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568

Origins of Resistances to Rust and Late Leaf Spot in Peanut (*Arachis hypogaea*, Fabaceae)[1]

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The cultivated peanut (Arachis hypogaea, *Fabaceae) is believed to have originated along the eastern slopes of the Andes in Bolivia and northern Argentina. The crop is now grown throughout tropical and warm temperate regions. Among diseases attacking peanuts, rust caused by* Puccinia arachidis *and late leaf spot caused by* Phaeoisariopsis personata *are the most important and destructive on a worldwide scale. Both pathogens, restricted in host range to* Arachis, *probably originated and coevolved in South America along with their hosts. In recent years there has been much emphasis on screening of peanut germplasm for resistance to these diseases. At the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India, some 10,000 peanut germplasm accessions were screened for resistance to rust and late leaf spot during 1977–1985 and sources of resistance indentified for either or both pathogens. Of the resistant genotypes, about 87% belonged to* A. hypogaea *var.* fastigiata *and 13% to var.* hypogaea; *84% originated in South America or had South American connections. A high percentage (75%) had their origin in Peru (believed to be a secondary gene center for var.* hirsuta *and var.* fastigiata*), suggesting that resistance to rust and late leaf spot diseases might have evolved in that country.*

Origine des Sources de Résistance à la Rouille et à la Cercosporiose Tardive de l'Arachide (*Arachis hypogaea*, Fabaceae). *L'arachide cultivée (*Arachis hypogaea, *Fabaceae) serait originaire du versant oriental des Andes, en Bolivie et en Argentine du Nord. Cette culture est maintenant pratiquée dans toutes les régions tropicales et tempérées relativement chaudes du monde. A l'échelle mondiale, la rouille,* Puccinia arachidis, *et la cercosporiose tardive,* Phaeoisariopsis personata, *sont les deux principales maladies de l'arachide. Les deux agents pathogènes, dont* Arachis *est l'hôte unique, sont probablement aussi originaires de l'Amérique du Sud, où ils se seraient développés avec leurs hôtes. Au cours des dernières années, un effort particulier a été fait pour cribler les ressources génétiques pour leur résistance à ces maladies. A l'Institut International de Recherches sur les Cultures des Zones Tropicales Semi-Arides (ICRISAT), en Inde, quelque 10,000 génotypes d'arachide ont été criblés, entre 1977 et 1985, pour leur résistance à la rouille et la cercosporiose tardive, et des sources de résistance à l'un ou l'autre, ou aux deux agents pathogènes ont été identifiées. Près de 87% des génotypes résistants appartenaient à* A. hypogaea *var.* fastigiata *et 13% à var.* hypogaea; *84% d'entre eux provenaient d'Amérique du Sud, ou pouvaient être apparentés à des sources sud-américaines. Un fort pourcentage (75%) provenait du Pérou (centre génique secondaire généralement reconnu de var.* hirsuta *et var.* fastigiata*), suggérant ainsi que les sources de résistance à la rouille et la cercosporiose tardive se seraient développées dans ce pays.*

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It is generally accepted that the primary and secondary gene centers of cultivated plants are the best locations to find genuine sources of resistance to common pests and pathogens (Dinoor and Eshed 1984; Leppik 1970). During the coevolution of host and parasite, both participants develop complementary genetic systems if they have long been associated in their centers of origin (Anikster and Wahl 1979; Browning 1974; Dinoor 1970; Harlan 1976; Leppik 1970; Segal et al. 1980). The evolution of new and more virulent races of the pathogen may be counterbalanced by the development of higher levels of resistance in its host system due to selection pressure in the coevolution (Flor 1956). Gene centers of many cultivated plants have been well established, but the origin and evolution of the parasites of these plants are still unexplored even after Leppik (1970) emphasized this point. Some investigations have shown that certain specialized parasites and their distribution on particular plant groups can serve as reliable indicators that help to trace back the origin and evolution of their hosts (Leppik 1966).

Systematic exploration in the gene centers for sources of resistance to some pests and diseases has been carried out for a few crop species (Qualset 1975). Very little is known regarding the relationship between the gene centers of the cultivated peanut (*Arachis hypogaea* L., Fabaceae) and sources of the resistance to diseases. Hennen et al. (1976) and Leppik (1971) suggested that the exploration of gene centers of peanut in South America may provide new germplasm for varietal improvement and breeding for resistance to pests and diseases. Our report discusses evolution of resistances to two major foliar diseases on the basis of screening of *Arachis* germplasm collected from gene centers and maintained at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT).

