COFFEE LEAF RUST, HEMILEIA VASTATRIX, ESTABLISHED IN BRAZIL

GERHARD GOTTSBERGER

Departamento de Botânica, Faculdade de Ciências Médicas e Biológicas de Botucatu, Botucatu, Estado de São Paulo, Brazil

A profound study and a good knowledge of a disease are the first steps for its control and combat. The intention of the present article is to discuss the general biology of the coffee leaf rust and some aspects of research into it in Brazil. From this we may obtain new ideas regarding the life cycle of the fungus, its origin, its spore-dispersal and its establishment. The conclusions here made are based not on my own work, but on a critical revision of the literature. Some of the conclusions have been discussed with agronomy and biology students during the cryptogamic botany course I have been giving in the Faculty of Medical and Biological Sciences in Botucatu, São Paulo State.

Coffee is still the most important Brazilian export, accounting for 30% of the value of all exports. Since January, 1970, when Hemileia vastatrix BERK. & BR. was discovered in the State of Bahia, the coffee leaf rust caused by this fungus has threatened coffee crops and thus the progress and expansion of the Brazilian economy. It is therefore not astonishing that the Brazilian government together with the Instituto Brasileiro do Café has made and is making supreme efforts to bring the rust under control. In a very short time hundreds of scientists, especially phytopathologists and agronomy experts were induced to do research on Hemileia vastatrix (see MONTEIRO, 1970; IBC, 1970). The coffee leaf rust is at the moment considered to be enemy number one if we restrict ourselves to internal economic questions. On the other hand the fungus perhaps should also induce us to treat another aspect. It clearly shows us that any botanical, zoological, or in a general sense, ecological, question cannot be settled satisfactorily without profound and basic biological knowledge. Ingenious application makes sense only after knowing biology. One may hope, and the African Hemileia vastatrix shows us this in a quite instructive way, that "pure" biology should be studied as much as "applied" biology, also in underdeveloped countries.

The origin of Coffea arabica, Arabian (really Ethiopean) coffee, and its leaf disease, Hemileia vastatrix, are not at all obscure. Kaffa, a province in southwest Ethiopia (Abyssinia) is said to be the country of origin of Coffea arabica. Concerning the origin of Hemileia vastatrix it is assumed: "Both in Ceylon and in East Africa local study and old herbarium material suggest that the rust existed as an innocuous parasite on wild coffee, turned loose by the monoculture." (GRAM, 1960:324). It is clear that the place of origin of coffee has to be also the place of origin of its leaf disease. Hemileia vastatrix is specialized on coffee, it has evolved along with this rubiaceous genus. Therefore, if we think about the East African region as the original center of *Coffea*, then it seems logical to look first for *Hemileia*, its disease, in the same region (see also WELLMAN, 1957). We will return to that question later when we discuss the existance of a possible intermediate host of *Hemileia*.

Plants of *Coffea arabica* that are believed to have been growing wild in East Africa were taken to southern Arabia (Yemen) and placed under cultivation there about 500 years ago. At the end of the 17th century, with the increasing popularity of coffee, the propagation of the plant spread rapidly from southern Arabia first to Ceylon (1658) and later to other places in the Asian and African tropics. In 1723 it was brought to the New World, first to Martinique and in 1727 to Brazil. To plant coffee up to the year 1868 was a profitable enterprise in many tropical countries of the Old World. However, in that year, *Hemileia vastatrix*, although already known in a moderate form from Africa, for the first time in history appeared as a violent disease in Ceylon. This new serious disease form of *Hemileia vastatrix* started to spread to coffee plantations in Asia and Africa and has recently reached the first coffee plantations of the New World. Where it passes, it destroys; control is extremely difficult and extinction of the disease in many cases means extinction of coffee.

