance he scores is a clear underestimation of reality (Parlevliet and Van Ommeren 1975).

Table 2. Number of barley leaf rust (race 1-2) uredinia per tiller of 4 barley cultivars at 3 field-plot situations (Parlevliet and van Ommeren 1975).

Cultivars	Field-plot situation: Plots (3 × 4 m), isolated	Adjacent plots: 4 rows (1.0 m)	Adjacent plots: 1 row (0.25 m)
L94	5000	1250	2500
Sultan	1000	750	800
Julia	17	100	250
Vada	1.1	35	100
range,*	4500 ×	36 ×	25 ×

This partial resistance is the cumulative effect (over several cycles of reproduction) of differences in latent period (LP), infection density (ID), and rate of sporulation (SR) per pustule. Vada has a considerable longer LP, lower ID, and lower SR than L94. The variations in these components of partial resistance are highly associated; a longer LP goes nearly always together with a reduced ID and SR. Partial resistance therefore is highly correlated ($r = 0.9$) with LP (Parlevliet and Van Ommeren 1975). Genetic analysis showed that LP, and so partial resistance, is inherited in a polygenic way (Parlevliet 1978a). Vada is assumed to carry 5-6, Julia 4-5, Sultan 2-3, and L94 zero polygenes for a longer LP.

This polygenic resistance, though, does not follow the race-nonspecific pattern. Three partially-resistant cultivars were tested against 5 barley leaf rust races (Table 3), and although the pattern is, by and large, of a race-nonspecific nature, there was one significant differential interaction, between cultivar Julia and race 18 (Parlevliet 1978b). This interaction was traced back to a reduced LP of Julia for that race and Parlevliet (1978b) assumed that the effect of one of the polygenes of Julia was overcome by race 18.

Apparently polygenic resistance also shows race-specificity, although the effects are small. Race-specific resistance is considered to be based on a gene-for-gene action. Each resistance gene in the host has a corresponding virulence gene in the pathogen. It seems that the polygenic, partial resistance is also based on a gene-for-gene action.

Table 3. Percentages of leaf area affected (covered with lesions) of 3 barley cultivars infected with 5 barley leaf-rust races. Each plot was separated from all others by wide strips of a non-host crop (Parlevliet 1978b).

	Races				
Cultivars	11-1	18	1-2	22	24
Berac	8.1	6.7	3.1	5.0	0.9
Julia	4.5	12.1	1.8	1.1	0.6
Vada	0.8	0.5	0.6	0.2	0.1

In case of no cultivar × race interaction the value should have been ca. 3%

However, histological studies (Niks and Kuiper 1983, Niks 1983) clearly showed that the hypersensitive type of resistance and partial resistance represent two distinct resistance mechanisms that do not interact with one another. The former mechanism appears to operate after the haustoria are formed inside the host cells, the latter before the host cells are penetrated.

There is also a marked difference in durability between the two types of resistance. The hypersensitive type of resistance is not only highly race-specific, but it also lacks durability. Partial resistance, however, seems to be very durable (Habgood and Clifford 1981, Parlevliet 1981) as it has been exposed in Western Europe already for a long time over a large area without any signs of adaptation in the pathogen population despite small race-specific effects.

Selection for partial resistance

In the absence of major genes for hypersensitivity, selection for partial resistance is not difficult in the case of barley and barley leaf rust. Selection appeared possible in the seedling stage in the greenhouse as well as on adult single plants and single lines in the field. The selection among adult plants was more efficient than selection among seedlings (Parlevliet et al. 1980).

It is also possible to select in the greenhouse for one of the components, LP. In the cross Vada × Cebada Capa, Parlevliet and Kuiper (1985) selected in the F_3, F_4, F_5 and F_6 the plants with the longest LP from the lines with the longest LP (mature plants). In this way it appeared possible to obtain F_6 lines that carried most of the polygenes of Vada and Cebada Capa (together), giving a LP considerably beyond that of Vada. These F_6 lines had a partial resistance also far beyond that of Vada, the cultivar with the approximately highest level of partial resistance among the European barley cultivars (Table 4) (Parlevliet et al. 1985).

If, however, major genes that are not completely overcome are present, selection for partial resistance is more difficult. The major genes may hide the partial resistance, and in the field it is very difficult to discern the two types of resistance. When the two types of resistance occur together one should, if possible, avoid testing with a mixture of races. Parlevliet (1983) showed that using mixtures of races, when partly-effective major resistance genes are present, selection for apparent partial resistance is largely a selection for the partly-effective major genes.

One should always bear in mind that genes with large effects are more easily recognized than genes with small effects. Major-genic resistance tends to have a higher heritability than polygenic resistance. This means that:

1. Intense selection for resistance tends to favor major genes, and
2. Mild selection for resistance, which is the same as selection against susceptibility, tends to favor minor genes.

Table 4. Latent periods (LP) relative to that of L94 (= 100) and partial resistance expressed in number of uredinia per tiller 1-2 weeks after heading of several barley cultivars and lines affected by barley leaf rust.

Cultivar Line	Relative LP	No. of uredinia per tiller
L94	100	
Akka	113	5000
Sultan	137	1000
Vada	185	100
42-1-9	212	35
139-8-4	234	7
17-5-16	281	0.4
26-6-11	291	1.0

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Inheritance of Rust Resistance in Groundnut

D.A. Knauft[1]

Abstract

Three rust-resistant groundnut genotypes (PI 314817, PI 350680, PI 315608) were crossed with the rust-susceptible genotype UF-439-16-10-3 (a component of the multiline Florunner), using the susceptible genotype as both male and female parent. Rust severity was recorded under natural disease pressure on F_2 and F_3 progenies and on parents. No reciprocal differences were found. Genotype PI 315608 is a poor source of rust resistance in Florida, and continues to segregate for susceptibility. Rust resistance in PI 314817 and PI 350680 appears to be controlled by duplicate recessive genes. All rust resistance and susceptibility does not seem to be explainable by this two gene system, especially where lines show only moderate levels of resistance.

