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Coffee Rust in the Americas

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With a Foreword by Richard A. Frederiksen

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FOREWORD

Coffee rust affects both large and small farmers in the coffee-producing areas of South and Central America. Even more important, it affects the foreign exchange of these countries and their potential for development.

The coffee rust symposium that produced the chapters in this book became a reality under the leadership of G. A. Zentmyer while he was chairman of the Tropical Plant Pathology Committee of the American Phytopathological Society. The suggested program was enthusiastically supported by the Society's Program Committee as a symposium topic for the 1982 annual meeting. Coffee workers representing the Americas, Europe, and Africa traveled to Salt Lake City, where many of them met for the first time. A generous grant from USAID helped to cover travel costs and other expenses for the symposium and for the publication of this volume. The Tropical Plant Pathology Committee also expresses deep appreciation to Jeanne Hale, "Secretary Exceptionale," Department of Plant Sciences, Texas A&M University, for her invaluable contributions in typing and technical editing of the initial draft.

The American Phytopathological Society is concerned with plant diseases in the tropics and continues to work toward their solution.

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DISTRIBUTION AND SPREAD OF COFFEE RUST IN LATIN AMERICA

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Coffee rust, incited by Hemileia vastatrix Berk. & Br., was first found in the western hemisphere by Medeiros (80) early in the 1970s in Brazil. The disease has since spread to 11 western hemisphere countries: six in South America (Brazil, Paraguay, Argentina, Bolivia, Peru, and Ecuador); four in Central America (Nicaragua, El Salvador, Honduras, and Guatemala); and, recently, one in North America (Mexico). The last seven detections of the rust, occurring in the past four years, were in Bolivia (1978), Peru (1979), El Salvador (late in 1979), Honduras (late in 1980), Guatemala (December 1980), and Ecuador and Mexico (summer of 1981) (Figs. 1 and 2).[1]

This chapter covers aspects of 1) the dissemination of the urediospores of H. vastatrix by wind,

[1]Since the coffee rust symposium held in 1982 in Salt Lake City, rust has been found in Colombia and in Costa Rica (1983).

This chapter is dedicated to the late distinguished Professor James G. Dickson, who greatly inspired the senior author in the study of tropical rusts.

humans, and seedlings, 2) the spread of the rust in the western hemisphere from 1970 to early 1982, and 3) the races of the pathogen now found in Latin America.

Fig. 1. Spread and distribution of H. vastatrix in South America. (Reprinted, by permission, from [128]).

Fig. 2. Spread and distribution of H. vastatrix in Central America.

DISSEMINATION OF UREDIOSPORES BY WIND, HUMANS, AND SEEDLINGS

Since coffee rust was detected in Bahia, Brazil, early in 1970, much has been learned about the means of dissemination of the urediospores of H. vastatrix. Wind played an important role in the dissemination of the rust within the coffee regions of Brazil, as the senior author observed during several study trips to that country in the 1970s. In 1972, Schieber (122) compared the diverse studies of coffee rust made during the 1960s in East Africa with the observations and studies made in Brazil, especially in the state of Sao Paulo. Martinez et al showed clearly in 1971 that urediospores of H. vastatrix were disseminated by wind as the rust moved into the state of Parana from Sao

Paulo. (His research, done in 1971, was not published until 1975 [74]). Very soon thereafter, the rust was detected also in Paraguay, following the prevailing wind currents in that region.

The invasion of Sao Paulo by the rust provided an excellent opportunity to study spread in a different way than the studies that were carried out previously in Africa (45,74). The rapid spread of the rust from Bahia to Parana within Brazil and into Paraguay and Argentina demonstrated the importance of wind in the dissemination of the disease (80). Later, Becker (5) showed that wind was also an important factor in the dissemination of the rust in East Africa. The spread of the rust within the Carazo region in Nicaragua, where it was detected in November 1976, has also been attributed to wind currents (124). Different foci within the Carazo region showed a pattern of spread according to prevailing wind currents.

The rust, of course, did not spread from Brazil to Nicaragua by wind, because of the prevailing natural geographical barriers. The situation in Nicaragua constitutes a good example of spread by humans, since we know that wind could not play a role in the introduction of the rust in the Carazo region. The same is true in El Salvador, where evidence indicates that the rust was introduced by people immigrating to that country (Table 1).

Bolivia provides a good example of spread of coffee rust on coffee seedlings. There is good evidence that rust was introduced into Beni in Bolivia by seedlings from Acre, Brazil. It is also possible that the rust may have spread from Africa to Brazil on seedlings, not necessarily coffee plants but possibly other tropical plants carrying the rust spores (121).

SPREAD OF THE RUST IN THE WESTERN HEMISPHERE

The spread of coffee rust in South America has been similar to our prediction; the rust invaded Paraguay and Argentina from Brazil, then spread to Peru and Bolivia (Table 2). However, the spread of the rust in Central America has been different than predicted. The rust was detected in December 1979 in

the eastern part of El Salvador, whereas expectations were that the western part of Costa Rica would be invaded by the rust coming from nearby Carazo (80-100 km) in Nicaragua (124). Our prediction was based on the fact that Costa Rican coffee grows close to the Nicaragua-Costa Rica border near Carazo.

Table 1. Possible factors involved in the introduction of H. vastatrix into Latin American countries

Country	Possible means of introduction
Brazil	Plants from Africa
Paraguay	Wind currents
Argentina	Wind currents
Nicaragua	Humans (migrant workers and others)
Peru	Seedlings
Bolivia	Seedlings
El Salvador	Humans
Honduras	Humans
Guatemala	Humans and wind currents
Mexico	Humans and wind currents

Table 2. Detection of coffee rust (H. vastatrix) in the Americas

Country	Date of detection
Brazil	January 1970
Paraguay	1972
Argentina	1972
Nicaragua	November 1976
Peru	January 1979
Bolivia	May 1978
El Salvador	December 1979
Honduras	Late 1980
Guatemala	December 1980
Ecuador	August 1981
Mexico	Summer 1981

The introduction and detection of the rust in Latin America in the past five years will be presented chronologically as follows: 1) situation of the rust in Nicaragua, 2) introduction into Bolivia, 3) introduction into Peru, 4) recent spread into Ecuador, 5) detection in El Salvador, 6) invasion of Honduras, 7) spread into Guatemala, and 8) spread into Mexico. The information on the spread of the rust is based on data available when this chapter was completed at the end of June 1982.

Present Situation of the Rust in Nicaragua

Nicaragua is the only country in Latin America where an eradication effort was implemented when coffee rust was discovered. The rust was first found in the Carazo region in November 1976. The comprehensive eradication program showed promising results when the data were first reported by the Organismo Internacional Regional de Sanidad Agropecuaria (OIRSA) in 1976 (97) and by Schieber (124) in 1977. A total of 2,068 foci were detected in November 1976, while only 15 were found from April 22 to June 3, 1977. By June 1977, Nicaragua had spent 35 million cordobas (US$5 million) on eradication of the rust (125).

The methods used in the attempt to eradicate coffee rust in Nicaragua were described in 1977 by Schuppener et al (129) and by Llano (70). Infected coffee trees were sprayed with an emulsion made of 4 L of paraquat, 1 kg of copper, 6.6 L of diesel fuel, a detergent, and an adhesive mixed in 208 L of water. The emulsion was applied in a 30-m radius from the affected plant or group of plants. Three days later the trees with dry foliage were pruned to 1 ft in height. An area of 50-60 m from the infection center was sprayed with a systemic fungicide (pyracarbolid [Sicarol]) mixed with copper to make a "protection zone" around the 30-m radius.

The eradication effort continued until the civil war in Nicaragua stopped the program. In 1977, the number of foci was 30,000; by 1978, while spraying and pruning continued in the Carazo region, there

were only 11,000 foci. In 1979 before the civil war, the number of foci was estimated at 2,500. However, the program was interrupted by the unrest in the area, and by August 1979 rust in the Carazo region had increased 400-1,000%. Ninety percent of the spraying equipment was destroyed, as was reported in a meeting of the Ministers of Agriculture of Central America held in El Zamorano, Honduras, in August 1979.

In the senior author's opinion, the temporary success of the eradication program in Nicaragua was due to the avoidance of fire in the technology used. Fire often produces wind turbulence, which can increase the dissemination of rust spores that escape heat. A system that we have called "the wet system," using a weed killer instead of fire, was successful.

The confinement of the rust in the Carazo region through the eradication program saved time and money in the rest of the Central American countries that grow coffee and were still free of rust.

It is of interest that rust did not spread to the Matagalpa region of Nicaragua until early in 1982. Because the rust was spreading very rapidly in northern Central America and Mexico, the slow spread within Nicaragua is puzzling.

Introduction of the Rust into Bolivia

Coffee rust was found in Bolivia in May 1979 in the region of Alto Beni, located northwest of the capital of La Paz. In 1975, Schieber (123) commented on the danger of the discovery of coffee rust in the isolated region of Acre in Brazil (Fig. 1). It is believed that the rust was introduced into Beni, Bolivia from Acre on coffee seedlings and was spread from this region to Alto Beni by humans. These regions grow coffee known as Typica, which is susceptible to rust.

When rust was detected in Bolivia, one of the first steps taken was the institution of quarantine measures to prevent the disease from spreading from the Alto Beni region to the "Las Yungas" region, where coffee and other tropical crops grow. Spraying with copper fungicides was started in some areas; however,

the country was not prepared to control the rust immediately, and no eradication program could then be implemented. One positive step that had been undertaken beforehand by the University of Florida and the Agency for International Development (AID) was the introduction of some resistant varieties into Bolivia for further tests. Some seed of the rust-resistant varieties Catimor, Kaffa, and Agaro were introduced before the rust spread to Bolivia. The Andean Pact has provided some assistance to the Ministry of Agriculture of Bolivia in relation to the coffee rust problem.

Detection of Coffee Rust in Peru

Early in 1979 coffee rust was detected in a coffee-growing region of Peru, the province of Satipo, in the Department of Junin (Fig. 1). The region was immediately surveyed, and rust was found along the highway that connects Satipo with Maxamari and Satipo Concepcion. Concepcion is located northwest of Huancayo, an important city in the Andes. By the time the rust was detected, it had already spread to approximately 1,200 ha of coffee plantings. How the rust was introduced into Peru is not known; however, one possible means is on seedlings, as in Bolivia (121).

Measures were taken immediately to prevent the rust from spreading to the important coffee region of Chanchamayo. The emergency program included strict quarantine measures (Ing. Cesar Wandemberg, Andean Pact, personal communication). Even with this emergency program, Peru was aware that it could not eradicate the rust, in contrast to the effort made in Nicaragua to eradicate the rust in the Carazo region.

By the spring of 1980 the situation in Peru had changed. Rust was still found in the region of Satipo; however, today it also occurs in the region of Chanchamayo in the central part of the country. More recently, the Cuzco region (the valley of Convención and the river of Apurimac areas), the Department of San Martin (in the areas of Tarapoto and Lamas), and the Tingo Maria region were also

invaded by the rust. Rust has also been reported in a region near Ecuador, in the Department of Amazonas. This last spread constitutes a potential threat to Ecuador.

Spread into Ecuador

Early in 1980 coffee rust was detected 60 km from the town of Zumba, which is located in the eastern Amazon region of Ecuador (Fig. 1). Quarantine measures were immediately established at the Ecuador-Peru borders. By August 1981 rust had spread into Ecuador, probably by windborne spores from Peru.

Detection of the Rust in El Salvador

We had predicted that the rust would first spread from Nicaragua to neighboring Costa Rica because of its proximity, but the rust was next detected in El Salvador. El Salvador, Guatemala, and Costa Rica are the three major coffee-producing countries in Central America.

Rust was first reported in El Salvador in December 1979 by the owner of a coffee planting in the Municipio of Santiago Maria, Department of Uzulután, in the eastern part of the country. The Instituto Salvadoreño de Investigaciones del Café (ISIC), one of the oldest institutions working on coffee problems in Central America, then surveyed the region and determined that the rust had already spread to approximately 7,000 ha. It is significant that the rust was first found near the Pan-American Highway, with small outbreaks (foci) scattered between the important eastern city of Uzulutan and El Triunfo.

One of the factors responsible for this recent outbreak in El Salvador may have been the movement of people in that area, especially the intensification of movement because of political factors. It is very possible that the rust was brought in by people moving from Nicaragua to El Salvador. Some of the immigrants started to work in coffee plantations. There is no question that in this case wind did not play an important part, because as Schieber (123) pointed out

in 1977, the wind currents in the Carazo region were from the north toward the Pacific Ocean.

OIRSA, headquartered in El Salvador, together with the government of El Salvador, immediately established several quarantine posts to try to confine the rust to the region north of Uzulutan. One measure was the spraying of cars passing on the Pan-American Highway and on the highway along the Pacific coast. When the rust was discovered in eastern El Salvador, ISIC started research programs that included the study of the disease cycle under the ecological conditions of that area and also the identification of races of the pathogen, as will be discussed later in this chapter. It should be emphasized that El Salvador has been one of the most advanced countries in the area in introducing resistant coffee hybrids, including the famous Hibrido de Timor and crosses such as the promising Catimor (124).

Late in September 1980 the rust was found to have spread to the central and western regions of El Salvador. This situation naturally alarmed neighboring Guatemala. By the end of the month, five additional foci had been detected in central and western El Salvador, three in Sacatecoluca and two in Izalco in the Departmento of Sonsonate. Later the rust was reported in the Departmento of Ahuachapan bordering Guatemala.

Invasion of Honduras

Honduras is located to the north of El Salvador. Coffee rust was discovered in Honduras in December 1980 in the county of Marcala, La Paz Province (Fig. 2). Heavy outbreaks were later reported from Santa Barbara, Cortes, and Lempira provinces. Santa Barbara alone produces 30% of the coffee in Honduras. The Instituto Hondureno del Cafe (IHCAFE) has varietal trials in Santa Barbara and also a collection of resistant hybrids, including Catimor (126).

Spread of the Rust into Guatemala

As soon as the news came that coffee rust had been found in neighboring El Salvador, Guatemala reinforced quarantine measures at its borders and established a "security zone" where surveys were conducted to detect the rust immediately if present. No rust was found in Guatemala during the fall of 1980. Early in 1980, as a preventive measure, the Asociación Nacional del Café (ANACAFE) and the Ministry of Agriculture began a spraying program at the Guatemala-El Salvador and Guatemala-Honduras borders. Copper sprays were used on healthy coffee plants.

Even with these measures implemented, on December 10 a coffee farmer reported to ANACAFE the presence of coffee rust in the area of Tierra Blanca, Municipio of Chiquimulilla in the Department of Santa Rosa (Fig. 2) (127). This first outbreak in Guatemala mobilized the Ministry of Agriculture, the recently established Mexico-Guatemala joint commission for the prevention and control of coffee rust, and ANACAFE to eastern Guatemala to attempt to eradicate this disease, which was found in an area of about 5 manzanas (3.5 ha).

By December 20 other foci had been detected in eastern Guatemala, one in El Molino, another in Oratorio in the Department of Santa Rosa, and a third in the vicinity of Atescatempa in Jutiapa Department. All these foci are located, as was expected, near El Salvador in eastern Guatemala. On December 23 another outbreak of rust was detected in northeastern Guatemala, in El Chispal and Champona, Los Amates, in the Department of Izabal. Since this locality is close to Honduras, it is possible that the rust there crossed the Guatemala-Honduras border.

On the last day of 1980, the rust was detected in the Municipio of San Francisco Zapotitlán in the important Pacific coast coffee region of Guatemala. The rust was found on five coffee farms, including two large plantations located in the Department of Suchitepequez in southwestern Guatemala. This outbreak in the Pacific coast has serious consequences, because the solid coffee belt in this region connects

with the coffee-growing region in Chiapas, Mexico. This outbreak, in our opinion, ended any hope of eradicating the rust in Guatemala.

A point of interest is that the invasion by and rapid spread of the rust in Guatemala happened during the dry season. Even under apparently unfavorable climatic conditions (Director of the Dirección General de Sanidad Vegetal, Mexico City, personal communication), the rust continued spreading rapidly, heading toward the Department of Retalhuleu and Quetzaltenango early in 1981 (January and February). In 1970, Schieber (121) had observed that rust was severe in dry regions of Brazil and Africa, even though the litera- ture points out that the pathogen *H. vastatrix* needs high humidity to spread and develop.

The rapid spread of the rust in El Salvador and recently in Guatemala is similar to the rapid spread observed in Brazil (122,126). As in Brazil, people and wind currents have played important roles in the spread of the rust in northern Central America, which is now also threatening Mexico, with its important coffee regions in Chiapas.

Spread of the Rust into Mexico

During the summer of 1981 the state of Chiapas in southern Mexico, the country's most important coffee-producing state, was invaded by the rust (Director of the Dirección General de Sanidad Vegetal, Mexico City, personal communication). Rust was found on a few plants in Tapachula County near the Guatemalan border.

By the summer of 1982 the rust had spread through most of the state of Chiapas and into the region of Soconusco. It has not yet been found in the coffee-growing state of Veracruz.

In Chiapas coffee rust was soon found in remote areas in the mountains (Nuevo Huixtan - Margaritas in northern Chiapas), even though the wind currents were not in that direction. Urediospores were most likely carried to the very remote areas of this part of Mexico by coffee pickers migrating from one region to another.

RACES OF H. VASTATRIX IN LATIN AMERICA

The first coffee rust outbreak in Bahia, Brazil, in 1970 was identified as race II, which is now the most widespread race in Latin America. It is present in all of the Central and South American countries that have been invaded by the rust (Table 3). Five other races (I, III, XV, XVII, and XXIV) are now known from Latin America. All six races are found in Brazil. Race I was recently identified in Central America by ISIC research workers in El Salvador (49). Research is needed in Nicaragua to determine if race I is also present in that country. Significantly, race I is also present in Brazil (122).

In 1975 Schieber (123) stated, "It is of prime importance to follow the appearance of new rust races in South America, because breeding programs must focus on new trends in the production of resistant varieties." With the spread of the rust through Central America and into Mexico, this aspect of rust

Table 3. Races of H. vastatrix in the Western Hemisphere

Country	Races
South America	
Brazil	II, XV, III, I, XVII, XXIV[a]
Paraguay	II
Argentina	II
Bolivia	II
Peru	II
Central America	
Nicaragua	II
El Salvador	II, I[b]
Guatemala	II
Honduras	II

[a]Identified by Galvez et al (49).
[b]Detected in the Instituto Biologico greenhouse in Sao Paulo, Brazil, in 1980 (44).

research is certainly of prime importance in the newly invaded regions.

CONCLUSION

In this chapter we have attempted to summarize and update the current situation on this serious threat to all coffee-producing countries in Latin America. The explosive spread of coffee rust in northern Central America in the past two years creates serious agricultural and economic problems for El Salvador, Guatemala, and Mexico. The danger is highlighted in the following statement made by Wellman and Echandi (142) in 1980: "In Latin American coffee countries, in which only arabica coffee is grown, there are at present hundreds of millions of trees wholly susceptible to rust." Concentrated and unified efforts to use all possible control measures are of utmost urgency.

The rapid spread of the rust in South and Central America in one decade has demonstrated the importance of humans in the spread, as well as wind currents in certain cases. The eradication attempt in Carazo, Nicaragua, was a notable success, in our opinion, because the rust was confined to a relatively small area for several years, and consequently spread to the rest of Central America was retarded.

A puzzling aspect of the epidemiology of rust spread in some locations in Central and South America is the obvious rapid development under very dry conditions during the dry season; this phenomenon has been observed, for example, in Minas Gerais and Campinas, Sao Paulo, in Brazil, and in certain areas of Central America.

LEAF RUST IN AFRICA AND WHAT IT MEANS TO AMERICAN PROGRAMS

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Coffea is predominantly an African genus and is indigenous in three important commercial varieties: C. arabica L. (90% of the world's coffee), C. canephora (9%), and C. liberica (1%). C. arabica (arabica coffee) is grown at moderately high altitudes (2,000 m) near the equator but may also be grown near sea level at the limits of the tropics. C. canephora (robusta coffee) is grown at lower altitudes mostly in Africa and Asia. C. liberica (liberia coffee), also a low-altitude coffee, is grown in small amounts in West Africa and Southeast Asia (46).

Arabica coffee requires very fertile, deep, and free-draining soils with a minimum rainfall of 1,200-1,400 mm per annum. In Kenya most coffee is produced in the high cultural areas on soils derived from volcanic lava or ash, on the slopes of the Aberdares and Mount Kenya at altitudes between 1,400 and 2,300 m where rainfall is adequate and temperatures are within the optimum range.

IMPORTANCE OF THE COFFEE INDUSTRY IN KENYA

During 1977-1981, arabica coffee was the leading foreign exchange earner in Kenya, with an average annual value of US$230 million. The area under coffee cultivation by smallholders (a majority of coffee growers have less than 0.5 ha of coffee) tripled from

28,000 ha in 1963 to an estimated 90,000 ha in 1980, while the area under coffee cultivation in large estates fell slightly over the same period from 34,000 ha to about 30,000 ha. Production gradually increased from 34,000 t in 1963 to 99,000 t in 1981. The contribution of the small coffee holders to the total coffee crop increased from 26% in 1963 to more than 65% in 1981, mainly as a result of an increase in the area planted with coffee. Production per hectare in the smallholder coffee sector remained at 500-800 kg, well below the mean of 1.0-1.5 t for the large estates (26).

There are about 265,000 small-scale coffee farmers, who are organized into cooperative societies with their own coffee-processing factories; large coffee estates number about 740. It is estimated that more than 10% of the 16 million people in Kenya depend on coffee for their livelihood (137).

COFFEE LEAF RUST

The coffee leaf rust fungus belongs to the order Uredinales, family Pucciniaceae, and genus Hemileia. Altogether about 40 species of Hemileia are known. They attack 11 families of flowering plants. Sixteen of the 40 species occur on the Rubiaceae family, and two species, H. vastatrix and H. coffeicola, attack the genus Coffea (83).

H. vastatrix is an obligate parasite on the genus Coffea. Infection results in the formation of pale spots up to 15 mm in diameter on the lower surfaces of the leaves, often with slight chlorosis of the upper side. Urediospores are produced from hyphae that protrude through the stomata of these lesions, and eventually the surface becomes encrusted with these spore masses, forming the characteristic bright orange pustules. There is only one report of the occurrence of teleutospores in East Africa and this was on dried herbarium material. The presence of even one pustule will cause premature abscission of the leaf (95).

Leaf rust (H. vastatrix) affecting wild coffee was discovered in 1861 in the region of Lake Victoria in

Kenya. The disease was later reported from coffee-growing areas in different parts of the world (Table 1). H. vastatrix has been present on C. arabica in Kenya since the turn of the century (33) but caused only locally severe losses until the 1950s, when the disease became severe in the coffee region below 1,656 m (122). Serious leaf rust infection (over 40%) was recently recorded, however, at the high altitude of 1,935 m. The economic importance of coffee rust, therefore, is increasing in Kenya.

EPIDEMIOLOGY OF LEAF RUST

Leaf rust has been studied in Kenya for more than 60 years; these studies were reviewed in 1970 by Nutman and Roberts (95). Until 1972, workers in East Africa assumed that the urediospores were dispersed mainly by rainwater (17,22,94). However, studies conducted at the Coffee Research Station, Ruiru, Kenya during 1973-1974 showed that spore release and dispersal occurred mainly by wind. Other dispersal agents such as rain splash, insects, plant material, and people may sometimes take part in the release and dispersal of spores but are of minor importance (6).

Table 1. First reports of coffee leaf rust in Africa

Year	Location	Year	Location
1861	Lake Victoria (Kenya)	1918	Central Africa, Zaire
		1940	Mozambique
1880	Mauritius	1946	Zanzibar
1883	Tanzania	1952	Ivory Coast, Dahomey
1886	Madagascar	1953	Sudan
1894	Uganda	1954	Togoland
1904	South Africa	1955	Liberia
1913	Kenya-Cameroons	1962	Guinea, Nigeria
1916	Zimbabwe	1966	Angola

[a]Data from Monaco (83).

DEVELOPMENT OF CONTROL MEASURES

Two factors besides rainfall and temperature strongly influence the severity of rust epidemics, namely the amount of primary inoculum and the degree of canopy foliation (18). In Kenya, leaf rust infection is normally at its lowest point before the "short rains" in October-November, and it has been verified that there is a close relationship between the amount of infection at this time and the severity of subsequent outbreaks (51). For this reason, control of leaf rust is particularly important at the time of the short rains--one well-timed spray can reduce disease to a negligible proportion for many months. When sprays during the short rains are augmented by sprays at the beginning of the "long rains" (March-May), excellent control can be achieved throughout the year (18) (Fig. 1). However, when sprays are omitted during the long rains, disease incidence during May-October often exceeds that noted in unsprayed coffee. As a result, the amount of inoculum available for the next short-rains period is increased (Fig. 2). This can be attributed mainly to the changed pattern of foliation brought about by spraying: because of their "tonic effects" and rust control, copper sprays during the short rains result in more heavily foliated trees on which more infections can develop rapidly (51) (Fig. 3).

