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ADVANCES IN COFFEE RUST RESEARCH

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INTRODUCTION

World coffee production is worth about $15 billion annually, providing important export revenues and labor opportunities for tropical countries (23). Coffee rust, induced by *Hemileia vastatrix* Berkeley and Broome, is a major disease of *Coffea arabica,* which constitutes about 75% of total coffee production. It has been estimated that crop losses in Brazil would be about 30% if no control measures were taken (93). On this basis, world crop losses from the disease may be roughly calculated at $1–2 billion annually (23, 57). Coffee rust is therefore one of the seven most important diseases and pests of tropical crops (68).

Marshall Ward's pioneering experiments with coffee rust, which were instrumental in proving that fungi are the causal agents of plant diseases, established it as a classical disease (139, 140). It is considered to have originated on wild coffee in Ethiopia (140), but was first reported in cultivated coffee in Sri Lanka in 1869 (12). Since then it has spread to most coffee growing countries (57). The western hemisphere was free from coffee rust until 1970 when it was reported in Brazil. Its further spread within a decade to other Latin American countries alerted governmental organizations and research institutions to improve their research capabilities. For many of these countries this marked a new era of scientific advancement. The application of

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modern technology has made possible the control of coffee rust, once thought to be a menace because of the lack of effective control measures. Various reviews are available on the history, biology, and control of coffee rust (22, 46, 56, 113). In this article advances in coffee rust research are discussed from the viewpoint of epidemiology, resistance, and management.

BIOLOGY AND EPIDEMIOLOGY

Life Cycle of the Fungus

The coffee rust fungus, *H. vastatrix,* in nature produces only the uredinial, telial, and basidial stages; the pycnial and aecial stages are still unknown (47). The fungus is perpetuated by its anamorphic urediniospores and the function of teliospores and basidiospores remains unclear. It is generally considered to be heteroecious even though the alternate host and the aecial and pycnial stages of the pathogen are unknown. However, some consider it to be autoecious, a short-cycled derivative of the long-cycled form, with urediniospores, uredinoid-aeciospores and basidiospores occurring on coffee (110, 124). Since such a phenomenon is not commonly observed in nature, only the urediniospores are thought to be of epidemiological and economic significance. Thus the remainder of this discussion is restricted mainly to the uredinial stage of the pathogen.

A Systems Approach to Epidemiology and Management

Systems analysis is a structured approach to the study of complex biological processes that can provide a framework to understand the complex processes involved in plant disease epidemics. Some of the major steps involved in systems analysis are: (*a*) definition of objectives, (*b*) system design, (*c*) system model, (*d*) model evaluation, and (*e*) system management (129). A brief description of the design of an epidemiological system and its management is given below.

Plant disease epidemics can be considered as biological systems consisting of complex, interlinked epidemiological processes. Thus they are polycyclic processes (142), with each process consisting of a series of monocyclic processes, which in turn are made up of noncyclic subprocesses and sub-subprocesses. For *H. vastatrix* three subprocesses can be recognized: infection, sporulation, and dissemination. The host and environmental factors influencing the epidemic can be understood by studying their effect on, or by developing submodels for, each individual subprocess under controlled environmental conditions. Management of an epidemic can be achieved either directly by controlling each subprocess, or indirectly by manipulating the factors influencing these subprocesses. According to the equivalence

theorem, all subprocesses are equal in their effects, and eventually all reduce the rate of disease development. Changes in these subprocesses can be measured and manipulated to achieve economic management of epidemics (59, 135, 142).

Infection Process

The infection process involves the growth of the urediniospore from inoculation until lesion production, and can be subdivided into germination, penetration, and colonization. For simplicity, the former two will be dealt with together and the latter separately.

GERMINATION AND PENETRATION PROCESSES The urediniospore germinates only in the presence of free water. It often produces two to three germ tubes simultaneously, with a maximum of four as there are four germ pores. The germ tubes, either directly or after branching, produce appressoria on stomata. On the dorsal surface the appressorium produces a vesicle that is a cytoplasm sink. This in turn penetrates the stomata by means of an infection hypha and thus gains entry into the substomatal cavity (47, 54, 89, 111, 116, 134).

In the absence of free water, exposure to high relative humidity levels is insufficient to induce spore germination (102, 139). Loss of moisture following germination inhibits the whole process and it does not recover even when moisture is reintroduced, unless the dry period has been less than a couple of hours (102). Various studies have been conducted on spore germination on different substrata, on water agar, leaf surfaces, etc (29, 58). Spore germination percentages are higher on young leaves than on intermediate and old leaves (102). Autoinhibition of spores is found at high spore concentrations of 2 mg/ml or greater (98).

Spores contaminated with the hyperparasites, *Verticillium hemiliae* and *V. psalliotae*, show reduced germination (67, 131). The hyperparasites penetrate the urediniospores and eventually kill them.

Equations have been developed to predict infection as a function of the duration of leaf wetness during the urediniospore germination and penetration periods (60):

$$PINF = 1 - 1.996 \exp(-0.1089\ HRWET) \quad 1.$$

where *PINF* is the proportion of maximum infection or lesions per leaf and *HRWET* is the duration of wetness in hours after inoculation.

On wet leaves, temperature is the most important environmental factor influencing spore germination. The amount of infection can be predicted as a function of temperature while the leaf is wet from the following equation (60):

$$PINF = sin^2 (188.1\ TE - 41.6\ TE^2 - 151.3\ TE^3) \quad 2.$$

where *PINF* is the proportion of maximum infection or lesions per leaf and *TE* is the temperature equivalence, $TE = (T_{ob} - T_{min}) / (T_{max} - T_{min})$, in which *T* is the temperature in °C observed *(ob),* minimum (min = 12.5C) and maximum (max = 32.5C) for infection. The mathematical function for infection can be improved by including various combinations of temperature and leaf-wetness duration levels in the experiment.

COLONIZATION PROCESS The infection hypha ramifies intercellularly in the substomatal cavity and nearby tissues and penetrates cells by means of haustoria (89). The external manifestation of this process is the presence of a lesion on the leaf surface, which depends on the extent of hyphal ramification and on environmental conditions. The mycelium then produces protosori that generally emerge through the stomata.

The colonization process consists of all subprocesses from the formation of the infection hyphae until the manifestation of lesions or the formation of protosori (58). In practice, the colonization process can be quantified as the incubation period, the time between inoculation and formation of lesions, or as the latency period, the time from inoculation to the formation of sporulating lesions. Calculation of the mean incubation or the mean latency period is therefore appropriate (130).

