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RESEARCH ARTICLE

AN OVERVIEW OF PHYSIOLOGICAL SPECIALIZATION OF COFFEE LEAF RUST – NEW DESIGNATION OF PATHOTYPES

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ABSTRACT

Coffee leaf rust is the most important disease thorought the world. The disease caused by a biotrofic fungi *Hemileia vastatrix* Berk. & Br. has been a serious threat for the sustainability of all coffee growing areas of the world. It caused the destruction of the coffee crop in Sri Lanka (Ceylon). Today, coffee leaf rust causes losses from 35 – 50 % on average in Brazil and more tham 50% of the entire Central American coffee park. Coffee rust probably originates in southwestern Ethiopia and was identified in 1860. Then the disease spreaded across the Indian and Pacific Oceans (Philippines, Madagascar and Java). In the 1950s and 1960s, rust advanced across West Africa. In January 1970, the disease was identified in Brazil. In the 1970s-90s, leaf rust advanced to South America, Central America, Caribean and Mexico. Currently, more than 50 *H. vastatrix* physiological races have been identified by using coffee differentials clones of CIFC in the world. The most comum and widespread *H. vastatrix* race II is presente in all over the world. The CIFC diferential clones has nine resistance genes (S_H1, S_H2, S_H3, S_H4, S_H6, S_H7, S_H8 and S_H9) alone or in combination. Races are identified by the differential interaction of genes of the host and of the pathogen. Molecular biology technique, found two different genes in HdT 832/1 and HdT 832/2 not yet identified in differential clones (S_H1-9), named as S_H10 and S_H11. In the present review, we are proposing the name pathotype to refer the isolates of *H. vastatrix* that could not be differentiated into races, according to the CIFC system. Several pathotypes was found in several countries. It became evident that race nomenclature based on a set of differentials of CIFC was not enough to characterize complex isolates from HdT derivatives into races. The resistance of the differential clones HdT 832/1 (S_H 6,7,8,9,? - $v_{6,7,8,9}$,?) and HdT832/2 (S_H 6,7,8,9,? - $v_{6,7,8,9}$,?) was only supplanted in India by isolates colleted in the field; but their resistance was not supplanted in any other part of the world. On the other hand all the progenies derived from HdT 832/1 and HdT 832/2 cossed with arabica coffee lost the complete resistance to *H. vastatrix* in the field in all the coffee growing areas of the world. The only gene that complete resistance was not suplanted yet is S_H3, in the dominant form, from *C. liberica*. This finding is very important due to the fact that cultivars containing the gene S_H3 may be attacked only by the race that has the gene v_3, which is absent in most of the coffee growing countries. For these reasons coffee breders must consider in their breeding programs cross HdT 832/1 and 832/2 (S_H 6,7,8,9) with S 288-23 (S_H3). Since there is no complete resistance to the disease all over the world growers has to rely on the chemical control of the disease. Finaly this overview will discuss designation of races and pathotypes according CIFIC system and Flor gene for gene theory. By the CIFC system the pathogen is recessive and virulent (v_{1-9}) and the host plants are dominant and resistant (S_H1-9) and the interaction is susceptible (S). In our proposed system, the pathogen is avirulent (Avr1-9) and the host plant is also dominant (S_H1-9) and the interaction is resistant (R) characterizing the hypersensitive reaction.

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INTRODUCTION

Coffee originates in Africa, more specifically in the regions of Café and Enária, in Ethiopia, where it occurs spontaneously (McCook, 2006). Commercial cultivation took place with the Arabs, who later took the coffee crop to Egypt in the 16th century and then to Europe in the 17th century.

From the European continent, the grain spreaded to the rest of the world, establishing production in the newly conquered territories in South, Central and Caribbean America. Since then, drink consumption of coffee has increased around the world, breaking records year after year. According to the International Coffee Organization (ICO), the world's largest coffee producing countries in decreasing order in 2020, were:

Brazil, Vietnam, Colombia, Indonesia, Ethiopia, Honduras, India, Uganda, Mexico and Peru. Brazil is the largest producer, exporter and the second in the ranking of largest coffee drink consumers. The cultivation and consumption of coffee around the world follows a growth trend, showing significant increases since the 1990s. The coffee sector follows a growth rate of 2% per year, and production is estimated to reach 208 million bags until 2030. Demand for coffee consumption increases more rapidly in those regions that are not traditional importers, such as Asia, Oceania and Africa. The ICO in 2019 reported an average increase of more than 4.0% on the three continents. However, Europe remains the region in the world that buys most grain. In 2019, 167.47 million bags were produced on a global scale, of which 104.01 million bags of arabica coffee and 63.5 million bags of robusta according to the ICO in 2019. Coffee cultivation is divided between Arabica (*Coffea arabica*) and Robusta (*Coffea canephora*). Brazil exports 35% of world production, Vietnam second with 18,3%, followed by Colombia with 18%, Indonesia with 6%, Ethiopia with 5%, Honduras with 5% and India with 3%. Brazil has been the largest producer of beans in the world for more than 150 years according to the ICO in 2019 and 'Observatório do café – Embrapa', in 2019. This review deals with the economic importance, geografical distribution, pathotypes and the new designation of races of *Hemileia vastatrix*.

Economic importance: Coffee leaf rust disease caused by *Hemileia vastatrix* Berk. & Br. has been a serious threat for the sustainability of Arabica coffee plantation in Asia, Africa, and America. (Avelino *et al*., 2015; Jefuka *et al*.; Talhinhas *et al*., 2017). In Ceylon (Sri Lanka), in the 1860s, leaf rust caused the destruction of the coffee crop. Ceylon was the world's third largest coffee exporter, in that time. Fifteen years later, Ceylon's coffee industry had practically collapsed to such an extent that coffee crop was replaced by tea. In the 1830s, the East African hemisphere produced about a third of the world's coffee, however by 1905, the production decrease for 5% due to the leaf rust attack. In the Philippines, the disease has destroyed the coffee industry and their smaller islands. In Madagascar and Java, the disease expelled Arabica coffee from the humid plains, where the epidemic was particularly severe (Mc Cook, 2006). Since, at that time, scientists could not control the disease epidemic. Then they started looking for coffee trees, including other especies, which showed some resistance to the disease, as *Coffea liberica* discovered in the 1870s, in India. This species was widely planted in Ceylon in the 1870s and in the Dutch East Indies in 1890. In these two places, however, *C. liberica* "lost" its resistance after several years. In the 1930s, British scientist Wilson Mayne discovered that the apparent loss of resistance involved the emergence of physiological races of *H. vastatrix* (Large, 1940).

Nowaday, coffee leaf rust causes losses of around 35% on average in Brazil, where climatic conditions are favorable the disease development. In conditions of prolonged drought in periods of greater disease severity, losses in production can reach more than 50%. The main damages caused by rust are the early fall of the leaves and the dryness of the branches, which, as a result, do not produce fruit in the next year (Zambolim, 2016); The disease in Central America was discovered in Nicarágua in 1978 (Stephanie, 2015). The Nicaragua government then started a campaign to eradicate the disease, with technical and financial help from other producing countries in Central America and an international agency. Around 1979, the Nicaraguan government spent more than $ 20 million to control rust. In 1980, the government initiated a program to renew the coffee crop in the country, but the rust spread quickly to the new plantations (Waller, 1982). In the 1970s-90s, the rust advanced to other countries in South America, Central America and Mexico (McCook, 2006; Schieber & Zentmeyer, 1984, Avelino *et al*., 2015). In Central America, leaf rust has caused one of the worst epidemics in the producing countries. According to data from Promecafé, the effect of rust on regional coffee production in the 2012/13 crop year was estimated at 2.7 million bags, costing around US $ 500 million. On average, more than 50% of the entire Central American coffee park, has been affected by the disease. The disease incidence rates were as follows: El Salvador 74%, Guatemala 70%, Costa Rica 64%, Nicaragua 37% and Honduras 25% (Avelino *et al*., 2015). In Honduras, the damage caused by the disease was low, due to the use of the rust-resistant cultivar Lempira in the main regions of the country. However, in 2017, the qualitative resistance of cv. Lempira was supplanted by the new races of the pathogen. In addition to economic losses, there was also a significant social impact. Most of Central America's coffee belong to small coffee growers, who did not have the financial means to absorb the expected losses. It is estimated that around 374,000 jobs disappeared in 2012/13 due to rust, as the labor used for the harvest would not be necessary. In addition, in many areas the loss of revenue by coffee growers was reflected in food security.