Since 1978, attempts have been made to develop a flexible anti-rust spray program based on rainfall patterns rather than on the currently recommended fixed calendar schedule of spraying in October, November, February, March, and May (Fig. 4). Data collected from field trials conducted during 1979-1980 showed that the plots that received sprays of cuprous oxide (Perenox 50% WP, 7.7 kg/ha) after every 50 mm of rainfall (with a minimum interval of one week between the sprays) had significantly less leaf rust ($\underline{P}$ = 0.05) than plots that received sprays timed according to the fixed calendar schedule (Fig. 5). Plots that were sprayed according to the flexible schedule also had high yields (Table 2). The flexible anti-rust spray program is being evaluated in

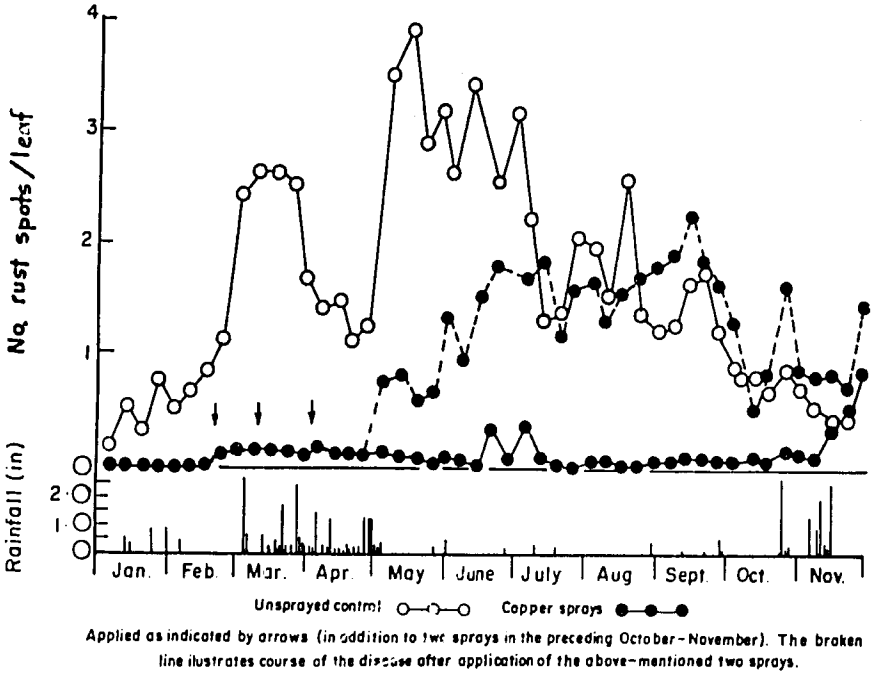

Fig. 1. Rainfall and incidence of coffee rust in the East Rift districts of Kenya. (Reprinted, by permission, from [18])

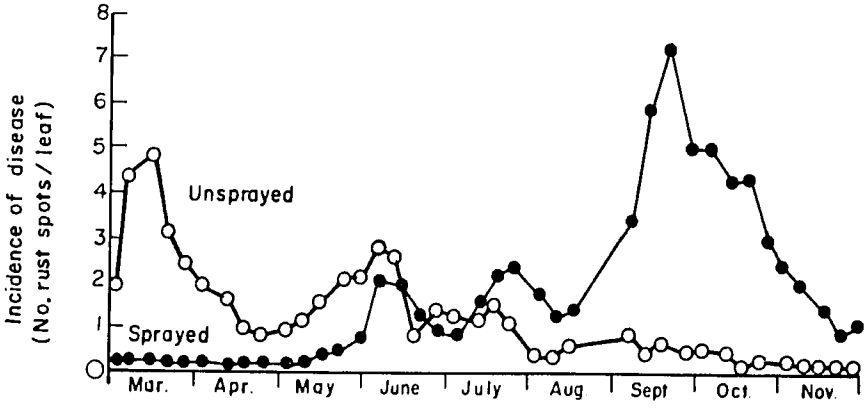

Fig. 2. Incidence of rust on unsprayed coffee trees and on trees sprayed the previous November. (Reprinted, by permission, from [18])

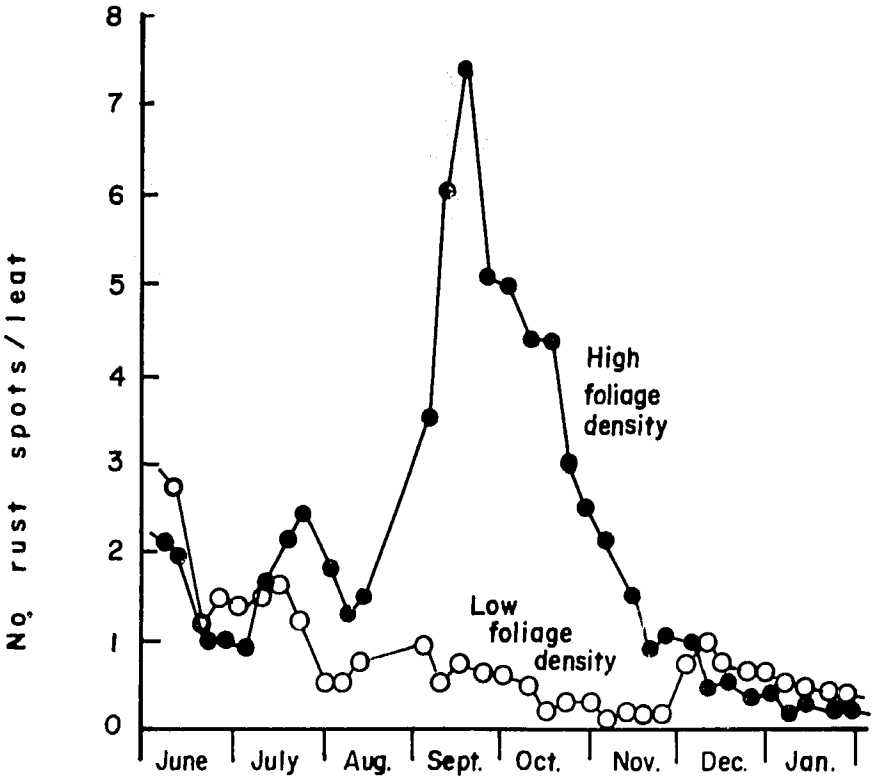

Fig. 3. Course of leaf rust development on coffee trees with high and low foliage density. (Reprinted, by permission, from [18])

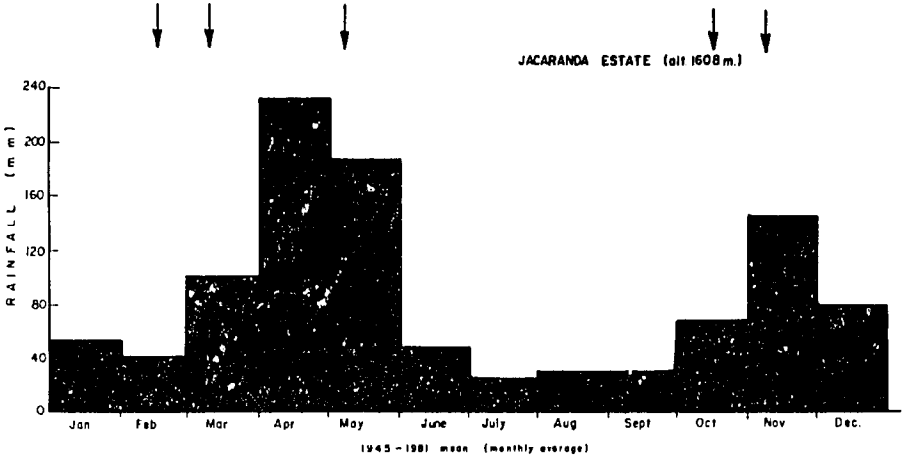

Fig. 4. Recommended antirust spray program, East Rift districts, Kenya.

different coffee-growing areas of Kenya before it can be recommended to coffee farmers. It is hoped that in dry years, the flexible spray program will reduce the number of sprays needed to achieve the same degree of control of leaf rust (63).

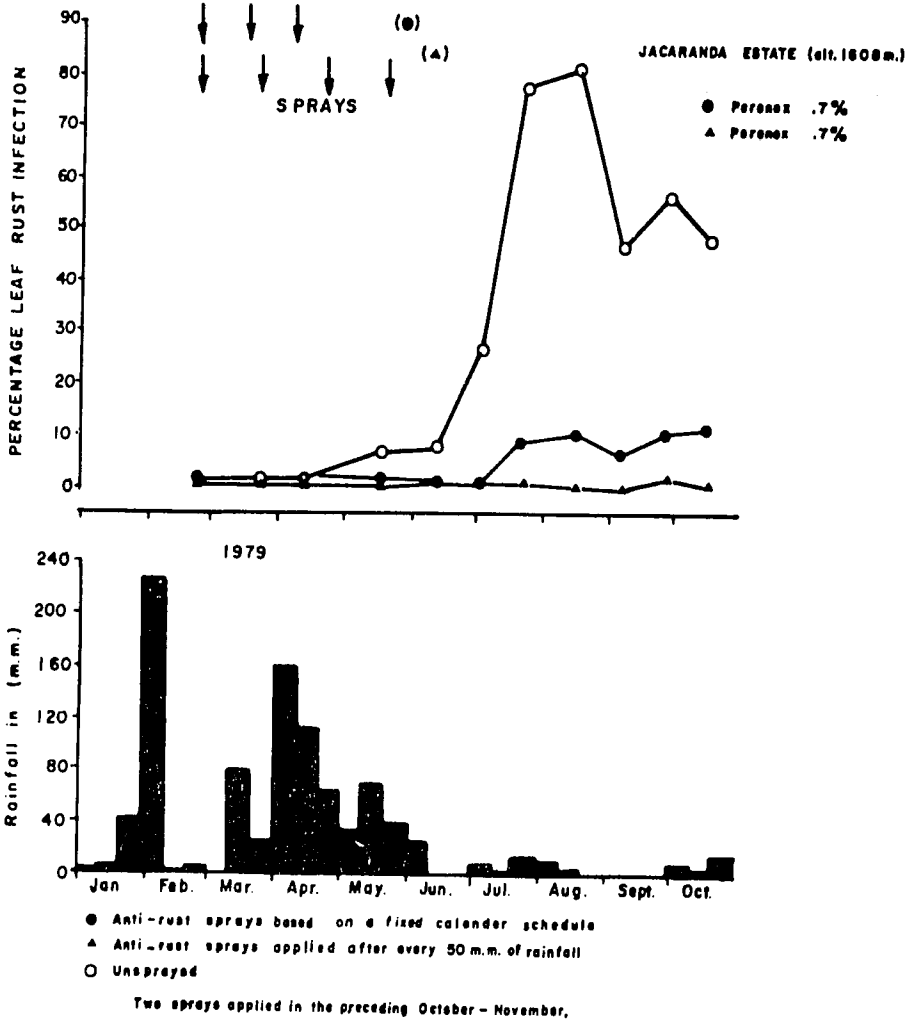

Fig. 5. The efficacy of flexible spray program against leaf rust in CRS Plot 8 in 1979.

Table 2. The efficacy of spray programs to control leaf rust in Coffee Research Station plot 8 in 1979

Treatment	Rate[a] (kg/ha)	No. of sprays applied	Peak infection, 8/15/79 (%)	Clean coffee yield (kg/ha)[b]
Standard fixed calendar[c]	7.7	5	11.7	814
Flexible schedule[d]	7.7	6	0.6	1,107
Unsprayed (control)	--	--	81.9	728

[a]Perenox 50% WP.
[b]1,330 trees per hectare.
[c]Sprays in October, November, February, March, and May.
[d]Sprays applied after every 50 mm of rainfall.

FUNGICIDES RECOMMENDED FOR LEAF RUST CONTROL IN KENYA

Fifty-Percent Copper Formulations

Leaf rust in Kenya has been controlled for several decades by the use of 50% copper formulations (Table 3). The fungicide should be applied three weeks before the onset of the short rains (October-November), and if the rains have not started within three weeks of the application, a second pre-rain spray is necessary. One or two more sprays are applied just before the onset of the long rains (March-May). If rust is detected in April or May, a final spray of copper is applied to prevent high levels of infection during July.

Table 3. Fungicides for coffee leaf rust control

Common name	Proprietary names and formulation	Rate (kg/ha)
	50% Copper Formulations	
Cuprous oxide (Red copper)	Copper-Sandoz MZ 50% WP	3.8
	Copper Nordox 50% WP	3.8
Cupric hydroxide (Blue copper)	Kocide 101 50% WP	3.8
Cupric chloride (Green copper)	Cobox 50% WP	7.0
	Vitigran Conc. 50% WP	7.0
	Recop 50% WP	7.0
	Cupravit 50% WP	7.0
	Pereclor 50% WP	7.0
	Other Fungicides	
Dithianon	Delan 75% WP	3.3
Pyracarbolid	Sicarol 15% OD	4.0[a]
Triadimefon	Bayleton 25% WP	2.0[b]
Fentin hydroxide	Du-Ter Extra 47.5% WP	2.75

[a]L/ha.
[b]Apply Bayleton 25% WP sprays only after the level of leaf rust infection in the field is approximately 20%.

The 50% copper formulations, particularly the cuprous oxides (Copper-Sandoz MZ and Copper Nordox) and cupric hydroxide (Kocide 101), have been found effective against leaf rust in field trials at a reduced rate of 3.8 kg/ha, compared to previously recommended rates of 7.0 kg/ha (63) (Fig. 6).

Fentin Hydroxide

In 1972, fentin hydroxide (Du-Ter Extra 47.5%WP) was recommended for leaf rust control. This product

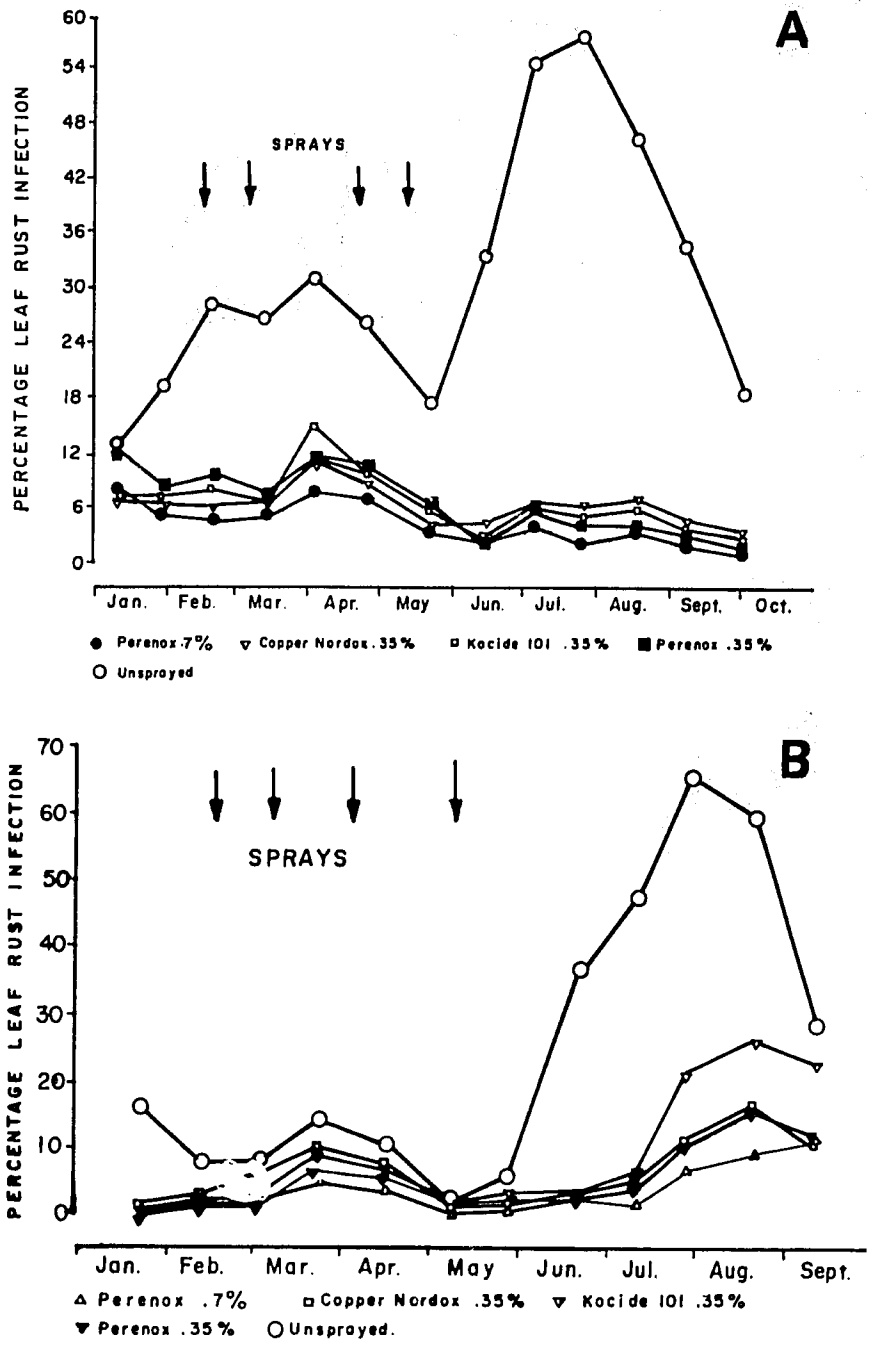

Fig. 6. The efficacy of reduced rates of application of Perenox, Copper Nordox, and Kocide 101 against leaf rust in Azania Trial I during 1979 (A) and 1980 (B).

gives adequate control of leaf rust at 2.7 kg/ha but is more effective as a repellent for the giant looper (138). When this pest is present, fentin hydroxide may be substituted for the copper spray in the program.

Pyracarbolid

Pyracarbolid (Sicarol 15% O.D.) was recommended for leaf rust control in 1974 and was found to be as effective as the proprietary copper formulations (87). Pyracarbolid should be applied at 4.0 L/ha three weeks before the onset of the short rains and long rains and three weeks after these rain periods have started. Pyracarbolid accelerates the abscission of infected leaves and inhibits further lesion development and disease spread in the plantings.

Triadimefon

Triadimefon (Bayleton 25% WP) was recommended for the control of leaf rust in 1978. Bayleton 25% WP at 2.0 kg/ha gives excellent control (Figs. 7-9) compared to copper or fentin hydroxide (61-64).

Plots treated with five or six sprays of Bayleton (2 kg/ha) in one season gave yields significantly lower than unsprayed control plots (Table 4). Further trials with Bayleton confirmed that the yield loss on these sprayed plots was mainly due to the stimulation of coffee berry disease (CBD) in the trials (61,62). Further timing trials with Bayleton 25% WP showed that if the product was applied after 20% leaf rust levels were recorded in the field (and if not more than two sprays of Bayleton were applied in a season), the final yield was not affected significantly (63).

In Kenya, at the medium-altitude coffee-growing areas (1,562-1,700 m), CBD (Colletotrichum coffeanum) is also a major problem besides leaf rust, and any anti-rust fungicide that would interact with or stimulate CBD in the field would cause serious crop loss. Therefore, systemic fungicides like triadimefon, pyracarbolid, and oxycarboxin can be freely used in Latin America for controlling leaf rust under

Table 4. Yield and peak leaf rust infection in coffee plots sprayed with recommended fungicides in Thika River Trial I, 1979-1980

Treatment	Rate of Application (kg/ha)[a]	Peak leaf rust infection (%)[b]		Clean coffee yield (kg/ha)[a]	
		8/3/79	6/27/80	1979	1980
Perenox 50% WP	7.7	3.0 (9.8)	0.1 (2.1)	1,956	1,620
Bayleton 25% WP	2.2	0.0 (1.4)	0.0 (1.4)	1,103	781
Du-Ter Extra 47.5% WP	2.7	8.8 (17.0)	0.9 (5.1)	1,771	1,200
Unsprayed (control)	--	66.9 (55.1)	15.5 (23.0)	1,669	1,039
LSD (P = 0.05)	--	-- 6.46	-- 3.44	218.66	224.29
CV	--	-- 27.88%	-- 35.19%	9.14%	13.43%

[a]1 ha = 1,330 trees.
[b]Figures in parentheses are transformed percentages (arcsin of the square root of the percentage.

severe epidemic conditions without adverse effect on the yield, as CBD is not yet present.

SPRAY APPLICATION

In the case of both manually operated knapsack sprayers and tractor-drawn or -mounted sprayers, the pressure should be adjusted from 1.1-2.8 kg/cm^2

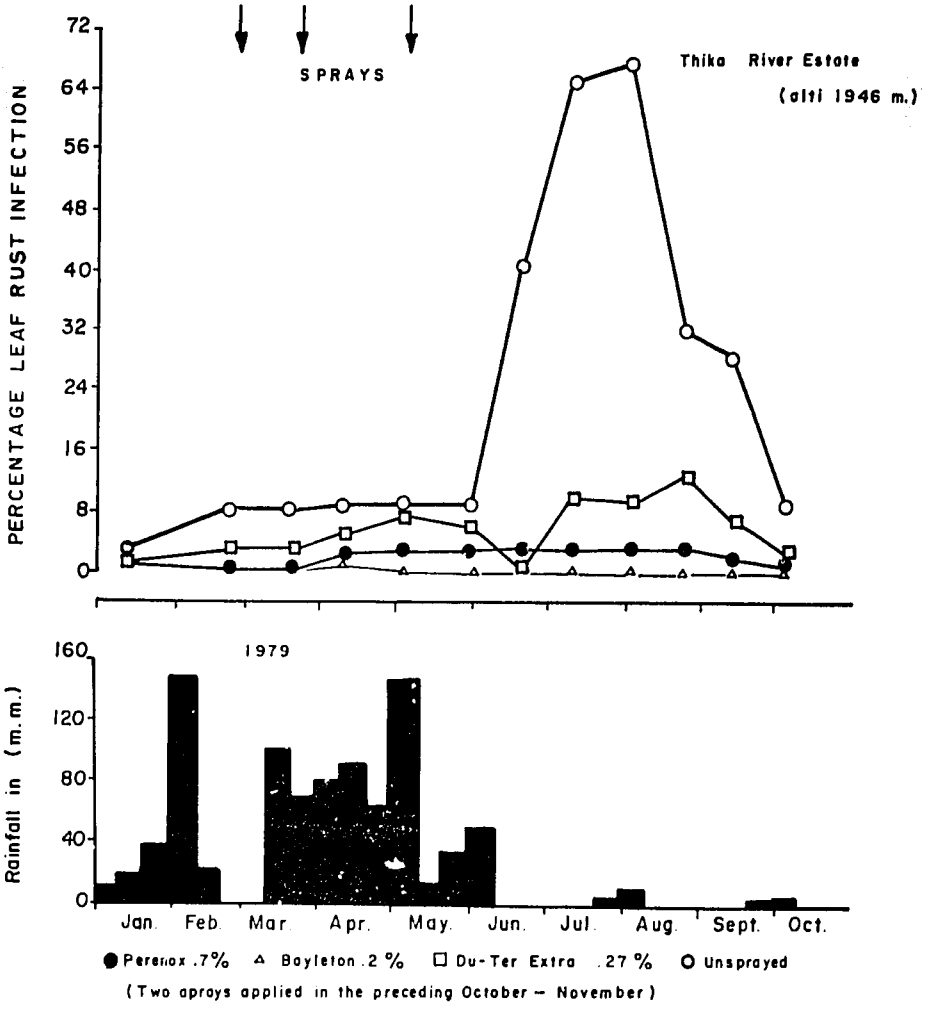

Fig. 7. The efficacy of recommended fungicides against leaf rust in Thika River Trial I in 1979.

(20-40 lb/in.^{2}) per nozzle in order to achieve effective spray mist for good control. If coffee is planted 2.74 m X 2.74 m (1,320 trees per hectare), variation in spray volumes of 670-1,345 L/ha does not affect the degree of disease control (141).