Unlike the germination and penetration processes, colonization is not significantly influenced by the duration of leaf wetness. However, it is greatly influenced by temperature, which exerts its effect mainly on the duration or rate of the process rather than the survival ratio, unless the ambient temperature is either extremely high or low during colonization (115). Incomplete host resistance also influences the colonization period (37, 58).

Rayner developed an equation to predict latency period as a function of daily minimum and maximum temperatures in Kenya (54):

$$LP = 90.61 - 0.408\ MAX - 0.44\ MIN \quad 3.$$

where *LP* is the latency period in days, and *MAX* and *MIN* are the mean daily maximum and minimum temperatures in °F for the latency period.

Similar equations have been developed for the Brazilian States of São Paulo (Equation 4) and Minas Gerais (Equation 5) (66, 95):

$$LP = 103.01 - 0.98\ MAX - 2.1\ MIN \quad 4.$$

$$IP = 53.12 + 1.78\ MAX - 3.99\ MIN \quad 5.$$

where *IP* is the incubation period and the mean temperatures are in °C. It should be noted that in these equations the two temperature variables are not independent but are highly correlated. Also, after the manifestation of lesions (in *IP*) the appearance of sporulating lesions (in *LP*) is influenced by relative humidity in addition to temperature. Thus the factors influencing sporulation may make the latency period equation less stable.

Sporulation Process

Sporogenous cells are produced from the protosori. Each protosorus produces 1–7 sporogenous cells that emerge through the stomatal opening (89). Spore buds are produced at the apex of these cells or fascicles, and more buds continue to produce at the apex as the cell grows. Initially, the spore buds are covered with a membrane that is reabsorbed as the spores mature (49). Immature spores are hyaline; mature spores are yellowish-orange, reniform, echinulated dorsally, and smooth ventrally. Coffee rust differs from the cereal rusts in that the individual disease spot is a lesion rather than a pustule, each lesion consists of many uredosori. In a lesion the new flushes of spores are produced, not only within each uredosorus but also by the formation of new uredosorus in the peripheral zone of each lesion. A single uredosorus can produce 4–6 crops of spores over 3–5 months. Each lesion can produce about 300–400,000 spores. As it expands the center portion stops sporulating and becomes senescent (89).

The sporulation process consists of all subprocesses from sporogenous cell formation until the maturation of the spores with prominent echinulations (58).

Sporulation is influenced by temperature and relative humidity. However, very little work has been done in this area. Furthermore, the amount of spores produced and their viability are significantly influenced by the presence of hyperparasites (71, 131).

Dissemination Process

The dissemination process in *H. vastatrix* consists of three subprocesses from the mature spore to the deposited spore stage: spore liberation, dispersal, and deposition. Since various studies conducted on dissemination involve a mixture of subprocesses, dissemination as a whole is discussed here.

The urediniospores are mainly wind disseminated. The introduction of rust from one continent to another has been attributed to wind currents and the transport of contaminated coffee seeds and other plant materials (57, 58). Within Latin American countries it has been attributed mainly to wind, the movement of workers, and planting materials (10, 57, 58, 128, 138).

Within a field, urediniospores are dispersed by wind. The highest concen-

tration of spores was found at 1.25 m above ground, and decreased as height increased (7, 9). Although a maximum of 4400 spores/day has been trapped on the heavily affected coffee canopy in Kenya, only 300 spores/day have been trapped in Brazil (7, 45). Compared to cereal rusts these numbers are very small.

High spore catches were often associated with high wind velocities of >10 km/hr. However, the relationship between wind velocities above 4 km/hr and spore catches was not significant (76).

The amount of spores found in air above the crop canopy was linearly related to the disease severity (8):

$$SPOR = 20.14 + 290.94\ \%LAR \qquad 6.$$

where *SPOR* is the number of spores trapped per day and *%LAR* is the % leaf area rusted.

The urediniospores are diurnal in their periodicity of spore liberation (7, 9, 15), with the highest number dispersed around noon. However, this trend is not clear during the rainy season.

Rain also plays a major role in the dispersal of spores—indeed it was once considered the most important agent (15, 103). Rain also provides free water required for spore germination. Under field conditions, rain is often associated with substantial wind velocity, so it is very difficult to quantify their contributions separately. A maximum of 402 spores/day has been trapped in rain using pluviometer funnels (9). Days with high rainfall were associated with the highest spore catches, but there was no specific relationship between the amount of rainfall and the number of spores caught. Thus, a complete model for sporulation should include the amount of spores present on the plant, and the influence of wind and rain.

Insects and animals, including man, also play an important role in the dispersal of spores (3, 4, 9, 26). However, insects are thought to have a limited impact on rust epidemics (7, 9).

Factors Influencing Disease Development

HOST The major host factors influencing the rate of disease development are the host density, level of cultivar susceptibility and predisposition of host due to high yield. The most widely cultivated coffee is *Coffea arabica,* the species most susceptible to rust.

In coffee both complete and partial resistance to rust have been reported. Specific major gene resistance, from *C. canephora,* has been transferred to *C. arabica*. Some of the major genes are quite durable. The resistance major genes in Catimor and Icatu populations, originally obtained from *C. canephora,* have been transferred to many cultivars and are being grown

commercially in many countries around the world (37). Most of these cultivars are effective until a new race appears (37, 59). Partial resistance has been reported from various populations originating from *C. canephora* (37). A lower rate of disease development is observed in the Catuai and Mundo Novo cultivars than in the cultivar Ibaarê (59). Resistance is discussed in detail later.

Disease severity is positively correlated with host density, the lower the host density the slower the rate of disease development (2, 9, 15, 85). However, in general, high and low host densities were also associated with high and low yields, respectively. The independent contribution of host density and yield on the rate of disease development is not clear. The annual variations in host density and yield are not only specific to cultivars but are also dependent on the rust severity in the previous year, as severe rust induces severe defoliation (64).

Plant susceptibility to rust attack increases with berry yield (1, 41, 73, 93). When berries are removed while immature, disease severity reduces to almost half.

PATHOGEN The race and level of inoculum are the most important pathogen factors that influence the development of rust. Though there are more than 30 races, only a few occur regularly and the number and pattern vary regionally. Race II is most common.

The survival of inoculum, after the dry season in Kenya and after the winter months in Brazil, plays a significant role in the annual development of rust (16, 50, 60, 61). In Brazil initial inoculum is important, but the high incidence in September can be reduced to insignificance if a dry period extends until November and causes defoliation (21, 50, 60, 62). The amount of initial inoculum in early October depends on the disease severity in the previous year and on the extent of defoliation during the winter months. The amount of secondary inoculum produced plays a major role in the rate of rust development (60, 61).