The rust epidemic in Central America has also caused greater migratory pressure towards North America. In terms of the world coffee market, Central America (excluding Mexico) produced 15.8 million bags in 2011/12, accounting for about 12% of world production. The expected losses for 2012/13, with an estimated volume of 2.7 million bags, would represent a decrease of 17.1% in relation to the previous year. This situation, moreover, had significant consequences for consumers of specialty coffees, given the great importance of Central America, as a source of quality washed Arabicas. In Central America, this fungus caused major damage which implicated loss jobs of around 1.7 million coffee workers and loss income around $3.2 billion in 2017. Currently, leaf rust still causes severe damage to coffee growing in the countries of South America (Brazil, Ecuador, Peru, Venezuela and Colombia), Central America (Guatemala, Honduras, Nicaragua, El Salvador, Costa Rica and Panama) and the Caribbean (Dominican Republic) and Mexico. The vertical or qualitative resistance of varieties originated from the crossing between Híbrido de Timor (HdT) and commercial varieties (Caturra, Catuaí, Vila Sarchi and Mundo Novo) grown in these countries, has been suplanted. Growers that have planted resistant or suscetible varieties selected in their countries are spraying against leaf rust with protector (coopper compounds) and systemic fungicides (triazols and or strobilurin). Therefore, chemical control of the disease has been used by coffee farmers in these countries (Zambolim, 2016; Zambolim & Caixeta 2018).

Distribution of coffee leaf rust in the world: Coffee rust probably originates in southwestern Ethiopia and was identified in 1860. The pathogen is a biotrophic fungus that attacks only plants of the genus *Coffea*. In the 1860s, the fungus was accidentally transported from East Africa to Ceylon (Sri Lanka). The dense monocultures of Ceylon coffee

with favorable temperature and humidity, made it a place especially conducive to the epidemic. In the following decades, the epidemic spreaded across the Indian and Pacific Oceans. The disease hit coffee culture in the Philippines, Madagascar and Java (McCook, 2006). In the early 1900s, Dutch producers introduced *Coffea canephora* var. *robusta*, in the Dutch East Indies, known as robusta coffee, considered to be resistant to rust. Robusta therefore became an important crop in Java, Uganda, Madagascar, Portuguese and French West Africa (Cramer, 1957; Clarence-Smith, 1870-1914). After 1905, the Old World began to recover its share of world coffee production - but most of it was robusta coffee. Around 1950, coffee growers in Africa, Asia and the Pacific - where rust was present - produced low quality and low value "robusta". The coffee-producing countries of the Americas up to that time, still free of rust, produced high-quality Arabica coffee. The epidemic had been effectively postponed since 1930s. In the 1950s and 1960s, rust advanced across West Africa. The region's two largest coffee producers - Côte d'Ivoire and Angola - were affected in 1954 and 1966, respectively. Since most of the coffee grown in the region was *C. canephora*, the rust did not affect the total coffee production. However, the epidemic has become very close to the Americas. Therefore, According to Mc Cook (2006), coffee rust spread in the Asia and Africa in the following countries: Ethiopia in 1860; Sri Lanka (Ceylon) in 1860; Philippines, Madagascar, Java and India from 1860-66); Ivory Coast in 1954 and Angola in 1966.

In the 1950s and 1960s, as the epidemic spreaded across West Africa, some scientists began to express concern about the risk of coffee in the Americas. Hence, phytopathologist Frederick Wellman was assigned to work at the Inter-American Institute of Agricultural Sciences in Costa Rica to travel to Africa and Asia to study the rust epidemic on these two continents. In his report, he concluded that the western hemisphere had escaped the disease "more by luck than by any other factor". In addition, he recommended that researchers in the Americas begin to grow or select coffee plants resistant to rust or explore other forms of disease control (Wellman, 1957). In response to this recommendation, in 1955 the government of Portugal created the Coffee Rust Research Center (CIFC), in Oeiras, financed by the United States government. The CIFC started to work on the identification of *H. vastatrix* races and on the genetic improvement of coffee, aiming at the incorporation of resistance in susceptible varieties. Besides, they initiated selections and hybridization of Hibrido de Timor (HdT) coffee with susceptible varieties of high commercial value such as Caturra and Vila Sarchi. HdT coffee is a spontaneous hybrid of *C. arabica* and *C. canephora*, discovered in the Portuguese colony of East Timor, in the 1920s. In the late 1950s, HdT plants was taken to Oeiras, Portugal by CIFC researchers. From the CIFC, improved descendants of HdT were sent to coffee breeding programs in Brazil, Colombia and Costa Rica, where they were crossed and backcrossed with local Arabica coffee (Avelino *et al*., 1999). In Latin America, productive Arabica varieties were grown such as Caturra, Bourbon and Catuaí, but they are very susceptible to leaf rust. With the establishment of rust in the new areas of West Africa, Wellman reported that there was 'an increasing danger that rust would spread throughout the Americas'. For the first time, areas attacked by rust are in the direction of the winds and storms that link rust-contaminated African countries to coffee plantations in the Americas (Wellman, 1957). As warned, rust spread from West Africa to Brazil. In January 1970, Brazilian researcher Arnaldo Gomes Medeiros identified coffee rust in Bahia state. Four months later, the disease was spreaded to all coffee growing states in Brazil, scattered by the wind (Chaves *et al*., 1970). So far, it is not clear how rust reached the New World. Even though wind currents spread rust over long distances in Africa, some scientists have doubted its ability to travel across the ocean. Once the disease settled in Brazil, it spreaded very quickly. The disease had taken 50 years to cross Africa from east to west; but it spreaded across the Americas in less than 15 years. As in previous outbreaks, wind was the biggest factor in the expansion of *H. vastatrix* spores at the local and regional level. In the late 1970s and early 1980s, coffee leaf rust spread beyond its focus in Brazil. From the Brazilian focus, it advanced over some areas of Paraguay and Argentina, in 1972, and then, significantly, to plantations in Acre, in the extreme west of the Brazilian Amazon, in 1975. The rust may have been carried from Acre to Bolivia in diseased seedlings. From Bolivia, the disease apparently went to the north of the Andes, possibly carried by seedlings or by the wind. The first country in Central America where leaf rust was detected was Nicaragua, in 1978, which has been growing coffee since the late 1800s (Stephanie, 2015). In the 1970s-90s, leaf rust advanced to other countries in South America, Central America and Mexico (McCook, 2006; Avelino *et al*., 2015). Leaf rust in the Americas in addition to Brazil in 1970, was reported in the following countries: Peru 1979 (McCook 2006); Guatemala 1980 (McCook 2006); Ecuador 1981 (McCook 2006); Mexico 1981 (Schieber and Zentmeyer 1984); Colombia 1983 (National Coffee Research Center - Cenicafé Colombia); Cosa Rica 1989-90 (McCook 2006; Avelino *et al*. 1989); Honduras 1995-96 (McCook 2006); Nicaragua 1978 (Schieber *et al*., 1984) and El Salvador 1989 (McCook 2006).