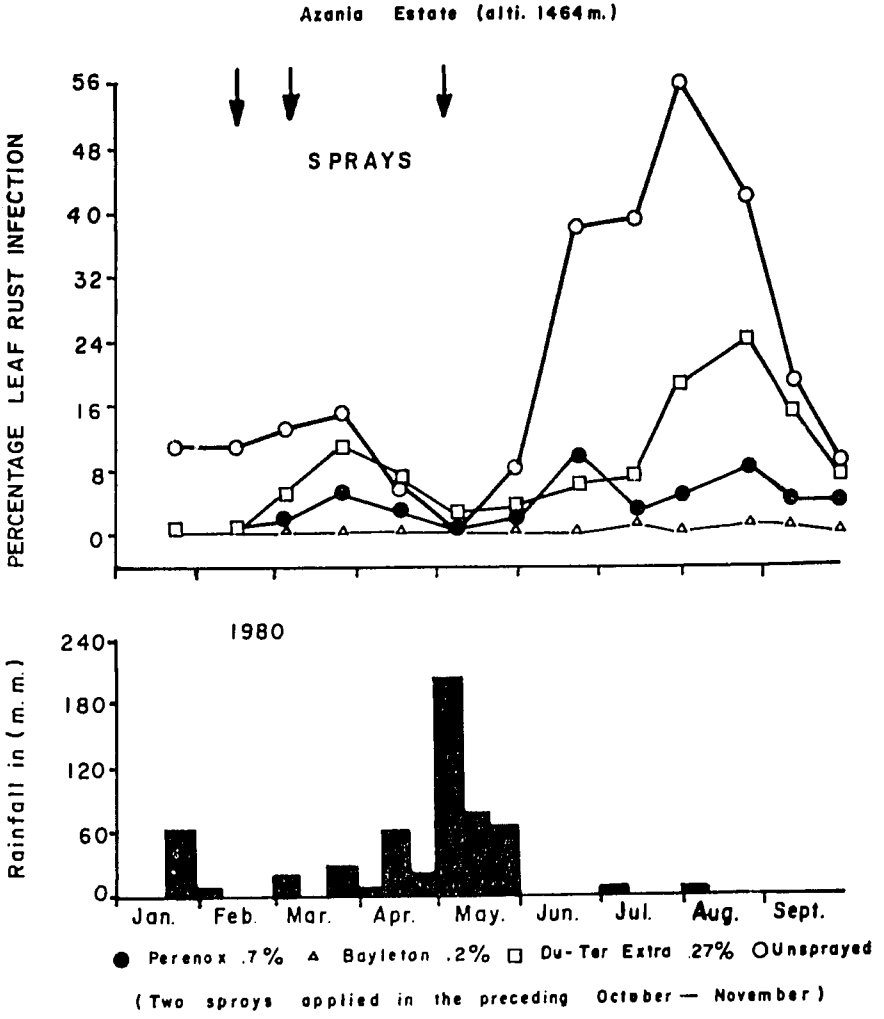

Fig. 8. The efficacy of recommended fungicides against leaf rust in Thika River Trial III in 1980.

EFFECT ON YIELD

Coffee trees demand a high carbohydrate supply for the successful maturation of crop, which utilizes not only the current production but also draws heavily on reserves. For this reason the defoliation caused by leaf rust does have serious consequences (95).

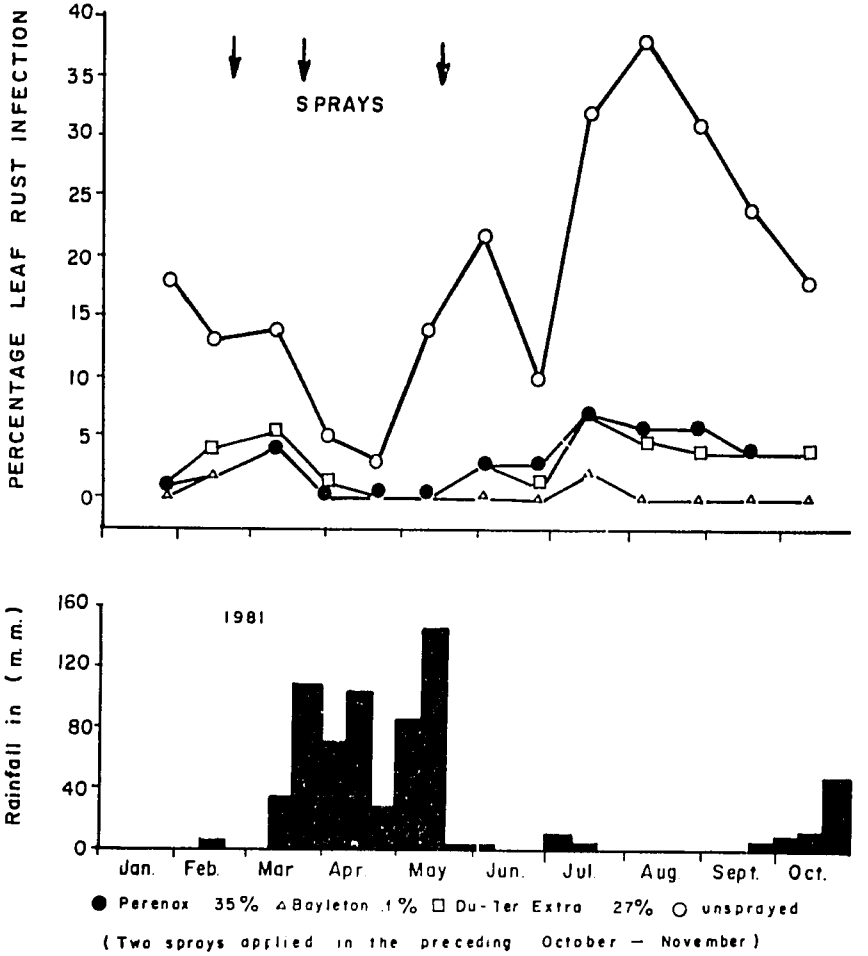

Fig. 9. The efficacy of recommended fungicides against leaf rust in Azania Trial I in 1981.

H. vastatrix attacking C. arabica was first reported in Ceylon in 1868. Within five years from its first report, the disease had spread all over the island. Productivity was reduced from 450 to 200 kg/ha. Consequently, the coffee plantations were abandoned and soon replaced by tea. In Uganda, an estimated loss of 30% has been reported, whereas the Philippine coffee industry was abandoned a few years after inoculation of rust in 1889 (83).

In Kenya, we find it very difficult to determine crop loss precisely, since the most serious disease of C. arabica in Kenya is CBD. In the absence of chemical control measures, the crop loss due to CBD could be 70% or more (52). Both CBD and leaf rust attack the same plant; therefore, to discriminate the crop loss due to leaf rust alone is not easy, but we are now trying to develop methods to look into this aspect.

In brief, newly developed antirust fungicides will require a careful field evaluation not only against leaf rust but also against other diseases, if any, at the same time making sure that fungicides applied to control leaf rust do not interact or stimulate the other diseases to cause any possible crop loss.

COST OF PRODUCING ONE TON OF CLEAN COFFEE IN KENYA

In Kenya, since 1979, the country's coffee earnings have fallen. The coffee growers have suffered a loss both net and absolute at the time when capital is of even greater importance to the industry. Since coffee prices are impossible to predict, the Kenyan grower has to strive to increase yields with higher inputs and more efficient growing methods to cover overhead, which is always rising due to inflation. Due to higher prices of chemicals, fertilizers, and fuels, the cost of farm inputs consumes the farmer's return. The cost of producing coffee these days varies from 650 to 870 Kenyan pounds (approximately $1,215-$1,626 in U.S. dollars) per ton, assuming a production range of between 1 and 1.5 t per hectare (Table 5) (92).

Table 5. Trends in coffee production costs, 1976-1980

Cost component (Kenyan pounds/t)	Year 76-77	77-78	78-79	79-80
Coffee Management Company "A"				
Field costs	335	403	350	400
Crop costs	137	146	147	217
Overhead	148	193	268	213
Interest	37	45	48	49
Total	657	787	853	879
Coffee Management Company "B"				
Field costs	115	281	260	258
Crop costs	116	136	154	228
Overhead	145	175	142	124
Depreciation	30	46	47	42
Total	406	638	603	652
Rukera Research Development Farm				
Field costs	172	195	372	NA
Crop costs	150	170	264	NA
Overhead	80	104	211	NA
Interest	25	28	51	NA
Total	427	497	898	NA
Rukera Levels of Management Trial[a]				
Total variable costs[b]	381	207	558	NA
Fixed costs	128	126	248	NA
Total	509	333	806	NA

[a]Average cost for the four levels of management A, B, C, and D.
[b]Includes both crop and field costs.

RUST-RESISTANT VARIETIES

Six physiologic races of rust fungus are known to cause damage in Kenya (115). These races are I, II, VII, XV, XX, and XIV. Of these, race II occurs throughout the main coffee-growing areas of Kenya, whereas race I is favored by low altitudes and warmer and more humid conditions. Coffee varieties such as K7, SL-6, and KP 532 have immunity to race II but are susceptible to race I. K7 appears to show a considerable resistance to leaf rust and has proved valuable where other varieties are attacked by rust. The plant breeding program started in 1971 has now reached the final stage. Catimor is being crossed to a locally produced resistant hybrid in order to get a hybrid plant that will be resistant to both CBD and leaf rust (138). It is hoped that the hybrid coffee seeds will be issued to the growers in 1986 (Fig. 10). Kenya really needs a compact type of resistant plant so that it could be planted at high density. Coffee-growing areas in Kenya are limited; therefore, the future of the coffee industry depends upon a resistant plant suitable for high-density planting.

CULTURAL MEASURES AND LEAF RUST CONTROL

In addition to fungicidal spraying, several control measures can be taken to reduce infection and lessen the effect of defoliation caused by leaf rust attack. Free circulation of air around and within the trees will reduce infection by allowing rapid drying of the leaves during handling and de-suckering. As soon as it is possible to estimate the extent of infection, it is advisable to prevent overcropping by reducing the crop. Nitrogen fertilizer is applied to encourage the growth of new leaves.

IMPLICATIONS FOR LATIN AMERICAN PROGRAMS

Leaf rust is a serious disease of C. arabica and, under favorable conditions of rust development, it can cause severe defoliation. Repeated epidemics may weaken the trees so much that eventually no worthwhile

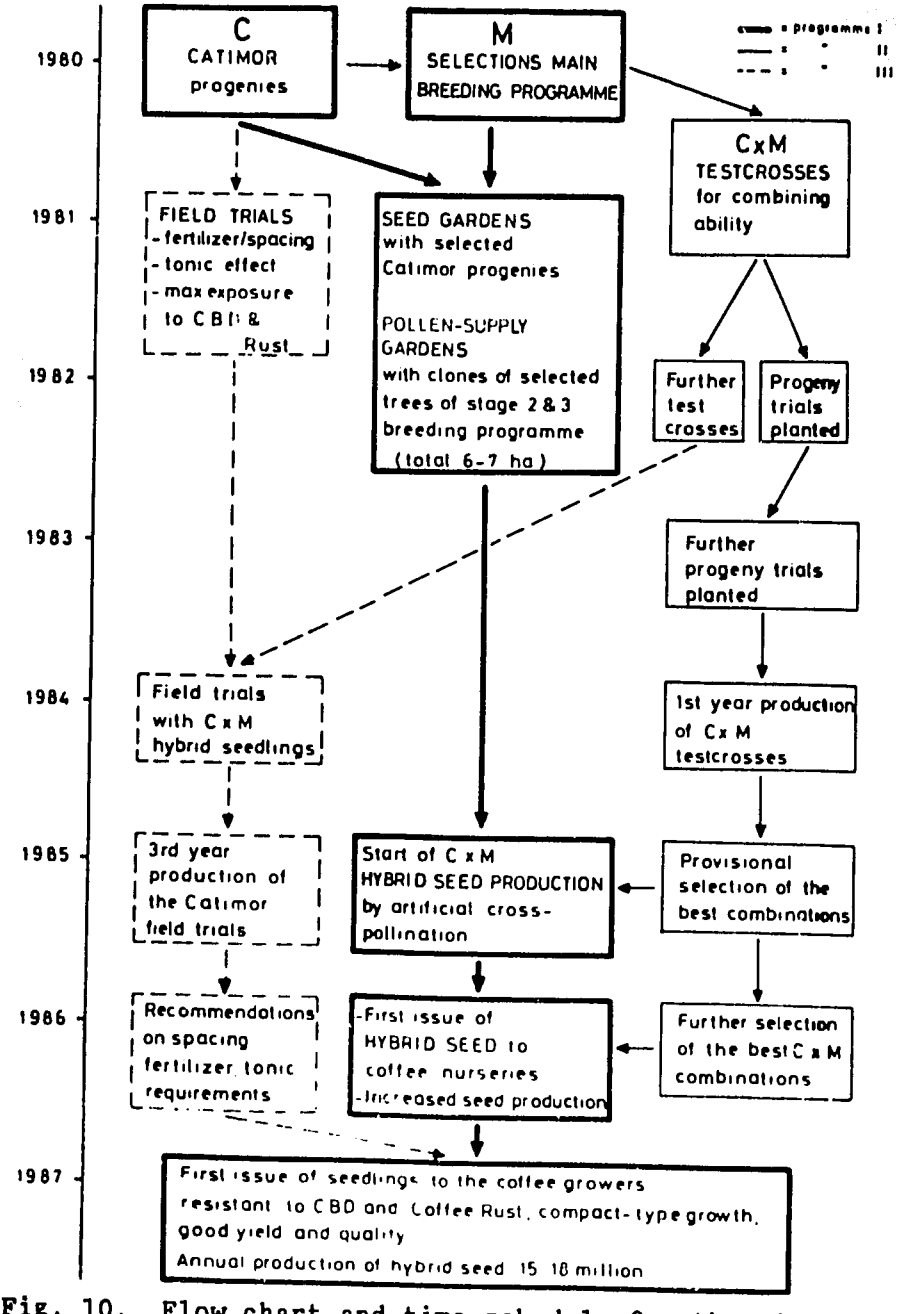

Fig. 10. Flow chart and time schedule for the plan of action of a program to produce well-tested disease-resistant and compact-type plant material of arabica coffee in Kenya through hybrid seed. (Reprinted from [137])

crop is produced. However, in most cases leaf rust can be effectively controlled by five to six well-timed copper (50% copper formulations) sprays, and fungicides like triadimefon (Bayleton) and pyracarbolid (Sicarol) can arrest an already advanced epidemic outbreak.

It is fully recognized in Kenya that leaf rust can be controlled adequately through efficient application and timely use of tested and approved chemicals. The use of these chemicals is prescribed to coffee farmers through Coffee Research Station (CRS) technical circulars. These circulars specify the chemical to use and the rate, frequency, and time of application for different coffee-growing areas of Kenya.

The timing of fungicidal sprays is very critical for the control of leaf rust. Therefore, individual countries in the Americas in which leaf rust has become endemic will have to develop their own spraying schedules for its control. The main objective should be the prevention of infection during the wet periods. Once control sprays have been applied, they must be continued as each rust cycle approaches; otherwise, "induced" outbreaks (Fig. 2) will occur.

Like a Kenyan smallholder, if a smallholder in the Americas fails, due to lack of funds, to follow the recommended spraying schedules to control leaf rust and applies only a few fungicidal sprays during the season, he could end up with higher levels of leaf rust. Poorly timed or inadequate spraying, although giving short-term control, may result in an increase in disease severity in the following season. Thus leaf rust could become a constant threat to the major source of cash income.

EPIDEMIOLOGY AND SPREAD OF *HEMILEIA VASTATRIX*

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Knowledge of the different factors that determine the epidemiological behavior of a disease is essential--not only when one must decide the right control measures to take (including the ecological zonification of the crop or the time and frequency of fungicide application) but also in deciding the necessary quarantines as protection for those countries that are still free of a particular plant disease.

EPIDEMIOLOGY

From the days of Marshall Ward at the end of the last century, scientists have been studying the different factors that influence epidemics of coffee leaf rust, caused by *Hemileia vastatrix* Berk. & Br. Climatic conditions, primarily humidity and temperature, play a major role in the buildup of a coffee leaf rust epidemic. Rust is a disease whose etiology is that of warm conditions for both germination of the urediospores and rapid development in the leaf; consequently it tends to be more severe in warmer areas. Due to the sensitivity of the fungus to temperature maxima during the incubation period, slight changes in temperature maxima can alter the multiplication rate of the disease. In general, the incubation period is shorter in months with higher temperatures and longer in months with lower temperatures as well as in higher

coffee-growing areas (due to lower temperatures there). Under the favorable conditions in India, with constant high humidities and high temperatures, the incubation period requires only about 15 days, while in the subtropical regions of Brazil the incubation period is about 21 days under the most favorable conditions. In East Africa there is a well-defined correlation between climate, altitude, and disease development: in altitudes between 1,200 and 1,500 m NNE of the Rift Valley, high temperatures of 24 C and leaf dew lead to the fast development of the rust. The incubation period is relatively short (18-19 days), the number of rust generations is high, and in spite of less rainfall, which sometimes is supplemented by irrigation, there are no interruptions in the buildup of the epidemic as occur in higher altitudes with lower temperatures. The damage to the coffee tree under these conditions can be enormous because of excessive leaf loss and poor recuperation resulting from little rainfall.

In altitudes between 1,500 and 1,800 m NN, the environmental conditions correlate more or less for the coffee plant and the fungus, and here leaf rust can be kept under control by chemical products. In altitudes between 1,800 and 2,000 m NN, the average temperatures are already quite low. This results in prolonged incubation periods of up to seven weeks, which furthermore cause fewer rust generations per year and, because the coffee is not irrigated, disease development stops during the dry season, with a corresponding drop in inoculum pressure. And in altitudes above 2,000 m NN, where coffee growing diminishes, the temperatures are too low and in spite of sufficient humidity leaf rust is not a problem.

Laboratory studies from Kenya indicate that the urediospores of coffee leaf rust germinate best at 22 C, with no germination occurring below 15.5 C or above 28 C. In Brazil, the optimum temperature for germination was found to be 23.7 C.

If there are two rainy seasons per year, then there are usually two peaks in the annual rust cycle, the rise in disease level starting soon after the onset of each rainy season with the maximum disease

intensity extending into the following dry period. Toward the end of the latter, the level of disease incidence drops, largely as a result of the rust-induced premature leaf fall when most of the infected leaves abscise. If the rainfall pattern is more uniform, only one annual outbreak of leaf rust occurs. The damage caused, however, can be more severe due to prolonged rains and no dry periods to interrupt the buildup of inoculum potential. This latter point corresponds mainly to the situation in West Kenya. Generally, the increase is faster when rainy periods alternate with sunny intervals, while heavy and prolonged rains seem to slow down the increase of disease incidence. This may be due to a certain washout effect on the inoculum.

In Brazil, we find somewhat similar conditions, with only one rainy season and one epidemic buildup. The incubation period is usually 28 days, shorter than the normal 30-35 days, because of the higher temperatures that occur during January-March. Thus, we note one major epidemic wave in the April to August period.

Thus, the leaf rust infection curve lags behind the rain patterns in developing only one maximum of infection, usually toward the end of the dry season, provoking accelerated premature leaf fall that may leave trees with little foliage at the onset of the rainy season when flowering starts again. Contrary to what might be expected, in Brazil it was found that during the summer when temperatures rise above 30 C, rust epidemics are delayed and the infection stops at the "fleck" stage, before urediospores develop in the lesions. High temperatures (above 28 C) in Brazil apparently lead to abortion of rust pustules and a sort of heat-dormant period. However, when the temperatures decrease, the pustules start sporulating again. It is postulated, therefore, that the mycelium of the fungus retains its viability through this period of dormancy for up to 60 days. Thus, the multiple regression equation established by Rayner under East African conditions, in which maximum and minimum temperatures were used to predict the duration of the incubation period, leads to different

results under Brazilian conditions whereby lower temperatures cause higher infection rates. Here, the higher field temperatures may delay the typical disease development, although other climatic factors may be favorable.

As a third climatic factor, the effect of light on leaf rust development can vary according to the stage. Direct bright light inhibits the germination process almost completely, whereas diffused light, such as the light intensity at the underside of the leaves in the field under shade trees or in dull weather, is low enough to permit germination. Previous exposure of urediospores to full light also may reduce the germination capacity of the urediospores. In Brazilian coffee plantations, the incubation period was found to be much longer in the hot season without shade than with shade trees, but in the cooler months the opposite situation prevails--in the plantations with shade trees the incubation period is much shorter. Observations from Central America also confirm a longer incubation period, i.e., 33 days, during the dry hot season.

Furthermore, the intensity of the leaf rust outbreak induced by each wet season depends on the amount of residual infection present at the time when the first showers of more than 7.5 mm occur. If there is little inoculum left from the previous year's epidemic, the buildup of the disease will not be rapid.

The density of the foliage is another important parameter. When only a few leaves remain on the tree, much of the inoculum dispersed falls to the ground because it is not intercepted by the suscept leaves. On trees with dense foliage, however, there are many surfaces on which spores can be retained, and high concentrations of inoculum can build up; the number of pustules per leaf also tends to be higher. In Brazil, the maximum infection was observed on trees of the Bourbon varieties, with a total leaf area of 50 m^2 per tree. This leads to another factor we have to consider--namely, coffee tree phenology. Observations over several years from Brazil and Kenya show that when crop yield is high, the intensity of leaf rust infection is also very high. This means that the

coffee leaf rust is a cyclical disease with high yield and high infection in the first year, and low yield and low infection in the second year, due to the growing habit of the plant. When there is a heavy crop on the tree, the branches grow only a little, but with a small crop, the branches grow more and produce more leaves, which are susceptible to rust from the second pair onward. Consequently, the actual total leaf area is a very important parameter for epidemic development in coffee leaf rust.

DISSEMINATION OF THE DISEASE

The history of the geographic spread of coffee leaf rust led to early speculation about the mechanism of the dissemination and propagation of the urediospores of H. vastatrix. For a long time it has been a source of discussion whether wind or rain plays the more important role. Research work from Kenya and Brazil, however, clearly shows that the urediospores are mainly disseminated by wind. For example, in Brazil urediospores were found at altitudes of 1,000 m in coffee regions that at that time were still free of rust. All attempts to create a natural barrier by eradicating coffee plants failed.

Detailed studies in Kenya about the influence of climatic factors such as wind and rain, insects, or other plants and people (coffee pickers) on the propagation of this disease led to the conclusion that wind is the most important factor in the detachment and dispersal of leaf rust urediospores.

Continuous recording for 28 months of urediospore intensity by volumetric spore traps located between, above, and outside infected coffee plantations revealed that urediospores of the pathogen become continuously windborne in varying quantities. Although spore densities generally decrease with increasing height and distance, urediospores still could be tracked up to 1,000 m above coffee plantations in varying concentrations due to air turbulence.

Spore dispersal by rain splash between and to nearby trees could also be verified. This vehicle, however, is less important as rain occurs less

frequently than wind. Insects play a supplementary role in the dissemination of the spores, which may be important for local tree movement but which is insignificant for long-distance dissemination.

Propagation of the disease by infected plant material from nurseries, which may already carry small pustules or only spores in their leaves, is also highly possible and may provoke an accelerated dissemination in large geographic areas. This is especially dangerous in the case of new coffee plantations where favorable conditions for the development of the leaf rust fungus exist. Also possible could be the introduction or propagation to new countries through other plant species imported from rust-infected countries.

In laboratory and field experiments we could also verify the possibility that leaf rust spores can be dispersed by human beings. Quite a number of urediospores may remain on the skin or on clothing of people who casually brush against infected leaves in the field and who thus may carry them to areas still free of leaf rust.

Comparing the significance of these different means of spore dispersal, one can conclude that wind plays the most important role in releasing and dispersing urediospores of H. vastatrix, but that the disease may nevertheless be introduced to other areas or other countries accidentally or even purposely by people. Quarantine measures are therefore vital and indispensable, not only at the border between countries, but also at the plantation level.

Dissemination of leaf rust in Central America most likely was due to human movement or travel, because shade trees hinder wind dissemination, contrary to the situation in Brazil, particularly in the south.

The spread of leaf rust throughout the world is a typical example of the propagation of a plant disease by human agency, although under normal conditions in coffee plantations the wind is the primary vehicle for its spread.

COFFEE RUST RACES AND RESISTANCE

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Centro de Investigação das Ferrugens do Cafeeiro, Oeiras, Portugal

Research on coffee leaf rust has been discontinuous through the years since the epidemics in Sri Lanka in the 1870s. There has been, however, a more or less permanent concern about it on the part of coffee pathologists and other coffee research workers. Some of these (Ward, Mayne, Nutman, Roberts, Rayner, etc.) have expressed their concern by investigating the disease and by making excellent contributions to its understanding; others (Wellman, Cowgill) by promoting conditions for the study of the disease and for the protection of coffee growing on the American continent, still others (Sylvain, Bechetel, Meyer, etc.) by collecting for study coffee seed and rust samples from different parts of the world. In the past 25 years, however, a great impetus has been given to this research with the foundation in 1955 of the Centro de Investigação das Ferrugens do Cafeeiro (CIFC) in Oeiras, Portugal, and the centralization of part of the rust research in this center in an international cooperative scheme. The invasion of the American continent by the disease in 1970 also stimulated coffee institutions there to become involved in breeding for rust resistance, chemical control, and other studies. Some of these institutions have produced very valuable work and are entitled to the appreciation of all coffee growers.

This chapter summarizes the work done on rust race differentiation and on the search of Coffea arabica

and interspecific hybrids for rust resistance. If a major emphasis is given to the work of the CIFC, it is because this center was to some extent the pioneer in these investigations. All of the credit for this pioneering work should be given to Professor B. d'Oliveira.

RACES

The existence of races in Hemileia vastatrix was first proved in India by Mayne (79), who differentiated in the local rust samples three physiologic races corresponding to races I, II, and VIII of the present CIFC rust collection. No other studies were made on the physiologic specialization of the fungus until d'Oliveira initiated a world survey of coffee rust races in 1953 in Portugal (30,31). When the CIFC was founded in 1955, quite a number of rust samples from different parts of the world started arriving at the center. Work since then has corroborated the existence of Mayne's races in addition to describing 27 additional ones (115).

Geographic Distribution

The rust races identified in 938 rust isolates from 37 countries are shown in Table 1. The origin of each race has been given by Rodrigues et al (114) and by Lopes and Godinho (71). The most prevalent races (determined as the number of times, in percentages, that each race was identified in the 938 isolates) are race II (58.2%), race I (14.4%), race III (8.9%), and race XV (3.6%). All the other races occur only in traces. The distribution of the races in the 37 countries follows the same pattern, with race II present in 34 of the surveyed countries, race I in 18, race III in 14, and race XV in 8.