ENVIRONMENT Among physical environmental elements, rain plays the most important role in the rate of rust development. It provides not only the moisture for spore germination but also aids in dispersal. The seasonal development of rust is related to the rainfall pattern of the region (16, 21, 60, 85). In Kenya two peaks of rust progress curves are observed in the eastern Rift Valley region, where there are two rainy seasons (16).

Seasonal fluctuations in temperature also influence the rate of rust development. In certain parts of Brazil winter temperatures are often less than 15°C, which is the lower limit for spore germination (60, 61). At extreme temperatures, $<10°$ C and $>35°$ C, lesion enlargement is limited (115). The amount of inoculum survival also depends on the winter temperature (61).

In general, lower rust intensities have been observed at higher altitudes, where the seasonal and daily fluctuations in temperature are greater, and the night temperatures are lower. In such areas rust is normally not an economic problem (25, 27, 118).

RESISTANCE

Nearly all *C. arabica* varieties are susceptible to common rust races whereas varieties of *C. canephora* are generally quite resistant. Varietal resistance is the cheapest method of control and is an alternative to chemical control that may sometimes increase pest incidence, as has been indicated for copper fungicides in relation to coffee leaf miner and mites (107, 108). Resistance is of fundamental importance where lack of water, difficult terrain, or financial considerations for smallholders, preclude chemical control. Resistance is also important in high density coffee plantations that favor disease intensity and make chemical control difficult.

Evaluation of Resistance

RESISTANCE TESTS Traditional resistance screening has involved inoculation of young leaves of greenhouse-grown plants with dry rust spores, which are then wetted (28), and also by inoculation of detached leaves or leaf disks in the laboratory (101). However, as resistance may vary with leaf age, inoculation of young leaves alone may not represent the level of resistance of the whole plant (43). Use of calibrated spore suspensions as inoculum has permitted quantitative evaluation of resistance. Inoculation of leaf disks or detached leaves enabled evaluation of complete as well as incomplete resistance (31, 69, 101) with a minimum of space, inoculum, and time. Leaf disks have been successfully used in new race detection, in determining the resistance of plants grown away from the laboratory and also for biochemical or physiological studies on resistance (31, 34, 88, 101).

REACTION TYPE AND DISEASE INTENSITY Reaction type (RT) has traditionally been evaluated by using a descriptive scale for individual lesion types (28), adapted from cereal rust research. As this scale is less suited for evaluating intermediate heterogeneous reaction types that are frequently found in diploid coffee species and interspecific hybrids, a 0–9 point scale has been proposed to evaluate reaction types of whole leaves, branches, or plants (42). This scale reflects increases in lesion size, within resistant RTs, and in sporulation frequency and intensity for heterogeneous or more susceptible RTs. The scale can effectively assess variation for complete as well as incomplete resistance to coffee rust (33). Other 0–9 point pictorial scales have been designed for rapid assessment of disease intensity in the laboratory,

greenhouse nursery, and field (42). These are useful for evaluating variation that is not expressed by reaction type and may also be used for evaluating fungicide trials (46).

COMPONENTS OF RESISTANCE Components of incomplete resistance to coffee rust, e.g. infection efficiency (IE), latency period (LP), spore production (SP) and infectious period (IP) have been evaluated in different ways (37). IE has been measured as lesion density (LD, number of lesions per leaf area unit) or more meaningfully, as sporulating lesion density (SLD). IE, LP, and SP have also been evaluated together by calculating a disease intensity index ranging from 0–1 (69). In repeated leaf-disk tests LP, LD, SLD, and SP together accounted for about 80% of the variation in field disease incidence present in *C. canephora* cv Kouillou (31). SLD was the component with the highest coefficient of determination ($r^2 = 0.67$). Components of resistance are quite well related among each other (31, 25, 38, 137). LP and SLD are highly correlated with RT that, by definition, is also correlated to SP. Therefore, most variation for incomplete resistance can be efficiently, and more simply evaluated by RT, using the 0–9 scale.

However, a resistance component not measured by RT is IP evaluated as the leaf-retention period (LRP, number of days between onset of sporulation and leaf-fall). For some susceptible *C. arabica* varieties, LRP varies significantly, with longer LRP values related to higher disease intensities in the field. However, rapid leaf-shedding upon infection may be correlated with low productivity (36). This phenomenon has also been observed in *C. racemosa* (28; A. B. Eskes, unpublished data), which may partly explain its high field resistance despite being used as a universal suscept for race studies in the greenhouse (121).

Factors Influencing Resistance

LEAF AGE Highly susceptible and highly resistant plants do not show much variation in resistance between leaves of different ages (43), although older leaves of susceptible plants grown in greenhouses may be more difficult to infect (28). Plants with incomplete race-specific resistance often show high resistance in young and lower resistance in older leaves, as observed in derivatives of the Hibrido de Timor and in the Icatu population (38, 43). Furthermore, in *C. canephora* cv Kouillou adult leaf resistance has been identified (43); this is mainly expressed by low LD on adult leaves, with young and old leaves more susceptible (35).

LIGHT INTENSITY Coffee leaves exposed to high light intensity (LI) generally become more susceptible to rust. With susceptible *C. arabica* varieties, LD may vary up to tenfold depending on pre- and post-inoculation LI (31, 32). Bright sunlight may also kill the fungus in the leaves. Rust development

on susceptible varieties would therefore be most favored by medium levels of shade. Plants with incomplete resistance to coffee rust generally show lower LD and RT with lower LI. Some *C. canephora* cv Kouillou plants may change in reaction from resistant to susceptible, depending on LI. The S_H4 resistance gene is affected by LI (32). Test conditions for resistance screening and inheritance studies should therefore be appropriately chosen to obtain useful results. The effect of light intensity may partly explain why rust is often less severe on wild coffee growing in the dense forest than on coffee growing in openings in the forest or the open air (13, 133).

YIELD It has long been realized that overbearing of coffee may exacerbate rust intensity (90). In Brazil, rust epidemics are generally more severe in high-yielding years than in off-years (93). Unproductive but susceptible plants like sterile dihaploids or triploid plants have shown little infection in the field. About 40% of variation in rust intensity observed in *C. arabica* cvs Mundo Novo and Catuai could be explained by variation in yield (36). Plants with high levels of incomplete resistance may show rust attack only in years of high yield. Leaves supporting rapidly growing coffee berries are more susceptible to rust infection than leaves that only support vegetative growth (41). Consequently, high-yielding coffee varieties are more likely to be attacked by rust in the field than low-yielding varieties.