Identification of *Hemileia vastatrix* races: For race characterization, samples of uredospores of *H. vastatrix* were collected from diseased leaves of *Coffea* spp. and interspecific hybrids in the coffee grown field, coffee species collections and greenhouses. Each sample of uredospores of *H. vastatrix* can be stored for a couple of weeks in ampoules maintained inside a desiccator contained a sulfuric acid solution (density of 1.8 and concentration of 32.6%) to maintain the relative humidity around 50% at 5^0C. The uredospores can also be kept in glass ampoules in liquid nitrogen at -196 ° C (Zambolim and Chaves 1974) or at -80^0C inside glass ampoules in a frezer. Next step is to get monopustule of the fungus for each sample collected. *Coffea arabica* var. Caturra leaves with 3 months old should be inoculated with uredospores of *H. vastatrix* either diretly from the field or with uredospores stored at 5^0C, liquid nitrogen or freezer at -80^0C. The incubation is generally at 22^0C with relative humidity approximately 100%. After 48 hours, the inoculated plants is taken to a chamber at 22^0C with 16 h of fluorescente light and 8 h in a dark. The isolated pustules on the leaves is harvested separately to be inoculate again in Caturra variety in order to obtain the amount of uredospores necessary for physiological race characterization. Only uredospores with a viability superior to 30% are considered appropriate for the inoculation tests. The inoculations can be done directly on the leaves of the differential clones. The inoculation of the uredospores from each multiplied monopustule of *H. vastatrix* is individually inoculated with a dried spores using camelhair brush or a suspension of 10^5 spores/mL with manual sprayer, over the abaxial surface of the leaves of each coffee

differential clone proposed by CIFC (Table 1 and 2). Distinct races or pathotypes of *H. vastatrix* have been identified through the differentiation of isolates of the pathogen on a set of coffee host materials with different resistance gene combinations (D'Oliveira, 1954−57). Physiologic races of plant pathogens are identified by their interaction with a set of host genotypes termed differentials (Flor, 1971). Currently, 23 coffee clones compose the differential coffee set (Zambolim & Caixeta, 2018).These clones was established by CIFC at Oeiras, Portugal (Rodrigues *et al*. 1965; Noronha-Wagner and Bettencourt, 1967) and sent to several research institutions in different continents in the world such as Asia, Africa, South America (Brazil) and Central America (Costa Rica). The clones are mantained by vegetative propagation from the original collection of coffee leaf rust disease centre at CIFC. The characterization of the physiological races of *H. vastatrix* is based on the readings of the phenotypic expression (absence or presence of uredospores) in the pustule on the inoculated coffee leaves or leaf discs (Eskes 1982). The evaluation starts when the first uredospores formed on the susceptible control (Caturra). Four evaluation should be done at 7-day intervals and the recorded results is compared with the races and differential clones designated by CIFC (Rodrigues *et al*., 1965; Noronha-Wagner and Bettencourt, 1967; Bettencourt and Lopes, 1968; Rodrigues *et al*., 1975; Várzea and Marques 2005).

Genetic diversity of *Hemileia vastatrix:* The geographical distribution of *H. vastatrix* races seems to be dependent on the coffee genotypes planted locally, and the prevalence of certain races in a given area thus seems to occur accordingly (Bettencourt, 1981). Races of *H. vastatrix* identified in the Asia and Africa are on the Table 3. Twenty four races (I, II, III, VII, XI, XII, XV, XVI, XVII, XX, XXII, XXIII, XXIV, XXV, XXVI, XXVII, XXVIII, XXIX, XXX, XXXIII, XXXIV, XXXIX, XLI, XLII) was reported in Asia and Africa since the decade of 1930 (Table 2). However, the number of races could be much greater then the 24 reported. A survey did by D'Oliveira & Rodrigues (1961) and Rodrigues *et al*. (1965) around the world related 45 and 54 races, respectively, but they did not mention the races. In India, the apparent loss of resistance in coffee cultivars highlighted the attention of Mayne in the early 1930s. By means of experimental inoculations, he was able to differentiate, with local rust samples and host differentials, four physiologic races of *H. vastatrix* (Mayne 1932; 1942; Meyer 1965). India was the country that registered the highest number of *H. vastatrix* races in the world, being more than 37 (Prakash *et al*., 2005; Prakash *et al*., 2015). However, the number of races today could be more than 50. This country holds the most ancient breeding programme for coffee leaf rust resistance in the world, involving regular and massive introductions of new or experimental resistant coffee materials into the field, to which usually follows the appearance of new pathotypes with enlarged virulence spectra (Várzea and Marques, 2005; Prakash, 2005). The most complex races has been identifyied in India due to the cultivation of germplasm of coffee varieties derived from HdT (Prakash, 2005; Prakash *et al*., 2015). In 1952 a world survey of coffee leaf rust was initiated by Branquinho D'Oliveira from Coffee Rusts Research Center (CIFC), in Oeiras, Portugal (D'Oliveira 1954-1957). The work enabled the characterization of about 45 rust races (D'Oliveira and Rodrigues, 1961; D'Oliveira, 1965; Rodrigues *et al*., 1965; Bettencourt *et al*., 1965; Rodrigues *et al*., 1975; Rodrigues *et al*., 1993; Várzea *et al*., 2002; Várzea & Marques, 2005). Rodrigues & Bettencourt (1975) related 32 races and Gichuru *et al*. (2012) reported 49 races. Considering that Ethiopia is the center of origin of *C arabica* and most probably of *H. vastatrix* as well, it is probable that host and parasite have undergone a parallel evolution, and that the work of natural selection has given rise to resistant plants on one side and to a number of physiologic races of the pathogen on the other (D'Oliveira, 1951). However, the screening of 66 rust samples received from several areas of Ethiopia on different occasions (D'Oliveira 1951; Bettencourt; Lopes, 1966) led only to the identification of races I, II, III, and XV. In a study on the decade of 1950-60, Rodrigues *et al*. (1965) and Bettencourt & Lopes (1966) identified 24 physiological races, using 13 differentiating coffee clones. Four of them, races XII, XIV, XVI and XXIV were obtained from cultures of *H. vastatrix* already established by the CIFC, in which they existed as a mixture or were developed through mutation or heterokaryosis (Bettencourt & Carvalho, 1968).

Following the survey of phsiological races of *H. vastatrix* around the world, carried out by the CIFC, with 779 rust samples from over 30 different regions of the world and with a vast collection of coffee germplasm, led to the differentiation of a total of 30 physiologic races (Rodrigues *et al*., 1965) on a set of 17 differential hosts. In the America continent (South and Central Amércia, Caribean and México), 18 races (I, II, III, X, XV, XIII, XVI, XVII, XXII, XXIII, XXIV, XXV, XXIX, XXX, XXXIII, XXXVI, XXXVII and XXXIX) were reported (Table 4). The most comum and widespread *H. vastatrix* race II in the America continent acquiring a generalized occurrence, probably is due to the uniform genetic background of most *C. arabica*cultivars planted in the field. Race II reflected the susceptible varieties cultivated in South and Central America, Caribean and Mexico. When HdT and interespecif hybrids from CIFC was cultivated in the field in Brazil and Central America, Caribean and Mexico in trials and in coffee collections,other complex races appeared (Talhinhas *et al*., 2016; Zambolim & Caixeta, 2018).

Selection pressure exerted by coffee resistance genes (HdT and other interespecific hybrids derivatives) probably explain the great variability of *H. vastatrix* races in Brazil and other countries. The virulence profile characterization, particularly of isolates infecting HdT derivatives, can onlybe performedif genotypes from the collection of differentiating clones can differentiate them. The unavailability of differential coffee genotypes results in many pathotypes with incomplete characterization or entirely unidentified. As presumed from the dynamic host–pathogen co-evolutionary arms race, in which short-term selection of pathogen strains with fitness advantages is promoted, new pathotypes with increased virulence have been continuously appearing. Currently, more than 50 *H. vastatrix* physiological races have been identified by using coffee differentials clones of CIFC, in several countries: Portugal, India, Kenya, Indonesia, Etiopia, Tanzania, Costa Rica, Honduras, Mexico, Colombia, Venezuela, Guatemala, El Salvador, Nicarágua, Dominican Republic and Brazil (Zambolim *et al*., 2005; Silva *et al*., 2006; Prakash *et al*., 2005; 2015; Várzea *et al*., 2005, 2009; Gichuru *et al*., 2012; Talhinhas *et al*., 2016; Talhinhas *et al*., 2017; Zambolim & Caixeta, 2018). Although there are many reports relating 50 races of the pathogen in the world, even though the number could be higher, there is no comprovation yet.