Résumé

Hérédité de la résistance à la rouille de l'arachide : *Dans le croisement effectué de trois génotypes d'arachide résistants (PI 314817, PI 350680, PI 315608) à la rouille avec le génotype sensible (UF-439-16-10-3, composant de Florunner multiligne), le génotype sensible a servi à la fois de parent mâle et femelle. L'intensité de l'incidence était notée sous conditions naturelles de la maladie chez les descendances F_2 et F_3 et chez les parents. On n'a trouvé aucune manifestation de différences réciproques. Le génotype PI 315608 n'est pas une bonne source de résistance en Floride due à l'apparition de la sensibilité suite à la ségrégation. Chez PI 314817 et PI 350680, la résistance est conditionnée par des gènes récessifs doubles. Cependant, ce système à deux gènes ne peut expliquer tous les phénomènes de résistance et de sensibilité surtout en cas de niveaux moyens de la résistance.*

The first person to describe the genetics of resistance to rust in any crop plant was Biffen from England, who showed in 1905 that resistance in wheat to yellow rust was controlled in a Mendelian fashion (Littlefield 1981). When he crossed susceptible with resistant plants he obtained an F_2 ratio of 3 susceptible to 1 resistant. Although Biffen found resistance was recessive, most of the reports of rust resistance in crop plants indicate the resistance is dominant.

Rust organisms attack many food legumes besides groundnut. In spite of the importance of the plants, only a few legumes have been studied to determine the mode of inheritance of resistance to the rust organisms. In the common bean, *Phaseolus vulgaris*, one or more dominant or incompletely dominant genes control resistance to rust (*Uromyces phaseoli*) depending on the host race combination. Ballantyne (cited in Meiners 1981) found 18 races of rust attacking beans and identified 10 dominant, single genes for resistance. In cowpea, *Vigna unguiculata*, resistance to *Uromyces unguiculata* is controlled by a single dominant gene (IITA 1976). In soybean, *Glycine max*, Bromfield and Hartwig (1980) reported a single, dominant gene for resistance to soybean rust, *Phakopsora pachyrizi*. Little additional work has been done on the inheritance of resistance to rusts in the food legumes.

In order to study the mode of inheritance of rust (*Puccinia arachidis* Speg.) resistance in groundnut (*Arachis hypogaea* L.), sources of resistance must be available. Plants from a number of wild *Arachis* species have been shown to be immune or highly resistant to *P. arachidis*. They include *A. batizocoi*, *A. duranensis*, *A. spegazzinii*, *A. correntina*,

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A. stenosperma, *A. cardenasii*, *A. villosa*, *A. apressipila*, *A. paraguariensis*, *A. pusilla*, *A. villosulicarpa*, *A. hagenbeckii*, and *A. glabrata* (Subrahmanyam and McDonald 1983). Not all wild species have been reported to be immune or highly resistant; *A. monticola*, *A. prostrata*, *A. marginata*, and a selection of *A. glabrata* have been reported to be susceptible (Subrahmanyam et al. 1983).

Most of these species do not cross readily with *Arachis hypogaea*, and sources of resistance within the cultivated species have been sought. Mazzani and Hinojosa (1961) reported that the "variety" Tarapoto was resistant to rust. Tarapoto consists of several different plant inventory (PI) numbers, including 259747, 341879, 350680, 381622, and 405132. Bromfield and Cevario (1970) found PI 314817 (also known as DHH 200) and PI 315608 (also known as Israel Line 136) to be rust resistant. PI 298115 is also known as Israel Line 136. Cook (1972) reported PI 315608 as resistant. Bailey released 14 lines of peanut with resistance to rust (cited in Hammons 1977).

Subrahmanyam et al. (1980) reported several sources of resistance, including two land races, (NC Ac 17090 and PI 76446) and several other accessions (NC Acs 17020, 17132, 17129, 17135, and 17124). Subrahmanyam et al. (1983) recently reported a number of additional PI numbers that have shown resistance in Puerto Rico, India, and China. Therefore, there is currently available a considerable number of different genotypes which carry at least moderate levels of resistance. They are listed by Subrahmanyam and McDonald (1983).

In spite of the importance of rust disease, and the large numbers of different genotypes showing resistance to rust, the mode of inheritance of resistance to this disease has not been well established. Bromfield and Bailey (1972) reported that a natural cross between PI 298115 and an unknown pollen donor segregated for susceptibility and resistance in a ratio suggesting bigenic control for rust resistance, with two homozygous recessive genes necessary for resistance. A preliminary version of this report was given at the American Peanut Research and Education Society meeting in North Carolina, USA in 1983 (Knauft and Norden 1983). There appears to be little other information in the literature on inheritance of rust resistance in groundnut.

Materials and Methods

Genotypes PI 314817, 350680, and 315608 were used as rust-resistant parents and were crossed with one of the component lines of Florunner, UF 439-16-10-3 (Table 1). Crosses were made using the susceptible genotype as both male and female parent. PI 298115 was used as a parent in crosses, but both this parent, and the segregating offspring were so unproductive under our conditions, that insufficient material was available to warrant inclusion in this discussion. PI 315608 was also crossed with PI 314817 to test for allelism.

Table 1. Crosses to study inheritance of rust resistance in groundnut.

PI 314817 × UF 439-16-10-3[1]
PI 350680 × UF 439-16-10-3
PI 315608 × UF 439-16-10-3
PI 315608 × PI 314817

1. One of the component lines of the Florunner cultivar

The F_1 seed was increased in Puerto Rico using fungicide applications to insure availability of large quantities of F_2 seed. Because of the fungicide application, no resistance data is available for F_1 plants. The segregating seed was grown with the cooperation of the Mobay Chemical Company at their experimental farm near Vero Beach, Florida, USA where natural rust levels are severe enough each year to kill susceptible plants before maturity. The F_2 progenies and parents were grown in 1981, and F_3, F_4 and parents were grown in 1982, along with the Tifrust lines 1-14 that were grown to examine the resistance reactions that these lines had to the natural rust populations in southern Florida.

All the screened material was sown in rows 91 cm apart, with 30 cm spacing between plants. Every third row was sown with cultivar Florunner to provide both a check and a source of rust inoculum. Seed were sown on 8 Jun 1981 and 9 Jun 1982. Standard groundnut production practices as recommended by the Florida Cooperative Extension Service were used, but no fungicides were applied.