Race Genotypes

There are known in H. vastatrix six genes for virulence (v_1, v_2, v_3, v_4, v_5, and v_6) whose existence has been assumed by the application of the

Table 1. Geographic distribution of the races of *Hemileia vastatrix*

Physiologic races and their origin	No. of times each was identified	Physiologic races and their origin	No. of times each was identified
Angola		Central African Empire	
Race I	11	Race II	1
Race II	37	Race IV	6
Race III	14	Race XIX	1
Race VII	1	Race XXVII	1
Race XV	15	Ethiopia	
Race XXIV	1	Race I	1
Race XXVII	16	Race II	30
Race XXX	2	Race III	37
Argentina		Race XV	1
Race II	1	Guinea (Conakri)	
Brazil[a]		Race II	3
Race I	1	India	
Race II	107	Race I	3
Race XV	2	Race II	1
Cameroon		Race III	3
Race II	21	Race VIII	4
Race III	2	Race XII	1
Cambodia		Race XIV	1
Race II	8	Race XVI	1
Race VI	1	Race XVII	2
Race XI	3	Race XXIII	4
Comores		Race XXIV	4
Race II	1	Race XXV	1
Congo (Kinshasa)		Race XXVIII	1
Race I	1	Race XXXI	1
Race III	5		

[a]Races III (106), X (38), XVII (42), and XXIV (44) have also been reported.

(continued on next page)

Table 1 (continued)

Physiologic races and their origin	No. of times each was identified	Physiologic races and their origin	No. of times each was identified
Indonesia		New Caledonia	
Race I	3	Race I	1
Race III	1	Race II	8
Race XV	3	Papua	
Ivory Coast		Race I	1
Race II	25	Race II	2
Kenya		Peru	
Race I	80	Race II	1
Race II	89	Philippines	
Race III	3	Race I	2
Race VII	1	Race II	9
Race XV	2	Race X	1
Race XX	3	Race XIII	1
Race XXIV	1	S. Tome	
Laos		Race I	1
Race II	4	Race II	23
Madagascar		Race III	1
Race I	1	Race VII	1
Race II	9	Race XV	1
Race XI	2	Race XVIII	1
Mauritius		South African Republic	
Race II	1	Race II	1
Mexico		Sri Lanka	
Race II	4	Race I	12
Malawi		Race II	34
Race II	1	Race XV	6
Mozambique		Race XXX	4
Race VI	14	Tanzania	
Nicaragua		Race I	6
Race II	3	Race II	9
Nigeria		Race III	8
Race II	7	Race XI	1
Race III	4		

(continued on next page)

Table 1 (continued)

Physiologic races and their origin	No. of times each was identified	Physiologic races and their origin	No. of times each was identified
Tanzania (cont.)		Uganda	
Race XVII	3	Race I	1
Race XX	1	Race II	10
Race XXIV	2	Race IV	3
Thailand		Race XXI	1
Race II	25	Race XXXII	1
Race III	1	Vietnam	
Timor (East)		Race I	1
Race I	4	Race II	1
Race II	49	Zambia	
Race III	1	Race I	6
Race IV	1	Race II	15
Race XV	3	Race III	3
Race XXII	20	Race XV	1
Race XXV	1	Zanzibar (Tanzania)	
Race XXVI	6	Race III	1
Race XXIX	4	Race VI	11
Race XXX	2	Race XV	1
		Zimbabwe	
		Race II	7

Flor gene-for-gene relationship (13,93) to the *C. arabica*-*H. vastatrix* complex (Table 2). Genotypes of some races that attack mainly the diploid coffees are, however, not known.

Gene v_5 has been found alone (race II) and in association with the other genes, unlike the other genes, which so far have been found only associated. It is the most widespread since it overcomes the S_H5 resistance gene present in the most prominent arabica cultivars (Typica, Caturra, Mundo Novo, etc.). Gene v_5 is absent from races IV, XI, XIX, XX, XXI, XXVII, and XXXII, which are unable to infect these cultivars but do infect Matari (the universal suscept of arabica

species), and in races VI and XVIII, which do not attack arabica.

Gene v_1 has been found mostly associated with v_5 in race III, widely available in Ethiopia where Geisha type coffees are widespread.

Gene v_2, mainly associated with v_5 (race I), was first detected in India, overcoming Kent's initial resistance. With the introduction of this cultivar in Kenya and the further selection of its derivatives, it became widespread in this country.

Gene v_3 has been found associated with other genes, except gene v_6, as races VII (v_3v_5), VIII ($v_2v_3v_5$), XII ($v_1v_2v_3v_5$), and XIV ($v_2v_3v_4v_5$). It is also present in race XVI ($v_1v_2v_3v_4v_5$), which was isolated only once in the greenhouse from race XIV (114) after several years of subculturing. This gene very likely resulted from a selection pressure exerted by resistance gene S_H3 of C. liberica origin. Its presence in races VIII, XII, and XIV is restricted to India.

Gene v_4 is mainly associated with v_5 as race XV. This gene is present in a number of countries, despite the Ethiopian origin of host gene S_H4. When associated with gene v_1 in several combinations like races X ($v_1v_4v_5$), XIX (v_1v_4), XX (v_1v_4?), XXIII ($v_1v_2v_4v_5$), and XXVII ($v_1v_4v_6$?), it induces intermediate reactions in the majority of the hosts.

Gene v_6 has been characterized, associated with other genes, in rust material collected on C. canephora X C. arabica derivatives from Timor and India, and on C. canephora from Angola and the Central African Empire. This virulence gene seems to have resulted from a selection pressure exerted by the resistance gene S_H6 tied up to C. canephora.

New Races of H. vastatrix

Although new rust races have not been reported in the CIFC since 1975 (115), there are at present some indications that new rust genotypes will be characterized in the near future. There are, however, some difficulties concerning the reproduction of intermediate reaction types in some differential hosts such

as H.420/2. This concern implies that, at least for some host-rust interactions, the surrounding environmental or physiologic conditions of the hosts have a bearing on the final reaction (see also the section Effect of Heat and Light). Some similar observations made in Brazil corroborate these considerations. In a leaf disk experiment conducted in the laboratory, an isolate of race II produced some sporulation on disks of S_H3 plants (37). This isolate was re-isolated and sporulated also on leaf disks of the differential clone CIFC 33/1. After multiplication, this isolate was used for inoculation in the nursery on the same differential; only resistant reactions with no sporulation were obtained. The screening of this isolate at Oeiras showed it to be race II.

Recently, some research workers (39) have given indications about the existence of four new races obtained from rust spores collected in plants of Icatu, Catimor, and the cultivar Kouillou of C. canephora, in Brazil. The rust material, when inoculated at Oeiras on the CIFC differentials, has indicated the presence of race II, but the hypothesis of the above plants being new differentials is not ruled out. Additional studies are under way at CIFC to clear up this situation.

RESISTANCE

By virtue of the narrow genetic base of most cultivated arabicas (Typica, Bourbon, Mundo Novo, Caturra, etc.) regarding rust susceptibility, a systematic search for resistant germ plasm has been conducted over the past 25 years, not only among the arabicas and interspecific hybrids, but also in other coffee species. This search has been conducted mainly at CIFC, where thousands of coffee seedlings from different origins have been screened with known physiologic races and categorized into physiologic groups. The selected resistant material has been used by CIFC and, furthermore, provided by the center to foreign institutions for breeding purposes.

Coffee Physiologic Groups and Genes for Rust Resistance

The coffee physiologic groups are characterized according to the different reaction spectra presented to the known rust races and are named arbitrarily by letters and numbers. The coffee grouping system has proved very convenient when the resistance genes are not known (Table 2) because it allows standardized classification of the coffee plants for rust resistance.

Twenty-four groups have been screened (115) and 16 synthesized at CIFC through crossing (A. J. Bettencourt, unpublished). This fundamental research has made possible the determination of six genes for rust resistance in C. arabica and tetraploid interspecific hybrids with the arabica phenotype which confer resistance to a number of races (13,14,93). In pure arabicas, genes S_H1, S_H2, S_H4, and S_H5 have been found singly or associated in the following coffee groups and selections: S_H1--group α (Dilla and Alghe); S_H4--group γ (S.12 Kaffa); SH5--group E (Typica, Bourbon, Caturra, Catuaí, Mundo Novo, etc.); S_H2 associated with S_H5--group D (Kent from India; Kent's derivatives K.7 and SL6 from Kenya; series KP, F, H, X from Tanzania; S.16 Wollamo from Ethiopia).

These same genes have been found associated as S_H1 S_H5 in group C (Geisha, Yrgalem, Dalecho, Sudan Barbuk), S_H1 S_H4 in group I (S.12 Kaffa), S_H4 S_H5 in group J (S.4 Agaro), S_H1 S_H4 S_H5 in group W (S.12 Kaffa) all from Ethiopia, and S_H1 S_H2 S_H5 in group L. Group β (Matari), also from Ethiopia, is considered the universal suscept of the arabica coffees.

In the interspecific hybrids with arabica phenotype, genes S_H3 and S_H6 have been found in the following groups and selections: S_H3 associated with S_H5--group G (S.288) from India; S_H3 associated with S_H2 and S_H5--group H (S.353, S.795) from India; S_H6--group R (Hibrido de Timor-2) from East Timor.

Within the interspecific hybrids there are groups such as A, 1, 2, 3, and M whose genotypes are not known. The most desired of all coffee groups is group A, which includes the coffee populations with resis-

tance to the 30 known races. These populations have been found in hybrids between C. arabica and C. canephora, either spontaneous like Hibrido de Timor (HDT) or man-made like Icatu. Since no pure arabicas have been detected so far in this group and since many diploid species, including C. canephora, are resistant to all the known rust races, the resistance of the above interspecific hybrids is most likely provided by the diploid parent. Groups Q, P, K, B, N, and F of unknown genotype are found only in diploid coffees.

Breeding for Rust Resistance

GENERAL TRENDS

C. arabica has been bred for rust resistance in several experimental centers of various countries. A general account of this work has been given elsewhere (115). Basically, the following orientation has been followed:

a) To select coffee plant material with known S_H genes for rust resistance and possessing vigor, yield, and quality similar to those of the traditional arabicas. Work performed along this line proved that the introductions bearing one or two S_H genes for rust resistance, coming from Ethiopia, India, Kenya, and Tanzania, presented enough yield variability so that this characteristic was not a limiting factor in the selection program. On the contrary, the grain abnormalities found were important obstacles in the selection process, mainly of the Ethiopian and Indian material (25).

b) To synthesize hybrids with several genetic combinations, mainly by introducing known S_H genes in good commercial cultivars. This line of research resulted from the observation that the direct use of the sources of resistance as indicated in a) would imply a long selection process in order to attenuate the grain abnormalities in the selected material. To overcome this difficulty, numerous hybrids have been

developed at CIFC and in other institutions, among them Caturra X Geisha, Caturra X S.4 Agaro, Caturra X S. Cioiccie, Caturra X S.795, etc The inclusion of the Caturra (Ct gene for compact growth) cultivar in a great number of crosses originated the dwarf and high-yielding progenies, capable of being used in intensive exploitation systems (high planting densities with short production cycles followed by plant renovation).

c) To introduce into the commercial varieties the resistance of group A coffee plants such as HDT. This may be the most important and advanced research line, not only because crossing with HDT introduces resistance to all known rust races but also because it provides high genetic variability. This research line has been under way at CIFC since 1960, and at Centro Nacional de Investigaciones de Cafe (CENICAFE) (Colombia) since 1965. Since 1970, the Universidade Federal de Vicosa (UFV) in Brazil has worked with F_2 and F_3 populations of the hybrids HW.26 and H.46 provided by CIFC. HDT has also been crossed at the CIFC institute with cultivars bearing other known S_H genes.

HDT AND ITS DERIVATIVES

HDT is a population derived from a single tree, very likely a spontaneous hybrid between C. arabica and C. canephora, discovered around 1927 in East Timor (50). It presents a predominant arabica phenotype, the majority of plants with resistance to the 30 known races of H. vastatrix, and a high genetic variability concerning morphology and yield. In 1956, HDT progeny were expanded to practically the whole territory to replace the local arabica (Typica), which had been seriously debilitated by rust. Since HDT characteristics offered good grounds for selection, this process was initiated in Timor (50) but had to be interrupted for political reasons. It is still under way in some countries (27,91). In Brazil, plants of some selections of HDT give yields higher than Mundo

Novo, a cultivar already considered a good yielder (91).

The principal drawbacks of HDT are, however, the large amount of abnormal grains produced and the difficulty of adapting it to some coffee areas. Its normal growth characteristic is also considered to be a disadvantage versus the compact growth. It is, however, looked at as a unique genetic material with which to introduce resistance to coffee leaf rust into C. arabica. It has shown a durable type of resistance; in India, seven progenies of the HDT lines S.2252 and S.2253, confronted since 1965 with local rust races I, II, III, VIII, XII, XIV, XVII, XXIII, XXIV, XXV, XXVIII, and XXXI, have remained rust-free (27). Besides, some plants of HDT present resistance to coffee berry disease (CBD) caused by Colletrichum coffeanum (137) and to Meloidogyne exigua (90).

HDT was first used for breeding purposes in Portugal by crossing two plants of the resistant HDT, CIFC 832/1 and CIFC 832/2, with the compact type susceptible Caturra Vermelho CIFC 19/1, which produced the hybrids CIFC HW.26 and H.46, respectively. All the F_1 was of the compact growth type and resistant to all known races.

Seventy-four progenies F_2 to F_5 of these two hybrids were analyzed at the CIFC greenhouses and in field experiments in Angola and Brazil. The screening made at CIFC showed variation in segregation for resistance (groups A, 1, 2, 3, R, and E) among the progenies. Successive selections were made over 20 years on these progeny based on data concerning yield, vigor, small percentage of abnormal grains, and resistance to the rust races. Some very promising F_4 and F_5 progenies were then chosen, namely, four derived from the coffee plant UFV 387-45 (F_3 of CIFC HW.26). These progenies are predominantly coffee seedlings of group A and some seedlings of groups 1, 2, and 3, and are homozygous for the allele Ct. A detailed account of this work was given by Bettencourt et al (12). The populations obtained from HW.26 and H.46 were designated in Brazil as Catimor. Catimor derived from HW.26 has been propagated in CIFC greenhouses and

distributed to other coffee areas for adaptation studies and multiplication purposes.

In Colombia, since 1967 special emphasis has been given also to the crosses involving HDT and the commercial varieties better adapted to Colombia, such as Typica, Bourbon, San Bernardo, San Ramon, and, in particular, Caturra (25). However, the HDT parent used, provided by CIFC in 1960, was CIFC 1343, a different introduction from that used in Oeiras. Progenies F_3 and F_4 of the hybrid Caturra Amarelo X HDT, evaluated in six locales, have shown yield, grain, and liquor characteristics similar to those of Caturra, a well-accepted variety in Colombia. The large genetic variation found in the progenies allowed for further selection in later generations (23). As far as rust resistance of these progenies is concerned, the screening made at CIFC indicates segregation for the same resistant types previously found in Catimor (12), namely A, 1, 2, 3, R, and E. However, note that the percentage of group E plants is smaller than 1% (23).

The number of resistant genes present in the hybrids with HDT is not known, but the identification of gene S_H6 (14) in clone 1343/269 of HDT and the segregation of coffee physiologic groups 1, 2, and 3 indicate that these hybrids must possess several genes, single or associated, different from those previously identified in C. arabica, with the exception of S_H5. This fact, besides conferring on the Caturra X HDT populations a complex vertical resistance when all the genes are present, further indicates the presence of high genetic variability. Coffee breeders wish to take advantage of this variability and to use the HDT derivatives as a composite cultivar. This cultivar will be named variedade Colombia, and the first seed was released in 1982 in Colombia (24).

The success achieved with the single crosses between Caturra and HDT has shown that backcrosses for the recurrent parent apparently were not necessary. Likewise, there was a certain fear that backcross would induce lowering of resistance and of genetic variability. In Portugal, however, several plants of

the original hybrid HW.26 have been backcrossed one or more times to several cultivars or selections such as Blue Mountain (H.283), SL 14 (H.285), SL 28 (H.306), Bourbon (H.373), Caturra Vermelho (H.504), Catuai Amarelo (H.528), Mundo Novo (H.369), etc. Information is available about the characteristic behavior in Brazil of some of this material, namely the progenies F_3 of the hybrid CIFC H.520 [Catuaí amarelo X (Caturra X HDT = HW 26/13)]. The screening for rust resistance of eight F_2 progenies of this hybrid selected at UFV and tested at CIFC indicates that group A coffee plants still predominate in the segregation (11). This hybrid has received the designation Cavimor.

OTHER C. ARABICA X C. CANEPHORA DERIVATIVES

Icatu. Icatu is a population derived from a cross made in 1950 at the Instituto Agronómico de Campinas (Brazil) between the duplicated C. canephora Co 254 and the C. arabica Bourbon Vermelho H.2460, backcrossed to Mundo Novo, Caturra Vermelho, and Bourbon Vermelho. Icatu is similar to HDT in that it presents high variability regarding vigor, morphology, yield, and other marketable characteristics. It also presents a wide spectrum of resistance to the rust races to which it has been submitted as has been proved by inoculations conducted at CIFC (73). In field experiments laid out in Paraná (Brazil) with Icatu with Catuaí Vermelho and Mundo Novo as controls, some progenies of Icatu such as H.3349-7C 1353, H.4782-7C 567, and H. 4782-10C 2196 showed yields higher than the Catuaí Vermelho LLCM 20 77-2-5-81, and the great majority presented yields intermediate between Catuaí and Mundo Novo (105). Icatu presents, however, undesirable traits such as aneuploidy, high percentage of abnormal seeds, and great heterogeneity in yield within plants of the same progeny.

Devamachy Derivatives. The derivatives of a spontaneous robusta X arabica (Coorg) hybrid found in India backcrossed with S.1403 (first generation of S.795), S.288, S.333, and S.881 (Rume Sudan) are known as Devamachy derivatives. The progeny S.1961 (S.1403-64 X Devamachy) is one of the best yielders

(27). Information on rust resistance and other characteristics is not available. F_2 and F_3 progenies of Devamachy X S.881 present promising yields and high resistance to leaf rust.

S.274 Robusta X S.450 Kent Arabica. This artificial hybrid already backcrossed twice with Kent has shown some progenies with good performance regarding yield and good cup quality. Information on rust resistance is not available (27).

HYBRID SEED PRODUCTION

The direct use of Catimor as a new variety is said to be unsuitable in Kenya because its liquor quality is still below the required standard (137). CBD is economically more important in Kenya than coffee rust, and Catimor resistance to CBD is determined by only one major gene (T-gene); this is considered another strong reason for Catimor not to be used directly in this country, despite the indications that this CBD resistance is likely to be stable. For these reasons, the purpose of the Kenya breeding program is to provide in the near future F_1 hybrid seed resulting from crosses between the best combinations of Catimor selections (supplied by Colombia) and genotypes of their main breeding program. These genotypes are backcrosses to SL 28 and SL 34 of multiple crosses involving Rume Sudan (with R- and K-genes for CBD resistance), HDT for rust and CBD resistance, and Bourbon, SL 28, SL 34, and K.7 for bean size and liquor quality. This F_1 hybrid will then theoretically provide resistance to the rust races and CBD and will have acceptable liquor quality and compact growth. F_1 hybrid seed has also been produced at CIFC by crossing Catimor with Catuaí.

Breakdown of Resistance

APPEARANCE OF NEW RACES

Periodic breakdowns of vertical resistance in agricultural crops due to the appearance of new races are well documented. In the history of coffee growing, similar examples can be found. For instance, Kent's cultivar, discovered in India in 1911, was

resistant to the prevalent race II of H. vastatrix but nevertheless succumbed to rust after several years of cultivation due to the appearance of race I. The same situation applied to other C. arabica selections introduced from Ethiopia into Kenya; resistant to races I and II, they became infected by other races. This tradeoff between arabica genes for resistance and coffee rust genes for virulence has been observed all over the world, even in Ethiopia, which is the origin of C. arabica. But in Ethiopia a balanced host-pathogen system (coexistence) (15) has been achieved through the years so that leaf rust is not a serious problem in the semi-wild forest (113). Whether this balance has been obtained as a result of the development of a natural multiline system and/or host horizontal resistance is yet to be ascertained. The presence of genes S_H1, S_H2 (rare), S_H4, and S_H5 and their combinations in the Ethiopian coffee material points out a multiline effect, but laboratory (40) and field (9) evidence indicates that horizontal resistance could be effective as well.

Insofar as Catimor and other HDT derivatives are concerned, some doubts arise as to the future stability of their rust resistance. However, the historical background of these hybrids in regard to the rust races now known seems to indicate that their resistance is stable. The important factors supporting this are: 1) durable resistance derived from HDT and proved in Timor and in other countries (27); 2) the polygenic vertical resistance in group A plants of these hybrids conferred by genes different from those found in C. arabica except SH_5; 3) the rare occurrence of polygenic vertical pathogenicity; and 4) the likelihood that these hybrids like Catimor have horizontal resistance as well (28).

EFFECT OF HEAT AND LIGHT

There are some indications that heat and light may affect the level of resistance to rust of some coffee progeny. As far as heat is concerned, a remarkable increase in susceptibility has been observed in all the susceptible plants whose leaves were given a heat treatment (water bath at 45 C for 1.5 hours) before

inoculation (112,117). This increase in susceptibility is indicated by the fact that the first flecks appear three to four days earlier on these plants and that more sporulation is produced on these plants than on the controls. These observations indicate that even plants considered highly susceptible to rust possess some degree of resistance that is decreased by the heat treatment. The effect of the heat treatment may be still more drastic and may transform a totally resistant reaction into a partially resistant one. In fact, when leaves of resistant plants are given the same treatment, some leaves that would normally react with flecks have been observed to produce urediospores. If susceptible plants are treated four to six days after inoculation, however, a typical susceptible leaf becomes resistant, and flecks and tumefactions appear instead of pustules (117).

Susceptible plants exposed to high light intensity before inoculation produced more pustules than plants submitted to several degrees of shade (41). This evidence is in agreement with the general observation that coffee plants grown under heavy shade are, in general, less severely attacked by rust.

Histopathology of the Resistance Reaction: Induction of flt and of Microscopic Alterations by Leachates of Urediospores

The process of infection of coffee leaves by rust urediospores follows the general stages described for other rusts. In the incompatible combinations characterized by flt (flecks plus tumefactions) symptoms, the fungus growth stops around the third or fourth day after the penetration, in general at the anchor stage (108). An occasional hypha might, however, cross the mesophyll without any branching. The number of haustoria is greatly reduced; besides the two formed in the subsidiary cells, only one or two can be observed in the mesophyll. During the infection process, the volume of the mesophyll cells increases progressively, and the intercellular spaces consequently disappear (107).

In the case of so-called immunity, i.e., when no

external symptoms are observed (110), microscopic alterations (stained with cotton blue) can be detected in the surface view as small islets about 100 um in diameter standing out from the remaining healthy tissue. In cross section, areas stained blue, corresponding to different stages of fungus development, can be observed in the penetration points. These stages range from the apparent absence of any fungus structure to penetration hyphae that have reached the anchor stage but are surrounded by larger cells that seem to block their further growth (110). The fact that some microscopic alterations appear to be produced even without the penetration of the fungus suggests that some inducing substance(s) released from the rust urediospores may be responsible for such alterations. This assumption has been proved by inducing flt or merely microscopic alterations via drops of leachates of live and autoclaved urediospores placed on detached coffee leaves (117).

Resistance and the Production of Antifungal Substances: Induced Protection

Some evidence has been given that antifungal substances are produced when coffee leaves are inoculated with avirulent races of H. vastatrix (115) or with several rusts not pathogenic to coffee (81). Further work (M. E. M. Guedes and C. J. Rodrigues, Jr., unpublished) seems to indicate that, at least in the coffee-rust association, some preexisting substances in the coffee leaves are enhanced after inoculation with avirulent races. This fact is in accordance with the observed partial inhibition of urediospore germination caused by the diffusates of noninoculated leaves as compared with the water controls. Spraying the leaves of susceptible coffee seedlings with lyophilized diffusates of incompatible combinations before inoculation reduced the percentage of pustules 60% when compared with controls.

Induced protection of coffee leaves against virulent races of H. vastatrix has been achieved by prior inoculation with avirulent races of this rust (115)

and also with water suspensions of some nonpathogenic bacteria and fungi (8,75). Some protection has also been achieved by spraying leachates of autoclaved urediospores of virulent races (7).

CONCLUDING REMARKS

The advances of coffee rust research have been significant in the past two decades. Coffee growers can now look ahead with confidence because they know what hybrid material they can use with a certain degree of safety to replace their highly susceptible cultivars. Most of the coffee plantations of many countries are old and debilitated, and their replacement is urgent, not only because they are unproductive but also because they are highly susceptible to rust. In many Latin American countries, chemical control is not practical because of the steep, mountainous terrain where coffee is grown. One alternative is to use resistant varieties with yields and quality similar to the traditional variety Typica. Catimor, besides being resistant to rust, has yields similar to or in some cases higher than Caturra, which largely surpasses the average yield of Typica. Catimor also has a compact growth characteristic, which is another advantage over the traditional varieties because it can be used easily in high-density planting systems.