Genes for coffee resistance and for *Hemileia vastatrix* virulence: *H. vastatrix* races are identified and characterized in a coffee host material bearing different resistance gene combinations under prescribed testing conditions (Table 1).Races are described as sequential roman numerals in order of detection (D'Oliveira, 1954−57; Noronha-Wagner and Bettencourt, 1967). Noronha-Wagner and Bettencourt (1967), by allelism test and inoculation of different coffee plants and the progenies from their crosses, found four resistant genes and named them as S_H. Using 12 physiologic races of *H. vastatrix*, they identified the gene S_H1 in clone 87/1 Geisha, S_H2 in 32/1 DK 1/6, S_H3 in 33/1 S.288-23 and S_H4 in 110/5 S4 Agaro. Some combinations of these genes have also been found in other clones. Further studies identified the genes S_H5, S_H6, S_H7, S_H8 and S_H9, alone or in association, in different coffee clones (Bettencourt & Noronha-Wagner, 1971; Bettencourt et al., 1980, Bettencourt et al., 1992). Table 1 shows the coffee clones and their respective S_H genes.

gene-to-gene theory (Noronha-Wagner and Bettencourt, 1967).Thus, as no further genetic confirmation has been possible so far, inferred rust race genotypes comprise virulence genes ranging from v_1 to v_9 in isolates derived from *C. arabica* and tetraploid interspecific hybrids, whereas those of the races that attack diploid coffee species are not known. Given this direct correlation with the coffee host resistance genotypes, virulence genes v_1, v_2, v_3 and v_5 can be traced back to an Arabica-type origin (v_1/S_H1 from 'Geisha'; v_2/S_H2 from 'Kent's'; v_4/S_H4 from 'Kaffa'; v_5/S_H5 from nearly all cultivars). The v_3/S_H3 was indentified in genotype with *C. liberica* introgression. The genes v_6 to v_9 reflect the additional *C. canephora* heritage of S_H6 to S_H9 genes present in HdT and other interspecific hybrids. HdTs are natural hybrids between *C. arabica* and *C. canephora* and received from the latter the major genes responsible for rust resistance (S_H6, S_H7, S_H8, S_H9) and others not yet identified biologicaly (Rodrigues et al., 1975; Bettencourt & Rodrigues Jr., 1988; Várzea & Marques,

Table 1. Differential clones, genes of resistance and virulence of *Hemileia vastatrix*

Host differentials	Resistant Genes S_H (1–9)	Virulence Genes $v_{(1-9)}$	Races
19/1 – Matari	S_H5	v_5	II, III, VII, VIII, X, XII, XIII, XIV, XV, XVI, XVII, XXII, XXIII, XXIV, XXV, XXVI, XXVIII, XXIX, XXX XXXI, XXXIX, XXXV, XXXVI, XXXVII, XXXVIII, XXXIX, XL, XLI, XLII.
128/2 - Dilla & Alghe	S_H1	v_1	III
635/2 S. 12 Kaffa	S_H4	v_4	X, XIV, XV, XVI, XIX, XX, XXIII,XXIV, XXVI, XXVIII, XXXV, XXXVI, XXXVIII, XXXIX, XXXV, XXXVI, XXXVII, XXXVIII.
63/1 – Bourbon	S_H 5	v_5	II, III, VII, VIII, X, XII, XIII, XIV, XV, XVI, XVII, XXII, XXIII, XXIV, XXV, XXVI, XXVIII, XXIX, XXX. XXXI, XXXIX, XXXV, XXXVI, XXXVII, XXXVIII, XXXIX, XL, XLI, XLII.
1343/269 - H. Timor	S_H 6	v_6	XXII, XXV, XXVI, XXVII, XXVIII, XXIX, XXX, XXXI, XXXIX, XXXV, XXXVI, XXXVIII, XXXIX, XL.
32/1 - DK 1/6	S_H 2,5	$v_{2,5}$	VIII, XII, XIV, XVI, XVII, XXIII, XXIV, XXVIII, XXXI, XXXIV, XXXV, XXXVI, XXXVII, XXXVIII. XXXIX, XL, XLI, XLII,
33/1 - S. 288-23	S_H 3,5	$v_{3,5}$	VII, VIII, XII, XIV, XVI
644/18 H. Kawisari	S_H ?	$v?$	XIII
H 148/5	S_H1,3,4,5	$v_{1,3,4,5}$	XVI
H 147/1	S_H 2,3,4,5	$v_{2,3,4,5}$	XXIV, XXVI.
H 152/3	S_H 2,4,5	$v_{2,4,5}$	XIV, XVI, XXIII, XXIV, XXVIII, XXXV, XXXVI, XXXVIII, XXXIX
H 153/2	S_H 1,3,5	$v_{1,3,5}$	XII, XVI
H 151/1	S_H 3,4,5	$v_{3,4,5}$	XIV, XVI
H 419/20	S_H 5,6,9	$v_{5,6,9}$	XXIX, XXXI, XXXVII, XXXIX.
H 420/2	S_H 5,8	$v_{5,8}$	XXIX, XXX, XXXVI, XXXVIII, XLI, XLII.
H 420/10	S_H 5,6,7,9	$v_{5,6,7,9}$	XXIX, XXXVII, XXXIX.
H 535/10	S_H2,3,5,6	$v_{2,3,5,6}$	XVI, XXVIII, XXXI, XXXVII, XXXVIII, XXXIX.
H 537/18	S_H 2,5,6	$v_{2,5,6}$	XVI, XXVIII, XXXI, XXXVII, XXXVIII, XXXIX, XL
H 538/29	S_H 1,5,6	$v_{1,5,6}$	XL
H 539/8	S_H 1,4,6,	$v_{1,4,6}$	XXVII
H 440/7	S_H 5,6	$v_{5,6}$	XXV, XXVI, XXVII, XXXVIII, XXIX, XXXI, XXXVII, XXXIX, XL.
H 150/8	S_H1,2,3,5	$v_{1,2,3,5}$	XL
H 581/17	S_H 3,5,6	$v_{3,5,6}$	-
H 583/5	S_H 4,5,6	$v_{4,5,6}$	XXVI XXII, XXV, XXVI, XXVIII, XXIX, XXXI
7960/15 = 7963/117-Catimor	S_H 5,7 ou S_H 5,7,9	$v_{5,7,9}$ ($v_{5,7}$)	XXXIV, XLII
829/1	S_H ?	$v?$	-
635/2 S 12 Kaffa	S_H 4	v_4	X, XIV,XVI, XIX, XXIII, XXIV, XXVI, XXVII, XXVIII, XXXV, XXXVI, XXXVIII, XXXIX.
1006/10 - KP 532 (pl 31)	S_H 1,2,5	$v_{1,2,5}$	XII, XVI, XVII, XXIII, XXXVIII, XL.
635/3 S 12 Kaffa	S_H 1,4,5	$v_{1,4,5}$	X, XVI, XXIII, XXXVIII,
HW 17/12	S_H 1,2,4,5	$v_{1,2,4,5}$	XVI, XXIII, XXXVIII
832/1 H. Timor	S_H 6,7,8,9,?	$v_{6,7,8,9,?}$	-
832/1 H. Timor	S_H 6,7,8,9,?	$v_{6,7,8,9,?}$	-
134/4 - S 12 Kaffa	S_H1,4	$v_{1,4}$	X, XVI, XIX, XXIII, XXVII, XXXVIII
87/1 – Geisha	S_H 1,5	$v_{1,5}$	III, X, XII, XVI, XVII, XXIII, XXXVIII, XL
110/5 S 4 Agaro	S_H 4,5	$v_{4,5}$	X, XIV, XV, XVI, XXIII, XXIV, XXVI, XXXV, XXXVI, XXXVIII, XXXIX
7962/164 Catimor HW 26/5(F6)	S_H 5,7 ou S_H 5,7,9	$v_{5,7\,ou}$ $v_{5,7,9}$	XXXIII

In the patossystem *Coffea-H. vastatrix*, the sexual stage of the rust is not known. Therefore, it is not possible to analyze the genetical bases of the pathogenicity. The virulence genes (v) in the pathogen are inferred based on resistance gene (S_H) found in the differential coffee set, according the Flor's

2005; Diniz et al., 2012). However, so far, we do not know the genes for resistance and virulence of the differentials host 849/1 Matari, *C. dewevrei excelsa* Longikoi (168/12,), *C. congensis* Uganda (263/1), *C. canephora* Uganda (829/1, 681/7 and 162113) and 644/18 Kawasari Hybrid (Table 2).