Coffee Differentials, Inheritance and Rust Races

Screening for resistance and rust races has mainly been done at the Centro de Investigação das Ferrugens do Cafeeiro (CIFC) at Oeiras, Portugal, from the early 1950s onward. Detailed results have been reviewed on a number of occasions (14, 37, 119, 120, 121). A minimum set of 18 coffee differentials and 31 rust races obtained from different countries are maintained at CIFC (14). Nine resistance factors have been identified as S_H1 to S_H9, corresponding virulence being indicated as v_1 to v_9 (14, 120). S_H1, S_H2, S_H4 and S_H5 are from *C. arabica*, S_H3 probably originates from *C. liberica* (121) and S_H6 to S_H9 from *C. canephora* (14).

S_H1, S_H2, S_H3, S_H4 and S_H6 appear to be dominant and monogenic (14, 121). Depending on test conditions, the S_H4 gene may be partially dominent or even quite recessive (32). No inheritance studies have been published yet on S_H5 (37), and studies on S_H7 to S_H9 are to be published soon (14). Two monogenic resistance factors, which are likely to differ from S_H1 to S_H9, have been detected in Brazil, one in *C. canephora* cv Kouillou and one in the Icatu population (33, 37). Recent results suggest that two or three more major genes are present in Icatu (39). Still other, unidentified resistance factors must be present in diploid coffee species (120). Inheritance patterns for diploid coffee species and interspecific hybrids have generally been more complex than would be expected from dominant gene action alone (37). Several genes are

likely to be incompletely dominant, as apparently is the case in Icatu and Catimor (14, 56, A. B. Eskes et al, unpublished results). Complex inheritance suggestive of action of polygenes has also been shown in *C. canephora* (35, 37). Some types of resistance appear to be recessive in interspecific hybrids, as for the adult leaf resistance in *C. canephora* cv Kouillou (37, 44).

No new coffee differentials have been selected at CIFC since 1975 and only one new rust race, obtained by mutation, has been added to the collection (14, 120). The low number of new races detected at CIFC may be explained by: (*a*) predominance of rust race II (v_5) on *C. arabica* varieties, which mainly possess the S_H5 resistance factor only, (*b*) the limited rust sampling done on derivatives of interspecific hybrids and on wild species, (*c*) lack of adequate differentials for race identification in interspecific hybrid populations or diploid species, and (*d*) the greater durability observed so far of resistance genes derived from *C. canephora*.

Intermediate Virulence and Residual Resistance

Coffee differentials tested at CIFC may react as R (resistant), MR (moderately resistant), MS (moderately susceptible), or S (susceptible) to different rust races, which suggests that more than two levels of virulence may be present in relation to known resistance factors. The differential for S_H3, for example, reacts like R, MS, or S to different races (121). In Brazil, isolates with some virulence to S_H3 have been obtained from field plants with S_H3, which were classified as avirulent on S_H3 at CIFC (C. J. Rodrigues Jr., personal communication). Thus four levels of virulence may exist, a hypothesis that indicates that either the virulence to S_H3 is more complex than expected from a gene-for-gene relationship or that the S_H3 factor is more complex than imagined. Intermediate virulence has also been demonstrated in relation to two resistant genes from *C. canephora* (34, 35, 37). As has been discussed (33), intermediate virulence in dikaryotic rust fungi might be explained by incomplete dominance of avirulence alleles, by multiple alleles for virulence, or by interallelic interactions. The occurrence of intermediate virulence indicates that the level of residual resistance of major genes, after they have been matched by virulent races, may depend on the rust genotype (34, 37).

Stabilizing Selection

Distribution of virulence factors in *H. vastatrix* has predominantly followed the presence of resistance genes in local coffee populations (119–120), with simple races prevailing when no resistance genes are present. This suggests that unnecessary virulence is selected against in nature, a process that has been called "stabilizing selection" (136). Difference in the ability to survive or in pathogenicity between simple and more complex races in relation to *C. arabica* genes may be too small to be observed in regular resistance tests, but might be observable in competition studies of races of *H. vastatrix* inoculated in mixture onto susceptible *C. arabica* plants (56).

Virulence of some new Brazilian rust races in relation to *C. canephora* genes appeared to have considerable side effects on pathogenicity of these races expressed as lower virulence to certain other coffee genotypes. For example, isolate 2, with higher virulence than race II to several Icatu plants, showed slightly lower virulence to Brazilian coffee cultivars and was avirulent to some Catimor plants that are susceptible to race II. Likewise, isolate 10, with virulence to some Kouillou plants, showed lower virulence than race II to other Kouillou plants. On the other hand, isolates were detected with virulence intermediate between race II and isolate 2 or 10 that showed few or no pronounced side effects (34). In heterogeneous coffee populations, high levels of virulence may therefore be less favorable for the fungus than intermediate virulence and could help to stabilize the pathogen population.

Type and Durability of Resistance

Different types of resistance to coffee rust can be found and inferences can be made on their possible durability and usefulness for coffee breeding, depending on their characteristics.

BASIC RESISTANCE LEVEL A basic level of incomplete resistance seems to be present in *C. arabica* and also in other coffee species. Such resistance may be strongly affected by stress conditions, such as high light intensity and yield, that in monocyclic inoculation tests may induce a two- to five-fold increase in susceptibility measured by lesion density (32). Such resistance seems to be race-nonspecific and may be effective in the natural forest habitat of coffee. However, it may be insufficient to protect high-yielding *C. arabica* varieties under modern cultivation techniques. In the field in Brazil, little variation has been detected within *C. arabica* for such resistance; this suggests that effective selection for higher levels of this resistance might be difficult (36).

ADULT LEAF RESISTANCE There appears to be a type of race-nonspecific resistance in *C. canephora* cv Kouillou that is expressed mainly by lower lesion densities on adult leaves, with young and old leaves more susceptible. Such resistance is also affected by light intensity and yield. Great variation for this resistance can be found, with some plants being far more susceptible than *C. arabica* varieties while others can be nearly immune. Inheritance seems polygenic, but in crosses with *C. arabica* it is quite recessive (35). Attempts are underway to introduce it into *C. arabica* cultivars (44).