The main drawback regarding the Catimor expansion is, at the moment, the shortage of available seed. The amount that has been supplied by CIFC to 20 countries for adaptation studies and seed multiplication should give rise, however, to many tons of seed within the next five to six years. The dominant preservation of Catimor resistance to the rust races cannot be fully ensured; however, the facts already pointed out provide strong reasons to be optimistic. Progressive replacement of the old susceptible plantations by resistant material would then be most suitable. In the few countries that are still rust-free, the presence of resistant plantations would prevent the settlement and multiplication of the most common races and, logically, the possibility of their mutation.

HOST-PARASITE INTERACTIONS IN THE COFFEE-*HEMILEIA VASTATRIX* SYSTEM

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The resistance mechanisms through which plants defend themselves against the attack and establishment of pathogens are one of the most exciting and fascinating subjects in the phytopathological sciences. During the last 25 years remarkable progress has been made in studies about host-pathogen interactions in plants. However, in spite of all the progress achieved, many aspects of the interaction processes between host and parasite still remain obscure.

It is well known that in spite of the large number of pathogens existing in nature, only a few of them can effectively parasitize any specific plant or group of plants and cause disease, due to the successful interactions between them. Certainly, plants have developed through their evolution some very complex and highly efficient systems of defense. These mechanisms are genetically controlled, being triggered whenever necessary, and involve several biochemical changes in the cells of the host tissues. These biochemical changes may be independent of the kind of invading organism; however, the magnitude, extension, and velocity of the changes can be the difference between the susceptibility or resistance shown by the host toward the invader.

In a symposium about coffee leaf rust it is quite impossible, even considering the importance of the subject discussed here, to analyze all aspects of

host-parasite interactions and resistance mechanisms in plants. Some more general aspects will be considered and discussed later, but our main objective deals with the host-pathogen interactions in the Coffea arabica-Hemileia vastatrix system.

Coffee leaf rust is certainly the most economically significant disease for the coffee-growing countries. Coffee represents a high percentage of the export products of many countries, involving billions of dollars. Today the disease has spread so that it is the most immediate menace to the coffee business in the international market, and can cause severe financial losses for all coffee-growing countries where the disease occurs. In the last century coffee leaf rust was responsible for the almost complete devastation of coffee crops in Ceylon, and the breaking down of the economy of several other countries. In Brazil, the disease was reported for the first time in early 1970 by Medeiros (80) in the state of Bahia. Since then it has spread through many countries of South and Central America such as Paraguay, Argentina, Bolivia, Ecuador, Peru, Nicaragua, Mexico, and, very recently, Colombia.

Coffee leaf rust is caused by H. vastatrix Berk. et Br., an obligate parasite that belongs to the order Uredinales. It parasitizes the genus Coffea, and to my knowledge no alternate host is known up to now.

The fungus H. vastatrix comprises about 30 physiologic races which, in spite of not being killing organisms themselves, can cause severe damage to their hosts and can even cause death by successive attacks.

SPECIFICITY IN HOST-PARASITE INTERACTION

Incompatibility and Hypersensitivity

It is always very difficult to start a paper without making some preliminary considerations about scientific terms and concepts which will be systematically used throughout the discussion. However, to define concepts and terms is not always easy as it may involve several philosophical and personal considerations that many times are not completely shared by all

readers. Thus, we will be restricted at present to our personal point of view regarding the most discussed basic concepts. Among the plant pathogens occurring in nature (viruses, bacteria, or fungi) we will direct our attention only to the fungi, and among these mainly to the obligate parasites because our main interest deals with coffee rust, which is caused by an obligate parasite.

By "obligate parasites" we mean those fungi that can live together with their host in a relatively harmonious relationship, obtaining nutrients for growth from the host cells through the formation of haustoria. The pathogen referred to specifically as an obligate parasite does not cause extensive harm to the host tissue, as it depends on the living host cells to survive and grow. The term obligate parasite as applied to rusts, downy mildews, and powdery mildews seems not to be the most appropriate because some of them can be cultured in artificial media without the presence of living host tissue. For this, Luttrell (72) proposed the name "biotrophs" to designate those parasites that in nature live in a close relationship with their hosts from which they obtain the necessary nutrients, regardless of their ability to grow in artificial culture media. Among the plant-pathogenic fungi, the biotrophs are undoubtedly those which show the greatest specificity toward their hosts, especially when, as in the case of H. vastatrix, they consist of physiologic races, each one restricted to particular genotypes of a host species, or to a very few related host species. The specificity in this case is considered at the host cultivar level. It is worthwhile to mention at this point that in the case of rusts, some of them must alternate between two hosts to complete their life cycles. In this case there is a preferential specificity to each one of the alternate hosts during each respective phase of their life cycles. Concerning H. vastatrix, as mentioned, no alternate host is known, and the complete life cycle is also unknown.

The concepts of susceptibility and resistance of the host to a particular pathogen, as in the case of H. vastatrix, have a special significance because a

cultivar that is resistant to a certain physiologic race can be susceptible to another race. Thus, the preferred use of the terms compatible and incompatible to designate the combination between particular host genotypes susceptible to particular virulent parasite genotypes and the combination between particular host genotypes resistant to specific avirulent parasite genotypes, respectively. According to this, "compatibility" could be defined as a highly specific biochemical and physiologic affinity between a host cultivar and a physiologic race of the parasite, which live in a close association. In a compatible combination, the host does not react immediately to the presence of the invading parasite, which is allowed to grow and develop inside the host tissue and eventually sporulate. As a final consequence of this peculiar association the host will show macroscopic symptoms accompanied by biochemical changes in the infected tissues, which will characterize the disease caused by that particular parasite, as well as the signs of sporulation of the fungus.

In case of incompatibility the cells of the host tissue react to the presence of the invader, due to the lack of affinity between them, and react against its establishment by excluding it, preventing its growth, or even killing it. Sometimes the reaction by the infected host cells is so drastic that they die, and symptoms of this event are shown together with other biochemical changes in spite of the absence of the symptoms characteristic of the disease. This rapid response of the host, followed more or less simultaneously by death of host cells and stoppage of fungal growth, is called the hypersensitive reaction (133) and depends in fact on the ability of the host to react as soon as possible to the presence of the invader through a defense mechanism.

However, in host-parasite systems involving biotrophs such as the rusts, hypersensitivity cannot be studied apart from considering in both resistant host and avirulent parasite the time course of events after inoculation, such as 1) appressorium formation and penetration, 2) recognition by host cells of the presence of the parasite, 3) haustorium formation,

response and death of host cells, and finally, death or interruption of hyphae growth. Many attempts have been made to determine the sequence of events following inoculation in an incompatible combination which will result in the hypersensitive reaction.

The study of this sequence of events is very important to determine the time during the infectious process when the host-parasite interaction takes place, host cell death occurs, and the fungal growth is stopped in the incompatible combinations. Depending on this, hypersensitivity can be considered as a cause or a consequence of the resistance. However, these two statements are highly controversial.

Brown et al (21) and Ogle and Brown (96), working with several cultivars of wheat and Puccinia graminis f. sp. tritici, demonstrated that in the highly incompatible combinations the necrotic area in the host tissue was larger than the fungal colony within it. They interpreted this as a sign that fungal growth was limited by the hypersensitive reaction which, in this case, acted as the cause of resistance. In the compatible combinations, as was expected, the fungal colony exceeded many times in size the negligible necrotic area. However, in combinations where intermediate resistance reactions were observed, the areas of fungal growth were larger than the necrotic areas due to the hypersensitivity. In this case, hypersensitivity cannot be considered as the cause but as the consequence of the resistance, because the fungus continued its development in spite of the death of the host cells.

Kiraly et al (68) also defended the idea that hypersensitivity was the consequence and not the cause of resistance in wheat and beans to the infection caused by P. graminis f. sp. tritici and Uromyces phaseoli, respectively. According to those authors, unknown factors in the cell could be responsible for stopping the fungal growth that in turn would release toxic substances which would kill the host cells. Other authors such as Mayama et al (78) also found evidence that supported this hypothesis. However, there is good evidence that hypersensitivity, instead of being a consequence, is a cause of resistance in

many plants. This implies that the fungal growth within the cell is either stopped due to starvation or is under the effect of toxic substances liberated by the dead cells. The fungus continues to grow, although delayed, even after the first symptoms of hypersensitivity have appeared in the host cells (131,132,135).

Heath (55,56), working with several hosts and nonhosts inoculated with U. phaseoli var. vignae, demonstrated that the interaction between host cells and the parasite takes place at different stages during the infection process. The specificity can be expressed at each one of these stages, which were referred to as "switching points."

Later, Tani et al (134), using incompatible combinations of oat and P. coronata f. sp. avenae, observed that the events which determined the resistance response by the host cells occurred at the prehaustorial stage of fungal development, and the limitation of fungal growth was not caused by the death of the host cells. In this case it seems that the limitation of the fungal growth was due to the production of antifungal substances by host cells.

In the C. arabica-H. vastatrix system, very little is known about the interaction between the two organisms. The initial development of the parasite after inoculation is the same in both compatible and incompatible combinations. According to Rijo (107) and Rijo and Rodrigues (109), the differences between the two combinations start to appear only about the third day after the inoculation. In the incompatible combinations, fungal growth stopped in the prehaustorium stage or sometimes after their formation in the subsidiary cells.

Studies being undertaken in our laboratory using the fluorescence technique have shown no differences until the haustoria have formed in mesophyllic cells. Under our conditions this starts to occur not earlier than three days after inoculation. The course of events in the interaction is being studied in close association with cytologic and biochemical changes in the host cells and parasite hyphae in order to

determine the first steps in the interaction between C. arabica and H. vastatrix.

The macroscopic symptoms of the hypersensitive reaction in coffee leaves are already known. The hypersensitive reaction is characterized by the appearance of chlorotic flecks (fl) which many times are associated with small tumefactions, usually called type t reaction (107). This hypersensitive reaction can also be induced in the absence of the parasite. According to Rodrigues et al (118), similar symptoms of tumefactions can be induced by treating coffee leaves with the wash-water filtrate of urediospores of either avirulent races of H. vastatrix or non-pathogens such as U. phaseoli typica, U. fabae, and U. transversalis. In this case, the results suggest that a nonspecific mechanism of defense is involved rather than a species specific one. The coffee host cells respond similarly with a hypersensitive reaction to the presence of metabolites or toxins released into the water-washes from at least these three fungi which are nonpathogenic to coffee plants.

Considering the contradictory arguments about the relation between hypersensitivity and resistance response in plants, it would seem more prudent to undertake further studies on this subject mainly with C. arabica-H. vastatrix before drawing conclusions about whether hypersensitivity is the cause or consequence of resistance in the host.

Compatibility and incompatibility are intimately associated with the genetic potential present in both the host and the parasite. Thus, the concepts of susceptible or resistant host behavior toward the invader become strictly dependent on the degree of genetic relationship between the host and the parasite during their interaction. In other words, for our system a particular coffee cultivar will behave as a compatible or an incompatible host toward two different physiologic races of H. vastatrix according to the genetic relationship between them. But not only is the genetic relationship important, environmental factors also can play an important role in the final host behavior.

According to Flor's theory (48), the specific race resistance shown by a particular host cultivar results from the interaction at the molecular level of resistance genes in the host and avirulence genes in the parasite. However, it is obvious that this interaction does not occur between the genes themselves but between their end products whose syntheses are genetically controlled by the respectively mentioned genes. Thus, an end product of a specific gene for avirulence in the parasite is necessary to elicit a specific resistance response in the host. Both end products show the same specificity as the genes that control their syntheses. This concept is very important because it suggests that no specific end product would be formed unless at least one dominant gene of a pair of genes was not present.

Bettencourt and Carvalho (10), working with the C. arabica-H. vastatrix system and following Flor's theory of matching genes in host and pathogen, concluded that there were at least six genetic factors for resistance (S_H1-S_H6) in the host and a putative set of six matching virulence factors (V_1-V_6) in the pathogen. Their work was based on inoculation studies of 18 physiologic races of the rust, a set of differential host cultivars, and test crosses of the host.

At this point it is important to make an observation about the nomenclature used for the genotypes for resistance in the host. In spite of genes being dominant and controlling resistance in the host, they are indicated by symbol S_h which gives the idea of genes for susceptibility to H. vastatrix. However, they should not be considered as genes for susceptibility since they are used to determine the resistance in C. arabica and Hibrido de Timor.

Black et al (16) and recently Habgood (54) have proposed new systems of nomenclature for the genetic inheritance of resistance and virulence, which were used for the coffee-H. vastatrix system. Robinson (111) presents an extensive review of this new approach.

Continuing in a compatible combination, the presence of a virulence gene v in the urediospores would be responsible for the lack of some specific

substance(s) produced as end product(s) of the avirulence gene and required to interact with specific end products of the resistance genes in the host and to stimulate the resistance response in this host.

Both end products of resistance and avirulence genes would be considered as the primary step in the host-parasite specificity through a specific mechanism of recognition between the host cells and the parasite.

SPECIFIC RECOGNITION MECHANISMS

Since the beginning of this chapter we have been moving to our main objective, the host-parasite specific interactions at their most primary steps--the molecular level.

As was mentioned, the specificity in systems that follow the gene-for-gene theory depends upon the interaction between the end products coded by both resistance genes (R) in the host and avirulence genes (A) in the parasite. A "hybrid" molecule resulting from this interaction could act as a "stop signal" (103) and trigger the resistance mechanism in the host. This would be expressed through the hypersensitivity response involving several cytologic and biochemical changes in the host tissue. The substances involved as end products in this interaction have not been identified. However, it seems probable that they are macromolecules such as proteins, glycoproteins, or even complex polysaccharides.

Host cell membranes contain many proteins, glycoproteins and polysaccharides of unknown functions, but it has been verified that they have carbohydrate-binding activity (20,66,67,130). Such molecules referred to as lectins are widespread among plants and could be involved in the specific recognition mechanism between host and parasite by binding sugar residues from complex carbohydrates found in cell walls or in haustorial membranes of the pathogen. Thus, the resultant specific interaction could represent the most primary step of the recognition mechanism. Several hypotheses have been postulated as attempts to explain this specific interaction.

Albersheim et al (3,4) suggested that the end product of an avirulence gene A is a specific glycosyl transferase, active in the synthesis of complex carbohydrates which are located in the cell surface of the parasite hyphae and/or via glycoproteins secreted by it. On the host side, these authors proposed the existence of specific receptors in the cellular membranes genetically controlled by a resistance gene R, which are able to "recognize" and interact with the sugar residues from the complex polysaccharides or glycoproteins found in the surface of the parasite. This interaction mechanism represents a highly specific recognition system different from nonspecific recognition mechanisms. According to this theory the glycosil transferase would code for a particular residue or groups of sugar residues present in the cell walls of the infectant fungal hyphae. Those residues would be "recognized" by the host, to the extent that they could be bound to specific receptors present in the wall of host cells. The chemical nature of receptors is also still unknown, but several authors defend the idea that they are lectin-type proteins or enzymes. However, their relationship and varietal specificity is contestable. In the case of compatible combinations, due to the lack of one or both resistance and avirulence genes, the corresponding "receptor" in the host and/or the "inducer" in the parasite would be lacking and thus no interaction would take place.

One of the most interesting examples of the importance of lectin-like substances in specific mechanisms of defense, such as agglutinating factors of microorganisms, was presented by Uritani et al (136). According to them, an agglutinating factor of high molecular weight, consisting of polysaccharide and protein extracted from sweet potato, was able to agglutinate in vitro spores of incompatible races of Ceratocystis fimbriata, but not the compatible ones.

Also, fungal extracellular enzymes possessing carbohydrates in their molecules could interact specifically with the host lectins. Some of them were even considered as possibly taking part in the host-parasite specificity. However, the experimental data

did not support this hypothesis and the mechanism involving the interaction was considered nonspecific (2,3).

Interestingly, not only proteins, glycoproteins, and polysaccharides were suggested as taking part in the host-parasite specificity. Several researchers (59,60,119,120) showed that nucleic acids (RNA) can be directly involved in the resistant reaction of wheat to P. graminis f. sp. tritici. The authors isolated a gene-specific RNA which was able to induce necrosis in the wheat cells. Independently of the chemical nature of those specific end products involved in the primary recognition mechanism, it is quite probable that they are associated with the host plasma membrane and with the hypha and/or haustorium membranes in the parasite. This concept is particularly important for those fungi wherein the first cytologic contact is fully accomplished during the haustorium penetration. This fact does not imply that other nonspecific recognition mechanisms cannot act in earlier phases of the fungal penetration into the host tissue. Elicitation of antimicrobial substances, the so-called phytoalexins, can be an example of those early nonspecific recognition mechanisms (2). Elicitors from different parasites can act similarly in the same host, stimulating phytoalexin accumulation in host tissues. Another important point regarding this type of nonspecific response mechanism through a nonspecific recognition mechanism is that the same elicitor can stimulate the accumulation of all of the phytoalexins produced by a determined host plant.

The formation of phytoalexin-like substances in leaves of incompatible combinations, but not in the compatible ones, is shown in the C. arabica-H. vastatrix system (82,116). Moraes et al (86) and Martins et al (77) also demonstrated the formation of phytoalexin-like substances in mesocarp of unripe coffee berries and leaves from compatible and incompatible combinations. Coffee berries, even from a compatible cultivar, react with any specific race of coffee rust to give an incompatible combination. The chemical nature of the antimicrobial substance(s) elicited in coffee plants has yet to be identified.

Preliminary studies showed that it was a low-molecular-weight substance, soluble in ethyl acetate and insoluble in water, being biologically active against spore germination and hyphal growth of other fungi, pathogenic or not to coffee plants.

One of the most important theories regarding the host-parasite specificity that has kept the attention of researchers is the concept of common antigens. According to this theory, both host and parasite have identical antigens which are referred to as "common" antigens. Using this theory, it may be possible to know why plants can recognize "non-self" particular parasites and react to them.

The theory of identical antigens started with Doubly et al (32) and followed Flor's theory (48) of the gene-for-gene relationship between flax cultivars and physiologic races of the flax rust Melampsora lini. These authors, using isogenic lines of flax resistant to different physiologic races of flax rust, prepared antigens from each one of these isogenic lines as well as from each one of the physiologic races of the flax rust. The preparations were also used to make the respective antisera to each one of the antigens. Through serologic tests between all possible combinations of the several antisera and antigens, the authors observed that in compatible combinations both the susceptible cultivars of flax and the virulent races of flax rust had some indentical antigens which they called common antigens. Later, Wimalajeewa and De Vay (143) working with the maize-Ustilago maydis system showed that the identical antigens of both were proteins.

De Vay and Adler (29) claimed that the antigens that were identical in both host and parasite may account for the host-parasite specificity. They also demonstrated that the identical antigens are present in both resistant and susceptible cultivars but at different proportions.

In spite of all the work done and data obtained to date, there is no conclusive evidence that identical antigens play a role in pathogen specificity and in the specific recognition mechanism. Considering the system C. arabica-H. vastatrix, it is already

known that among the substances present in the surface of urediospores that can also be released into the water washes are the so-called common or identical antigens. They can also be extracted from the walls of urediospores through a mild acid hydrolysis (1). However, when filtrates of water washes of autoclaved urediospores were used, no reaction for identical antigens was detected. When different host-parasite combinations are studied, the subject is truly fascinating.

According to Alba et al (1), preparations from coffee leaves of physiologic groups D and E, resistant and susceptible respectively to H. vastatrix race II, were assayed in double-diffusion tests against antisera from filtrates of triturated urediospores. The data suggested that the identical antigens in the urediospores and coffee leaves precipitate at 80% ammonium sulfate and at 60% ethanol. The fraction of ethanol precipitate obtained from preparations of coffee leaves of group E reacted with the antisera (i.e., at lower levels of protein and carbohydrate concentration) than equivalent amounts obtained from preparations of coffee leaves of group D. This agrees with the hypothesis of antigenic disparity between host and parasite which was observed earlier (1), suggesting that the identical antigens have heterogeneous characteristics. Further studies are suggested on the chemical nature and structure of the identical antigens as well as on their role in the host-parasite interaction.

As already mentioned, complex carbohydrates, proteins, and glycoproteins are present on the surface of urediospores of H. vastatrix and are easily released into their water washes. Enzymes such as esterase-like compounds were also detected in urediospore filtrates (88,89), but their action during the germination process was not validated. During the infection process the fungal hyphae may produce other substances which, being released into the host tissue, can reach the host cell membranes and interact with their "receptor" sites.

However, we do not know what kind of substances may be involved in this interaction. Proteins,

glycoproteins, polysaccharides, and nucleic acids could be involved. Experiments are being conducted to obtain more information.

INDUCED PROTECTION IN HOSTS TO PARASITES

By induced protection we mean the phenomenon through which a plant can be protected against a parasite by a previous treatment with a nonpathogen, an avirulent race of a pathogen, a heat-killed pathogen, or with abiotic inducers such as light, metabolites, temperature, metal ions, and ultraviolet rays, to name a few.

For several years, researchers all over the world have been trying to demonstrate that plants, like animals, can react to a kind of immunization and acquire a certain degree of protection or resistance to a pathogen. We will not present the historical data, but we want to stress the work done by Johnston and Huffman (65) on the induced protection in wheat plants to rust by self-inhibitors released by urediospores of oat rust. Yarwood (145) also verified the efficacy of urediospores of bean rust (U. phaseoli) in inducing protection in sunflower (Helianthus annuus) against sunflower rust (P. helianthi).

Recently, Littlefield (69) induced resistance in susceptible cultivars of flax to virulent races of M. lini by previous inoculation with avirulent races of the pathogen.

Protection can be induced locally or systemically in plants. Most of the research on this subject was done with nonbiotrophic fungi. According to Elliston et al (34-36) and Rahe et al (104), two distinct types of induced resistance to Colletotrichum lindemuthianum can be observed in Phaseolus vulgaris plants. The first type, locally induced resistance, was obtained by first inoculating with a nonpathogenic race of Colletotrichum lindemuthianum followed by inoculating the same site with a pathogenic race. The second type, systemically induced resistance, was obtained by first inoculating with a nonpathogenic race of Colletotrichum lindemuthianum followed by inoculating a different site (a short distance away from the

first) with a pathogenic race. Data suggested that cultivars of Phaseolus vulgaris, apparently susceptible to all known races of Colletotrichum lindemuthianum, were locally and systemically protected from later inoculation with the pathogen. Also a nonpathogen such as Colletotrichum lagenarium was able to induce protection in green bean to Colletotrichum lindemuthianum (36).

In the C. arabica-H. vastatrix system, Moraes et al (85) and Beretta et al (7) demonstrated that a previous treatment of coffee plants from physiologic group E with filtrates of water washes of H. vastatrix race II urediospores (compatible combination) could induce protection in the host from further inoculations with the same physiologic race of the pathogen. Interestingly, the protection was obtained at a distance from the site of the inducer application, suggesting a systemic reaction of the host to the inducer.

Later, Martins et al (76) showed that other rusts and facultative parasites nonpathogenic to coffee plants were also able to induce resistance in coffee plants to a virulent physiologic race of H. vastatrix. Bacteria can also act as inducers of protection to coffee plants (76). Among them, Bacillus megaterium and Xanthomonas manihotis gave the best results when used in suspension as inducers.

The biochemical mechanism through which the induced protection is stimulated in the host is unknown. It appears that a nonspecific mechanism is involved and that substances present in the filtrates, assayed as inducers, activate physiologic and biochemical changes in the host in such a way that it becomes resistant to further attacks by the parasite. The length of time during which the plant is protected is short-lived, but it could possibly be increased by successive treatments before the inoculation with the pathogen. This will be the object of future investigations, as well as to determine the efficacy of the inducer from urediospores of H. vastatrix supplying protection in other systems.

Regarding the chemical nature of the inducer in our system, the data suggest that it is polysaccharide

and heat-stable, with a wide-ranging molecular weight (84). Further studies are being undertaken to determine the precise chemical structure of this inducer and its mode of action.

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CHEMICAL CONTROL OF COFFEE LEAF RUST IN CENTRAL AMERICA

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Leaf rust (Hemileia vastatrix Berk. et Br.), today's major disease of coffee in the Americas, has spread north from the original foothold in Nicaragua to now encompass El Salvador, Honduras, and Guatemala in its debilitating grasp. The chemical control programs for this invasion were not evolved but simply transferred from the control experienced regions of Africa, then Brazil, and finally to today's Central American arena. The required fungicides for this campaign went to the proprietary coppers plus a new unique systemic curative, triadimefon (144).

As given, we have at hand today's chemical tools for economic control which are in use as the checkmates for leaf rust. Now, let us review the melding of basics, known and prognosticated, as our stepping stones to better understand the spray programs suitable to coffee culture in Central America. These basics will include the target, the pathogen's field dynamics, field survey assessments for spray scheduling, and the behavior and use of chemicals in relation to this overall panorama.

THE TARGET

All of the commercially important coffee species are evergreen woody perennials. They have a single

main stem which elongates vertically and remains vegetative, with leaves and flowers being produced on the lateral branches. The lateral or side branching growth depends on age. The lower branches, which are the oldest, show the greatest growth. Therefore, coffee trees in general have a typical conical shape with all new foliar growth on the outer shell of this cone.