Table 2. Coffee clones, genes for resistance and virulence of *Hemileia vastatrix* to distinguish races of the pathogen according CIFC system*

Host differentials	Resistance genes (Virulence genes)	Host differentials	Resistance genes (Virulence genes)
128/2 Dilla & Alghe*	S_H1 (v_1)	34/13 S 353 4/5	S_H2,S_H3 ($v2,v3$)
635/2 S.12 Kaffa*	S_H4 ($v4$)	H 440/7	S_H5,S_H6 ($v5,v6$)
63/1 Bourbon*	S_H5 ($v5$)	H 539/8	S_H1,S_H4,S_H6 ($v1,v4,v6$)
1343/269 H. Timor*	S_H6 ($v6$)	H 538/29	S_H1,S_H5,S_H6 ($v1,v5,v6$)
87/1 Geisha*	S_H1,S_H5 ($v1,v5$)	34/10 S.3534/5	S_H2,S_H3,S_H5 ($v2,v3,v5$)
32/1 DK 1/6*	S_H2,S_H5 ($v2,v5$)	H 537/18	S_H2,S_H5,S_H6 ($v2,v5,v6$)
33/1 S.288-23*	S_H3,S_H5 ($v3,v5$)	H 581/17	S_H3,S_H5,S_H6 ($v3,v5,v6$)
110/5 S4 Agaro*	S_H4,S_H5 ($v4,v5$)	H 583/5	S_H4,S_H5,S_H6 ($v4,v5,v6$)
134/4 S.12 Kaffa*	S_H1,S_H4 ($v1,v4$)	H 150/8	S_H1,S_H2,S_H3,S_H5 ($v1,v2,v3,v5$)
H 420/2*	S_H5,S_H8 ($v5,v8$)	H 148/5	S_H1,S_H3,S_H4,S_H5 ($v1,v3,v4,v5$)
1006/10 KP532 pl.31*	S_H1,S_H2,S_H5 ($v1,v2,v5$)	H 535/10	S_H2,S_H3,S_H5,S_H6 ($v2,v3,v5,v6$)
H152/3 (32/1x110/5)*	S_H2,S_H4,S_H5 ($v2,v4,v5$)	832/2 H. Timor	S_H6,S_H7,S_H8,S_H9($v6,v7,v8,v9?$)
H 419/20*	S_H5,S_H6,S_H9 ($v5,v6,v9$)	HW 18/21	S_H1,S_H2,S_H3,S_H4,S_H5 ($v1,v2,v3,v4,v5$)
635/3 S.12 Kaffa*	S_H1,S_H4,S_H5 ($v1,v4,v5$)	829/1 *C. canephora* Uganda	Unknown
H151/1 (33/1x110/5) *	S_H3,S_H4,S_H5 ($v3,v4,v5$)	168/12 *C. dewevrei excelsa* Longikoi	Unknown
H 153/2*	S_H1,S_H3,S_H5 ($v1,v3,v5$)	263/1 *C. congensis* Uganda	Unknown
HW 17/12*	S_H1,S_H2,S_H4,S_H5 ($v1,v2,v4,v5$)	681/7 *C. canephora* Uganda	Unknown
H 147/1*	S_H2,S_H3,S_H4,S_H5 ($v2,v3,v4,v5$)	162113 *C. canephora*Uganda	Unknown
H 420/10*	S_H5,S_H6,S_H7,S_H9 ($v5,v6,v7,v9$)	849/1 Matari*	Unknown
7960/15 = 7963/117 Catimor*	S_H5,S_H7 ($v5,v7$) or S_H5,S_H7,S_H9 ($v5,v7,v9$)	644/18 Kawasari Hybrid *	Unknown
832/1 H. Timor *	S_H6,S_H7,S_H8,S_H9($v6,v7,v8,v9?$)		

Adapted from: *D'Oliveira, 1954−57; Rodrigues et al. (1965); Noronha-Wagner and Bettencourt (1967).

Table 3. Races of *Hemileia vastatrix* identified in Africa and Asia

Country	Races	Author
India	Four (no race designation)	Mayne (1932)
Collected in several Countries in Africa	Fourthy five (no race designation)	D'Oliveira & Rodrigues, (1961); Rodrigues et al., (1965); Bettencourt et al., (1965); Rodrigues et al., (1975); Rodrigues et al., (1993); Várzea et al., (2002)
Ethiopia	I, II, III, XV.	Bettencourt & Lopes (1965)
African countries	Twenty four (no race designation) (XII, XIV, XVI, XXIV-CIFC collection)	Rodrigues et al. (1965) Bettencourt & Lopes (1965)
Around the world	Thirty (no race designation)	Rodrigues et al. (1965)
Kenya	I, II, VII, XV, XX, XXIV	Thitai & Okioga (1977)
Kenya	III, XVII, XXIII, XXXVI, XLI, XLII	Gichuru et al. (2012)
Tanzania	I, II, III, XVII, XXIV, XI, XX	Rodrigues et al. (1975)
Tanzania	XXII, XXXIV	CIFC (2007)
Tanzania	XXIII, XXIV, XXV, XXVI, XXVIII,	Kilambo et al. (2013)
Tanzania	XV, XXX, XXXIII, XXXIV, XXXIX, XLI, XLII	Kilambo et al., (2013)
Indonesia	I, II, III, XV, XVII, XXII, XXV, XXVI, XXIX, XXX	Goujon (1971); Rodrigues et al. (1975)
Índia	I, II, VIII, XII, XIV, XVI, XXII, XXIII, XXIV, XXV, XXVIII, XXXIV	Rodrigues et al., (1975)
Índia	Over 37 (no race designation)	Prakash et al.(2005); Prakash et al. (2015)
Sri Lanka	I, II, XV	Rodrigues et al. (1975)
Angola	I, II, XV, XXVII	Rodrigues et al. (1975)
Portuguese Timor	I, II, III, XV, XXII, XXV, XXVI, XXIX, XXX	Rodrigues et al. (1975)
Java (Indonésia)	VII	Mawardi & Hulupi (1993)

Within this context, *H. vastatrix* races are atributed to isolates with distinct and unique combinations of virulence genes as inferred by Flor's gene-to-gene theory (Flor 1942, 1971). Accordinly to Flor (1942), "for each dominant gene responsible for resistance in the host there is a dominant specific gene for avirulence in the pathogen". He also mentioned that, for *Melampsora lini*, the infection of the virulent type appeared to be, in general, a recessive character and resistance to the rust fungi usually has been inherited as a dominant character. In 1955, Flor confirms this finding, and proposed that the resistance genes in the host could be identified by the pathogenicity of specific races of the parasite. In addition, the genes for pathogenicity in the parasite are identified by the reaction of specific genes on the varieties of the host. Acceptance of this hypothesis enables to construct

Table 4. Races of *Hemileia vastatrix* identified in the America's continent

Country	Races	Author
Brazil	I, II, III, X, XIII, XV, XVI, XVII, XXII, XXIII, XXIV, XXV, XXIX; XXX; XXXIII; XXXVII	Chaves & Pereira (1980) Cardoso et al., (1986, 1988) Zambolim et al. (2005) Fazuoli et al. (2005) Cabral et al. (2009) Toma-Braghini et al., (2015) Capucho et al. (2012) Silva; Zambolim; Caixeta (2019)
Brazil	I, II, III (*Coffea canephora*)	Zambolim, (2018-20)*
Guatemala	I, II, III, XXIII, XXV	Zambolim & Chocooj, (2018-20)*
Honduras	I, II, III, XIV, XX, XXII, XXXVI	Zambolim, Veras & Lizardo, (2018-20)*
Costa Rica	II, XXII, XXIX, XXXIII	CIFC[1]; Zambolim, (2018-20)*
El Salvador:	I, II, III	Gálvez et al., 1980; Zambolim, (2018-20)*
Nicaragua	I, II	Zambolim, (2018-20)*
Panamá	I, II	Zambolim, (2018-20)*
México	I, II, III	Zambolim, (2018-20)*
Venezuela	I, II, III, X, XV, XVI, XXIV, XXXIII	Silva et al., (1997) Zambolim & Ramirez, (2018-20)*
Colombia	Virulent factors v1,2,4,5,6,7,8, 9	Alvarado y Ruiz, 2005.
Colombia	II, XXII	Leguizamin et al., (1984); Gil Ocampo, (1998); Cristancho et al., (2007)
Colombia	XXIX or similar	Cristancho et al., (2007)
Dominican Republic	I, II, III, XXXIII	Zambolim & Quisqueya, (2018-20)*