For a better understanding of host and parasite we have to go to the center of origin of both, to East Africa. In general, the centers of origin of cultivated plants are said to be extremely important for studying and understanding genetic interaction between host and parasite. The gene-for-gene hypothesis of FLOR (1956) says that during correlative evolution of a host and its disease, both have developed a complementary genetic system. Each gene of the parasite which tends to cause virulence has caused a reaction in the host to evolve a reciprocal protective gene. Therefore, in these gene centers, which in most cases are also the centers of origin of the cultivated plants, we find a very fine controlled interaction of the host and its disease built up during millions of years. The parasite exists, but is controlled by the proper genetic system of the host (LEPPIK, 1967, 1968, 1970). This probably was also the situation with *Coffea arabica* and its parasite, *Hemileia vastatrix*, in East Africa. *Hemileia* has been known there for a long time (see RAYNER, 1960; GRAM, 1960); both host and parasite have lived together and have established complementary genetic systems which controlled each other. This must have been one of the reason why *Hemileia vastatrix* formerly had not become violent in East Africa. The same might be said for southern Arabia which lies quite close to or even within the gene center. Plant breeders knowing that the gene centers of cultivated plants are the best places to find genuine resistance to their diseases, nowadays collect wild plants of the cultivars with good perspectives for resistance in the countries of origin (see RAYNER, 1960; MEYER, 1966). It happened that *Coffea arabica*, once planted in places outside of its gene center and intensively cultivated in monoculture lost its immunity and became more and more susceptible to its own parasite. Intensively cultivated plants have no time to maintain or establish genetic systems against pest-susceptibility. Plant breeders try to change the genetic of the cultivated plants all the time; the cultivars have to become better and more productive. On the other hand the parasite may suffer mutations or recombinations and may change its former complementary genetic systems too. Both host and parasite have evolved away from each other genetically until the moment that the parasite becomes violent, or in other words, the host becomes susceptible. The indication given by GRAM (1960:324) that the rust existed as an innocuous parasite on wild, viz., unbred coffee in East Africa and Ceylon, offers facts to make us think that Hemileia vastatrix was introduced into Ceylon together with coffee. Because of monoculture and long breeding the blocking gene systems there were broken and the fungus became violent. The other possibility is that the spores were blown to Ceylon by the southwest monsoons from the Horn of Africa (RAYNER, 1960:222) and could there efficently attack coffee which in the meantime had genetically changed.

The spread of the disease from Ceylon to the other coffee-producing countries is still a riddle. RAYNER (1960) and BURDEKIN (1960) brought up strong evidence that the uredospores are dispersed over long distances from one region to the other by air currents. Their ideas were mostly neglected when NUTMAN, ROBERTS and BOCK (1960) and BOCK (1962) seemed to have proved that there is almost entirely a very local dispersal of spores by water-splash. NUTMAN et al. still admitted air dispersal at a very low rate, but later on for BOCK even this seemed unlikely. Nowadays the whole complex of spore dispersal of Hemileia vastatrix is in discussion again and recent results from Brazil showed that in opposition to the statement of BOCK (1962) that there is no wind dispersal at all, spore dispersal is in fact caused by the wind. At least floating spores were found between altidudes of 100 to 1000 meters (local newspapers: Folha de São Paulo, September 30, 1971, page 26; O Estado de São Paulo, October 2, 1971, p. 15). This proves that uredospore dispersal at least within a region is caused by local air currents among other factors. We also have good reasons to believe in long-distance dispersal, so convincingly described by RAYNER (1960), particularly if we observe the spread of the disease and compare this with the directions of the winds of the world. There are two general trends to be seen. The northeast and southwest monsoon circulations during the winter and summer season over Asia might be responsible for the spread of Hemileia within the Asian and Indonesian tropics. In 1868, Hemileia was discovered as a pest in Ceylon, in 1869 already in south India, 1876 in Sumatra and Java and in 1879 it reached its most eastern point in the Fiji Islands. There, at the limits of the monsoons, the disease was brought to a stop; a more eastern spread, for example to the western coast of South America, was hindered because of another main wind direction, the trade wind zones. The trade winds between latidude 30°N and 30°S, coming from northeast in the northern hemisphere and southeast in the southern hemisphere, are characterized by the steadiness of their direction and spead, especially over the oceans. Their general trend from east to west seems to be the reason that the disease did not spread to the east, with the exception of the places reached by the monsoons, but slowly and steadily westwards. Coming from Asia the violent rust was approaching the eastern parts of Africa: Mauritius Island in 1880, Reunion Island in 1882, Madagascar in 1886 and in 1894 it reached the African continent in Tanganyika. A further step in the western direction was Central Africa (1918) and the west coast of Africa between 1930 and 1950 (Ivory Coast, Angola and Nigeria). America was at that time still free of the pest, but RAYNER (1960) and others already warned: "Latin Americans have reason to look at the map of the winds of the world with great disquietude, for the north-east trades blow down along the coast in this part of Africa and then out across the Atlantic towards them." (p. 223). We certainly never will discover if the spores were brought by wind or by other agents to South America, but the great importance of the winds, even for long-distance dispersal (intercontinental spore dispersal discussed in SCHRÖDTER, 1960:222-223) cannot be ruled out. The great extension of the infected areas in the states of Bahia, Minas Gerais and Espirito Santo at the time when the disease was discovered (January, 1970), suggests that the rust probably arrived in Brazil a few years previously. Under the idea that wind may play a major role in spore dispersal, a 50 km broad safty strip between the cities of Rio de Janeiro and Belo Horizonte was established by eradicating coffee plantations just south of the infected areas. This could not stop the rust on its spread to the coffee centers in the southern states of São Paulo and Paraná. In fact the disease has already jumped the safety strip and has reached recently several places in São Paulo State and Paraná. Western countries of South America and Central America are still free of *Hemileia vastatrix*; at least the disease is not yet reported from there. Now they have reasons to look at the map of the winds of the world with great disquietude. Southeastern trades blow straight on from the infected Brazilian areas up to Colombia. That the rust will come to the western parts of South America and also Central America is to expected in a not too far future. Even quarantine stations and the most rigorous control will not prohibit the disease reaching its most western points on its general east-west travel around the world.