Natural rust infection was rated 140 days after sowing. The third, fourth, and fifth fully expanded leaves on each plant were rated using the modified Mazzani and Hinojosa (1961) scale, i.e., 0 = no rust pustules present; 1 = 1-10 pustule centers per leaflet; 2 = 11-30 pustules per leaflet; 3 = 31 or more; and a rating of 4 was used for plants that were dead. The abaxial sides of leaves were examined. Ratings represent an average of the 12 leaflets examined per plant. Plants with ratings of 0 or 1 were considered

resistant, while ratings of 2 or above indicated the plant was susceptible to rust.

Results and Discussion

Small quantities of seed from each of the Tifrust lines were grown at Vero Beach in the second year of the study to determine the levels of resistance that these lines showed to the natural rust populations present in southern Florida. Table 2 lists the Tifrust lines, the plant introductions from which they were selected and the parents used in this study. In Florida all the lines showed resistance relative to the Florunner check (which had an average rating of 3.8), although some of the lines showed only moderate levels of resistance, with Tifrust 3, 7, 10, and 13 showing average disease ratings of 2 or more. Several Tifrust releases were highly resistant in the Vero Beach environment, especially Tifrust 8, 9, and 14. Tifrust 8 also showed no late leaf spot under what was only moderate pressure at this location and is being further tested in Gainesville. Unfortunately, it has poor agronomic characteristics. Tifrust 14 was a selection from PI 314817, one of the plant introductions used in this study, and both Tifrust 14 and the plantings of PI 314817 from the seed source used for the parent in these studies showed essentially the same rust resistance.

Table 2. Disease reactions of the 14 Tifrust lines and parental lines used in crosses.

Line	PI Number	Disease rating[1]
Tifrust 1	215696	1.6
Tifrust 2	310593	0.5
Tifrust 3	390595	2.0
Tifrust 4	407454	1.3
Tifrust 5	393641	1.7
Tifrust 6	393643	1.8
Tifrust 7	393646	2.0
Tifrust 8	393516	0.4
Tifrust 9	393517	0.2
Tifrust 10	393526	2.0
Tifrust 11	393531	1.0
Tifrust 12	393527	1.9
Tifrust 13	315608	2.2
Tifrust 14	314817	0.3
PI 314817		0.4
PI 350680		0.5
PI 315608		1.5
Florunner		3.8

[1] Rating of 0 = no rust pustules found, 1 = 1-10 pustule centers present per leaflet, 2 = 11-30 pustule centers per leaflet, 3 = 31 or more pustule centers per leaflet, and 4 = plant death due to rust. Ratings are averages of 12 leaflets per plant.

The rating of another parent in this study, PI 315608, is somewhat misleading here, as it represents the average of some plants that were essentially free of rust and others that were given ratings of 3, rather than plants with ratings of 1 and 2. Tifrust 13, which represents selections made from this genotype, was the most susceptible of the Tifrust lines screened in the Vero Beach plantings, but was considered resistant in Puerto Rico, India, and China, three other locations where these lines were screened for resistance (Subrahmanyam et al. 1983). This same genotype, however, was reported to be susceptible by Cook (1972) in Jamaica. It is not known whether these disparate readings are from variable seed lots of this genotype and of Tifrust 13, or whether they are the result of a different genetic makeup of the rust populations at these different locations.

Data from the segregating generations of the crosses studied are listed in Table 3. No reciprocal differences were found, so data for the cross in the direction given have been pooled with data for its reciprocal. Also, no differences were found between years, so these data have also been pooled. In the cross PI 314817 × UF 439-16-10-3, 20 of the 263 F_2 plants were resistant. This gives an insignificant chi-square value of 0.82 when testing the hypothesis of a 1:15 ratio of resistant to susceptible plants. The F_2 from the cross of PI 350680 with UF 439-16-10-3 gave similar results, with 22 out of 304 plants showing resistance, and a chi-square value of 0.46 was calculated when testing the same 1:15 hypothesis. These results are in agreement with the observations of Bromfield and Bailey (1972) on a chance cross of PI 298115 with a (presumed susceptible) pollen donor of unknown origin.

In the F_3, the resistant F_2 plants should breed true for resistance, and the susceptible plants should segregate 1 resistant : 11 susceptible. This ratio is obtained because 7/16 of the F_2 plants have at least one gene homozygous dominant and will not show any resistant segregates, 4/16 of the F_2 plants are heterozygous for one gene and homozygous recessive for the other and will segregate 1:3, and 1/4 of the plants are heterozygous for both the genes and will segregate 1:15.

In the F_3, 34 of the 302 plants from cross PI 314817 × UF 439-16-10-3 were resistant. This fits an F_3 genetic ratio of 1:11 as the chi-square value of 3.38

Table 3. Resistance class distributions and probabilities for goodness-of-fit to designated ratios based on chi-square analysis.

Genotype	Number of plants		Ratio tested	Probability
	Resistant	Susceptible		
PI 314817 × UF 439-16-10-3 F_2	20	243	3:1	$0.5 > P \geq 0.20$
PI 314817 × UF 439-16-10-3 F_2	34	268	11:1	$0.10 > P \geq 0.05$
PI 350680 × UF 439-16-10-3 F_2	22	284	3:1	$P = 0.50$
PI 350680 × UF 439-16-10-3 F_2	33	262	11:1	$0.10 > P \geq 0.05$
PI 315608 × UF 439-16-10-3 F_2	1	162	3:1	$P < 0.01$
PI 315608 × UF 439-16-10-3 F_2	9	176	11:1	$0.10 > P \geq 0.05$

Table 4. Segregation patterns of F_3 families derived from F_2 susceptible plants.