*Surveys done from 2018 – 2020 (not published). [1]Personal information

Table 5. Pathotypes de *H. vastatrix* identified in Brazil. *H 419–1535/33 Mundo Novo x HW 26/13; **H 420–1535/33 Mundo Novo x HW 26/14; HW 26–Caturra vermelho x Híbrido de Timor 832/1

Patotipes	Genes for virulence of the pathotypes	128/2 Dila & Alghe	635/2 S 12 Kaffa	63/1 Bourbon	1343/269 H. Timor	87/1 Geisha	32/1 DK1/5	33/1 S. 288-23	644/18 Kawisari hybrid	110/5 S 4 Agaro	134/4 S12 Kaffa	*H420/2	1006/10 KP 532	H 152/3	*H419/20	635/3 S.12 Kaffa	HW 17/12	H 147/1	**H420/10	7963/117Catimor	832/1 H.Timor
		S_H1	S_H4	S_H5	S_H6	$S_H1,5$	$S_H2,5$	$S_H3,5$	$S_H?$	$S_H4,5$	$S_H1,4$	$S_H5,8$	$S_H1,2,5$	$S_H2,4,5$	$S_H5,6,9$	$S_H1,4,5$	$S_H1,2,4,5$	$S_H2,3,4,5$	$S_H5,6,7,9$	$S_H5,7,9$	$S_H6,7,8,9?$
H_{v01}	[1]*V1,5,6,7,8,9?* [2]*V2,3,4?*	S[3]	R	S	S	S	R	R	R	R	R	S	R	R	S	R	R	R	S	S	R
H_{v02}	*V1,5,6,8,9? V2,3,4,7?*	S	R	S	S	S	R	R	R	R	R	S	R	R	S	R	R	R	R	R	R
H_{v03}	*V5,6,7,9? V1,2,3,4,8?*	R	R	S	S	R	R	R	R	R	R	R	R	R	S	R	R	R	S	S	R
H_{v04}	*V5,8? V1,2,3,4,6,7?*	R	R	S	R	R	R	R	R	R	R	S	R	R	R	R	R	R	R	R	R
H_{v05}	*V,5,6 ? V1,2,3,4,8,9?*	R	R	S	S	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
H_{v06}	*V1,5,6,7,9? V2,3,4,8?*	S	R	S	S	S	R	R	R	R	R	R	R	R	S	R	R	R	S	S	R
H_{v07}	*V1,5,6,? V2,3,4,7,8,9?*	S	R	S	S	S	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
H_{v08}	*V1,2,5,6,7,8,9? V3,4?*	S	R	S	S	S	S	R	R	R	R	S	S	R	S	R	R	R	S	S	R
H_{v09}	*V1,5,6,8? V2,3,4,9?*	S	R	S	S	S	R	R	R	R	R	S	R	R	R	R	R	R	R	R	R
H_{v010}	*V1,4,5,? V2,3,6,7,8, ?*	S	S	S		S	R	R	R	S	S	R	R	R	R	S	R	R	R	R	R

[1]Virulent genes according to CIFC system; [2] Virulent genes according to the new proposed system; ;[3]Means susceptible to the pathogen (S); reaction to the others pathotypes are resistant (R).

hypothetical genotypes of host and pathogen in the absence of direct genetic studies by determining the reaction of a range of host varieties to a range of pathogen races. For the patossystem *Coffea-H. vastatrix*, this theory was applied by CIFC researchers (d'Oliveira, 1954−57; Rodrigues et al., 1965; Noronha-Wagner and Bettencourt, 1967). Based on the CIFC's system, race II of *H. vastatrix* with the recessive virulent gene v_5 infect *C. arabica* cv. Caturra that have the dominant gene S_H5, but do not infect the host with the resistant gene S_H1 (128/2 Dilla & Alghe). Following the same system, race XXIX with the virulent gene $v_{5,6,7,8,9}$ infect host plants 63\1 Bourbon (S_H5), 1343/269 (S_H6), 420/10 (S_H5,6,7,9), 420/2 (S_H5,8) and H419/20 (S_H5,6,9). Using this strategy, the reaction of susceptibility is considered to infer genes in the host and in the pathogen. Based on the Flor theory and the susceptibility found in the differential coffee clones (Table 1 and 2) the race XIII infect 644/18 *H. kawisari* (*SH*? – *v*?); the race XI infect H 581/17 (S_H3,5,6 – $v_{3,5,6}$) and 829/1 (SH? – v?); HdT832/1 (S_H 6,7,8,9,?–$v_{6,7,8,9}$,?) and HdT832/2 (S_H 6,7,8,9,? - $v_{6,7,8,9}$,?). On the other hand, HdT 1343/269 (S_H6) and other interespecif hybrids containing S_H6 (H 419/20 - S_H5,6,9; H 420/10 - S_H5,6,7,9; H 535/10 - S_H2,3,5,6; H 537/18 - S_H 2,5,6); H 538/29 - S_H 1,5,6; H 539/8 - S_H 1,4,6; H 440/7 - S_H 5,6; H 583/5 - S_H 4,5,6) have been attacked by *H. vastatrix*. The resistance of the differential clones HdT 832/1 (S_H 6,7,8,9,? - $v_{6,7,8,9}$,?) and HdT832/2 (S_H 6,7,8,9,? - $v_{6,7,8,9}$,?) was only supplanted in India by isolates colleted in the field; but their resistance was not supplanted in any other part of the world. In America (Colombia), Cristancho et al. (2007) reported that the resistance of HdT 832/1 was suplanted in the field, but this report needs confirmation. These results suggest that this HdT have other resistant genes not yet identified. More recently, Barka et al. (2020) and Almeida et al. (2020), using molecular biology technique, found two different genes in HdT 832/1 and HdT 832/2. As theses genes are not yet identified in differential clones (S_H1-9), here they were named as S_H10 and S_H11, respectively. S_H10 correspond to a resistance gene analogs (RGAs) and was compleley sequenced and characterized. This gene was detected in all the differential coffee with S_H6, in HdT 832/1 and in HdT 832/2 (S_H6, 7, 8, 9, ?). In addition, a conserved sequence was report in 128/2-Dilla & Alghe, previously considered to contain only the S_H1 gene, and in 644/18 *H. kawisari* with an uncharacterized S_H-gene.