The life cycle of *Hemileia vastatrix* very often is said to be uncompletely known. What we principally see from the rust are a great number of uredospores, seldom a few teliospores, which germinate immediately and produce basidiospores. Pycno- or aecidiospores, common in long-cycled rusts have not yet been discovered. From what we know we may classify *Hemileia* biologically as a Hemi-Uredineae (WETTSTEIN, 1935:260). Whether it is an autoecious or heteroecious rust is not settled yet. One should be careful, however, about calling *Hemileia* a heteroecious rust (CARVALHO, P., 1970:21) simply because the coffee plant carries two kinds of spores only and one expects the yet "not discovered" pycno- and aecidiospores on a hypothetical intermediate host. Not all rusts produce all kinds of possible spores (which might be true for Hemileia vastatrix), and even if they do it is not the rule that they are obligately produced on different hosts (WETTSTEIN, 1935:260; ALEXOPOULOS, 1966:376-377; MÄGDEFRAU, 1967:461). For a better illustrating of this idea we may first have a look at the long-cycled heteroecious stem rust, Puccinia graminis, which might serve as a model, and compare its life cycle with that of Hemileia vastatrix. Puccinia graminis produces all kinds of possible spores, viz., pycno-, aecidio-, uredo-, telio- and basidiospores. After having produced pycno- and aecidiospores on Berberis or Mahonia, the aecidiospores infect the second host, a grass of the subfamily Festucoideae. On this second host the rust repeatedly forms uredospores during the summer. In autumn the uredospores are substituted for by many teliospores, the so-called winterspores. In comparing uredo- and teliospore formation in Puccinia and Hemileia we will pay attention to the fact that uredospores are frequent and numerous in both rusts, whereas the teliospores in Puccinia are incomparably more numerous; we know they have to continue the life cycle in the next vegetative period. Teliospores in Hemileia are rarely formed (DIETEL, 1928:52). In comparison with the mass of uredospores they look surpressed and insignificant. This phenomenon perhaps needs some explication. Teliospores are said to conclude the vegetative period, or in temperate countries even to maintain the rust alive during the long winter. In tropical countries there is no real winter. Temperature may fall, precipitation and air humidity may change and the whole metabolism of plants may slow down. Hemileia is a tropical parasite living on a tropical host. Coffee normally maintains a great part of its leaves during winter. Therefore there is no necessity for Hemileia to form "winter"-spores for surviving and continuing its life cycle. Hypothetisizing, we could think that the rust during its correlative evolution with its host has strengthened the parts which have the best dispersal effect, the uredospores, and has diminuished at the same time the unnecessary winter-(telio-)spores. Pycno- and aecidiospores were completely repressed and the formerly long-cycled autoecious rust has become a short-cycled autoecious one. The few telio- and basidiospores in that case might be the remains of a formerly long-cycled rust. Exceptions with profuse production of teliospores sometimes occur (CHINNAPPA & SREENIVASAN, 1965) and might give an insight into a phylogenetically earlier condition. As a consequence of this reduction, basidiospores do not infect coffee any longer; telio- and basidiospores are a blind end of a reduced rust, which reproduces merely by uredospores.