LEAF RETENTION Resistance related to rapid leaf shedding after infection has been detected in *C. arabica* (36) and *C. racemosa* (A. B. Eskes, unpublished results). Rapid leaf abscission could be race non-specific, but it

could also possibly be a type of hypersensitivity at the level of the whole leaf. Selection for genotypes that shed their leaves quickly may not be rewarding, as such a selection is likely to be negatively correlated with yield (36).

MAJOR GENES The resistance genes of *C. arabica* S_H1, S_H2, S_H4 and S_H5, used either singly or in combination, do not provide effective resistance for more than a few years. However, the S_H3 resistance factor, which likely originates from *C. liberica* (121), as well as several genes from *C. canephora*, have so far provided more durable protection. Genes introduced from diploid coffee species would thus seem to be more effective than those from *C. arabica*. A similar finding has been reported for certain genes for resistance to wheat rusts introduced from diploid species into cultivated wheat (132). A tentative explanation could be that the predominating rust population is well adapted to resistance in *C. arabica* but lacks the capacity to quickly generate virulence to resistance genes from other species. Common rust races might be homozygous avirulent, virulence may be more complex as suggested for the S_H3 gene or newly generated virulence may have side effects on general or specific pathogenicity (34). Consequently, the combined use of resistance genes from *C. canephora* and *C. liberica* in *C. arabica* varieties may provide resistance of agronomically acceptable durability (37).

MINOR GENES Certain resistance genes may vary in effectiveness depending on test conditions, gene dosage, and probably also genetic background. Furthermore, different levels of virulence have been detected in relation to known major genes, which may under certain conditions appear as minor genes and vice versa. Incomplete monogenic resistance is apparently quite frequent in interspecific hybrid populations like Catimor and Icatu (37). Such resistance genes, when present alone, have so far not been very effective (34). There may be other types of more effective minor genes present in these coffee populations.

ADDITIVITY OF RESISTANCE FACTORS Recently, genetic analyses in Icatu and Catimor (37, 39; A. B. Eskes, unpublished results) have shown that additivity among resistance alleles may be frequent. This suggests that selection of the most resistant phenotypes, with extremely low reaction types, would result in selection of genotypes with a higher number of resistance alleles. This is important for practical selection as it would facilitate the accumulation of resistance genes in one genotype and thus likely provide more durable resistance.

Biochemical and Histopathological Studies

Biochemical and histopathological studies have given some insight into the resistance mechanism governing major genes. So far no evidence exists on the

involvement of constitutive barriers operating before infection, but, several defense mechanisms seem to be activated after infection with avirulent races. Some evidence exists on the accumulation of phytoalexins, although contradictory results have also been found (48, 83, 84, 119, 122). Furthermore, increased activity of peroxidase, polyphenoloxidase, cutinase and lamarinase, as well as the accumulation of phenolic compounds, lignification and callose deposits have been observed (83, 84, 96, 117, 123). Lignification has been related to the so-called "immune" response and to "tumefactions", and may actually be a secondary mechanism that can be observed after fungal growth has already ceased (117, 123). After infection, race-specific fungal elicitors may be found (84) that are related to increased enzyme activities. Further research is needed to confirm this hypothesis and possibly provide a clue to the primary gene products involved in incompatibility. Some problems facing biochemical research are lack of isogenic coffee lines and inconsistency of results, mainly with low molecular weight compounds. Studies have been mainly confined to major gene resistances. However, histopathological studies have shown that even in susceptible varieties, 50–75% of fungal penetrations can be aborted in the early stages of infection (78), which may be an expression of the basic level of non-specific resistance present in *C. arabica*.

Induced Protection and Resistance

Coffee leaves that have been pre-treated with dead urediniospores or spore extracts, and subsequently with viable spores, show localized, short-lived self-protection, which is mainly expressed by lower lesion density (88, 97). Results on systemic self-protection seem still contradictory (11, 56). Field observations indicate that self-protection may be of relatively little importance in reducing rust epidemics. Rust infections that are already established do not seem to induce systemic protection (37). The mechanism involved in self-protection is not clear, although a polysaccharide has been suggested as the inducing agent (96). Spore germination does not seem to be affected (88). Both localized and systemic protection can be obtained by pre-treating coffee leaves with a series of other microorganisms, such as rust pathogens of other hosts and also with bacteria (77). In the laboratory, high levels of protection have been obtained with *Saccharomyces cerevisiae* and *Bacillus thuringiensis* (125, 126). The feasibility of applying this interesting phenomenon under field conditions still remains to be determined.

MANAGEMENT

Disease Prediction Models

Regression models incorporating various biological and meteorological parameters have been formulated to predict coffee rust development, with the ultimate aim of scheduling fungicide applications.

The equation established for São Paulo state in Brazil, based on meteorological factors, was (2):

$$LPL = 14.417 - 0.329\ MAX + 0.214\ MIN - 0.009\ RAIN \qquad 7.$$

where *LPL* is the number of lesions per leaf on the date of prediction *(DP), MAX* and *MIN* are mean maximum and minimum temperatures in °C for 45 days before *DP,* and *RAIN* is total rainfall in mm for 45 days.

Various meteorological and biological factors have been considered in explaining the rate of rust development. The significant factors were identified by applying stepwise selection criteria in regression analysis (55, 62). As dependent variables, both the disease severity on *DP* and the intrinsic infection rate for an interval of 1 to 2 latency periods after the *DP* have been considered. The equation explaining the maximum variation in the infection rate was (55):

$$k'' = 0.031 + 4.881\ PLAS + 0.022\ PLNEW - 0.001\ MIN - 0.001\ MAX - 0.001\ RAIN \qquad 8.$$

where k'' is the intrinsic infection rate for an interval of 56 days after the *DP; PLNEW* is the proportion of new leaves formed during 14 days preceding the DP; *MIN* is the mean minimum and *MAX* is the mean maximum temperatures in °C for 14 days preceding *DP; RAIN* is total rainfall in mm between 14–28 days before *DP.*

Very high correlations were observed between independent variables that were considered in formulating equations to predict the rate of coffee rust development. As a result, some parameters that independently explained significant variation in the disease were eliminated due to multicolinearity (60). The predictive success of such models depends on the future occurrence of the different parameters, including those not used in the model, in similar combinations as they were observed. This may make the model less stable under field conditions, unless the function is based on many years of data. Although certain combinations of different parameters are required for specific processes of the pathogen, the relationships between the parameters tested in these equations do not explain the pathway of biological action.