Cross	F_3 family ratio			Chi-square
	3:1	15:1	all susc.	
PI 314817 × UF 439-16-10-3	7	4	8	1.04
PI 350680 × UF 439-16-10-3	5	4	10	0.38
PI 315680 × UF 439-16-10-3	1	2	9	4.03

was non-significant. The F_3 data from the cross of PI 350680 × UF 439-16-10-3 did not, however, fit the expected data very well. These data indicated many more resistant plants than expected. One of the twenty F_3 families produced 16 resistant plants, suggesting that the F_2 plant that was the source of this family was actually resistant, but was misclassified as susceptible. This skewed the F_3 data. Without this family the chi-square value is 3.15, which is not significant.

Although the number of different F_3 families sampled was small, the number of families fitting the expected segregation patterns was consistent with the numbers expected from the two-gene model. For both the cross with PI 314817 and with PI 350680 (Table 4), the 19 families (excluding the one from the latter cross mentioned above) should have had 5.1 families segregating 3:1, 5.1 segregating 15:1 and 8.9 not segregating (all susceptible). Chi-square tests were run on each of the F_3 families, which were then placed in the segregation categories they best fitted. The numbers of families segregating for each of these patterns were then analyzed with a chi-square test. All crosses segregated within the expected values for each of the segregation categories.

Analysis of crosses involving PI 315608 was more difficult. Of the 50 plants of this genotype observed, 14 were rated as susceptible. In the F_2 from the cross of this genotype with UF 439-16-10-3, only one plant was classified as resistant in the 2 years of this study. These data did not fit the 15:1 ratio according to the chi-square test. However, the F_3 data did fit the 11:1 ratio. Note, though, that for the other two crosses, all resistant classes had more observed resistant plants than expected. This was most likely due to escapes. However, in the cross with PI 315608 there were fewer observed resistant plants than expected. If a certain number of escapes occurred, this may explain the resistant plants from this cross. It is also possible that these resistant plants, many of which had ratings of 1, were actually showing a moderate form of resistance.

Genotype PI 315608 does not contain the same resistance genes as PI 314817. When the two lines were crossed, 44 susceptible plants were found out of 66 in the F_2, and 36 susceptible plants out of 74 in the F_3. The genetic makeup of this genotype is unclear. The 44 susceptible and 22 resistant plants fit a 5:3 ratio, which would occur if the genotype contained one dominant and three recessive genes. There are inadequate data from the F_3 to further test this hypothesis. Also, it would not explain why some resistant and some susceptible plants appeared in the parental plots.

Conclusions

Rust resistance in PI 314817 and PI 350680 appears to be controlled by duplicate recessive genes.

Genotype PI 315608, which is reported to be resistant to peanut rust, is a poor source of resistance to the rust populations found in Florida. The line itself continues to segregate for susceptibility; in a cross with another resistant line, susceptible plants appeared, suggesting that a different genetic system is in operation. In a cross with a susceptible parent, only 1 resistant plant (possibly an escape) appeared out of 163 F_2 plants.

All rust resistance and susceptibility does not seem to be explainable by a two-gene system. This is especially true of the lines in this study and elsewhere that show moderate levels of resistance. No studies appear to have reported on the presence of races of *Puccinia arachidis*, although there is much suggestive research. It may be the presence of differing proportions of these races at different locations that determine whether genotypes are classified as resistant or moderately resistant.

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Discussion

Chairman: J.P. Moss

Rapporteurs: M.J.V. Rao, A.B. Mohammed

J.E. Parlevliet (addressed to Knauft). What did you consider as resistant and as susceptible on the 5-point scale?

D.A. Knauft. Scores 0 and 1 as resistant, and 2, 3, and 4 as susceptible.

J.E. Parlevliet. Were the susceptible and resistant groups of plants in F_2 as susceptible resistant as the parents?

D.A. Knauft. Very few susceptible plants were as susceptible as Florunner and mostly scored 3 on the 5-point scale. In general, the resistant plants had the same level of resistance as the resistant parent.

P. Subrahmanyam. In some of the crosses between two resistant parental lines at ICRISAT Center, we came across some plants with more resistance than the parents under high disease pressure.

L.J. Reddy. It could be due to lower disease pressure, which would give an upward bias.

D.A. Knauft. Probably that is why we did not observe such differences.

R.W. Gibbons. Should we go for a detached-leaf scoring technique to look into this?

P. Subrahmanyam. Yes. We have plans to do this.

P. Subrahmanyam. Does J.E. Parlevliet think that it is advisable to study components of resistance in F_2 plants to get precise estimates of genetic patterns?

J.E. Parlevliet. If I had studied barley rust in the field, I would not have obtained the results that I have today. If you must study, you must take leaves of the same physiological stage and age. Maturity differences could influence the results. There are several advantages in greenhouse studies, particularly the elimination of effects of other factors. I think that in such studies, one must take into account only one of the components for genetic studies. Latent period and infection frequency are difficult to measure on a large scale, and they are related to one another, so I would not do genetic analysis on these.

R.W. Gibbons. I think that leaf spots complicate rust studies in the field and that genetic studies must be carried out separately. But, for practical plant breeding, dual resistance to rust and leaf spots should be the aim.

E.A. Salako. Could the discrepancies in results be due to differences in juvenile and adult plant resistances?

J.E. Parlevliet. The variation for resistance among commercial barley varieties was far smaller at the seedling stage than at the adult stage. This was also true for wheat brown rust, rye brown rust, barley yellow rust, and barley powdery mildew. Apparently, it is a general pattern that partial resistance is best expressed in the adult plant and only to a limited extent in the seedling stage.

R.N. Strange. Pisatin is an exceptional phytoalexin. In pigeonpea we have found 10 phytoalexins, which have quite complicated side-chain structure. In *Arachis* we have found 3 phytoalexins. I want to know what mechanism controls partial resistance.

J.E. Parlevliet. I agree with Dr. Strange regarding pisatin. Regarding mechanisms, in the hypersensitive reaction, the cell and the neighbouring cells collapse after the haustorium has been formed inside the cell. Recognition perhaps occurs and results in cell death. But in partial resistance, an early abortion occurs in about 30-40% of the cases, but no single haustorium forms. In the other 70%, we get at least one haustorium formed. In partial resistance, it happens before the cell is penetrated while in the hypersensitive reaction, it happens after the cell is penetrated. But, in both cases, initially haustorium and host cells interact.