ICRISAT, 25 km northwest of Hyderabad, Andhra Pradesh, India, has the world's largest collection of peanut germplasm: over 10,000 accessions (Ramanatha Rao 1987). During 1977–1985 these were screened against rust caused by *Puccinia arachidis* Speg. and late leaf spot caused by *Phaeoisariopsis personata* (Berk. & Curt.) von Arx; several sources of resistance were identified for either or both pathogens (Subrahmanyam and McDonald 1983, 1987; Subrahmanyam et al. 1980, 1982, 1983, 1985b).

ORIGIN AND DISTRIBUTION OF PEANUT

Arachis is confined to a region in South America, east of the Andes, south of the Amazon, and north of La Plata. The assumed center of origin of the genus is in the Mato Grosso of Brazil, close to the Gran Pantanal (Gregory et al. 1980). *Arachis hypogaea* is the only member of *Arachis* cultivated on a large scale. It is believed to have originated somewhere along the eastern slopes of the Andes in Bolivia (Gregory et al. 1980) and in northern Argentina (Krapovickas, pers. comm. 1984). *Arachis hypogaea* is broadly classified into two subspecies, each with two varieties (Krapovickas 1969). Krapovickas (1969, 1973) indentified five gene centers in relation to the distribution of subspecies and botanical varieties of *A. hypogaea* (Fig. 1):

(1) The Guarani region, which includes a large part of the basins of the rivers Paraguay and upper Paraná bordering northeastern Argentina (Corrientes and Misiones, eastern Paraguay, and southern Mato Grosso and western São Paulo in Brazil): subsp. *fastigiata* (var. *fastigiata* and var. *vulgaris*).