Methods for Scheduling Fungicide Applications

RAINFALL Timing of fungicides to control coffee rust was mainly based on the disease's seasonal periodicity and on the factors influencing its development. Some of the earlier epidemiological studies found the seasonal periodicity of rust to be associated with the rainfall pattern; consequently, sprays

were recommended during rainy seasons. In India and Kenya, fungicide applications were generally started before the onset of the rainy season to reduce the initial build-up of the disease. Further spraying followed during and after the rainy season to maintain the disease at a low level (4, 17, 52, 86, 112).

In India, the rust was managed to an economic level with 3–4 pre-monsoon sprays before April, followed by 2 mid-season sprays in August and September (4, 100).

In Kenya, 3–5 applications were made, depending on the rainfall. One treatment preceded the onset of rains, followed by 1–2 sprays at 3 week intervals. If rust appeared in April another spray was recommended (24). In East Rift Valley districts, spray scheduling recommendations were based on the amount of rain. Fungicides were applied at every 50 mm rainfall, with a minimum interval of one week between applications (52, 53).

CALENDAR SCHEDULE AND ITS MODIFICATIONS TO INCLUDE YIELD AND INOCULUM In order to find the appropriate months when fungicides should be applied in Brazil, copper fungicides were used at monthly intervals from October through May for many years and at differing locations (71, 106). As the time, and the frequency of fungicide applications varied, at different locations, a general schedule was recommended with 4–5 applications at 30–40 day intervals between October and May, depending on the locality (71). Such experiments usually assume that the host, pathogen, and environment have similar seasonal rhythms every year. However, further experimentation showed that initial inoculum levels and berry yield varied significantly from year to year, and consequently such variables were included in the timing of fungicide applications.

The yielding habit of coffee in different years varies from maximum to 10% of the maximum yield, depending on the coffee cultivar and on the extent of defoliation and yield during the previous year. Only 2–3 fungicide applications were required during the years with low yields, as compared to 4–6 during high-yielding years (71, 114).

Copper fungicides needed to be applied at inoculum levels corresponding to 10–20% leaves diseased, and systemic fungicides when 20–30% leaves were diseased (80, 92). The application of a mixture of systemic and protective fungicides once in January, when the inoculum was <20%, or twice in January and March if the inoculum was >20% leaves rusted, controlled the rust effectively (91, 92). At very high inoculum levels, with around 40% leaves rusted, systemic fungicides were necessary at 3–4 week intervals (24, 104, 141).

In Brazil during years with low yield and inoculum levels, one copper fungicide only was recommended for better leaf retention. When the yield

was medium, two applications of copper or one of a mixture of copper and triadimefon were applied between February and March. During years with high yield, if the initial inoculum level reached 5–10% leaves rusted, 3 applications of copper fungicides were required in January, February, and March, or two applications of a mixture of copper and systemic fungicides, during and after February, if the inoculum level reached 20–30% leaves rusted (59, 80, 81).

Development of Simple and Complex Forecast Systems

From our earlier discussions, the various factors influencing coffee rust development in the field clearly cannot be identified by a factorial experiment or by other classical statistical procedures. A more comprehensive model is required capable of explaining the pathway of biological action, and integrating the various factors that influence the system. A fundamental forecast system has been developed for coffee rust and is described here briefly (58–61).

SURVIVAL RATIO MODEL TO PREDICT COFFEE RUST The model employs regression analysis to predict the rate of coffee rust development from the net survival ratio for the monocyclic process of *H. vastatrix* values (*NSRMP* or disease severity values) (Figure 1). The dependent variable is the intrinsic infection rate (k'') for an interval of 28 days after the date of prediction *(DP)* (65). The independent variable is daily *NSRMP* values, as an average for 28 days before the date of prediction. The *NSRMP* value is derived as:

$$NSRMP = BSR * MPEE * MPEH = SRMP * MPEH \quad 9.$$

where *BSR* is the basic survival ratio, or basic units that produced inoculum, such as the proportion of leaves or leaf area rusted (PLR or PLAR); *MPEE* is the monocyclic process equivalent for environment; *MPEH* is the monocyclic process equivalent for host; *SRMP* is the survival ratio for the monocyclic process.

The *MPEE* is derived as:

$$MPEE = SPOEE * DISEE * INFEE \quad 10.$$

where *SPOEE* is the sporulation equivalent for environment; *DISEE* is the dissemination equivalent for environment; *INFEE* is the infection equivalent for environment. Because no function is available for sporulation, *SPOEE* = 1.0 is assumed.

The *DISEE* is calculated as:

$$DISEE = [ERAIN + 0.5\ EWIND)/28] * EHOSTDEN \quad 11.$$

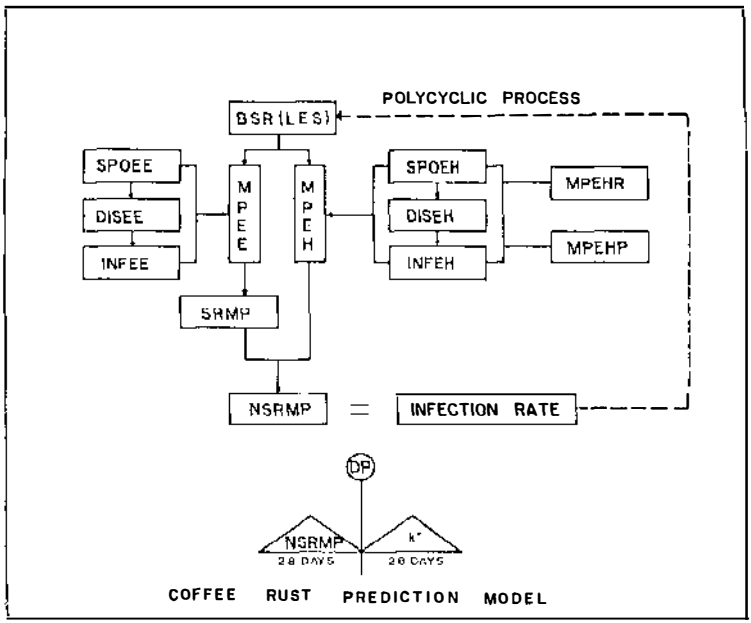

Figure 1 A schematic flow diagram of coffee rust prediction model indicating derivation of net survival ratio for the monocyclic process of *Hemileia vastatrix* (NSRMP). The daily NSRMP values, as an average for 28 days before the date of prediction (DP), were regressed against the intrinsic infection rate (k'') for 28 days after the DP. The acronyms are:
BSR basic survival ratio or inoculum producing units (proportion of leaves or leaf area rusted);
MPEE monocyclic process equivalent for environment (MPEE = SPOEE x DISEE x INFEE);
SPOEE sporulation equivalent for environment;
DISEE dissemination equivalent for environment;
INFEE infection equivalent for environment;
MPEH monocyclic process equivalent for host (MPEH = SPOEH x DISEH x INFEH or MPEH = MPEHR x MPEHP, the latter function was employed here);
SPOEH sporulation equivalent for host
DISEH dissemination equivalent for host
MPEHR is MPEH due to resistance;
MPEHP is MPEH due to predisposition of host from berry yield;
SRMP survival ratio for the monocyclic process of *H. vastatrix* (SRMP = BSR x MPEE);
NSRMP net survival ratio for the monocyclic process of *H. vastatrix* (NSRMP = SRMP x MPEH = BSR x MPEE x MPEH).
(Modified from Kushalappa et al (39))