Coffee leaves are ovate or elliptical with a wavy margin. The upper leaf surfaces have a slightly elevated midrib extending the leaf length, and the surface is glossy due to the high waxy cutin content. Two leaves at a time are borne at each node, presenting a horizontal arrangement as leaf pairs on the branches. These lateral branches are usually quite flexible and tend to bend downward in the younger, less woody parts, especially when they bear fruit. As based on tissue development within each expanding new leaf, the youngest tissue is marginally oriented and conversely the oldest is in the midrib region.

The horizontal position of all leaf pairs is most favorable for photosynthesis as well as receiving and bouncing impacting raindrops, urediospores, and fungicide sprays. The period of the flush of new leaf formation coincides with the spring rains and continues into that growing season producing a new pair of leaves from terminal growth about every 21-25 days. This paired leaf production period is dependent on the local climatic conditions of temperature, rainfall, and solar radiation (R. H. Fulton, unpublished).

FIELD DYNAMICS

An understanding of how the fungus operates in harmony with the host's seasonal physiological behavior is essential to the whys and hows of chemical control programs. In the field the coffee leaf rust seasonal cycle, which exists in three distinct phases, is typified as follows.

Phase I. The disease pressure is at its lowest field level during and at the end of the dry season. This also coincides with the period of leaf fall of both rusted and noninfected leaves.

Phase II. The initiation of the spring rains and a corresponding increase in field ambient temperatures. Herein, foliage development and growth begin and accelerate into the season with similar compounding of leaf rust infections.

Phase III. This phase is the typical real or explosively spectacular stage as the trees are at full foliar capacity, field temperatures are ideal for fungal development, and rains are frequent for pathogen dispersal. This culminates in local field epidemics, peaking after foliar expansion but in harmony with the next season's flower bud initiation-formation phase. Crop losses to leaf rust indirectly are initiated at this phase of the cycle by the draining of host reserves through leaf abscission and in turn debilitating the next season's flower bud potential.

The given phase analysis of coffee leaf rust epidemics is not confined to this disease but is a common denominator for other tropical crop foliar-fruit pathogens. Nonetheless, this information pinpoints that for successful chemical control programs one must start early on, during the spring rains, to keep the initial urediospore infection footholds to a minimum on the rapidly expanding foliar area.

Interestingly, the susceptibility of coffee leaves varies inversely with their age (95). Rust urediospore germinations on juvenile leaves of the proximal internode are 50% higher than the intermediate leaf node pairs of leaves and over 65% compared to leaves in node positions 4 to 5 (Fig. 1). Likewise, due to the later stages of leaf marginal meristem development, urediospore germinations in this more juvenile area were 30% higher than in the leaf midrib areas (17).

The dispersal of urediospores to the target is common during rains. The three-dimensional splash dispersal mechanism is clearly depicted in Figure 2. Water droplets containing urediospores move to the leaf tip or to an undulation on the leaf margin, and the impact of continued raindrops scatters these spores to adjacent leaves. A urediospore dispersal period is defined as a single or group of showers in excess of 7-8 mm. Upward splash dispersal of spore-

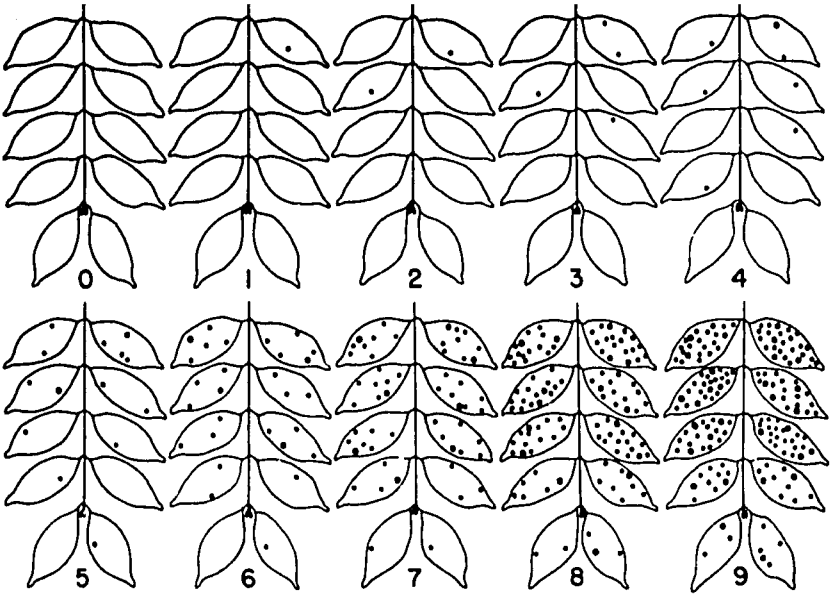

Fig. 1. Disease assessment scale as represented by the average disease incidence per diseased branch. (Reprinted, by permission of the Food and Agriculture Organization of the United Nations, from [43].)

laden droplets to the infection court occurs easily during precipitations of 14 mm or more (17,19,58). The movement of spores to the lower leaf surface has now been effected, with actual leaf invasion now being influenced by the concentration of these urediospores at this site. Noteworthy is that the threshold concentration for actual leaf infection is in the range of 16-20 urediospores per cm^2 and such concentrations of spores, or greater, will occur in a direct linear manner with rainfall intensity (95).

FIELD SURVEY DISEASE ASSESSMENT

A major aspect of evaluating fungicide products and importantly field implemented programs was the establishment of reproducible assessment methods on a quantitative measurement basis, simply a uniform

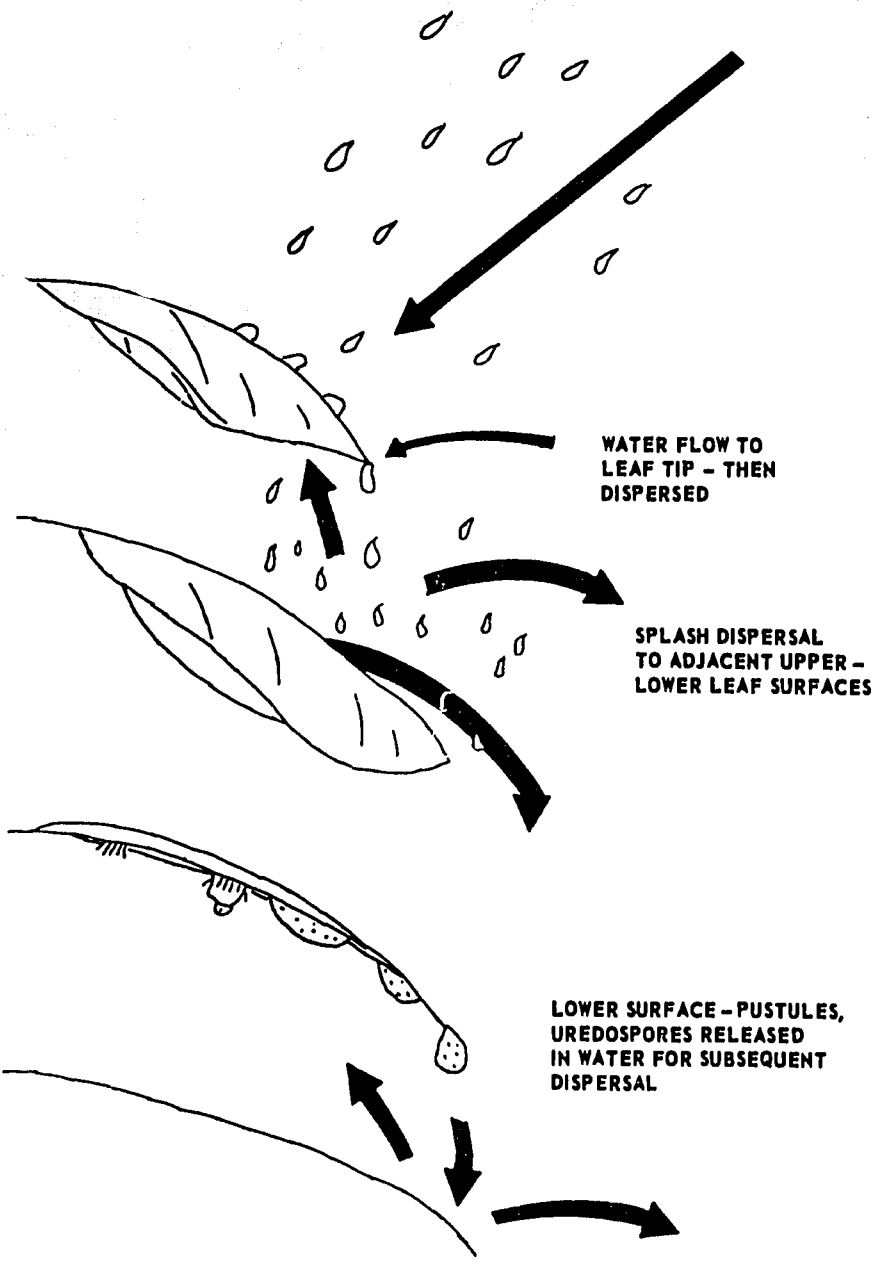

Fig. 2. Uredospore splash dispersal.

recording system for comparing data from diverse global areas and/or individual farms within a given region.

Leaf rust parameters that correlated well were the number of lesions per leaf and the percentage of diseased leaves. For measurement accuracy of rust incidence in the field, the number of lesions per leaf was the most reliable parameter. Through the collaboration of the FAO and the Instituto Agronomico of Campinas, SP, Brazil, field disease-assessment scales have been designed which give comparable results (Fig. 1) (43). The writer (unpublished) and researchers in the varied coffee regions of the world have in turn employed these scales or slight modifications of same for comparisons of control programs.

Figure 3, which employs the whole tree as an assessment unit, has been quite successful in delimiting focal disease pressure or "hot spot" areas of the

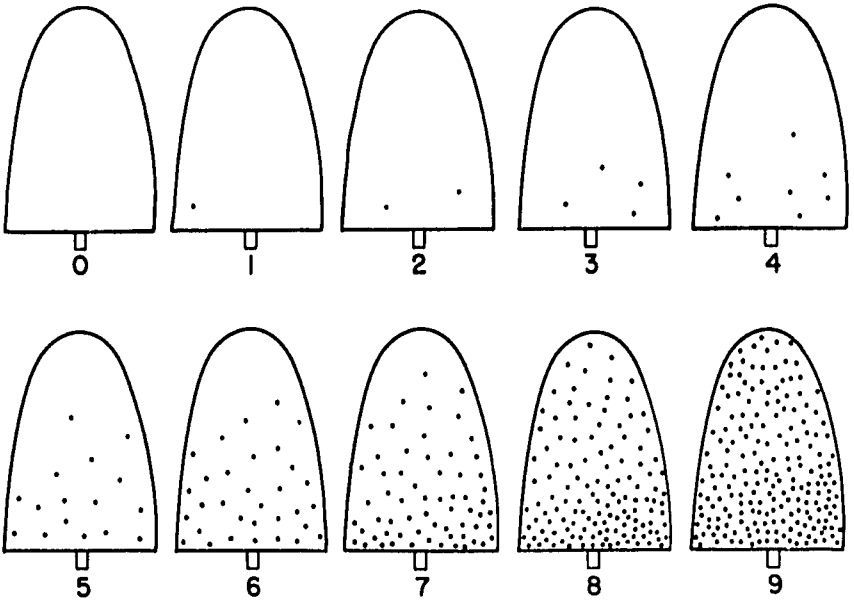

Fig. 3. Whole tree assessment scale. Each dot represents the number of diseased branches. (Reprinted, by permission of the Food and Agriculture Organization of the United Nations, from [43].)

field. In unshaded coffee, this assessment scale is advantageous since the initial and compounding epidemic builds up in the lower canopy of the tree, called the skirts. This is due to the open and exposed nature of this cultural growing method which enhances downward splash dispersal movement of the urediospores. In the Figure 1 assessment scale, each small dot represents a sporulating rust lesion; larger dots represent a coalescence of two lesions. This scale is realistic, since the older paired leaves on the branch are more visibly infected (completed incubation periods) than encountered in younger leaf pairs (i.e., disease in incubation).

Nonetheless, the use of such defined field survey methods has been of valid use for comparisons of integrated versus purely protectant schedules (99) as well as defining critical threshold levels of application for the curative-eradicative systemic triadimefon (144).

USE OF CHEMICALS FOR COFFEE LEAF RUST CONTROL

As in the past, today the copper protectant fungicides and at least one systemic will carry the major part of the control burden; and it seems likely that these control tools will continue to hold true for the foreseeable future. Their proper use in Central America has been, of course, a major theme of action on the local scene. An overview of these varied action phases follows in harmony with former basic leaf rust control studies.

The movement of the urediospores through the conical coffee tree foliage has been defined, and thus the placement of fungicide sprays over-the-top and on the peripheral areas of the trees has been the effective method of deposition for control (101,102).

The recorded amounts of rainfall to effect urediospore distribution closely approximate 7-8 mm, below which dispersal by leaf tip dripping does not take place (17,95). The rust pathogen penetrates the leaf tissues entirely via the stomata on the lower leaf surface, and urediospores reach this surface by rain droplets impacting on the upper surface of the

leaves (Fig. 2). Thus, the spore-laden rain splash incident droplet impacting on the underside of leaves will have first passed over the fungicide-deposited surfaces of the upper leaf canopy. These water droplet contacts with the fungicidal residues result in their redistribution from the initial residual deposits of the upper surface to that of the underside of the leaf (17,58,95,102). In retrospect, it is obvious that in unshaded coffee cultural areas the lower branches of the conically shaped coffee tree will have more infection, as is the case (19,43).

Considering that the urediospore and fungicide redistribution movement is within the host's conical sphere of area, then the key to control is early protectant coverage sprays of the young suscept leaves. This is logical, for the first rain dispersal period and infection outbreak is not derived from trees at a distance but from rust pustules at close range within the same tree (19,95).

Basic facts on the use of the proprietary coppers were essential so as to not repeat errors in history, as is common to early stages of chemical disease control programs. Salient facts were as follows: 1) spray intervals in excess of 21 days lead to control failure since new susceptible leaf pairs are formed about every 21 days (19,99; R. H. Fulton, unpublished); 2) copper deposits not only redistribute via splash dispersal during rains, but also their small satellite droplets are eroded from around the original droplet, limiting the final droplet zone of protection to the immediate area under the visible residue zone (57,58,102); 3) copper deposits do not possess the unique vapor phase zone of protection as is common with mancozeb or maneb, thus redistribution is the only compensation for poor canopy coverage (57); 4) tank mixes of proprietary coppers with mancozeb (ratios of 2:1 or 1:1) have been successful in control (R. H. Fulton, unpublished); 5) applications of either low- or high-volume (10-800 L/ha) have been equal in control efficacy (47,99,140); 6) an overall control key has been to apply proprietary coppers, at 3-5 kg/ha of product, with annual spray numbers based solely on foliage intensity; for example, four sprays

for little foliage and six sprays for farms of high foliage canopy and a good potential crop.

Although pure copper spray programs for years have been in the mainstream of coffee leaf rust control, this has not been without the adverse effects of field explosions of leaf miners (Leucoptera coffeella), spider mites (Oligonychus ilicis), increased coffee berry disease (CBD) (Colletotrichum coffeeanum Novack), and increasing accumulations of copper in the plantation soils. Accordingly, with these facts in mind there have been degrees of shifts from these historic pathways for the Central American programs. First away was that of high-volume sprays as water logistics posed an impasse because of terrain and unavailability. Lower volume sprays of 50-100 L/ha are common in the area. Next was that of the frequency of sprays since rain splash dispersal in shaded coffee was less intense, which in turn relegated spray numbers to a range of three to five per year. Then, too, it was verified that cupric hydroxide was less phytotoxic (99) than other proprietary coppers, so this compound remained as the program mainstay while the systemic triadimefon became the integration key for curbing explosive epidemics.

Triadimefon demonstrated curative and eradicative properties against leaf rust and in turn managed rust pustule outbreaks at thresholds of 20-40%. At the grower level, however, field assessments of these percentages were better handled at a minimal range of 15-20%. This is to maintain a substantial reduction of rust pustules in the foliar canopy and, in turn, fewer overall applications per year. In general, only one and occasionally two sprays of triadimefon are required per season.

In the end, the successful adaptation of the integrated program concept, the placement of protectant copper sprays early on in the season with the deployment of triadimefon to arrest the spread of rust via curative action on urediospores and inhibiting further sporulation, has placed the control of coffee leaf rust in Central America on sound economic footing.

CENTRAL AMERICAN COFFEE RUST PROJECT

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Coffee production is by far the most important agricultural business of the Central American area. It is now facing two serious problems, coffee rust (Hemileia vastatrix) and coffee berry borer (Hypothenemus hampei), which, if not handled effectively, will threaten coffee activity in the region as a whole. This in turn will have a negative impact on the social, economic, and political stability of the area.

Because of this, the countries of Mexico, Central America, and the Dominican Republic have turned to coffee improvement programs as a way to increase the economic efficiency of coffee cultivation and to tackle coffee problems from a technical standpoint. These programs have also facilitated access to the wealth of modern coffee technology that has been developed throughout the world during the last few decades.

In addition, the countries have joined in a regional endeavor (Regional Cooperative Program for the Protection and Modernization of Coffee Cultivation in Mexico, Central America, and the Dominican Republic, or PROMECAFE), creating a program to support their national effort. This effort, in turn, has received the support of other agencies, including the USAID Regional Office for Central American Programs, or ROCAP.

THE IMPORTANCE OF COFFEE TO CENTRAL AMERICA

Central America provides roughly 13.8% of total world coffee production (Table 1). An estimated 60 million bags of coffee will be exported this year by the cited countries. According to the Central American Bank for Economic Integration (BCIE), the value of exported coffee in billions of $CA (1$CA = 1$US) was 1.825 in 1977 and 1.636 in 1978.

The same publication further estimates that coffee exports represented 12.0% of the region's gross domestic product in 1977 and 9.9% in 1978. This income pays taxes that fund many of the country's development projects. According to the BCIE, coffee produced 352.8 million Central American pesos in 1977 and 270.2 million in 1978. Nicaragua and Panama are not included in these figures.

In regard to its impact on the labor force, coffee is estimated to provide full employment to half a million rural workers. In El Salvador alone, it is calculated that coffee provides employment to 19% of the economically active population. A study made in Colombia, which can be applied to Central America, concludes that a traditionally worked coffee planting of 1 ha having a population of 1,000 trees generates

Table 1. Coffee production in Central America

Country	Total production	Exportable production	Domestic consumption
Costa Rica	1,880	1,660	220
El Salvador	2,400	2,200	200
Guatemala	2,600	2,275	325
Honduras	1,312	1,200	112
Nicaragua	1,050	965	85
Panama	160	7	153
Total	9,402	8,307	1,095

Thousands of 60-kg bags, 1980-1981 harvest.

Source: USDA, Foreign Service, October 1981.

470 working days during seven years of investment and production. A similar area using moderate levels of technology, with 4,000 trees and regulated shade, generates 2,385 working days, and finally, a coffee plantation using high levels of technology, with 8,000-10,000 trees, generates 3,149 working days during the same period. This gives a ratio of 1:5:7, which means that 1 ha of traditionally farmed coffee provides permanent employment to 1.6 persons a year, whereas a farm using a maximum of technology will hire 10.5 persons during the same period. In addition, coffee activities provide employment in the areas of transportation, banking, sack and basket manufacturing, and many other areas in which people are indirectly employed as a result of coffee production.

Contrary to popular belief, coffee production is in the hands of small and medium-scale farmers (Table 2). Almost 86% of coffee producers are small or medium-scale farmers. In addition, all coffee production in the area is a national concern.

Of the countries, Costa Rica uses among the highest levels of technology. A study of its production costs for 1980-1981 revealed the breakdown shown in Table 3. These figures do not include export taxes, customs duties, export-level transportation, processing, profits for the processing plants, and other expenses. In any case, it is clear that the coffee dollar is broadly distributed among the inhabitants of a producing country.

Table 2. Number of coffee-producing farms

Country	All farms	Small farms
Guatemala	43,352	34,000
El Salvador	43,779	34,569
Honduras	38,800	37,881
Nicaragua	17,483	14,924
Costa Rica	65,000	55,250
Panama	30,742	29,000
Total	239,156	205,624

Table 3. Coffee production costs in Costa Rica, 1980-1981

Item		Expense (%)
Labor		10.6%
Agrochemicals		13.6%
Harvest expenses (coffee-picking)		25.5%
Other expenses		50.3%
Depreciation	2.8%	
Repairs	0.5%	
Administration	4.1%	
Taxes	0.5%	
Interest	37.9%	
Transportation (farm level)	0.5%	
Fences	0.5%	
Coffee and shade trees	3.5%	

PROBLEMS OF COFFEE CULTIVATION

Given the foregoing conditions, one can easily imagine what would happen to a country when coffee activities are affected by a disastrous disease like rust, or a pest like the borer. The situation is further aggravated by the low prices paid for coffee on the world market, the high costs of inputs necessary for production, the high cost of labor, and especially the low yields of small and medium-scale farmers who do not have access to credit or modern technology.

These conditions led the countries of the area to decide that a practical and efficient measure was necessary for joining their efforts to carry out research, staff training, extension, advisory, and other types of projects, and likewise to adopt basic measures that would help develop and protect regional coffee cultivation, especially among small and medium-scale coffee farmers.

This was the background against which PROMECAFE was founded in January 1978. The Program united the efforts of Mexico, Central America, and the Dominican Republic as well as those of the Inter-American Institute for Cooperation on Agriculture (IICA), the Tropical Agriculture Research and Training Center (CATIE), and the Regional International Organization of Plant Protection and Animal Health Care (OIRSA).

Since then, the Program has been at work at its headquarters in Costa Rica. It receives funding from the countries and from IICA. The head of the program is a horticulturist, who is assisted by a plant pathologist and a communicator.

During the short life of the Program, an intense exchange of publications has been established among coffee technicians; the great majority of the technicians have been involved in training with some phase of modern coffee cultivation; consultation service has been provided to several countries on specific subjects or problems; research has been conducted on matters at the specific request of the countries; numerous meetings of all kinds have been held which have not only provided communication among technicians, but also have increased the ties among coffee organizations in the area; improved genetic materials have been distributed to all the countries; and special attention has been paid to improving methods for transferring technology among extension agents working with coffee in the area.

Perhaps the best measure of PROMECAFE's work is the collaboration and support it has received. In late 1981 the Dominican Republic requested admission to PROMECAFE. The Brazilian Coffee Institute donated substantial funds to enable the Antillean countries to be included in some of the Program's activities. The French Coffee and Cacao Insitute assigned one of its technical specialists to work with the Program's staff during the last two years.

No less important has been the economic support that the member countries have provided, despite the very serious economic problems they are all facing,

and the support of CATIE and OIRSA. USAID/ROCAP donated funds to the Program for conducting research on the status of coffee production in the area and to determine the best type of support that can be provided to national and regional efforts to save coffee cultivation. The Central American Coffee Rust Project resulted from this study.

THE PROJECT

The Central American Coffee Rust Project is funded by a USAID/ROCAP donation of US$3.5 million, which was added to the US$1.576 million provided by the regional agencies involved and the US$2.073 million provided by the countries. The total of US$7.149 million will be invested over a five-year period and will serve to increase the actions in support of national and regional efforts already underway in order to expand, accelerate, and intensify them as much as possible. Although the project is administered by PROMECAFE, it is hoped that all the agencies involved will participate. Project results will be available to all, although the project is geared to be of special use to small and medium-scale farmers, who are seen as the prime beneficiaries of this effort.

The project contains six components:

Studies on the biology and epidemiology of rust. This project component will seek to accomplish two objectives. It will develop a basic understanding of the epidemiology of coffee rust and will determine the efficacy of available fungicides at the sites representative of the principal agroecological coffee-producing zones of the region.

To achieve these objectives, PROMECAFE will be responsible for ensuring that the necessary laboratory, greenhouse, and field studies are made, and will make available a long-term senior plant pathologist and several short-term specialists who will be funded under the project.

Studies on the biology of the coffee bean borer. This component will seek to develop an effective, economical control program for the coffee bean borer.

This pest is the second most serious threat to regional coffee production and has been found in Mexico, Guatemala, and Honduras.

OIRSA is currently engaged in a cooperative research effort, especially focusing on developing a more integrated methodology of control at the field level. PROMECAFE will make available a long-term senior entomologist and a short-term biological control specialist to work with OIRSA personnel. The project will also finance in-country travel costs, a greenhouse, limited laboratory equipment, field supplies, field equipment, and the preparation of training materials and part of the cost of short courses.

Residue analysis, control, and registration of pesticides. This component of the project will seek to develop a system, acceptable to the regional and national entities, for the analysis of pesticide residues and the establishment of standards for use and registration of pesticides in coffee production. The activity is closely linked with the efficacy studies of pesticides used in the control of rust, broca, and/or other coffee pests since coffee berry and plant tissue samples from those studies will provide the materials for analysis of residues.