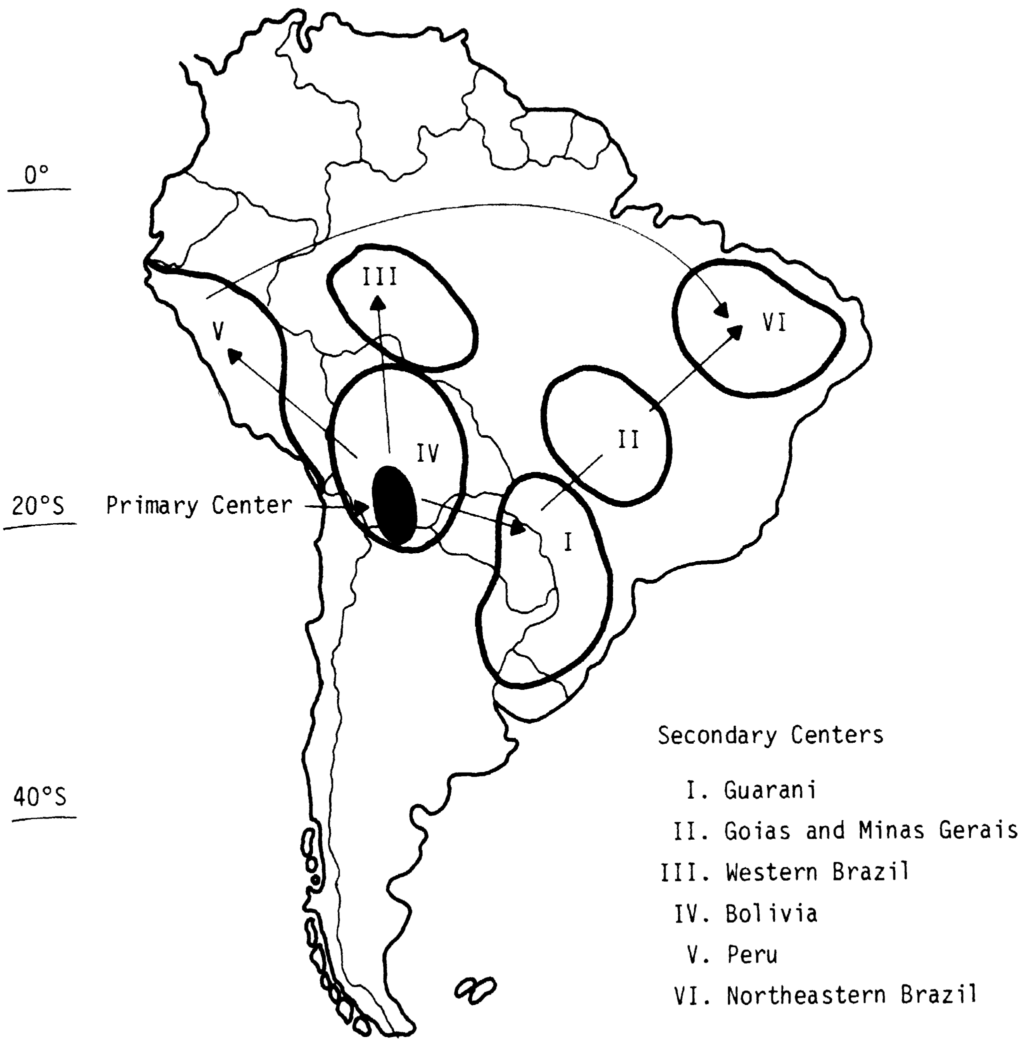

Fig. 1. Centers of origin and diversity of the cultivated peanut. Arrows indicate the spread (adapted from Gregory and Gregory 1976).

(2) The regions of Goiás and Minas Gerais in Brazil: subsp. *fastigiata* (var. *fastigiata* and var. *vulgaris*).

(3) The region of Rondonia and northeastern Mato Grosso of Brazil, which is part of the Amazon basin: subsp. *hypogaea* (var. *hypogaea*).

(4) The Bolivian region including the eastern foothills of the Andes: subsp. *hypogaea* (var. *hypogaea*) and a few subsp. *fastigiata* (var. *fastigiata*).

(5) The Peruvian region: subsp. *hypogaea* (var. *hirsuta*) and subsp. *fastigiata* (var. *fastigiata*).

Gregory and Gregory (1976) identified the sixth gene center to include northeastern Brazil: subsp. *fastigiata* (var. *fastigiata* and var. *vulgaris*). The Bolivian region is believed to be the primary gene center of *A. hypogaea*, and the other five regions are assumed to be secondary gene centers (Gregory et al. 1980) (Fig. 1).

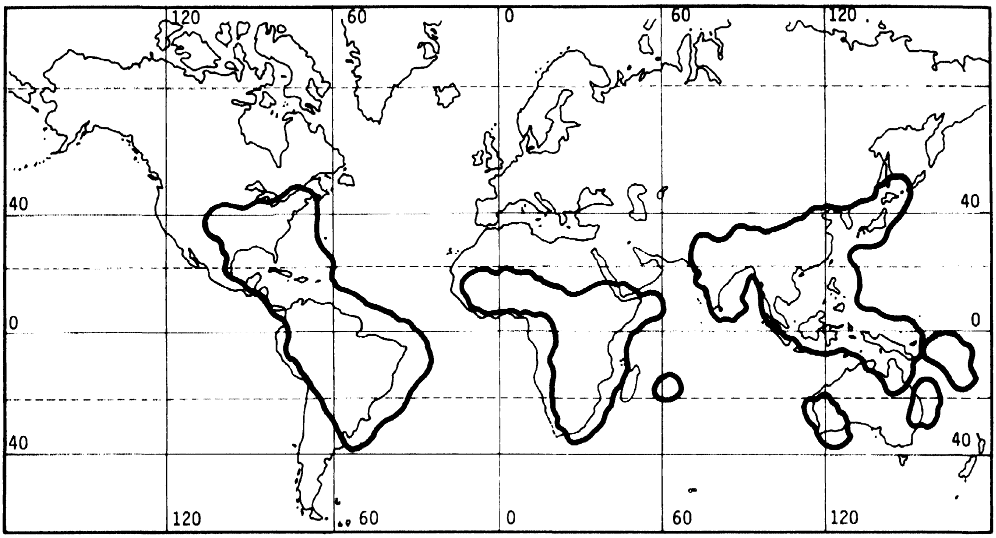

Fig. 2. Geographical distribution of peanut rust (based on Commonwealth Mycological Institute map 160 issued in 1980).

The peanut is grown throughout tropical and warm temperate regions, approximately between latitudes 40 N and 40 S. Peanuts are known to have been cultivated in Peru ca. 2000 B.C. (Hammons 1973; Krapovickas 1969); this country is a center of diversity for var. *hirsuta* and var. *fastigiata*. From its centers of origin, peanut spread to the rest of the world in post-Columbian times (Krapovickas 1969).