where *ERAIN*, *EWIND* and *EHOSTDEN* are dissemination equivalents due to rain, wind, and host density, respectively. *ERAIN* is the number of days with rainfall ≥1 mm (0–28 days); *EWIND* the number of days with rainfall <1 mm or no rain (0–28 days); *EHOSTDEN* the proportion of leaf area index (0–1.0, maximum *LAI* = 30 m^2 leaf area/m^2 of ground area). The *MPEE* value ranges from 0–1.0.

The *INFEE* is derived as:

$$INFEE = \sum_{i=1}^{n=28} (INFEE_{HW} * INFEE_T)/28 \qquad 12.$$

in which $INFEE_{HW}$ is *INFEE* based on the daily duration (hr) of leaf wetness (Equation 1); $INFEE_T$ is *INFEE* based on the temperature while the leaf is wet (Equation 2, but the maximum proportion of infection is adjusted to 1.0); n is the number of wet periods (in 28d). In the field, the daily duration of leaf-surface wetness is measured with a surface-wetness recorder, and the temperature is recorded with a thermograph (60, 61). The value of *INFEE* varies from 0–1.0.

The monocyclic process equivalent for the host *(MPEH)* is determined as:

$$MPEH = MPEHR * MPEHP \qquad 13.$$

where *MPEHR* is *MPEH* due to resistance, which is given a value of 1.0. *MPEHP* is *MPEH* due to predisposition of the host from high yield, which is derived as:

$$MPEHP = 0.5 + \left\{ \sum_{i=1}^{n=5} [(PY_i * 0.5/M_n) * (M_i)] \right\} \qquad 14.$$

where PY_i is the proportion of berry yield on the ith month; M_n is the number of months between blossom and maximum predisposition effect, which is considered as $M_n = 5$, and M_i is the number of months from blossom to the ith observation. The constant value 0.5 is based on the finding that the rust is reduced to half the maximum when the immature berries are removed.

After a two-year study in four locations in the eastern Brazilian state of Minas Gerais, equations were developed to predict k'' from *NSRMP*. The equations that have high coefficients of determination are:

$$k'' = 0.00044 + 14.766\ (NSRMP) - 2511.21\ (NSRMP)^2 \qquad 15.$$

$$k'' = 0.023 + 14.026\ (NSRMP) - 87.38\ (NSRMP)^2 \qquad 16.$$

in which the Equation 15 and 16 are used to predict disease severity and incidence, respectively. k'' is the intrinsic infection rate, expressed in monits (monit $x = ln\ (1/(1\text{-}x))$) for 28 days where $x_1 = X_{DP}/Y_{DP}$ and $x_2 = X_{DPILP}/Y_{DP}$, in which x is the proportion of disease, X is the number of leaves or total proportion of leaf area diseased and Y is the number of leaves. When calculating k'', the amount of leaf, Y, present on the date of prediction is

considered as the maximum amount of host available for infection during the whole prediction period, i.e. from *DP* to *1LP* after *DP*.

SIMPLE AND COMPLEX FORECASTS TO TIME FUNGICIDE APPLICATION A model to predict the total amount of disease at the end of one latency period after *DP* can be written as (59):

$$\text{monit } x_{DP\ 1LP} = \text{monit } x_{DP} + k'' \ 1LP \qquad 17.$$

The total amount of disease at the end of one latency period after *DP (DP 1LP)* depends on the amount of disease present on DP and on the increase between *DP* and *DP 1LP*. An increase of about 10% leaves rusted, or 0.26% leaf area rusted, would justify a fungicide application. Therefore a value of $k'' = 0.0026$ in Equation 15 for severity and a value of $k'' = 0.1$ in Equation 16 for incidence were substituted to derive the *NSRMP* limit to spray fungicide. The *NSRMP* limits to spray fungicides were 0.00015 based on inoculum producing units quantifed as disease severity, and 0.0057 based on inoculum producing units quantified as disease incidence. By grouping the values observed during a two-year period on *BSR, MPEHP,* and *MPEE* for Minas Gerais to certain convenient ranges, we derived the combinations of these values to reach the prefixed *NSRMP* limit (Table 1). The grower has to quantify inoculum producing units as percent leaves or leaf-area diseased, and yield as high or low, at two-week intervals. By substituting these data for a given month in the Table 1, a recommendation can be made whether or not to apply fungicides. After one spray no fungicide is applied for one month.

TABLE 1 A simple forecast[x] for coffee rust to time fungicide application (39)

MPEE[y] & MONTH	BSR or inoculum producing units (range)							
%LR	5–9		10–14		15–29		>29	
%LAR	0.12–0.25		0.26–0.37		0.38–0.74		>0.74	
YIELD	LO	HI	LO	HI	LO	HI	LO	HI
<0.04 (S)								
0.04 (O,A)	–	–		–	–	F	F	F
0.08 (N,M)		–	–	F	F	F	F	F
0.12 (D,F)	–	F	F	F	F	F	F	F
≥0.16 (J)	–F	F	F	F	F	F	F	F

[x] The grower has to quantify basic survival ratio (BSR) or inoculum producing units as % leaves or leaf area rusted (%LR, or %LAR) and yield (low or high) at every 14 days beginning September. He can make a decision based on the month of the year indicated in the first column, or he can determine MPEE values for his estate and make a decision according to those values independent of the month indicated in parenthesis.

[y] MPEE, monocyclic process equivalent for environment; F, apply fungicide immediately; subsequent applications of fungicides are made as shown but with a gap of at least 28 days after a spray; –, do not apply fungicide; –F, may require fungicide at high levels of MPEE.

For a complex forecast, all parameters, *BSR*, *MPEE*, and *MPEH*, have to be determined for each estate by the grower. Fungicide is then applied when the *NSRMP* threshold is exceeded. The use of forecasts depends on the grower's technical know-how. Both simple and complex forecasts can help in postponing the timing of fungicide application, thereby decreasing the number of applications or the dosage of fungicides. These methods are better than the previous local methods based on a fixed calendar schedule (63).