In support of this activity, the project will fund short-term specialists in pesticide chemistry and pesticide registration to augment current PROMECAFE and OIRSA staff. In addition, funding for collection and shipment of samples, residue analysis, preparation of training and promotional materials, and short-term training will be provided under the project. PROMECAFE/OIRSA will compare the analysis data to the international standards recommended by the CODEX Committee on Pesticide Residues and/or the USEPA Standards and recommend adoption of such standards by each country in order to achieve regional and international uniformity.

Development and reproduction of rust-resistant varieties. This component will seek to identify new varieties of coffee that combine the characteristics of rust resistance, high yields, and good quality and to multiply, as rapidly as feasible, those varieties that perform at acceptable levels. PROMECAFE/CATIE

will take the lead in screening and identifying promising varieties, introducing new germ plasm, distributing experimental seeds or plants to national entities, and sending materials to international institutions for testing.

In addition, the project will finance a long-term senior plant breeder, a short-term tissue culture specialist, and three local contract assistants to work with CATIE core staff. The project will also fund specialized short-term training of national research technicians in Brazil and Portugal on the techniques of identification of races of rust, screening procedures, and field trial methodology of rust research. The project will finance procurement and operation of a vehicle, a laboratory and equipment for tissue culture, small-scale coffee seed-processing equipment, a greenhouse, a program for pedigreeing, processing and distribution of seed, and screening for rust resistance in Brazil and Portugal.

Development and adaptation of methods for transferring appropriate technologies. This component is a major project activity aimed at using results from the research activities to develop sound technicalization and pest control programs appropriate for application by small to medium-sized coffee farms. They will be based upon area and farmer-specific profile samples that describe production resources and modules, to name several constraints such as size of farm, topography, age of planting, spacing, water availability, labor availability, current inputs and management practices, credit availability, and markets.

Since communications represent a critically important element in the successful transfer of improved technologies, PROMECAFE will assign a full-time staff specialist to this activity as well as a long-term, project-funded communications specialist. Implementation of this component clearly will require close cooperation by the national-level agencies and the regional project in developing solutions based upon research, to consolidate the results into appropriate recommendations, and to assist national-level agencies to improve their research and outreach efforts.

Information network and data bank development. The objective of this component is to expand the quantity of coffee research data available to the regional and national research entities. A substantial body of technical information on coffee pests and production techniques has been developed around the world. Access to this information is important in order to minimize duplication of research as well as to remain aware of new developments. In addition, there is a need to manage and analyze research data generated by the project within the region.

Computer-based data and information systems already exist at IICA, which has access to world research literature and data through the FAO (AGRS) and USDA (Agricola and CRIES) as well as the IICA (SINIA and AGRINTER) programs.

The project will provide limited financial support to assist in the collection, storage, and analysis of data and documentation, and these funds will be programmed through PROMECAFE to fill gaps not adequately addressed by current regional activities.

AN EFFORT TO CONTROL AND POSSIBLY ERADICATE COFFEE RUST IN NICARAGUA

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In looking back to review history, we realize the importance of the words frequently repeated by Dr. Frederick L. Wellman, one of the most eminent specialists on coffee:

> I am afraid that our good fortune may be running out in Latin America. One cannot hope for anything but the best, but we should be prepared also for the worst. A long history of studies shows that the Hemileia disease does not stay quietly within the limits of countries, nor even locked within a continent. This makes us realize the daily increasing certainty that our coffee trees in the Western Hemisphere are going to get the Hemileia disease by means of the winds and the storms. Now we are almost certain that this is the natural way this disease is spread. It [the disease] will probably come in future years.

When coffee rust appeared in Brazil in January 1970, it was evident that Dr. Wellman's words had become a reality. This reality became even more dramatic when coffee rust demonstrated its presence in Central America, making its debut in Nicaragua at the end of November 1976. It has now spread to all of Central America and Mexico, except Panama (100).

On November 23, 1976, the Department of Agriculture and Livestock of Nicaragua was informed of the existence of coffee rust (H. vastatrix) in their coffee plantations. Although there was no doubt about the validity of this information, given its importance, it was considered prudent to send two Nicaraguan experts with infected leaf samples to Brazil to verify the pathogen and the race. They were confirmed on November 28, 1976.

In the face of this serious situation, the Department of Agriculture summoned the Executive Director of the Organismo Internacional Regional de Sanidad Agropecuaria (Regional International Agency for Agricultural Health) (OIRSA) (Mexico, Central America, and Panama) to an emergency meeting which officially proclaimed the existence of the disease, in compliance with the provisions of the Second Agreement of San Salvador. Subsequently, the Executive Director of OIRSA announced to the governments of all the countries in the area the existence of coffee leaf rust and recommended strengthening quarantine measures, especially in Costa Rica, Honduras, and El Salvador, in order to prevent by all available means the spread of this destructive disease.

At the higher levels of the Nicaraguan government, the decision had been made to initiate a campaign of control and possible eradication. The following national and international institutions participated in the campaign:

National: Department of Agriculture and Livestock, Central Bank, National Bank, Department of Public Health, Civic Military Action, Instituto Nicaraguense del Cafe (INCAFE).

International: OIRSA, Instituto Interamericano de Ciencias Agricolas (IICA) (Interamerican Institute of Agricultural Sciences), Food and Agriculture Organization of the United Nations (FAO-PNUD), AID Regional Office for Central America and Panama (ROCAP), Nicaragua-Germany Cooperative Technical Program, Brazilian Coffee Institute, Colombian Technical Mission.

DETECTION OF THE DISEASE

The outbreak was detected 45 km from the city of Managua, 2 km from the city of Jinotepe on the Jinotepe-San Marcos highway, in the district of Carazo, on the "Santa Elisa" farm.

JUSTIFICATION

The decision reached in Nicaragua to establish a program to control and possibly eradicate leaf rust was justified on the basis that one year of disease control meant at least one or two years of freedom from the disease for all the countries in the area, from Mexico to Colombia. Each year that the disease could be kept under control would mean that Central America could maintain its production levels--which could decline in the range of $100 million per year for two or three years after the disease spread throughout the coffee plantation areas--with a foreign exchange savings of $60 million for the import of production items. Also, it was estimated that during the two-year respite, the area countries could retain $320 million in foreign exchange. Even more important, the time gained could be used to modernize the industry of the region to counteract some of the effects of leaf rust on the balance of payments, production, and employment in the surrounding countries.

FINANCING

The effects that leaf rust could have on the coffee production and economy of Nicaragua and consequently of Mexico, Central America, and Panama would be of alarming proportions if no action were taken. Thus, the Nicaraguan government made the first financial contributions to the campaign with funds from the Central Bank, placing those resources at the disposal of the Department of Agriculture and Livestock. At the same time, Nicaragua imposed a tax of US$5.00 on each quintal (100 lb) of coffee for export. Later, Nicaragua secured "soft money" loans from the Banco Centroamericano de Integracion Economica (BCIE)

(Centroamerican Bank for Economic Integration), with monies coming from the Fund for the Central American Program for the Prevention and Eradication of Plant and Livestock Diseases. The initial amount was US$12.2 million, established by contributions from the Central American countries, Mexico, and Panama.

SETTING UP THE CAMPAIGN

Objectives were set during the first meetings of the technical committees, which demanded immediate action, such as the isolation of the area known to be affected by coffee leaf rust. The spread of the disease to other coffee areas was to be prevented by controlling the outbreaks in the sites already identified and in newly detected sites. Ideally, accompanying these actions with internal quarantine systems would complement their success.

One objective that received priority was to determine the presence or absence of the disease not only in the rest of Nicaragua, but also in the other countries within the OIRSA region. The results of all the surveys were negative, thus making possible the establishment of a campaign to control and possibly eradicate the disease.

As the campaign developed, it became necessary to create an organization to define the roles and responsibilities of the groups involved. Briefly, the activities of the survey, chemical control, and quarantine areas were relegated to teams.

Inspection

Infected areas can be detected through foliar inspections of coffee plants for early recognition of disease foci.

Chemical Control

Chemical control is one of the most important elements of a program of eradication such as that adopted in Nicaragua. It includes methods that delay

or prevent the pathogen from invading the leaves or actually eradicate established infection loci.

The Method of Eradication

The method used in the campaign against coffee rust, once it is detected, would be used on the infected plants and in buffer areas around the infected sites. A radius of 30 m is marked around the infected plants to include the buffer zone. A mixture of chemicals is applied immediately to the foliage of the coffee plants within this radius and afterward to the buffer plants, at a height of 30-50 cm. These operations are combined with a protective application of curative and protective fungicides to the peripheral area.

The specific chemicals used in these operations were as follows:

Desiccant-eradicant: Paraquat, 4 lb; diesel, 10 L; 50% copper fungicide, 1.5 kg; water, 200 L

Eradicant-protectant: Sicarol, 1.5 L; 50% copper fungicide, 1 kg; Agral (spreader), 150 cc; water, 200 L

EVALUATIONS

OIRSA, acting in agreement with member countries, called for five field reviews by experts to evaluate the status of coffee rust and the possibility of its eradication in Nicaragua. These reviews (98) were performed by recognized experts from the OIRSA area, international agencies, and cooperative countries.

Some of the main observations and recommendations of these evaluations are summarized here.

First Evaluation

In the first evaluation, June 13-17, 1977, by representatives of Guatemala, El Salvador, Honduras, Costa Rica, Colombia, and OIRSA, it was stated that, taking into account the opportunity afforded by the

location of the disease, efforts should be continued to achieve total success in the eradication of rust in Nicaragua, with all possible support from the other countries in the OIRSA area. The experience gained in Nicaragua might result in similar eradication efforts in other countries of the area should the emergency arise. Therefore, the first evaluation concluded that eradication should be firmly considered and that a determined effort should be made to improve crop technology and modernize, basically through technical assistance and farm credits.

Second Evaluation

The second evaluation was conducted from October 30 to November 5, 1977, by representatives of Mexico, Guatemala, El Salvador, Honduras, Costa Rica, Panama, and OIRSA.

This evaluation revealed that the results of the activities developed by the eradicative campaign against leaf rust in Nicaragua clearly showed that the technique used was effective. In spite of the rainfall during September and October, the number of disease outbreaks detected was relatively small, and it was anticipated that it would be reduced to zero within a period of two to five months.

It is worth mentioning that all this activity on the part of Nicaragua was very costly, but the end results allowed sufficient time for the area countries to prepare their own national campaigns, to initiate or strengthen the modernization of technology in coffee cultivation, and to thereby reduce the high costs of an eradication program.

With the exception of one pustule, which was located in replanted areas, no new cases were detected. The direct effect of the sun, the resulting increased light, and the low humidity of these areas may have contributed to the elimination of the pathogen since the records kept up to that time indicated a higher number of rust foci in plantings under intense shade.

Third Evaluation

The third evaluation was performed on June 11-17, 1978, by representatives of Mexico, El Salvador, Honduras, Costa Rica, Panama, and OIRSA. The coffee rust situation in Nicaragua at that time was characterized by very low, even imperceptible, levels of visible inoculum via continued inspection of the coffee region.

Analysis of the records for 1977 and part of 1978 showed a decrease in the sites of inoculum, beginning approximately during the last two weeks of April, continuing during May to August, and only increasing in intensity the last two weeks of September.

The apparent decrease in inoculum was the most noteworthy characteristic for that portion of 1978 in contrast with 1977, undoubtedly as a result of the campaign, which had a functional and dynamic organization under a director with a group of experts who worked with dedication and fervor.

These control actions leading to eradication were favored at the beginning of the year because of the low level of inoculum as a result of previous campaign actions and also because of the unfavorable environmental conditions and the physiologic condition of the coffee plants.

Despite the positive aspects of the picture, we knew and took into consideration the fact that the pathogen was still present in some coffee-growing areas of the Carazo region. We did not know the means of biological dissemination, whether it occurred as spores in the atmosphere, on the ground, on fallen leaves, on parts of trees in the shade, on the coffee plants, or on the leaves themselves.

Analysis of the charts showing the behavior of the disease throughout 1977 and in comparison with the portion of the current year clearly showed a substantial decrease in the appearance of the disease, closely interrelated to rainfall.

Fourth Evaluation

The fourth evaluation was performed on January 21-28, 1979, by representatives of Mexico, Guatemala, El Salvador, Honduras, Colombia, Brazil, FAO, IICA, BCIE, and OIRSA (140).

The field surveys had shown that the campaign against the rust was successful in keeping the inoculum inside the quarantined area. This reinforced the decisions to place extreme emphasis on a possible eradication. Since the maximum time period for field inspections was 30 days, this allowed for the detection of the disease in due time before well-developed pustules were produced.

The surveys pointed out localized foci of the disease near footpaths or secondary roads, which indicated that the fungus was mainly being spread by individuals or on clothing.

The peripheral sampling performed twice in 1977 and three times in 1978 determined the presence of the disease only in the areas of Las Nubes and La Concha.

The evaluation concluded that the control campaign was structured in a highly efficient manner and that, if the system was placed into effect, it was capable of dramatically reducing the levels or the number of coffee leaf rust outbreaks in a specific zone. To achieve eradication in two to three years, it was decided that the campaign should structure certain priorities that the working groups defined as necessary, making the maximum effort during 1979.

Coffee plant restocking within a 50-m radius of the foci is considered critically important in that the foliage of infected plants is eliminated; a vital factor in reducing inoculum levels. Therefore, restocking should be done in all cases in which "hot spots" of the disease are found.

The months of March to June are considered critical in the epidemiology of the disease because the inoculum that survives these months allows rust to develop in July or later. Therefore, all the campaign activities, especially the surveys and chemical controls, must be increased to the maximum during March-June.

Notwithstanding the significant reduction in the number of disease outbreaks in 1978, the distribution had been extended within the exposed quarantined area. However, for the success of the campaign, it was essential to avoid this spread. The coffee pickers (harvesters) and farm workers were then considered to be the principal spreading agents. For this reason it was recommended that efficient prevention and/or protectant chemical measures be put into effect.

Fifth Evaluation

The fifth evaluation was conducted on December 11-16, 1979, by representatives of Mexico, Guatemala, Costa Rica, Panama, and OIRSA. It was evident that the situation of coffee rust had changed during the past months, so new approaches and strategies were considered to eradicate it from Nicaragua.

The OIRSA board of experts presented the two alternatives that could be taken to eliminate the disease: rust eradication using the restocking method, involving the procedures recommended in the fourth evaluation, or eradication by elimination of coffee plantations and cultivation renovation, which implies the elimination of 10,000 ha (24,710 acres) of coffee plantations and their replanting later on. Each alternative was analyzed in all details, including the appropriate recommendations and budgetary considerations.

Rust eradication using the restocking method. This alternative was the same as was being used with some of the fourth evaluation recommendations, such as extending the restocking area to 50 m, increasing to the maximum the number of survey and chemical control personnel, and increasing the number of internal quarantine posts at the farm level for the control of workers who might spread the disease.

Transforming and renovating the agronomic structure of 10,000 ha of coffee in the Carazo zone. Basically, this plan consisted of replanting 10,000 ha of coffee with new varieties planted following a system of contour lines; the shade trees would also be replaced, and shelterbelts would be set. To

facilitate the eradication of coffee rust, all the areas in which the disease was present would be cut down immediately after the harvest. The replanting would not be done until at least one rainy cycle had passed, so that the spores that had survived could germinate in the absence of the host plant. At the same time, careful and intensive searches would be conducted in the peripheral and northern zones, and in addition, preventive copper treatments would be applied.

The seedlings for the replanting would be cultivated in a zone outside Carazo to ensure the absence of the disease. If the pathogen could be eliminated from the infected area before the replanting began, the opportunities for complete eradication would be substantially increased. Any future occurrence of coffee rust, or of any other pest or disease, could then be treated more efficiently in the new plantations, since the means to control it would be economically feasible.

ECOLOGICAL IMPACT OF THE RESTOCKING PLAN

According to the blueprint for the eradication of the rust, the 10,000 ha of coffee plantations would be completely cut down, an operation that implied prior killing with herbicides. Once the plantations had been leveled, the soil would be plowed, and herbicides would be systematically applied to destroy any coffee seedlings that might emerge. These measures would be accompanied by spraying with a copper-based fungicide.

As can be appreciated, this would be a drastic operation in intensity as well as in magnitude, with an ecological impact of unpredictable dimensions. It is known that coffee plantations form one of the more stable agroecosystems because of the complexity of their components, which gives them the characteristics of a semiforest and, as a result, makes them practically free of pests and diseases compared to other less ecologically complex agroecosystems such as cotton. If this ecological balance were to break down as a result of such a drastic modification, the direct

impact on the 14,000 manzanas (28,840 acres), and the indirect one on other zones, might reach alarming proportions.

Physical Effects

The destruction of extensive areas caused by the absence of vegetative coverage could bring about changes in temperature and compactness which would affect the structure, texture, and composition of the soils. The erosion phenomenon might affect the fertility of the whole area.

The winds, as well as the rains, could carry chemical residues toward sites bordering the treated area, with direct or indirect effects, short- or long-term, on terrestrial and aquatic life forms.

Biological Effects

Coffee plantations derive their great ecological stability from their complexity; they support hundreds or thousands of different species of microorganisms (bacteria, fungi), annelids (earthworms), arthropods (spiders, acarids, insects), and vascular and phanerogamic plants. The majority of these organisms are very useful in maintaining the biological balance. It is not difficult to imagine the severe impact that the complete destruction of this habitat might have on this elaborate biotic system, destruction from which undesirable organisms might emerge as winners when their natural enemies were destroyed. New pests might appear, others might develop resistance to chemicals, producing population explosions of acarids, scales, jumping plant lice, leaf miners, aphids, and ants. The effect on other fauna, such as amphibians, reptiles, birds, and mammals, could also lead to undesirable ecological phenomena. The invasion of bird or rodent pests is a potential threat that should be carefully considered. Also not to be disregarded is the production of mutations in different organisms and the sudden appearance of rust races with unanticipated characteristics.

Effect on People

The human population living in the area to be cut down, and also that of the bordering zones, would also suffer from the effects of the eradication measures. The air, as well as the water, would be contaminated with residues from chemicals, dust, and detritus resulting from the operations, thus affecting the health of the population. There might be cases of poisoning and irritation, and for an extended period, life in those zones might be quite uncomfortable. This might displace people into towns and cities, with the attendant social consequences.

CONCLUSION

There is no doubt that the experience gained in the campaign for the control and possible eradication of coffee rust in Nicaragua has been of great importance and valuable help for the rest of the Central American nations, in containing or confining the disease. It has also given the area nations, especially those where coffee is grown with low-technology methods, the opportunity to establish training and financial programs that should allow them to improve their coffee production technology in order to coexist with the disease and to continue productive and profitable activity.

Unfortunately, the methodology that was adopted could not be carried through to its conclusion because the circumstances that befell the nation did not allow for any sequel to the process. This shows that any factor or event not under the control of the campaign can reduce or alter the anticipated success.

LITERATURE CITED

1. Alba, A. P. C., Guzzo, S. D., Mahlow, M. F. P., and Moraes, W. B. C. 1983. Common antigens in extracts of Hemileia vastatrix Berk. et Br. urediniospores and Coffea arabica L. leaves and roots. Fitopatologia Brasileira 8:473-483.
2. Albersheim, P. 1976. An introduction to the research on elicitors of phytoalexin accumulation. Pages 129-136 in: Cell Wall Biochemistry. B. Solheim and J. Raa, eds. Universitetsforlaget, Oslo. 487 pp.
3. Albersheim, P., and Anderson-Prouty, A. J. 1975. Carbohydrates, proteins, cell surfaces and the biochemistry of pathogenesis. Annu. Rev. Plant Physiol. 26:31-52.
4. Albersheim, P., Darvill, A. G., McNeil, M., Valent, B. S., Hahn, M. G., Lyon, G., Sharp, J. K., Desjardins, A. E., Spellman, M. W., Ross, L. M., Robertsen, B. K., Aman, P., and Franzen, L.-E. 1981. Structure and function of complex carbohydrates active in regulating plant-microbe interactions. Pure Appl. Chem. 53:79-88.
5. Becker, S. 1976. Untersuchungen zur Verbreitung der Uredosporen von Hemileia vastatrix Berk. & Br. in Kenia. Ph.D. dissertation. Justus-Liebig University, Giessen. 210 pp.
6. Becker, S. 1977. Diurnal periodicity of spore dispersal of Hemileia vastatrix in relation to weather factors. J. Plant Dis. Prot. 87:577-591.
7. Beretta, M. J. G., Martins, E. M. F., and Moraes, W. B. C. 1977. Induced protection to Hemileia vastatrix at a distance from the site of the inducing action in coffee plants. Summa Phytopathologica 3:66-70.

8. Beretta, M. J. G., Martins, E. M. F., and Moraes, W. B. C. 1980. Inducao de proteccão à Hemileia vastatrix em plantas de café susceptiveis por fungos não-patogénicos ao cafeeiro. Sociedade Brasileira de Fitopatologia, 13th Congresso Brasileiro, 6-11 July 1980.
9. Bettencourt, A. J. 1976. Avaliação da resistência à Hemileia vastatrix no melhoramento genético de Coffea arabica. 4th Congresso Brasileiro de Pesquisas Cafeeiras. Resumos, pp. 274-276. Caxambu/Minas Gerais, Brazil, 23-26 November 1976.
10. Bettencourt, A. J., and Carvalho, A. 1968. Melhoramento visando a resistência do cafeeiro à ferrugem. Bragantia 27:35-68.
11. Bettencourt, A. J., and Lopes, J. 1980. Resistência à Hemileia vastatrix de 32 retrocruzamentos (BC_1, BC_2 e BC_3) para Bourbon, Catuaí, Caturra e Mundo Novo do híbrido CIFC HW 26 (Caturra Vermelho CIFC 19/1 X Híbrido de Timor CIFC 832/1). 8th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 385-387. Campos do Jordão/São Paulo, 25-28 November 1980.
12. Bettencourt, A. J., Lopes, J., and Godinho, I. L. 1979. Transferência de factores de resistencia à Hemileia vastatrix do Híbrido de Timor para a cultivar Caturra Vermelho de Coffea arabica. Garcia de Orta (Serie Estudos Agronomicos) 6(1-2):11-18.
13. Bettencourt, A. J., and Noronha-Wagner, M. 1971. Genetic factors conditioning resistance of Coffea arabica to Hemileia vastatrix. Agron. Lusit. 31:285-292.
14. Bettencourt, A. J., Noronha-Wagner, M., and Lopes, J. 1980. Factor genético que condiciona a resistência do clone 1343/269 (Hibrido de Timor) à Hemileia vastatrix. Brotéria-Genética 1(76):53-58.
15. Bingham, R. T., Hoff, R. J., and McDonald, G. I. 1971. Disease resistance in forest trees. Annu. Rev. Phytopathol. 9:433-452.
16. Black, W., Mastenbroek, C., Mills, W. R., and Petersen, L. C. 1953. A proposal for an inter-

national nomenclature of races of Phytophthora infestans and of genes controlling immunity in Solanum demissum derivatives. Euphytica 2:173-178.

17. Bock, K. R. 1962a. Dispersal of uredospores of Hemileia vastatrix under field conditions. Trans. Br. Mycol. Soc. 45:63-74.

18. Bock, K. R. 1962b. Seasonal periodicity of coffee leaf rust and factors affecting the severity of outbreaks in Kenya. Trans. Br. Mycol. Soc. 45:289-300.

19. Bock, K. R. 1962c. Control of coffee leaf rust in Kenya Colony. Trans. Br. Mycol. Soc. 45:301-313.

20. Bowles, D. J., and Kauss, H. 1975. Carbohydrate-binding proteins from cellular membranes of plant tissue. Plant Sci. Lett. 4:411-418.

21. Brown, J. F., Shipton, W. A., and White, N. H. 1966. The relationship between hypersensitive tissue and resistance in wheat seedlings infected with Puccinia graminis tritici. Ann. Appl. Biol. 58:279-290.

22. Burdekin, D. A. 1960. Wind and water dispersal of coffee leaf rust in Tanganyika. Kenya Coffee 25:212-213.

23. Castillo, J., and Moreno, G. 1981. Selección de cruzamientos derivados del Híbrido de Timor en la obtención de variedades mejorades de café para Colombia. Cenicafe 32(2):37-53.

24. Castillo, J., and Moreno, G. 1982. Obtencion de materiales de cafe resistentes a Hemileia vastatrix en Colombia en ausencia de la enfermedad. Un programa cooperativo entre CENICAFE y el CIFC. Garcia de Orta (Serie Estudos Agronomicos) 9(1-2):119-128.

25. Castillo, J., Moreno, G., and Lopez, S. 1976. Uso de resistência genética à Hemileia vastatrix existente em germoplasma de café en Colombia. Cenicafé 27(1):3-25.