ORIGIN AND DISTRIBUTION OF THE RUST AND LATE LEAF SPOT PATHOGENS

Peanut yields are adversely affected by rust and late leaf spot diseases (Subrahmanyam et al. 1984). The first record of peanut rust dates back to 1827 or 1828 in a collection made in Surinam by C. Weigelt (Hennen et al. 1987). Prior to 1969, the disease was confined largely to South America, although occasional outbreaks in the peanut-producing areas of the southern U.S.A. were reported from 1918 onwards (Hammons 1977). However, peanut rust is not a serious problem in the U.S.A. (Mixon et al. 1983). By the early 1970s rust had spread to all major peanut-producing areas of Asia, Africa, Australasia, and Oceania (Bromfield 1974; Subrahmanyam and McDonald 1983) (Fig. 2). The source(s) of inoculum and means of spread responsible for this movement of rust from South America into these areas are undetermined. The pathogen is known almost exclusively by its uredinial stage. There are a few records of the telial stage on *A. hypogaea* and on wild *Arachis* spp. (Hennen et al. 1976, 1987), but the role of teliospores in the life history of the pathogen is not known. There is no record of occurrence of any collateral hosts of this pathogen outside of *Arachis*. It is not known whether the fungus produces pycnia and aecia or whether any alternate host is involved in its life cycle (Hennen et al. 1987). Hennen et al. (1976, 1987) speculated that the fungus produces its sexual life cycle in South America, and genetic diversity of the pathogen is predicted to have accumulated there. Understanding the races of the pathogen and their distribution would help to identify

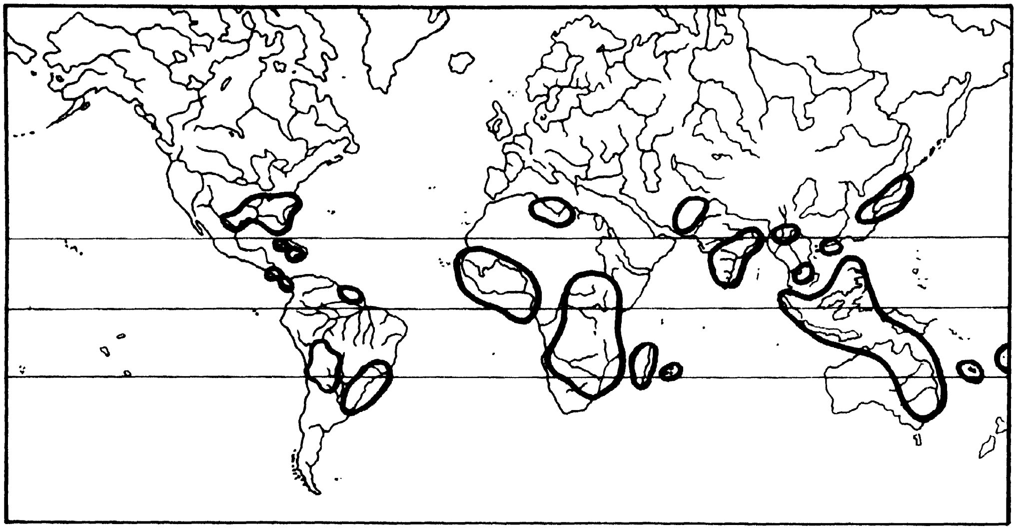

Fig. 3. Geographical distribution of peanut late leaf spot (based on Commonwealth Mycological Institute map 152 issued in 1967).

the center of origin. Peanut rust is thought to have originated in South America along with the domestication of the peanut in prehistoric times (Leppik 1971). The restricted distribution of the pathogen in South America until 1969, and its host restriction to members of *Arachis,* strongly support this hypothesis.

The late leaf spot pathogen occurs wherever peanuts are grown (McDonald et al. 1985) (Fig. 3). Members of *Arachis* are its only reported hosts (Subrahmanyam et al. 1985a). The restricted host range within *Arachis* suggests that the pathogen might have originated and evolved independently along with its hosts in South America. The present worldwide distribution of the pathogen is very likely not an indigenous condition, but the result of extensive cultivation of peanut by humans.

Rust and late leaf spot pathogens may have originated and coevolved along with their hosts in South America. However, there are several unanswered questions regarding the evolution and spread of these two pathogens. Why did the late leaf spot pathogen spread to the rest of the world from South America much earlier than rust? When did the late leaf spot pathogen spread to the rest of the world? How did rust and late spot pathogens spread to peanut-producing countries outside South America? What and how are the evolutionary changes, if any, in the centers of origin themselves—in the pathogen by itself, and under the influence of its host; in the host itself under the influence of pathogen(s)?