The sampling time required to quantify the *BSR* or the disease intensity level can be optimized by establishing sequential sampling procedures, depending on the spatial distribution of rust (18). The forecast model discussed here is quite flexible, and could be improved by establishing better functions for the various parameters included. If fungicide application is to be at a fixed interval, then dosage can be increased rather than decreasing the time interval between each application as the *NSRMP* values rise. Low dosages of copper fungicides (1–1.5 kg a.i. metallic Cu) effectively controls coffee rust during seasons when disease pressures are lower, whereas a higher dosage was required when they are high (3–3.5 kg a.i. metallic Cu) (50, 75). When the initial and predicted disease intensities are very high, systemic fungicides may be recommended (81, 87). Also, correction factors can be incorporated into the model to include fungicide efficiency and weathering (59).

The simple forecast developed for the Minas Gerais state of Brazil can be adapted to other states in Brazil and to other countries in Latin America, as it is a fundamental model. For its implementation the MPEE values (Table 1) for different months have to be established for each geographic or climatic zone.

Factors Influencing Fungicide Efficiency.

The efficiency of fungicides for controlling coffee rust depends on the active ingredient, dosage, tenacity, frequency and timing of application, distribution on the plant, etc.

Under field conditions copper fungicides are the most effective and economical. Efficiency depends on the amount of metallic copper (Cu^{++}), and, in general, copper fungicides have a long residual effect (87, 112). Among copper fungicides, copper oxychloride formulations are the best. Rust is effectively controlled at a dosage of 1.5 kg a. i/ha, though 1 kg is sufficient during years with low yield (50, 75). A higher concentration is required when the yield and rust severities are high (81, 87). In Kenya, cupric hydroxide and cuprous oxide treatments are the most effective (17, 51, 53, 104), but a higher dosage, 3.5 kg a.i/ha, is required due to high rainfall (52).

Among other protective fungicides, the dithiocarbamates have proven useful, despite their relatively short residual effect and chemical instability at

high temperature and humid conditions (50). Their performance is better when mixed with copper fungicides (59, 79).

Systemic fungicides have performed well under field conditions, the major drawback being high cost and the induction of severe defoliation. Among these triadimefon has been the best so far, with the most effective rust control and limited defoliation (52, 53, 59, 99, 141). However, in Kenya applications of triadimefon stimulated the coffee berry disease (52). In general, with continuous application of systemics, pathogens develop resistance against narrow spectrum fungicides.

Mixtures or alternate applications of protective and systemic fungicides have been very successful in controlling rust. The best control is obtained by either alternating or mixing copper oxychloride and triadimefon (53, 74, 81, 92).

Fungicide effectiveness also depends on the time of application. Applications at the wrong time or dosage often are wasteful (17). Furthermore, placement of fungicides at the site of infection is critical, as redistribution due to rain is very limited. This aspect can be improved by ensuring an adequate spray pattern, employing suitable spray equipment to control: (*a*) the volume of spray liquid; (*b*) the spray droplet size; and (*c*) spray coverage (82). All three parameters are interrelated and determine the equipment's efficiency.

There are high, medium, low, and ultralow volume sprayers, in which the liquid sprayed varies from >200 L to <15 L/1000 plants/ha. Uniformity of spray droplet distribution on the plant surface is also important, and depends on the spray nozzle, target, and environment (59). Spray distribution can be measured as percent leaf area covered, using a diagrammatic scale (109).

The most commonly used sprayers are hydraulic, air-carrier, or rotary. All three types have been modified, in the latter two by employing centrifugal or rotary nozzles for low and ultralow volume spraying (59, 81).

Breeding for Rust Resistance

For a detailed coverage, the reader is referred to the comprehensive reviews that have recently been published (14, 19, 56). The main obstacles in breeding for coffee rust resistance have been: (*a*) restricted variation for resistance within *C. arabica,* (*b*) variation in pathogenicity of the rust fungus, rendering the more easily available resistance genes ineffective, and (*c*) coffee's long breeding cycle, specially when interspecific hybrids are involved. Breeding in *C. arabica* initially involved the major genes present in this species, which proved to be relatively ineffective. Nowadays, attention is mostly concentrated on selection in interspecific hybrid populations, such as Catimor and Icatu, containing resistance genes from *C. canephora*. In Columbia, a locally

developed Catimor population has been successfully selected and a mixture of F5 lines is being distributed commercially under the name "Colombia" (20). Other Catimor selections are being used in new varieties released in Kenya and India (56). Several of these lines have shown problems of overbearing and early degeneration in Brazil as well as in other countries (19, 30). The Icatu population appears more vigorous and advanced selections will soon be released commercially in Brazil. New types of hybrids between *C. arabica* and *C. canephora* have been produced in Columbia and Brazil by using triploid F_1s backcrossed with *C. arabica*. Preliminary results with these populations have been promising (44, 105). New breeding methods like large scale in vitro propagation, the use of spontaneous haploids, anther culture and genetic male sterility are becoming available (56) and will be of great help in reducing the long selection cycle in coffee. The application of these techniques will permit more efficient exploitation of variability of rust resistance in heterozygous coffee populations.

Natural Enemies and Biological Control

The most important natural enemies of coffee rust reported so far are hyperparasitic fungi like *Verticillium lecanii* (formerly *V. hemileiae*), *V. leptobactrum, V. psalliotae, Cladosporium hemileiae* and *Paranectria hemileiae* (18, 38, 51, 67). In some countries, specially with high humidity conditions, these fungi frequently occur naturally (127). The best known fungus is *V. hemileiae,* commonly found in rust samples (28, 40, 127). Although effective in the laboratory, both this fungus and *V. leptobactrum* have a poor survival rate under field conditions in Brazil, the main limiting factor most likely being low humidity (40). The search for other, possibly more effective antagonists is an open area of research.

CONCLUSION

Advances made in the past two decades in forecasting methods, the discovery of new fungicides and fungicide application methods, in addition to host resistance, have enabled producers to combat coffce rust more economically. Future advancement is aimed at continuing improvement of these factors and the exploitation of biocontrol methods. Increased public awareness of health hazards caused by pesticides applied on coffee, as in other crops, should in future encourage more researchers to work on the improvement of forecasting systems to optimize fungicide usage and on the gcnetic engineering and plant breeding to obtain more resistant cultivars.

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