The other possibility, existance of a second host was and is the subject of studies and searches in many coffee regions. To day Brazilian are very enthusiastic to find this intermediate host. Eradicating this second host, they conclude, would (1) make it difficult for the rust to finish its life cycle and therefore diminuish the severity of the pest, or at least would (2) inhibit sexual recombination and hybridization. (Hyphae germinated from basidiospores form spermogonia and fuse with each other.) The first expectation can be excluded immediately. The teliospores are not frequent enough to continue the life cycle on another host in a decisive way. On the other hand it is known that uredospores are able to infect coffee during the whole year, even in winter months. Also the long-cycled Puccinia graminis shows its ability in tropical countries and in absence of the intermediate host (e.g. in Australia, DIETEL, 1928:33) to conclude and repeat its normally heteroecious cycle with only uredospores. Any alteration, viz., reduction of the leaf disease is not to be expected by combating the intermediate host. The second expectation, hindering sexual recombination, sounds at first noteworthy. Hemileia possesses quite a number of different races and as a matter of fact new races always appear (e.g. SREENIVASAN & CHINNAPPA, 1968). But perhaps there is another explanation for the appearance of these races than sexual recombination occuring on the hypothetical intermediate host. Plant breeders were very disappointed to hear that in addition to hybridization, mutation and successive selection, rusts can produce new forms also by heterocaryosis (LEPPIK, 1970:327). Dicariotic hyphae germinated from uredospores of different races of Puccinia graminis can fuse and change their nucleus (RODENHISER and HURD-KARRER, 1947; NELSON, 1956; WATSON, 1958; WILCOXSON et al., 1958; WATSON and LUIG, 1959). A similar phenomenon of fusion was found in Hemileia too (cited in CARVALHO, P., 1970:27). This author speaks about the frequently found anastomosis between hyphae germinated from uredospores. That, he concludes, although not proved yet experimentally, would indicate changing of nuclei between hyphae and could finally serve as an explanation for the variability of the fungus. One must agree with him and think of the already substantiated processes in Puccinia. An intermediate host more and more becomes superfluous. Its existence would be more interesting biologically than economically. If it ever existed and still exists, where could we find it ? Searching for the host in Brazil would be a hard job. It would be much easier to search in East Africa (which has been done extensively already), in the country of origin of both, parasite and host(s). One could even compare the flora of East Africa with that of Brazil and look for plants which are in common at both places. Plants in common should be investigated first in Brazil as potential intermediate hosts. The intermediate host has to be a plant phylogenetically older than coffee. Puccinia graminis has its origin on Berberis and Mahonia (aecial phase) and radiated later with the telial phase to phylogenetically younger grasses of the subfamily Festucoideae (LEPPIK, 1967:571). The aecial phase is said to be the phylogenetically older phase (LEPPIK, 1967). Rubiaceae, the host of Hemileia (telial phase) are, as members of the subclass Asteridae (CRONQUIST, 1968), within the most derived Angiosperms. It would therefore be extremely difficult or impossible to make any predictions as to where we would find a phylogenetically older intermediate host since the possibilities are so numerous. The alternate host, however, is very unlikely to be of the same family, Rubiaceae.

The disease has been known for more than a hundred years. Many people have searched for an intermediate host in many places of the world without results until now. Studying the life cycle of Hemileia vastatrix and its particularities we could come to the conclusion that it indeed is a short-cycled autoecious rust and that pycno- and aecidiospores and the intermediate host on which they are produced are absent. This, however, was presumed already by DIETEL in 1928 (p.51).

After having discussed some biological aspects of Hemileia vastatrix we may mention in a few words the prospect of combatting it in Brazil. The best, and in a long run, only possible form of control is to breed resistant races of coffee. This has been attempted for many years in the Centro de Investigações das Ferrugens do Cafeeiro in Oeiras, Portugal, by Prof. B. d'OLIVEIRA and his group. Brazil also seems to be prepared. Prof. A. CARVALHO from Campinas, São Paulo State, has occupied himself in breeding resistant coffee under Brazilian conditions for about 15 years. His studies were already quite advanced when the disease (race II) arrived. Today his cultivars and hybrids are going to be tested in natural conditions to replace the old susceptible coffee plants. Principally based on his work, Brazil hopefully will overcome its financial losses and economic difficulties of the coming years.

References

ALEXOPOULOS, C. J.: Einführung in die Mykologie. Stuttgart 1966.

BOCK, K. R.: Dispersal of uredospores of Hemileia vastatrix under field conditions. Trans. Brit. Mycol. Soc. 45:63-74 (1962).

BURDEKIN, D. A.: Wind and water dispersal of coffee leaf rust in Tanganyika. Kenya Coffee 25:212-213, 219 (1960).