SOURCES OF RESISTANCE TO RUST AND LATE LEAF SPOT

The most important peanut foliar diseases causing severe yield losses on a worldwide scale are the leaf spots (*Cercospora arachidicola* Hori and *P. personata*) and rust. Losses in yield due to leaf spots have been estimated at around 10% in the U.S.A., where fungicide application is normally practised (Jackson and Bell 1969). In the semi-arid tropics, where chemical control is generally prohibitive, losses in excess of 50% are common (Gibbons 1979). In India, combined attacks of rust and leaf spots cause around 70% yield losses (Subrahmanyam et al. 1984). Although these diseases can be controlled by certain chemicals (Smith and Littrell 1980), genetic control is decidedly the best solution. Identification of sources of genetic resistance is therefore highly important.

Screening for resistance to rust and late leaf spot has been intensively carried out by many workers, and a number of sources of resistance have been reported (Bromfield 1974; Bromfield and Cevario 1970; Cook 1972, 1981; Gorbet et al. 1982; Moraes and Salgado 1983). An intensive research program was started at ICRISAT in 1977 to search for resistance to all major peanut diseases, in both the cultivated and the wild *Arachis*, and to incorporate resistances into high yielding and commercially acceptable cultivars. At ICRISAT, rust and late leaf spot occur regularly and reach high levels on rainy season peanut crops, but early leaf spot is rarely severe enough to permit field screening. A collection of over 10,000 peanut germplasm accessions (Ramanatha Rao 1987) was screened against rust and late leaf spot during 1977–1985, and a number of sources of resistance were identified for either or both pathogens (McDonald et al. 1985; Subrahmanyam and McDonald 1983, 1987; Subrahmanyam et al. 1980, 1982, 1983, 1985b). These sources of disease resistances are listed in Table 1 together with details of their identity, botanical type, seed color, and country of origin.

DISCUSSION

Out of 10,000 germplasm accessions screened, 42 genotypes (36 *fastigiata* and 6 *hypogaea*) were resistant to rust, 5 (1 *fastigiata* and 4 *hypogaea*) were resistant to late leaf spot, and 39 (38 *fastigiata* and 1 *hypogaea*) were resistant to both rust and late leaf spot (Table 1).

Grouping of the foliar-disease-resistant genotypes based on botanical type indicated that about 87% of them belonged to var. *fastigiata*, 13% to var. *hypogaea*, but none to var. *vulgaris*. Among the var. *hypogaea* types, two of the genotypes from Honduras (ICG 7899 and ICG 7900) have in their pedigree a resistant parent belonging to var. *fastigiata*. These *fastigiata* types are distinct from the normal valencia peanut types in having typically ribbed, constricted, and prominently beaked pods. They also have comparatively long maturation periods.

Study of all the available foliar-disease-resistant genotypes at ICRISAT revealed that about 84% of them originated in South America or had South American connections; 74% originated in Peru (Fig. 4), which is believed to be a secondary gene center of the peanut (var. *hirsuta* and var. *fastigiata*). Seeds of ICG 6340 (PI 350680) were obtained from the Division of Tropical Research, Honduras, by the USDA; its identification was given as 'Tarapoto'. So it may well be originally from the Tarapoto region of Peru (Hammons 1977). The resistant accessions from Honduras have genes from the resistant parent, 'Tarapoto', which comes from Peru (Hammons 1977). Origins of accessions ICG 2716 (from Uganda) and ICG 6022 (from Sudan) were uncertain, but their pod characteristics suggest that they are introductions from South America, probably from Peru. The inclusion of some of these accessions in the ICRISAT program has shown that the pod characters could be transferred to other genetic backgrounds along with disease resistance (Nigam et al. 1980; Reddy et al. 1984, 1987). ICG 9185, from Israel, is a breeding line from a cross between *A. hypogaea* and an unknown male parent

TABLE 1. SOURCES OF RESISTANCE TO GROUNDNUT RUST AND/OR LATE LEAF SPOT DISEASES IDENTIFIED AT ICRISAT CENTER (UP TO 1985).