26. Coffee Board of Kenya. 1977-1981. Annual Reports.

27. Coffee Board Research Department. 1982. 34th Annual Technical Report, 1980-1981, pp. 43-63. Coffee Board Research Department, India.
28. Costa, W. M., Fazuoli, L. C., and Carvalho, A. 1980. Associação de diferentes factores de resistência à Hemileia vastatrix em Coffea arabica. 8th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 123-126. Campos do Jordão, São Paulo, 25-28 January 1980.
29. De Vay, J. E., and Adler, H. E. 1976. Antigens common to host and parasites. Annu. Rev. Microbiol. 30:147-168.
30. d'Oliveira, B. 1954-1957. As ferrugens do cafeeiro. Rev. Café Port. 1(4):5-13; 2(5):5-12; 2(6):5-13; 2(7):9-17; 2(8):5-22; 4(16):5-15.
31. d'Oliveira, B. 1958. Selection of coffee types resistant to the Hemileia leaf rust. Coffee Tea Ind. 81:112-120.
32. Doubly, J. A., Flor, H. H., and Claget, C. O. 1960. Relation of antigens of Melampsora lini and Linum usitatissimun to resistance and susceptibility. Science 131:229.
33. Dowson, W. J. 1921. Some problems of economic botany in East Africa. Ann. Appl. Biol. 8:83-100.
34. Elliston, J. E., Kuć, J., and Williams, E. B. 1971. Induced resistance to bean anthracnose at a distance from the site of the inducing interaction. Phytopathology 61:1110-1112.
35. Elliston, J. E., Kuć, J., and Williams, E. B. 1976a. Protection of Phaseolus vulgaris against anthracnose by Colletotrichum species non-pathogenic to bean. Phytopathol. Z. 87:117-126.
36. Elliston, J. E., Kuć, J., and Williams, E. B. 1976b. A comparative study of the development of compatible, incompatible and induced incompatible interactions between Colletotrichum spp. and Phaseolus vulgaris. Phytopathol. Z. 87:289-303.
37. Eskes, A. B. 1980. Ocorrência de um isolado da raça v_3 v_5 de Hemileia vastatrix pouco virulenta em cordições de laboratório. 8th Congresso Brasileiro de Pesquisas Cafeeiras,

Resumos, pp. 81-82. Campos do Jordão, São Paulo, 25-28 November 1980.

38. Eskes, A. B., Braghini, M. T., Carvalho, A., Ribeiro, I. J. A., and Paradela Filho, O. 1980. Detecção da raça de Hemileia vastatrix com genes de virulencia v_1 v_4 v_5 no Estado de São Paulo. 8th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 91-92. Campos do Jordão, São Paulo, 25-28 November 1980.

39. Eskes, A. B., Braghini, M. T., Levy, F. A., Carvalho, A., and da Costa, W. M. 1980. Indicações de raças novas de Hemileia vastatrix em relação a genes de resistência do Híbrido de Timor, de Icatu e da cultivar Kouillou de C. canephora. 8th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 78-80. Campos do Jordão, São Paulo, 25-28 November 1980.

40. Eskes, A. B., Braghini, M. T., and van de Weg, E. W. 1980. Grau de resistência à Hemileia vastatrix observado em várias introduções de C. arabica provenientes da Etiópia e em cruzamentos entre plantas de cultivar Kouillou de C. canephora. 8th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 217-219. Campos do Jordao, Sao Paulo, 25-28 November 1980.

41. Eskes, A. B., Kroon, S., and van de Weg, W. E. 1980. Efeito da luminosidade sobre o nível de resistência à Hemileia vastatrix. 8th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 83-86. Campos do Jordão, São Paulo, 25-28 November 1980.

42. Eskes, A. B., Ribeiro, I. J. A., Carvalho, A., and Paradela Filho, O. 1979. Raça de Hemileia vastatrix portadora dos genes de virulencia v_1 v_2 v_5 diferenciada no Estado de São Paulo. 7th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 122-123. Araxá, Minas Gerais, Brazil, 4-7 December 1979.

43. Eskes, A. B., and Toma-Braghini, M. 1981. Assessment methods for resistance to coffee leaf rust (Hemileia vastatrix Berk. & Br.). FAO Plant Prot. Bull. 29:56-66.

44. Fanucchi, M., Beretta, M. J. G., Martins, E. M. F., Moraes, W. B. C., and Figueiredo, M. B. 1980. Verificação da presença, no Estado de São Paulo, da raça fisiológica de Hemileia vastatrix portadora dos genes de virulência v_2, v_4, v_5. 13th Congresso Brasileiro de Fitopatologia, Universidade Federal Rural do Rio de Janeiro, Itaguí, Rio de Janeiro, 6-11 July 1980.
45. Firman, I. D. 1972. Coffee rust in Brazil. FAO Plant Prot. Bull. 20:121-126.
46. Firman, I. D., and Waller, J. M. 1977. Coffee berry disease and other Colletotrichum diseases of coffee. Commonw. Mycol. Inst., Kew, Surrey, England.
47. Firman, I. D., and Wallis, J. A. N. 1965. Low volume spraying to control coffee leaf rust in Kenya. Ann. Appl. Biol. 55:123-137.
48. Flor, H. W. 1956. The complementary genic systems in flax and flax rust. Adv. Genet. 8:29-54.
49. Galvez, G. C., Flores, M. B., Portillo, D., and Rios Lazo, F. A. 1980. Determinación de razas fisiológicas de la roya del cafeto (Hemileia vastatrix Berk. & Br.). Instituto Salvadoreño de Investigaciones del Café, Tech. Bull. 4 (NS).
50. Gonçalves, M. M., Rodrigues, M. L., Mexia, J. N., and Doenhardt, E. 1977. Amélioration de la caféiculture à Timor face à Hemileia vastatrix. 8th Colloque, Association Scientifique Internationale du Café, Abidjan, 1977, pp. 515-522.
51. Griffiths, E. 1972. Negative effect of fungicides in coffee. Trop. Sci. 14:79-89.
52. Griffiths, E., Gibbs, J. N., and Waller, J. M. 1971. Control of coffee berry disease. Ann. Appl. Biol. 67:45-74.
53. Guedes, M. E. M., Morais, M. L., and Martins, J. M. S. 1982. Production of stress metabolites in coffee leaves infiltrated with Pseudomonas syringae. Garcia de Orta (Serie Estudos Agronomicos) 9(1-2):243-248.
54. Habgood, R. M. 1970. Designation of physiological races of plant pathogen. Nature 227:1268-1269.

55. Heath, M. C. 1972. Ultrastructure of host and nonhost reactions to cowpea rust. Phytopathology 62:27-38.
56. Heath, M. 1974. Light and electron microscope studies of the interactions of host and non-host plants with cowpea rust--Uromyces phaseoli var. vignae. Physiol. Plant Pathol. 4:403-414.
57. Hislop, E. C. 1967. Observations on the vapor phase activity of some foliage fungicides. Ann. Appl. Biol. 60:265-279.
58. Hislop, E. C. 1969. Splash dispersal of fungus spores and fungicides in the laboratory and greenhouse. Ann. Appl. Biol. 63:71-80.
59. Howes, N. K., Kim, W. K., Rohringer, R., and Samborski, D. J. 1976. Studies on a gene-specific RNA involved in the resistance of wheat to stem rust. Pages 80-83 in: Biochemistry and Cytology of Plant-Parasite Interaction. K. Tomiyama, J. M. Daly, I. Uritani, H. Oku, and S. Ouchi, eds. Kodansha Ltd., Tokyo. 236 pp.
60. Howes, N. K., Samborksi, D. J., and Rohringer, R. 1974. Production and bioassay of gene-specific RNA determining resistance of wheat to stem rust. Can. J. Bot. 52:2489-2497.
61. Javed, Z. U. R. 1981a. Field trials with new and recommended fungicides for leaf rust control during 1979. Kenya Coffee 46:19-24.
62. Javed, Z. U. R. 1981b. Field trials with new and recommended fungicides for leaf rust control during 1980. Kenya Coffee 46:239-246.
63. Javed, Z. U. R. 1981c. Leaf rust. Pages 117-119 in: Coffee Research Station Annual Report, 1979-1980.
64. Javed, Z. U. R. 1982. Field trials with new and recommended fungicides for leaf rust control during 1981. Kenya Coffee 47:199-205.
65. Johnston, C. D., and Huffman, M. D. 1958. Evidence of local antagonism between two cereal rust fungi. Phytopathology 48:69-70.
66. Kauss, H. 1976. The possible physiological role of lectins. Pages 347-358 in: Cell Wall Biochemistry. B. Solheim and J. Raa, eds. Universitetsforlaget, Bergen. 487 pp.

67. Kauss, H., and Bowles, D. J. 1976. Some properties of carbohydrate-binding proteins (lectins) solubilized from cell walls of Phaseolus aureus. Planta 130:169-174.
68. Kiraly, Z., Barna, B., and Ersek, T. 1972. Hypersensitivity as a consequence, not the cause, of plant resistance to infection. Nature (London) 239:456-458.
69. Littlefield, L. J. 1969. Flax rust resistance induced by prior inoculation with an avirulent race of Melampsora lini. Phytopathology 59:1323-1328.
70. Llano, A. 1977. The orange coffee rust in Nicaragua. Plant Dis. Rep. 61:999-1002.
71. Lopes, J., and Godinho, I. L. 1976. Physiologic specialization of Hemileia vastatrix. Garcia de Orta (Serie Estudos Agronomicos) 3(1-2):13-16.
72. Luttrell, E. E. 1974. Parasitism of fungi on vascular plants. Mycologia 66:1-15.
73. Marques, D. V., and Bettencourt, A. J. 1979. Resistência à Hemileia vastatrix numa população de Icatu. Garcia de Orta (Serie Estudos Agronomicos) 6(1-2):19-24.
74. Martinez, J. A., Palazzo, D. A., Karazawa, M., Monteiro, M. V. M., and Rea, N. R. N. 1975. Presenca de esporos de Hemileia vastatrix Berk. & Br. agente causal da ferrugem do cafeeiro, em diferentes altitude nas principais áreas cafeeiras dos Estados de Sao Paulo e Paraná (Brasil). O Biológico 41:77-88.
75. Martins, E., Beretta, M. J., and Moraes, W. 1980. Indução de proteccão à Hemileia vastatrix em plantas de café susceptíveis por bactérias não patogénicas ao cafeeiro. Sociedade Brasileira de Fitopatologia, 13th Congresso Brasileiro, 6-11 July 1980.
76. Martins, E. M. F., Beretta, M. J. G., Roveratti, D. S., and Moraes, W. B. C. 1984. Comparative induced protection to Hemileia vastatrix in coffee plants by non-specific inducers from different fungal and bacterial origins. Fitopatologia Brasileira (in press).

77. Martins, E. M. F., Roveratti, D. S., Beretta, M. J. G., and Moraes, W. B. C. 1982. Indução de síntese de compostos tipo-fitoalexinas em folhas de cafeeiro. (Abstr.) 5th Congresso Paulista de Fitopatologia, p. 30. Piracicaba, São Paulo.
78. Mayama, S., Daly, J. M., Rehfeld, D. W., and Daly, C. R. 1975. Hypersensitive response of near-isogenic wheat carrying the temperature-sensitive SR_6 allele for resistance to stem rust. Physiol. Plant Pathol. 7:35-47.
79. Mayne, W. W. 1932. Physiologic specialization of Hemileia vastatrix. Nature 129:150.
80. Medeiros, A. G. 1970. Informe sobre Hemileia vastatrix en café, en Bahia, Brasil. Comi. Exec. Pl. Recup. Econ. Rural Lav. Cacaueira, Rio de Janeiro.
81. Medeiros, E. F., and Rodrigues, C. J., Jr. 1977. Production of phytoalexin-like substances in Coffea arabica leaves inoculated with several rusts not pathogenic to coffee. 8th Colloque, Association Scientifique Internationale du Café, pp. 511-512. Abidjan, 28 November-3 December.
82. Medeiros, E. F., and Rodrigues, C. J., Jr. 1978. Produção de substancias do tipo das fitoalexinas em folhas de Coffea arabica L. inoculadas com ferrugens não patogênicas para o cafeeiro. Garcia de Orta (Ser. Est. Agron.) 5:15-18.
83. Monaco, L. C. 1977. Consequences of the introduction of coffee rust into Brazil. Ann. N.Y. Acad. Sci. 287:57-71.
84. Moraes, W. B. C., Martins, E. M. F., Beretta, M. J. G., and Guzzo, S. D. 1981. Studies on the induced protection in coffee plants to Hemileia vastatrix. IV. Chemical analysis of the inducer. (Abstr.) Colloque International sur les Cultures Tropicales, Lyons, France.
85. Moraes, W. B. C., Martins, E. M. F., Musumeci, M. R., and Beretta, M. J. G. 1976. Induced protection to Hemileia vastatrix in coffee plants. Summa Phytopathol. 2:39-43.
86. Moraes, W. B. C., Martins, E. M. F., Roveratti, D. S., and Beretta, M. J. G. 1978. An antifungal substance produced by mesocarp of green

coffee berries. (Abstr.) 3rd International Congress of Plant Pathology, Munich.

87. Mulinge, S. K., Baker, C. J., and Pereira, J. L. 1974. Effect of pyracarbolid on coffee rust in Kenya. Phytopathology 64:147-149.

88. Musumeci, M. R., Nicholson, R. L., Moraes, W. B. C., and Kuć, J. 1973. Observations on an esterase activity associated with uredospores of Hemileia vastatrix Berk et Br. J. Coffee Res. 3:46-49.

89. Musumeci, M. R., Nicholson, R. L., Moraes, W. B. C., and Kuć, J. 1974. Esterase activity associated with uredospores of Hemileia vastatrix. Arg. Inst. Biol. 41:15-18.

90. Netto, K. A., Ferreira, A. J., and Pereira, J. B. D. 1979. Selecção de cafeeiros portadores de resistência ao nematoide M. exigua e ao fungo H. vastatrix. 7th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 251-254. Araxá, Minas Gerais, Brazil, 4-7 December 1979.

91. Netto, K. A., and Pereira, J. B. D. 1980. Estudo de selecções de Híbrido de Timor procedentes do CIFC, Oeiras-Portugal, em Caratinga-Minas Gerais. 8th Congresso Brasileiro de Pesquisas Cafeeiras, Resumos, pp. 104-106. Campos do Jordão, São Paulo, 25-28 November 1980.

92. Njagi, S. B. C. 1981. Current costs in coffee farming and the farmer's profit. Kenya Coffee 46:49-57.

93. Noronha-Wagner, M., and Bettencourt, A. J. 1967. Genetic study of the resistance of Coffea spp. to leaf rust. I. Identification and behaviour of four factors conditioning disease reaction in Coffea arabica to twelve physiologic races of Hemileia vastatrix. Can. J. Bot. 45:2021-2031.

94. Nutman, F. J., and Roberts, F. M. 1960. Method of uredospore dispersal of the coffee leaf rust fungus Hemileia vastatrix. Trans. Br. Mycol. Soc. 43:509-515.

95. Nutman, F. J., and Roberts, F. M. 1970. Coffee leaf rust. PANS 16:606-624.

96. Ogle, H., and Brown, J. F. 1971. Quantitative studies of the post-penetration phase of infection by Puccinia graminis tritici. Ann. Appl. Biol. 67:309-319.
97. OIRSA. 1976. Informe sobre la situación y acción tomada en la República de Nicaragua con relación a la roya del café (Hemileia vastatrix). Departmento de Sanidad Vegetal, OIRSA, San Salvador, El Salvador. 30 pp.
98. OIRSA. 1977-1979. Primera, segunda, tercera, cuarta y quinta evaluacíon sobre la situacion de la roya del cafeto, Hemileia vastatrix Berk y Br., y la posibilidad de su erradicacion en la Republica de Nicaragua. OIRSA, San Salvador, El Salvador.
99. Okioga, D. M. 1978. The role of copper fungicides in the control of coffee diseases. Kenya Coffee 43:221-230.
100. Otero, G. R. 1980. Roya en Centroamerica. Presented at a seminar on coffee rust organized by the Asociacion de Amigos del Centro de la Universidad Vieja, Guatemala.
101. Pereira, J. L. 1972. Multi-row spray application for coffee disease control. Int. Pest Control 14(1):6-10, 19.
102. Pereira, J. L., Mapother, H. R., Cooke, B. K., and Griffiths, E. 1973. Redistribution of fungicides in coffee trees. Exp. Agric. 9:209-218.
103. Person, C. O., and Mayo, G. M. E. 1974. Genetic limitations on models of specific interactions between a host and its parasite. Can. J. Bot. 52:1339-1347.
104. Rahe, J. E., Kuć, J., Chuang, C. M., and Williams, E. B. 1969. Induced resistance in Phaseolus vulgaris to bean anthracnose. Phytopathology 59:1641-1645.
105. Rebel, E. K. 1980. Comportamento de progénies e linhagens de Icatu no Noroeste do Paraná. 8th Congresso Brasileiro de Pesquisas Cafeiras, Resumos, pp. 175-176. Campos do Jordão, São Paulo, 25-28 November 1980.

106. Ribeiro, I. J. A., Sugimori, M. H., Moraes, S. A., and Monaco, L. C. 1975. Raças fisiológicas de Hemileia vastatrix no Estado de S. Paulo. Summa Phytopathol. 1:19-22.

107. Rijo, L. 1972. Histopathology of the hypersensitive reaction t (tumefaction) induced on Coffea spp. by Hemileia vastatrix Berk et Br. Agron. Lusit. 33:427-431.

108. Rijo, L., and Rodrigues, C. J., Jr. 1977. The infection process of Hemileia vastatrix in susceptible and resistant cultivars of Coffea arabica. 8th Colloque, Association Scientifique Internationale du Café, pp. 509-510. Abidjan, 28 November-3 December.

109. Rijo, L., and Rodrigues, C. J., Jr. 1978. Processo de infecção de Hemileia vastatrix Berk et Br. em cultivares suscetíveis e resistentes de Coffea arabica L. Garcia de Orta (Ser. Est. Agron.) 5:23-24.

110. Rijo, L., Rodrigues, C. J., Jr., and Vasconcelos, M. I. 1980. Immunity on the coffee-orange rust association. Histopathological aspects. Presented at 9th Colloque, Association Scientifique Internationale du Café, London, 16-20 June 1980.

111. Robinson, R. A. 1976. The gene-for-gene relationship. Pages 35-43 in: Plant Pathosystems. Springer-Verlag, Berlin. 184 pp.

112. Rodrigues, C. J., Jr. 1975. The coffee rusts: Hemileia vastatrix and H. coffeicola. 7th Colloque, Association Scientifique Internationale du Café, pp. 401-408. Hamburg, 9-14 June 1975.

113. Rodrigues, C. J., Jr. 1981. Coffee leaf rust. Consultant report to Ethiopia. FAO Consultancy Report ETH/78/004. FAO, Rome. 17 pp.

114. Rodrigues, C. J., Jr., Bettencourt, A. J., and Lopes, J. 1965. Study of the physiologic specialization of the coffee rust Hemileia vastatrix and selection of coffee clones for the establishment of a standard range of differentials for this rust. Centro de Investigação

das Ferrugens do Cafeeiro. Progress Report 1960-65:21-27.

115. Rodrigues, C. J., Jr., Bettencourt, A. J., and Rijo, L. 1975. Races of the pathogen and resistance to coffee rust. Annu. Rev. Phytopathol. 13:49-70.

116. Rodrigues, C. J., Jr., Medeiros, E., and Lewis, B. G. 1975. Relationship between a phytoalexin-like response in coffee leaves (Coffea arabica L.) and compatibility with Hemileia vastatrix Berk et Br. Physiol. Plant Pathol. 6:35-41.

117. Rodrigues, C. J., Jr., Rijo, L., and Medeiros, E. F. 1981. Induction of flecks and tumefactions on coffee leaves by incompatible and compatible, viable and non-viable uredospores of Hemileia vastatrix and of other rusts, and by their leachates. Presented at Colloque International sur la Protection des Cultures Tropicales, Lyons, 9-11 June 1981.

118. Rodrigues, C. J., Jr., Rijo, L., and Medeiros, E. 1981. Induction of flecks and tumefaction on coffee leaves by washout of coffee rust urediniospores. (Abstr.) International Conference on Tropical Crop Protection, Lyons.

119. Rohringer, R. 1976. Evidence for direct involvement of nucleic acids in host-parasite specificity. Pages 185-196 in: Specificity in Plant Disease. R. K. S. Wood and A. Graniti, eds. Plenum Press, London. 354 pp.

120. Rohringer, R., Howes, N. K., Kim, W. K., and Samborski, D. J. 1974. Evidence for a gene-specific RNA determining resistance in wheat to stem rust. Nature (London) 249:585-588.

121. Schieber, E. 1970. Viaje al Brasil y el Africa para estudiar y observar el problema de la herrumbre del café. Rep. Org. Int. Reg. Sanidad Agrop. OIRSA, San Salvador, El Salvador. 109 pp.

122. Schieber, E. 1972. Economic impact of coffee rust in Latin America. Annu. Rev. Phytopathol. 10:491-510.

123. Schieber, E. 1975. Present status of coffee rust in South America. Annu. Rev. Phytopathol. 13:375-382.
124. Schieber, E. 1977. Some aspects of the coffee rust outbreak in Central America. Paper presented at the 17th Annual Meeting of the Caribbean Division of the American Phytopathological Society, Miami Beach, FL.
125. Schieber, E. 1979. The coffee rust in Latin America: Analysis of its economic consequences. Pages 11-18 in: Coffee Rust Control. Report on a seminar held in Paipa, Colombia, in 1977. GTZ, Eschborn, West Germany.
126. Schieber, E. 1981. Recent developments on spread of coffee rust in Central America. Tropical Plant Pathology Discussion Session, 1981 Annual Meeting of the American Phytopathological Society, New Orleans, LA.
127. Schieber, E., and Sanchez de Leon, A. 1982. First report of coffee rust in Guatemala. Plant Dis. 66:855-856.
128. Schieber, E., and Zentmyer, G. A. 1984. Coffee rust in the Western Hemisphere. Plant Dis. 68:89-93.
129. Schuppener, H., Harr, J., Sequeira, F., and Gonzales, A. 1977. First occurrence of the coffee leaf rust Hemileia vastatrix in Nicaragua, 1976, and its control. Café, Cacao, Thé 21:197-201.
130. Sequeira, L. 1978. Lectins and their role in host pathogen specificity. Annu. Rev. Phytopathol. 16:453-481.
131. Shimony, C., and Friend, J. 1975. Ultrastructure of the interaction between Phytophthora infestans and leaves of two cultivars of potato (Solanum tuberosum L.) Orion and Majestic. New Phytol. 74:59-65.
132. Skipp, R. A., and Deverall, B. J. 1972. Relationship between fungal growth and host changes visible by light microscopy during infection of bean hypocotyls (Phaseolus vulgaris) susceptible and resistant to physiologic races of

Colletotrichum lindemuthianum. Physiol. Plant Pathol. 2:357-374.

133. Stakman, E. C. 1915. Relation between Puccinia graminis and plants highly resistant to its attack. J. Agric. Res. 4:193-200.

134. Tani, T., Yamamoto, H., Onoe, T., and Naito, N. 1976. Primary recognition and subsequent expression of resistance in oat leaves hypersensitively responding to crown rust fungus. Pages 124-135 in: Biochemistry and Cytology of Plant-Parasite Interaction. K. Tomiyama, J. M. Daly, I. Uritani, A. Oku, and S. Ouchi, eds. Kodansha Ltd., Tokyo. 236 pp.

135. Tomiyama, K. 1955. Cytological studies on resistance of potato plants to Phytophthora infestans. 2. The death of the intracellular hyphae in the hypersensitive cell. Ann. Phytopathol. Soc. Jpn. 19:149-154.

136. Uritani, I., Oba, K., Kojima, M., Kim, W. K., Oguni, I., and Suzuki, H. 1976. Primary and secondary defense actions of sweet potato in response to infection by Ceratocystis fimbriata strains. Pages 239-242 in: Biochemistry and Cytology of Plant-Parasite Interaction. K. Tomiyama, J. M. Daly, I. Uritani, H. Oku, and S. Ouchi, eds. Kodansha Ltd., Tokyo. 236 pp.

137. van der Vossen, H. A. M., and Walyaro, D. J. 1981. The coffee breeding programme in Kenya: A review of progress made since 1971 and plan of action for the coming years. Kenya Coffee 46:113-130.

138. Vine, B. H., Vine, P. A., and Griffiths, E. 1973. Some problems of evaluating fungicides for use on coffee in Kenya. Ann. Appl. Biol. 75:377-385.

139. Waller, M. J. 1979. Informe final, consultor de FAO, roya del cafeto. 15 February 1979.

140. Wallis, J. A. N., and Firman, I. D. 1962. Spraying Arabica coffee for the control of leaf rust. East Afr. Agric. For. J. 28:89-104.

141. Wallis, J. A. N., and Firman, I. D. 1967. A comparison of fungicide spray volumes for the

control of coffee berry disease. Ann. Appl. Biol. 59:111-122.

142. Wellman, F. L., and Echandi, E. 1981. The coffee rust situation in Latin America in 1980. Phytopathology 71:968-971.

143. Wimalajeewa, D. L. S., and De Vay, J. E. 1971. The occurrence and characterization of a common antigen relationship between Ustilago maydis and Zea mays. Physiol. Plant Pathol. 1:523-535.

144. Wybour, A., and Stripecke, W. 1980. Control of coffee rust (Hemileia vastatrix Berk. & Br.) with Bayleton in Brazil. Pflanzenschutz-Nachr. Bayer (Am. Ed.) 33:123-151.

145. Yarwood, C. E. 1956. Cross protection with two rust fungi. Phytopathology 46:540-544.