CARVALHO, P. C. T. de: Ferrugem do Cafeeiro - Epidemiologia. In: A ferrugem do cafeeiro, Univ. São Paulo, Secret. Agric. Est. São Paulo:15-39 (1970).

CHINNAPPA, C. C. and M. S. SREENIVASAN: Secondary sporidia in Hemileia vastatrix. Curr. Sci. 34:668-670 (1965).

CRONQUIST, A.: The evolution and classification of flowering plants. New York 1968.

DIETEL, P.: Unterklasse Hemibasidii (Ustilaginales und Uredinales). In: ENGLER, A. und K. PRANTL, Die natürl. Pflanzenfam. 6:1-98. Leipzig (1928).

FLOR, H. H.: The complementary genetic system in flax rust. Adv. Genet. 8:29-59 (1956).

GRAM, E.: 9. Quarantines. In: HORSFALL, J. G. and A. E. DIMOND, Plant Pathology, Vol. III:313-356. New York and London (1960).
IBC (Instituto Brasileiro do Café): A ferrugem do cafeeiro no Brasil. VIII Reunião Latino Americana de Fitotecnia, Bogotá, Colombia. 75 p., 1970.
LEPPIK, E. E.: Some viewpoints on the phylogeny of rust fungi. VI. Biogenic radiation. Mycologia 59:568-579 (1967).
-- Relation of centers of origin of cultivated plants to sources of disease resistance. Contrib. Agric. Res. Serv. U.S. Dept. Agric., Plant Introd. Invest. paper nº 13, 7 p. (1968).
-- Gene centers of plants as sources of disease resistance. Ann. Rev. Phytopath. 8:323-344 (1970).
MÄGDEFRAU, K.: Dritte Abteilung, Mycophyta, Pilze. In: STRASBURGER et al., Lehrbuch Bot., Ed. 29:430-473 (1967).
MEYER, F. G.: F. A. O. coffee mission to Ethiopia, 1964-1965. Kenya Coffee 31:123-125, 127 (1966).
MONTEIRO, M. V. M.: Ferrugem do Cafeeiro - Ocorrência da doença e providências para seu contrôle. In: A ferrugem do cafeeiro, Univ. São Paulo, Secret. Agric. Est. São Paulo:61-95 (1970).
NELSON, R. R.: Transmission of factors for urediospore colors in Puccinia graminis var. tritici by means of nuclear exchange between vegetative hyphae. Phytopath. 46:538-540 (1956).
NUTMAN, F. J., F. M. ROBERTS and K. R. BOCK: Method of uredospore dispersal of the coffee leaf-rust fungus, Hemileia vastatrix. Trans. Brit. Mycol. Soc. 43:509-515 (1960).
RAYNER, R. W.: Rust disease of coffee. I. Nature of the disease; II. Spread of the disease; III. Resistance. World Crops, May 1960:187-190; June 1960:222-224; July 1960:261-264 (1960).
RODENHISER, H. A. and A. M. HURD-KARRER: Evidence of fusion bodies from urediospore germ-tubes of cereal rusts on nutrient-solution agar. Phytopath. 37:744-756 (1947).
SCHRÖDTER, H.: Dispersal by air and water - The flight and landing. In: HORSFALL, J. G. and A. E. DIMOND, Plant Pathology, Vol. III:169-227. New York and London (1960).
SREENIVASAN, M. S. and C. C. CHINNAPPA: Occurence of a new physiological race of coffee rust (Hemileia vastatrix). Indian Coffee 32:94, 99 (1968).
WATSON, I. A.: Somatic hybridization in Puccinia graminis var. tritici. Proc. Linn. Soc. New South Wales 83:190-195 (1958).
WATSON, I. A. and N. H. LUIG: Somatic hybridization between Puccinia graminis var. tritici and Puccinia graminis var. secalis. Proc. Linn. Soc. New South Wales 84:207-208 (1959).
WELLMAN, F. L.: Hemileia vastatrix - Investigaciones presentes y pasadas en la herrumbre de café y su importancia en la America tropical. Fedecame, Sec. divulgación, nº 23, San Salvador (1957).
WETTSTEIN, R. von: Handbuch der Systematischen Botanik. Ed. 4, Leipzig, Wien 1935.
WILCOXSON, R. D., J. F. TUITE and S. TUCKER: Urediospore germ tube fusions in Puccinia graminis. Phytopath. 48:358-361 (1958).