ICG No.[a]	Genotype	Botanical type/variety	Seed color[b]	Country of origin
Resistant to rust alone				
1697	NC Ac 17090	*fastigiata*	Light tan	Peru
4746	PI 298115	*hypogaea*	Off-white	Israel/USA
7296	WCG 190	*fastigiata*	Tan	Peru
7320	NC Ac 17656	*fastigiata*	Tan with PS	–
7628	PI 275747	*fastigiata*	Light Purple	Peru
7629	PI 275748	*fastigiata*	Tan	Peru
7712	PI 262129	*hypogaea*	Tan	Peru
7882	PI 314817	*fastigiata*	Light tan	Peru
7883	PI 315608	*fastigiata*	Off-white	Israel/USA
7886	PI 390593	*fastigiata*	Light tan	Peru
7889	PI 393517	*fastigiata*	Off-white	Peru
7890	PI 393526	*fastigiata*	Purple	Peru
7891	PI 393527	*hypogaea*	Red	Peru
7892	PI 393527-B	*hypogaea*	Red	Peru
7893	PI 393531	*fastigiata*	Tan with PS	Peru
7895	PI 393643	*fastigiata*	Light tan	Peru
7896	PI 393646	*fastigiata*	Purple	Peru
7898	PI 407454	*fastigiata*	Purple	Ecuador
7899	PI 414331	*hypogaea*	Tan	Honduras
7900	PI 414332	*hypogaea*	Tan	Honduras
8298	NC Ac 18045	*hypogaea*	Tan	USA
9185	PI 343419	*fastigiata*	Red	Israel
10011	PI 476143	*fastigiata*	Tan	Peru
10014	PI 476145	*fastigiata*	Tan	Peru
10016	PI 476141	*fastigiata*	Tan with PS	Peru
10022	PI 476151	*fastigiata*	Purple	Peru
10024	PI 476161	*fastigiata*	Tan	Peru
10030	PI 476166	*fastigiata*	Tan with SPS	Peru
10031	PI 476168	*fastigiata*	Tan with PS	Peru
10032	PI 476168-1	*fastigiata*	Tan	Peru
10034	PI 476172	*fastigiata*	Tan	Peru
10037	PI 476174-1	*fastigiata*	Tan	Peru
10039	PI 476174	*fastigiata*	Purple	Peru
10046	PI 476178-1	*fastigiata*	Tan with LPS	Peru
10048	PI 476179	*fastigiata*	Tan	Peru
10051	PI 476180	*fastigiata*	Grey-orange	Peru
10057	PI 476184	*fastigiata*	Grey-orange	Peru
10061	PI 476186	*fastigiata*	Grey-orange	Peru
10062	PI 476187	*fastigiata*	Grey-orange	Peru
10067	PI 476191	*fastigiata*	Light purple	Peru
10068	PI 476192	*fastigiata*	Light purple	Peru
10070	PI 476193	*fastigiata*	Grey-orange	Peru
Resistant to late leaf spot alone				
2879	NC Ac 15989	*hypogaea*	Purple	Bolivia
6322	RMP 12	*hypogaea*	Tan with PB	Burkina Faso
6323	RMP 91	*hypogaea*	Tan	Burkina Faso
8069	NC Ac 2499	*hypogaea*	Tan	USA
9368	59-467	*fastigiata*	Red	South Africa

TABLE 1. CONTINUED.