C.D. Mayee. Phytoalexins are naturally formed as postinfectionary products. There are several fungal species that do not attack plants and I think it does

not fit into your scheme of nonpathogenic interactions. Do you suggest that screening for strong resistant genes would result in loss of minor genes especially in groundnut rust?

J.E. Parlevliet. I do not think that if you select for strong resistance, you would lose minor genes. But, you are favoring major genes. You may gain neither.

K.J. Middleton. Do you have any information on effects of inoculum pressure on latent period?

J.E. Parlevliet. Latent period is influenced by a number of factors such as inoculum level, infection frequency, location on leaf, etc. So, we should take these factors into consideration before studying latent period.

P. Subrahmanyam. We had the same problem when we inoculated the test plants with higher doses of urediniospores. Latent period came down from 19 days to 10 days in resistant lines. Is there any risk involved in selecting for minor genes under low disease pressure particularly for rust? If so, how do those selections perform when tested under high disease pressure?

J.E. Parlevliet. In barley, by selecting for latent parent, I could effectively select for partial resistance. Heritability for latent period is higher in the greenhouse than in the field. Partial resistance and latent period are strongly correlated. But in the field, I would use more or less the same system you are using.

S. Wongkaew. We have received some material from ICRISAT that seems to be more resistant than the parents from which they are derived. Why is this the case?

D.A. Knauft. We do not know why it is so. But, there could be major and minor genes involved. There are some studies showing dominance of resistance. Some others show simple recessive genes. Maybe there are two different mechanisms operating that have come together in the derivatives you mention.

P. Subrahmanyam. Observations on ICRISAT breeding lines, for example PI 259747 or PI 350680 derivatives, showed that some were more resistant to rust than were their resistant parents. In 1979, when we scored the F_3 populations in the field trials, some F_3 plants were more resistant than the resistant parent.

S. Nagarajan. Our observations in wheat rust have indicated that sometimes the greenhouse observations for resistance do not correlate with the field observations. Have you observed the same in your material?

J.E. Parlevliet. Seedling-stage screening is not very representative. But in barley rust, we have been able to select for partial resistance even in the seedling stage. However, the seedlings should be close together and the specific control cultivar should be adjacent to each set of seedlings for use as a reference.

S. Nagarajan. We always put the reference seed in the right side of each bread pan. We later transplant the seedlings in the field.

J.E. Parlevliet. Transplanting itself could influence results. I suggest you produce seed from the transplanted seedling and use that seed for evaluation.

T.P. Yadava. The chances of environmental interactions with genotype are much more in what you are suggesting than in transplantation.

J.E. Parlevliet. Partial resistance is not very sensitive to environment because I get the same ranking order in a range of environments.

General Discussions, Field Visit and Concluding Remarks

General Discussion

Chairmen: D. McDonald, R.W. Gibbons

Rapporteurs: P.T.C. Nambiar, P.W. Amin, P. Subrahmanyam, L.J. Reddy

Discussion of control measures

D. McDonald. In the various papers and discussions we have mentioned many of the factors that are important in the cultural control of rust disease. We should now consider these together and in greater depth.

Fertilizer

C.D. Mayee. One agronomic factor mentioned is the effect of fertilizer treatment on rust-disease severity. In trials in Maharashtra State we found that rust severity was greater when phosphorus levels were low than when there was a sufficient supply of this element. This has also been mentioned by Dr Salako from Nigeria and by Drs Zheng and Liu from the People's Republic of China.

A.S. Rao. Is the influence of phosphorus direct or through interaction with nitrogen?

P.T.C. Nambiar. Addition of phosphorus increases nitrogen fixation. However, application of fertilizer nitrogen does not influence rust-disease severity.

R.O. Hammc. Nonnodulating lines descended from Tarapoto crosses are susceptible to rust, but so are commercial varieties with good nodulation.

R.W. Gibbons. Did we find any relationship between nonnodulating lines and rust resistance?

P.T.C. Nambiar. No. Some of the nonnodulating lines were resistant and some susceptible to rust.

S. Wongkaew. Perhaps the reduction in rust severity following phosphorus application could be due to the improved growth and health of the plants.

R.O. Hammons. It may be difficult to separate the direct effect of fertilizers on rust disease from that of such factors as soil pH.

D. McDonald. Really very little is known of the effects of fertilizers, soil-nutrient levels, and pH on development of rust disease. This could be a useful subject for research and perhaps fertilizer trials could be used for this purpose. The involvement of physiologists would be essential for such work.

Cropping systems and plant population

R.W. Gibbons. We should study the factors influencing perpetuation and spread of groundnut rust in India, and perhaps also internationally.

F.P. Yadava. In southern India the multiple cropping of groundnut facilitates build up of rust disease and this is a threat to groundnut production in the north. Should we initiate studies on spread of rust in India?

P. Subrahmanyam. Yes. This could be studied through the AICORPO network.

S. Nagarajan. Trap crops could be used to monitor the disease as has been done for wheat rust. Such studies do require considerable cooperation and meteorological data are needed to assist with interpretation.

S. Wongkaew. Plant population can be an important factor in cultural control of foliar diseases.

P. Subrahmanyam. That is correct. At ICRISAT the pathologists and physiologists have been together investigating effects of plant population on severity of rust and leaf-spot diseases. At high populations there was more defoliation than at low populations. But not all of the defoliation was due to greater disease severity, and we found increase in defoliation with increased population in the absence of disease. This complicates disease-resistance screening.

D.L. Cole. What populations do Indian farmers use? In Zimbabwe some farmers plant groundnuts up to 1 m apart.

P. Subrahmanyam. The recommended spacing for spanish type groundnuts is 30 cm between rows and 10 cm between plants in the row.

D.L. Cole. Yes. But at what spacings do farmers actually sow?

R.W. Gibbons. Farmers in India sow groundnuts at very much higher populations than do most African farmers.

D. McDonald. Vegetative growth of groundnuts is generally poorer in India than in Africa and if plants are widely spaced they will not provide full ground cover.