The obtained results suggested that the cloned S_H gene loci have a characteristic polymorphism conferring different resistance phenotypes against coffee leaf rust (Barka et al. 2020). Resistante gene S_H11 was cloned based on a library of bacterial artificial chromosomes (BAC) of the the differential coffee HdT 832/2 and screened using a functional marker. A disease resistance gene analogue was cloned and characterized and showed a typical plant RLK motif (Receptor-Like Knase). The analysis of the presence/absence of this gene in a set of differential coffee suggested that the cloned candidate gene is not one of the nine S_H genes reported previously (Almeida et al. 2020). The main source of genes for resistance to *H. vastatrix* used in the world are: S_H1, 2, 4, 5 – *Coffea arabica*; SH 3 – *Coffea liberica;* S_H 6, 7, 8, 9 - *C. canephora var. robusta and C. canephora* var. *conilon*, and S_H 6, 7, 8, 9– Timor Hybrid. Probably there are other genes not characterized yet. The most important resistance sources (HdT 832/1 and HdT 832/2) with the genes S_H 6, 7, 8, 9were crossed and backcrossed with the elite cultivars as Caturra, Vila Sarchi, Mundo Novo and Catuaí, resulting in new resistant cultivar. However, the resistance of some of these cultivars where supplanted and were attacked by the isolates and pathotypes of the America's continent. The first hybrids using these resistance sources was obtained by CIFC. The hybrid H361 (Villa Sarchi CIFC 971/10 x CIFC HDT 832/2) was selected and seeds were distributed to many contries. The selected material of this hybrid was the starting point for further improvement and selection (Varzea et al. 2009). Progenies derived from H361 were designated as Sarchimor. Other important hybrids developed by CIFC researchers was the denominated Catimor (CIFC 19/1 Caturra x CIFC HDT 832/1). Derivatives of Sarchimor and Catimor were develeloped in breeding programs and have been under commercial cultivation in diferent coffee growing countries. However, the cultivars have lost their complete resistance to rust. Sarchimor seems to have more durable resistance than Catimor. Very few cultivar derived from Catimor are stil resistant under field conditions in Brazil.

Pathothypes of coffee leaf rust: The name pathotype has been used by many authors to refer the variability of plant pathogens (Buck, 2013; Takaoka et al. 2014; Kan-Fa (2015); Aghnoum et al., 2019). In the present review, we are proposing this name to refer the isolates of *H. vastatrix* that could not be differentiated into races according to the CIFC system. Surveys of approximately 225 isolates of *H. vastatrix* collected in Brazil, Honduras, Venezuela and Costa Rica from 2018 – 2020, on HdTderivatives that lost the resistance, could not be differentiated into *H. vastatrix* races. It became evident that race nomenclature based on a set of differentials of CIFC was not enough to characterize complex isolates from HdT derivatives into races. For this reason, the isolates have been named as pathotypes. Pathotype is a strain of an organism that is virulent in a wide host range. They are designated when virulent genes of the pathogen do not interact differentially with the genes for resistance of the host plant. Ten (Hv01to Hv10) and eight (Hv01to Hv08) *Hemileia vastatrix* isolates have been identified in Brazil and Honduras, respectively as pathotypes due to the fact that they do not fit in any possible combination of race on the coffee clones differentials (Table 5 and 6). In Colombia and Tanzania also many isolates of *H. vastatrix* from the field could not be differentiated into races (Gouveia *et al.,* 2005; Kilambo *et al.* 2013).

The three identified pathotypes in Brazil named H_{v01} ($v_{1, 5, 6, 7, 8, 9}$?), H_{v02} ($v_{1, 5, 6, 8, 9}$?) and H_{v08} ($v_{1, 2, 5, 6, 7, 8, 9}$?) have the virulence gene v8-9 pathogenic to H420/2 (S_H 8, 9) and H420/10 (S_H 5, 6, 7, 9) (Table 4). These pathotypes (Hv01, Hv02 and Hv08) did not infect HdT832/1, HdT832/2 and 644/18 Kawisari hybrid (S_H?), respectively. For these reasons, we can infer that HdT832/1, HdT 832/2 and Kawisari hybrid might have more resistant genes in their genome. Two identified pathotypes in Honduras Hv 03 ($v_{1, 2, 4, 5, 8}$), Hv 06 ($v_{1, 2, 4, 5, 7, 8}$) and Hv 08 ($v_{1, 2, 4, 5, 6, 7, 8, 9}$,?) has the virulence gene v_8 pathogenic to H420/2 (S_H 5, 8) (Table 5). But only the pathotypes Hv 01 ($v_{1, 2, 4, 5, 6, 7, 9}$,?) and Hv 08 ($v_{1, 2, 4, 5, 6, 7, 8, 9}$,?) has the virulent gene v_9. These pathotypes (Hv 01 and Hv 08) although have the virulent gene $v_{6,7,8,9}$,? do not infect 644/18 Kawisari hybrid, HdT832/1 and HdT832/2, respectively. The pathotype Hv 02 from Honduras with the virulent gene $v_{1,2,3,4,5}$ infected the clones H 147/1 (S_H2, 3, 4, 5) and 33/1 S. 288-23 (S_H3, 5). These findings are very important due to the fact that cultivars containing the gene S_H3 in Honduras might be attacked by the race that has the genev_3 already present in this country.

Table 6. Pathotypes of *Hemileia vastatrix* identified in Honduras

Patotipes	Genes for virulence of the pathotypes	128/2 Dila & Alghe	635/2 S12Kaffa	63/1 Bourbon	1343/269 H. Timor	87/1 Geisha	32/1 DK1/5	33/1 S. 288-23	644/18 Kawisari hybrid	110/5 S 4 Agaro	134/4 S12Kaffa	*H420/2	1006/10 KP 532	H 152/3	*H419/20	635/3 S.12 Kaffa	HW 17/12	H 147/1	*H420/10	7963/117 Catimor	832/1 H. Timor
		S_H1	S_H4	S_H5	S_H6	$S_H1,5$	$S_H2,5$	$S_H3,5$	$S_H?$	$S_H4,5$	$S_H1,4$	$S_H5,8$	$S_H1,2,5$	$S_H2,4,5$	$S_H5,6,9$	$S_H1,4,5$	$S_H1,2,4,5$	$S_H2,3,4,5$	$S_H5,6,7,9$	$S_H5,7,9$	$S_H6,7,8,9?$
H_{v01}	[1]*v1,2,4,5,6,7,9?* [2]*v3,8?*	S[3]	S	S	S	S	S	R	R	S	S	R	S	S	S	S	S	R	S	S	R
H_{v02}	*v1,2,3,4,5 v6,7,8?*	S	S	S	R	S	S	S	R	S	S	R	S	S	R	S	S	S	R	R	R
H_{v03}	*v1,2,4,5,8 v3,6,7?*	S	S	S	R	S	S	R	R	S	S	S	S	S	R	S	S	R	R	R	R
H_{v04}	*v,1,2,4,5 v3,6,7,8?*	S	S	S	R	S	S	R	R	S	S	R	S	S	R	S	S	R	R	R	R
H_{v05}	*v2,4,5 v1,3,6,7,8?*	R	S	S	R	R	S	R	R	S	R	R	R	S	R	R	R	R	R	R	R
H_{v06}	*v1,2,4,5,7,8 v3,6,7?*	S	S	S	R	S	S	R	R	S	S	S	S	S	R	S	S	R	R	R	R
H_{v07}	*v1,2,4,5,7 v3,6,7,8?*	S	S	S	R	S	S	R	R	S	S	R	S	S	R	S	S	R	R	R	R
H_{v08}	*v3?*	S	S	S	S	S	S	R	R	S	S	S	S	S	S	S	S	R	S	S	R

*H 419 - 1535/33 Mundo Novo x HW 26/13; *H 420 - 1535/33 Mundo Novo x HW 26/14; HW 26 – Caturra vermelho x Híbrido de Timor 832/1. Pathotypes from Hv_{01} to Hv_{08}were identified in the Lempira cultivar considered resistant to *H. vastatrix.* [1] Virulent genes according to CIFC system; [2]Virulent genes according to the new proposed system; ;[3]Means susceptible to the pathogen (S); reaction to the others pathotypes are resistant (R).