ICG No.[a]	Genotype	Botanical type/variety	Seed color[b]	Country of origin
Resistant to both rust and late leaf spot				
1702	NC Ac 17124	*fastigiata*	Tan with PS	Peru
1703	NC Ac 17127	*fastigiata*	Tan with PS	Peru
1704	NC Ac 17129	*fastigiata*	Light tan	Peru
1707	NC Ac 17132	*fastigiata*	Purple	Peru
1710	NC Ac 17135	*fastigiata*	Purple	Peru
1712	NC Ac 17142	*fastigiata*	Dark tan	Brazil
2716	EC 76446(292)	*fastigiata*	Purple	Uganda
3527	USA 63	*fastigiata*	Purple	—
4747	PI 259747	*fastigiata*	Purple	Peru
4790	Krap. St. 16	*fastigiata*	Purple	Argentina
4995	NC Ac 17506	*fastigiata*	Purple	Peru
6022	NC Ac 927	*fastigiata*	Purple	Sudan
6330	PI 270806	*fastigiata*	Purple	Zimbabwe
6340	PI 350680	*fastigiata*	Purple	Honduras
7013	NC Ac 17133-RF	*fastigiata*	Purple	Peru
7232	PI 262127	*fastigiata*	Purple	Peru
7291	PI 262128	*fastigiata*	Purple	Peru
7340	WCG 182	*fastigiata*	Tan	Peru
7353	PI 262129	*fastigiata*	Tan	Peru
7406	PI 262121	*fastigiata*	Purple	Peru
7411	PI 275745	*fastigiata*	Tan with SPS	Peru
7433	NC Ac 17518	*fastigiata*	Tan with LPS	Brazil
7620	NC Ac 17505	*fastigiata*	Tan with LPS	Peru
7630	204/66	*fastigiata*	Tan with PS	Peru
7881	PI 215696	*fastigiata*	Purple	Peru
7884	PI 341879	*fastigiata*	Purple	Peru
7885	PI 381622	*fastigiata*	Purple	Peru
7887	PI 390595	*fastigiata*	Purple	Peru
7888	PI 393516	*fastigiata*	White with RB	Peru
7894	PI 393641	*fastigiata*	Light tan with PS	Peru
7897	PI 405132	*fastigiata*	Purple	Peru
9294	58-295	*hypogaea*	Tan	Burkina Faso
9990	PI 476021	*fastigiata*	Tan	Peru
10000	PI 476030	*fastigiata*	Red	Peru
10010	PI 476143	*fastigiata*	Tan with SPS	Peru
10023	PI 476152	*fastigiata*	Tan	Peru
10028	PI 476163	*fastigiata*	Purple	Peru
10045	PI 476178	*fastigiata*	Tan with PS	Peru
10064	PI 476189	*fastigiata*	Tan	Peru

[a] ICRISAT groundnut accession number.

[b] Royal Horticultural Society Colour Chart, 1966. PS = purple stripes, SPS = short purple stripes, LPS = long purple stripes, PB = purple blotches, and RB = red blotches.

that could be a resistant Peruvian line. ICG 4790 (Krapovickas strain 16) may not be from Argentina since there is no collection with that number (Krapovickas, pers. comm. 1984). ICG 7296 (WCG 190) lacks records of origin, but could be from Peru since other collections of Dr. Gregory (e.g., 182 [ICG 7340]) are from there. The four accessions resistant only to late leaf spot are from countries other