R.O. Hammons. High plant densities could lead to longer retention of water on leaf surfaces and this could have interesting interactions with varietal resistance as Marion Cook has reported varietal differences in leaf wettability being related to rust resistance. Interactions between microclimatic effects and leaf wettability could influence rust resistance evaluation of breeding material. Someone should confirm or disprove Dr Cook's contention that leaf wettability is an important factor in rust resistance.

J.F. Hennen. Is anything known of the effect of weeds on rust disease? I am thinking of reports of some vascular plants inhibiting the growth of other vascular plants.

D. McDonald. I have not heard of any such inhibiting effect of weeds on groundnut rust. However, heavy weed growth in groundnut crops can have an effect on the microclimate similar to that of high crop-plant population. There was some evidence in Nigeria that heavy weed growth in groundnut fields led to increased severity of leaf-spot diseases.

Biological control

D. McDonald. There have been several comments on the possible use of biological control by hyperparasites. I was particularly interested in the comment on their occurrence late in the season and possible effects in reducing carry-over of viable urediniospore inoculum.

C.D. Mayee. Reduction of rust diseases on other crops by the action of hyperparasites has not been very effective.

D.L. Cole. The hyperparasites of groundnut rust are not likely to have a serious effect upon the disease unless the cycle can be changed in their favor.

S. Wongkaew. No teliospores have been found in Thailand and groundnut rust depends solely upon urediniospores for spread and perpetuation. The effect of hyperparasites in reducing urediniospore populations could be important, particularly late in the season.

P. Subrahmanyam. Application of conidia of the hyperparasite *Verticillium lecani* to groundnut foliage some 2 days prior to inoculation with the rust pathogen was effective in reducing infection and development of rust.

K.J. Middleton. There are reports of *Bacillus* spp being effective against leaf spots. Are there any reports of *B. subtilis* or *B. thuringiensis* being parasitic on or antagonistic to rust?

J.F. Hennen. I know of no record of bacteria affecting groundnut rust, but there are reports of bacteria being responsible for reducing the overwintering of cereal rusts in North America.

In Brazil it was difficult to find groundnut rust without hyperparasites, including insects.

A.S. Rao. Hyperparasites are generally favored by cool wet conditions: they are therefore not likely to be very effective in reducing rust severity in the semi-arid tropics.

D.L. Cole. Could Dr Subrahmanyam comment on the distribution of *Darluca* sp on groundnut rust in Malawi?

P. Subrahmanyam. I found *Darluca* sp. in both the cool highland and warmer Lake Shore regions of Malawi.

D. McDonald. It certainly seems that there are interesting possibilities for use of hyperparasites to reduce rust severity, and research should be encouraged, particularly in those areas where the hyperparasites commonly occur.

Chemical control

D. McDonald. Moving on to consideration of use of fungicides to control rust, I would like to indicate

a few areas for possible discussion. It is most important to obtain accurate data on crop losses from rust and associated foliar diseases, and on benefits that can be obtained from chemical control. In only a very few cases have research workers constructed proper response curves to show increase in yield associated with increase in concentration of fungicide and numbers of applications. There has not been sufficient involvement of economists in this work. We also have to investigate the possibilities of combining chemical control with use of resistant cultivars.

C.D. Mayee. What do you mean by proper response curves?

D. McDonald. A response curve can be obtained by plotting yield increases against numbers of fungicide applications, having previously determined optimum intervals between applications and optimum fungicide formulations and concentrations. Numbers of applications could be increased from 1 to as many as required to produce a virtually disease-free crop at harvest.

D.L. Cole. Are you talking specifically about rust disease?

D. McDonald. No. This approach covers both rust and leaf spots. We can obtain separate epidemics of rust and of leaf spots by use of specific fungicides but for practical purposes we should deal with foliar diseases together.

E.A. Salako. In Nigeria we have been investigating the application of fungicides with controlled-droplet application (cda) machines, but have had problems with using some formulations.

D.L. Cole. Filters can be used to improve the condition of the spray chemicals. In Zimbabwe we use a mixture of 1 kg of Dithane M 45 and 250 g of benomyl in 2.5 to 5 l water per hectare, and this is applied with cda machines. We get very good control of rust and leaf spots.

E.A. Salako. Good results have been obtained from use of fungicides to control rust and leaf spots. We have input from economists when considering recommendations for control. It is also important that recommendations should be easy to understand and simple for unsophisticated small farmers to implement.

D.A. Knauft. How readily available are cda machines?

E.A. Salako. They are available in Nigeria at a cost of around seventy naira.

R.W. Gibbons. Effective fungicide application is relatively easy in developed countries where farmers are given advice over the radio as to when they should spray their crops. In many developing countries the meteorological data on which such advice is based may not be available, nor may there be broadcasts to farmers. Recommendations are usually of the type that require a specific number of sprays to be given at specific intervals starting at a particular crop age or following appearance of the disease. If such a recommendation is strictly followed fungicides can be wasted when applied during drought conditions.

K.J. Middleton. Even in developed countries, but more importantly in developing countries, we should have a scouting system by which the farmer examines his crop for occurrence and severity of disease and from this decides whether or not to apply fungicides.

D. McDonald. There is always a danger of scientists being pushed into making general recommendations for regions that do not have uniform conditions. In some areas rust epidemics occur with great uniformity and severity e.g., in Hyderabad. In other areas the disease may be important in one season and relatively unimportant in the next. We have also to consider the risk of crop failure from such factors as drought and pest attack. Some farmers in marginal areas of India may lose one crop in three from drought. However, there are areas where farmers have good land and assured rainfall, or possibly supplementary irrigation facilities, and such farmers could well find it economic to follow a set procedure for foliar-disease control with fungicides.

R.W. Gibbons. Research should concentrate on cda fungicidal control of rust and leaf spots. Experience with control of cotton pests in Africa has shown that small farmers are quick to adopt cda technology although previously reluctant to apply the medium or high volume sprays recommended. This has much to do with difficulty in obtaining ready access to water in a semi-arid tropical environment and with problems of handling large amounts of water and spray.

R.O. Hammons. Insufficient attention is paid to problems of spray drift and this can be particularly important in the case of eda. We suspect that drift to nonsprayed plots in yield loss assessment trials can reduce severity of rust and leaf spots and lead to underestimation of yield losses.