Table 7. Designation of pathotypes of *Hemileia vastatrix* identified in Brazil and in Honduras according to CIFC system and new system proposed

Isolates from Brazil*			Isolates from Honduras		
Patothypes	CIFC system –virulent(v_{1-9}) and resistant genes(SH_{1-9})	Proposed system Avirulent (Avr_{1-9})and resistant genes (Flor theory)	Patothypes	CIFC system Virulent (v_{1-9}) and resistant genes (SH_{1-9})	Proposed system Avirulent (Avr_{1-9})and resistant genes(SH_{1-9}) (Flor theory)
H_{v01}	v1,5,6,7,8,9? S_H1,5,6,7,8,9?	Avr 2,3,4? S_H2,3,4?	H_{v01}	v 1,2,4,5,6,7,9? S_H1,2,4,5,6,7,9?	Avr 3,8,? S_H3,8?
H_{v02}	v 1,5,6,8,9,? S_H1,5,6,8,9?	Avr 2,3,4,7,? S_H2,3,4,7,?	H_{v02}	v 1,2,3,4,5 S_H1,2,3,4,5	Avr6,7,8 S_H6,7,8
H_{v03}	v 5,6,7,9,? S_H5,6,7,9?	Avr 1, 2, 3, 4, 8 ? S_H1,2,3,4,8,?	H_{v03}	v 1,2,4,5,8 S_H1,2,4,5,8	Avr 3,6,7 S_H3,6,7
H_{v04}	v 5,8,? S_H5,8?	Avr 1,2,3,4,6,7 S_H1,2,3,4,6,7,8	H_{v04}	v 1,2,4,5 S_H1,2,4,5	Avr 3,6,7,8 S_H3,6,7,8
H_{v05}	v5,6 ? S_H5,6?	Avr1,2,3,4,6,7,8,9? S_H1,2,3,4,6,7,8,9?	H_{v05}	v 2,4,5/ S_H2,4,5	Avr 1,3,6,7,8 S_H1,3,6,7,8
H_{v06}	v1,5,6,7,9? S_H1,5,6,7,9,?	Avr2,3,4,8,? S_H2,3,4,8?	H_{v06}	v 1,2,4,5,7,8 S_H1,2,4,5,7,8	Avr 3,6,7 S_H3,6,7
H_{v07}	v1,5,6,? S_H1,5,6,?	Avr 2,3,4,8,9 S_H2,3,4,8,9	H_{v07}	v 1,2,4,5,7 S_H1,2,4,5,7	Avr 3,6,7,8 S_H3,6,7,8
H_{v08}	v1,2,5,6,7,8,9? S_H1,2,5,6,7,8,9,?	Avr 3,4 S_H 3,4	H_{v08}	v 1,2,4,5,6,7,8,9? S_H1,2,4,5,6,7,8,9,?	Avr 3,? S_H3,?
H_{v09}	v1,5,6,8? S_H1,5,6,8?	Avr 2,3,4,9 S_H2,3,4,9			
H_{v010}	v1,4,5? S_H1,4,5,?	Avr 2,3,6,7,8 S_H2,3,6,7,8			

*Isolates form the state of Minas Gerais and Espírito Santo in Brazil.

In Brazil, all the surveys, so far, did not find races or pathotypes with the gene v_3 (Toma-Brachini, 2015; Zambolim & Caixeta, 2018). The virulent genes $v_{8,9}$ was not identified yet on the 16 identified races in Brazil (Zambolim *et al.*, 2005; Zambolim 2016; Zambolim & Caixeta 2018). The clone HdT1343/269 (S_H6) was susceptible to pathtypes Hv 01, Hv 02, Hv 03, Hv 05, Hv, 06, Hv, 07, Hv, 08 and Hv 09 from Brazil and, therefore, have the virulent gene v_6. It was observed that only the pathotype Hv 10 ($v_{1,4,5}$) had the virulent gene v_4. All of these pathotypes were identified after almost 50 years, since the discovered of coffee leaf rust in Brazil, was in 1970. As soon as the resistant varieties derived from HdT832/1 and HdT832/2 increased cultivation by coffee growers from the year 2005, the new pathotypes have been

identified. Almost all the coffee growing areas cultivated in Brazil have resistant varieties; those derived form HdT832/1 lost the resistance very rapidly and few varieties derived from HdT832/2 still remains resistant. Two identified pathotypes in Honduras Hv 03 ($v_{1, 2, 4, 5, 8}$), Hv 06 ($v_{1, 2, 4, 5, 7, 8}$) and Hv 08 ($v_{1, 2, 4, 5, 6, 7, 8, 9,}$?) have the virulence gene $v_8$pathogenic to H420/2 (S_H5, 8) (Table 4). But only the pathotypes Hv 01 ($v_{1, 2, 4, 5, 6, 7, 9,}$?) and Hv 08 ($v_{1, 2, 4, 5, 6, 7, 8, 9,}$?) have the virulent gene v_9. These pathotypes (Hv 01 and Hv 08) although have the virulent gene $v_{6, 7, 8, 9,}$? did not infect HdT832/1 and HdT832/2, respectively. These data corroborate to hypothesis that HdT832/1 and HdT832/2 might have more resistant genes in their genome. The virulent gene v_4 was identified in only one pathotype of Brazil (Hv 10 –$v_{1,4,5}$) (Table 5), but it was presented in Honduras in all the pathotypes from Hv 1 to Hv 8 (Table 6). A survey in Costa Rica isolates of *H. vastatrix* from 2018 – 2020 found the presence of the pathotype *v1, 5, 6, 7, 8, 9*, ? In Tanzania, Kilambo et al. (2013) reported that at least four isolates of *H. vastatrix* could not be differentiated into races. This could indicate that the differential clones of *Coffea* spp. of CIFC were not able to confirm the isolates into races but they are very importante to distinguish the pathotypes. The genome of the pathotypes are recognized based on the interaction of the isolates of the pathogen and the host differentials. According to the results the pathotypes are designated (Table 5 and 6). The pathotypes from Brazil and Honduras according to the results of Table 5 and 6 are completely different. Other pathotypes from Venezuela, Costa Rica and Ethiopia were also diffents (data not shown). Twenty host differentials was used to distinguish ten pathotypes from Brazil and eight from Honduras.

***New propose of pathotypes designation*:** As mentioned above, in the CIFC system, the designation of the pathotype follow the gene-to-gene theory. Accordinly of Flor works (Flor, 1942, 1946, 1947 and 1955), "the inheritance of avirulence and resistance or of virulence and susceptibility has been explained as result of specific genes in the host interaction with specific gene in the parasite". However, for the patossystem *Coffea-H. vastatrix*, CIFC system based the characterization of the genes on resistance of the coffee varieties and virulence of the fungus, instead resistance and avirulence. Besides, the susceptibility reaction is considering to infer the host and pathogen genes. Based on the Flor theory, resistant reaction is observed only when the plant has at least one allele of resistance (RR or Rr) and the fungus has at least one allele of avirulence (AA or Aa). Susceptibility reaction occur in three situations: 1) the plant and the fungus has no resistance gene (rr) and no avirulence gene (aa), respectively; 2) the plant has resistance gene (RR or Rr) but the fungus has no avirulence gene (aa); and, 3) the plant has no resistance gene (rr) and the fungus has avirulence gene (AA or Aa). For this reason, we are proposing the fungus and coffee gene prediction using the resistance reaction and the inheritance of avirulence and resistance. We expected that this new approach would facilitate the gene inference and also, help to join the data of inference with molecular characterization of the genes. The designation of the pathotypes followed the two systems is shown in Table 7. By the CIFC system the pathogen is recessive and virulent (v_{1-9}) and the host plants are dominant and resistant (S_H1-9) and the interaction is susceptible (S).In our proposed system, the pathogen is avirulent and dominant (Avr1-9) and the host plant is also dominant (S_H1-9) and the interaction is resistant (R). Following the CIFC system, the brasilian pathotype Hv_{01} has the virulent genes $v_{1,5,6,7,8,9}$ and infects the coffee diferentials with the resistant genes S_H1,5,6,7,8,9? On the other hand, in the new system, the pathotypeHv_{01} has the avirulent genes $Avr_{1,5,6,7,8,9}$?and do not infect the coffee diferentials with the resistant genes S_H1,5,6,7,8,9? For the isolate Hv_{01} from Brazil of *H. vastatrix*, CIFC system is pathogen virulent gene v1,5,6,7,8,9? and the resistant gene on the plant host is S_H1,5,6,7,8,9? (Table 7). The result is: *H. vastatrix* isolate is virulent on the coffee differential S_H1,5,6,7,8,9?. On the other hand we proposed a system based on Flor theory which the pathogen with the gene Avr 2,3,4? can not infect a coffee differential containing the resistant gene S_H2,3,4? (Table 7). Our proposed system is more simple and follows Flor theory straight forward. Furthermore the number of differentials of CIFC is enough to distinguish pathotypes instead of races.

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