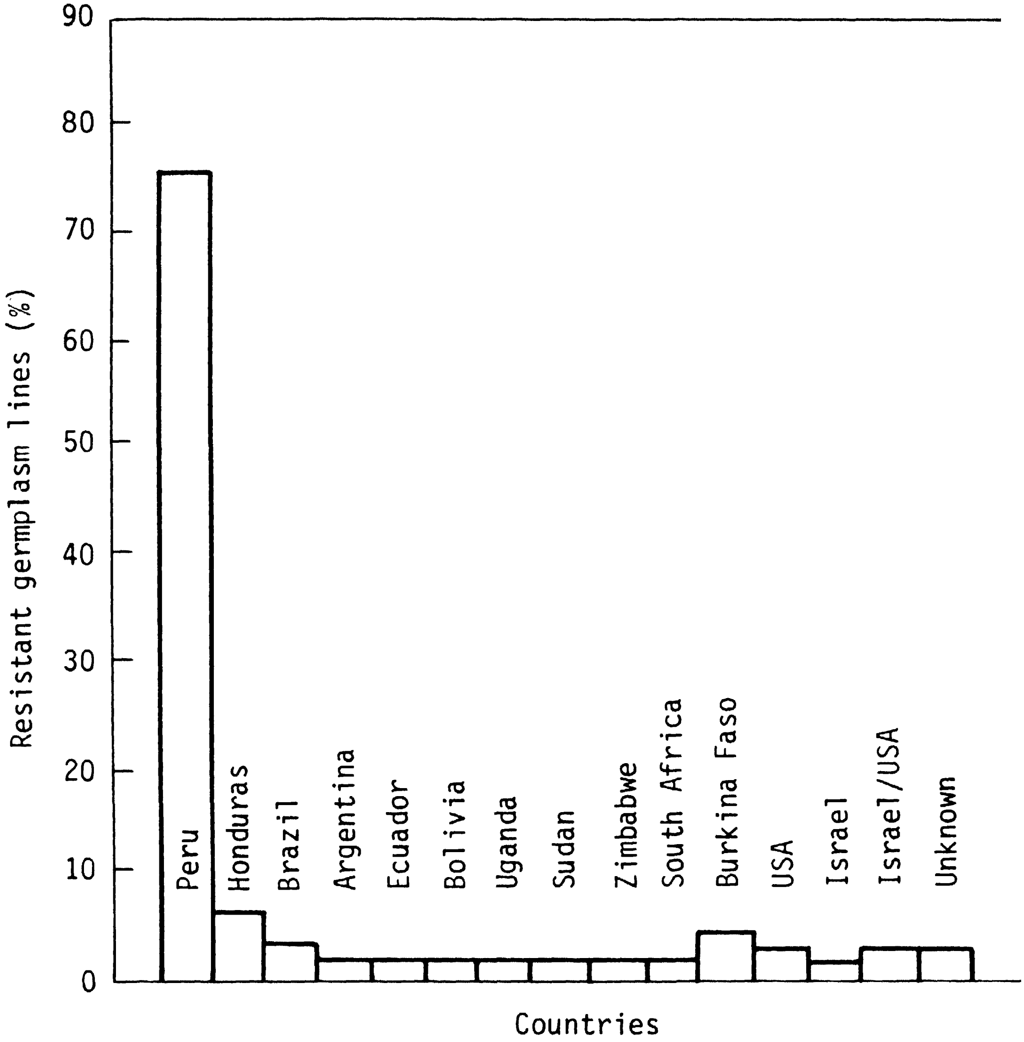

Fig. 4. Distribution of foliar-disease-resistant peanut germplasm accessions based on their origins (total of 10,000 accessions).

than Peru, and belong to var. *hypogaea*. Although we were unable to locate their exact identity/origin, it may be assumed that they were transgressed types, since generally the selection has almost always been towards *hypogaea* forms.

About 74% of the resistant lines are from Peru, while about 84% of them have some South American connection and, from the above analysis, may have originated in Peru. Of the 304 accessions from Peru at ICRISAT, 182 have been screened, and 47% are resistant to rust and/or late leaf spot diseases. Major collections in South America, including Peru, have been carried out by Drs. W. C. Gregory, A. Krapovickas, R. O. Hammons, and W. R. Langford, among others, but exact details of location and other collection data are incomplete in many cases. However, from available records (especially from collections by Winters and Clark, and by Tripp in 1974), the origin of most of the resistant types could be traced to the Tarapoto region of Peru. The assumption that peanut and the two diseases coevolved in Peru is further supported by the fact that Peru is one of the secondary centers where a predominance of primitive valencia types occur. The majority of rust and late leaf spot resistant peanuts are primitive valencia types. Such types have been under cultivation since about 2000 B.C. as evidenced by a number of archeological findings (Banks, pers. comm. 1985; Hammons 1973). This supports the view that human selection following a spontaneous mutation was largely responsible for the evolution of resistance.

Resistances to rust and late leaf spot diseases have clearly evolved in the Peruvian region. Since these diseases are commonly present in that region, we can reasonably assume that the resistance genes arose as mutations and were subjected to natural/human selection as the resistant types had advantages over the susceptible ones. Studies of association of resistances to a group of diseases would provide information concerning the evolution of adaptive gene complexes. This would, of course, need extensive examination of character association in the Peruvian peanuts.

Information on the frequency of distribution of sources of resistance to rust and late leaf spot in Peru and other regions of South America is limited, and there is no information on the reactions of the resistant genotypes to native pathogen populations. Studies must be carried out in Peru and other South American countries in natural ecosystems. Only then will it be possible to understand how the host and pathogen have evolved together.

CONCLUSIONS

Peruvian peanuts provide material for a study of evolution of resistances to rust and late leaf spot diseases. This is not such a clear cut case as that in barley (Qualset 1975), where resistance to yellow dwarf virus has not been found outside Ethiopia, the gene center of barley. However, studies on gene centers in relation to disease resistance in peanuts are of recent origin (Leppik 1971).

From careful interpretation of the available records we can say that the genes for resistance to the rust and late leaf spot pathogens are not randomly distributed (as they occur mostly in Peru), and even within Peru they occur non-randomly (in the Tarapoto region). It can also be hypothesized that the foliar-disease-resistance might have arisen as a mutation that has been subjected to natural/human selection. It is also apparent that we have only just begun to understand the evolution of the peanut, its pathogens, and its resistance to them. With the present knowledge, it is hypothesized that the host plant (*A. hypogaea*), the pathogens (*P. arachidis* and *P. personata*), and the disease resistances might have coevolved in Peru.

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