Genetic resistance

V. Arunachalam. Should we concentrate on a few specific rust-resistant genotypes in breeding or should we use as many sources as possible and try to obtain rust-resistant groundnut populations rather than single genotypes?

D.A. Knauft. Another question is, what levels of yield and resistance are we aiming at? At what level of resistance are we going to get yields as good as the farmers are currently obtaining? There should be a yield advantage.

R.O. Hammons. It is recognised that there is a strong relationship between resistance and yield, most resistant breeding lines having low yields.

D.A. Knauft. We don't know if there is a special linkage of resistance genes with low yield, or if the yields are low because the resistant genotypes have not been subject to selection for good agronomic characteristics.

R.W. Gibbons. We now have breeding lines with high levels of resistance to rust and moderate levels of resistance to late leaf spot. Some of these lines have acceptable quality and good yield potential. We are currently trying to get the resistances into shorter duration cultivars suitable for areas such as sub-Sahelian West Africa where rainy seasons are short.

D.A. Knauft. Breeding lines are now available at the University of Florida that can yield well (up to 5 t ha^{-1}) under severe late leaf-spot disease pressure.

R.W. Gibbons. It would be useful if the Florida and ICRISAT Programs could exchange foliar diseases resistant germplasm and breeding lines to compare their performance against leaf spots and rust diseases in both environments.

Disease-scoring methods

K.J. Middleton. We have had considerable discussion in the various sessions and in the field visit on the suitability of the 9-point scale and other methods for scoring of rust-disease damage. Could we now discuss this further?

R.W. Gibbons. Yes. It should be noted that each disease scale has its advantages, and each should be assessed in relation to the particular use for which it is intended.

S. Nagarajan. If there are definite susceptible and resistant pustule types, then the 9-point scale in its present form is not sufficient for disease-resistance screening. It is difficult to modify the 9-point scale unless we can establish that there is a definite host × parasite interaction. For most screening purposes it may be necessary to use the modified Cobb's scale.

J.E. Parlevliet. Considering the data presented in the ICRISAT publication on components of resistance to rust (Subrahmanyam, P., McDonald, D., Gibbons, R.W., and Subba Rao, P.V. 1983. Components of resistance to *Puccinia arachidis* in peanuts. Phytopathology 73 (2): 253-256), of the 26 genotypes studied 4 had a mean rust field score of 2.4 on the 9-point scale and had a mean incubation periods of 17.6 days. The next group of 9 genotypes had a field score of 2.9 and incubation periods of 14.6 days. The next group of 8 genotypes had a field score of 4.1 and incubation period of 9.9 days. The last, and most susceptible, group of 5 genotypes had a field score of 9 and incubation period of 9.1 days. From these data one can see that the relationship between field rust score and incubation period is not linear. A linear relationship might be achieved by modifying the 9-point scale which is after all an arbitrary one, perhaps by making it logistic.

K.J. Middleton. Are you basing this argument on the latent period (incubation period) being the most important factor in resistance? Could there be some other component of the field score that is not covered by latent period?

J.E. Parlevliet. From the data it is clear that latent period is important although it is not the only factor involved. For a disease-scoring scale to be most useful, each unit in it should represent a similar epidemiological distance; this not true of the 9-point scale in its present form.

R.W. Gibbons. If the 9-point scale was to be modified in this way, would it still be suitable for both resistance screening and genetic studies?

J.E. Parlevliet. Yes.

D.L. Cole. I have reservations about the suitability of the 9-point scale for use where statistical analysis is required. If it could be modified to a logarithmic scale then statistical analysis would be facilitated.

S. Nagarajan. I prefer a scoring system in which pustule type is taken into consideration as well as pustule numbers. We could probably work out such a system over the next few years.

R.O. Hammons. Fortunately, the breeding program is not dependent upon us resolving the question of what kind of scale to use. Field resistance is agreed to be the most important factor.

J.E. Parlevliet. For the practical purpose of selection almost any scale can be used. However, it would be useful to have a multipurpose scale. I agree that for breeding purposes scales should be based on field data and not necessarily on greenhouse or laboratory data. A uniform groundnut-rust scoring system is indeed desirable, but it should be remembered that it took many years to develop such a system for cereal rusts.

D. McDonald. In the meantime we shall continue to use the 9-point scale in rating the resistance of germplasm and breeding lines in the field. For research into genotype × pathogen × environment interactions and for study of disease-control systems we can use the modified Cobb's scale and make careful measurements of remaining green leaf.

R.W. Gibbons. ICRISAT physiologists should continue to work in close cooperation with pathologists and breeders to elucidate the various interactions between rust disease, resistant and susceptible genotypes, environmental factors and crop protection treatments.

Stability of resistance

P. Subrahmanyam. There is broad agreement in the disease reactions of genotypes to rust in different parts of the world. Some differences have been noted in the reaction of specific genotypes to rust between ICRISAT Center and the research farm of the Guangdong Academy of Agricultural Sciences, Guangzhou, but these have been from resistant to moderately resistant or vice versa. No genotype changed from resistant to susceptible or susceptible to resistant between the two locations.

T.P. Yadava. At how many locations in India has the ICRISAT International Groundnut Foliar Diseases Nursery been grown?

P. Subrahmanyam. It has been grown in 12 locations altogether.

D. McDonald. Feedback of information from the disease nurseries has been of variable quality. We are considering modifying the nursery and possibly reducing the number of locations.

K.J. Middleton. It is most important to have an international nursery to monitor possible breakdown of resistance. Such trials should be sited in problem areas, and it is important that they be visited by plant pathologists.

R.O. Hammons. Nurseries should be sited in locations where rust disease is severe. The link between Peanut CRSP and ICRISAT could be used to ensure maximum utilization of such trials in countries such as Thailand.

J.F. Hennen. Are there disease nurseries located in South America? It would be useful to site them in Peru and Brazil.

P. Subrahmanyam. One rust disease nursery was sent to Guyana. We would very much like to have more of them in South America, particularly in Peru where many of the rust-resistant genotypes have originated.

Origin, distribution, and spread of rust

J.F. Hennen. It would be interesting to learn where rust came from. Perhaps this could be investigated through study of the disease in wild *Arachis* species populations in South America. Rust could be collected from wild populations and used for cross-inoculation studies. The data could be examined from an evolutionary viewpoint. The rusts *Puccinia zoniae* and *Puccinia stylosanthis* should be studied to determine their relation to *Puccinia arachidis*.

R.W. Gibbons. We should encourage more research into groundnut rust in South America. It would be particularly useful if collecting teams visiting South America could include plant pathologists.

Field Visit

The group visited ICRISAT Center Farm and were shown the various field trials being done on rust and other foliar diseases. Considerable interest was shown in the field screening of germplasm and breeding lines for resistance to rust and late leaf spot. Comparison of resistant and susceptible genotypes stimulated discussion of reactions to rust and the suitability of various disease scoring methods for particular purposes.

Concluding Remarks

R.W. Gibbons. We have had several days of interesting and useful discussion on groundnut rust, and your comments and suggestions for improving our research on this important disease are much appreciated. It is gratifying that you have on the whole endorsed our approach to the problem, and our meeting will give rise to much useful cooperation in the future. Our discussions have concentrated on breeding for rust resistance and on the disease-screening methods available for use in this process. It is to be hoped that this will stimulate development of more accurate disease-assessment methods and that cooperative research will lead to the identification of genotypes for use in checking for pathogen variation. We shall continue to monitor the reaction of genotypes to rust worldwide, and this will be facilitated by ICRISAT's increasing inputs in both Africa and Asia. The importance of research on rust in South America involving the cultivated groundnut and its wild relatives has been noted, and we should all do our best to support Dr Hennen's plans for such work.

The progress being made in several countries towards breeding rust-resistant cultivars is commendable and we should soon see the release of material that should have particular relevance for use by small farmers in disease-prone areas. The integration of such cultivars with cultural, biological, and chemical control systems will require considerable research and extension inputs from all concerned and our ICRISAT Program will do all in its power to assist national programs in management of rust disease and associated leaf spots.

I thank you all for your contributions to making this a successful and useful meeting.

Meeting Organization and Participants

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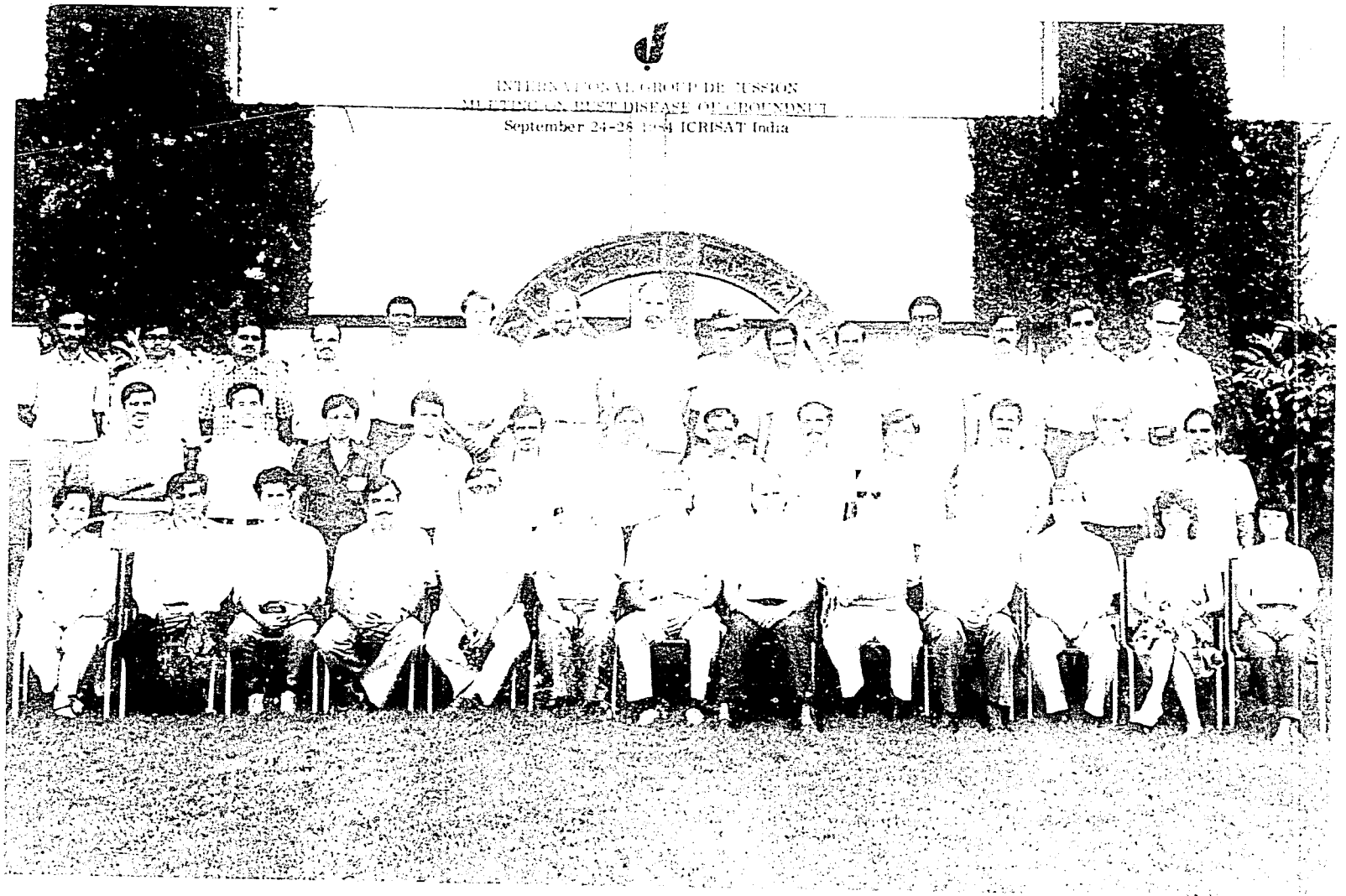

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