The effect of leaf age on incomplete resistance of coffee to Hemileia vastatrix

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Abstract

The influence of leaf age on incomplete resistance to race II of coffee leaf rust (Hemileia vastatrix), which is the most common race in Brazil, was tested in the greenhouse and in the field. Three stages of leaf age were distinguished: 'young' leaves which had just fully expanded and still had a shiny appearance on the day of inoculation, 'adult' leaves of 1 to 4 months old, and 'old' leaves of 6 to 12 months old which were formed in the foregoing growing season.

The effect of leaf age varied with the coffee genotype. With the susceptible Coffee arabica cvs Mundo Novo and Catuai no important effect of leaf age on latency period and reaction type was observed. Lesion density, depending on inoculation method, was affected to some extent, older leaves showing lower values. With genotypes of the C. canephora cv. Kouillou, which varied in level of incomplete resistance, adult leaves appeared to be more resistant than young and old leaves. This adult leaf resistance was expressed mainly by a lower lesion density, but also by a longer latency period and a lower reaction type.

Within the hybrid populations Icatu and Catimor, genotypes with race-specific incomplete resistance were tested and others of unknown specificity. Resistance was expressed mainly by a low reaction type. Generally, resistance decreased with increasing leaf age, which was occasionally associated with a complete change in reaction type. Contrary to cv. Kouillou, in Icatu and Catimor no higher susceptibility of young leaves than of adult leaves was observed.

The incomplete resistance to race I of the differential CIFC H152/3, heterozygous for S_H4, was also better expressed in young leaves, older ones becoming gradually more susceptible.

It is concluded that for screening incomplete resistance to coffee leaf rust leaves of different ages should be tested.

Additional keywords: Coffee leaf rust, coffee differentials, durable resistance, complete resistance, heterogeneous reaction type, components of resistance.

Introduction

Resistance to pathogens is often affected by the developmental stage of the plant or of the plant organ. Generally, plants become more resistant when they mature (Dickinson and Crute, 1974; Hooker, 1967; Hyde, 1977; Zadoks, 1961). but conflicting results have been reported (Hooker, 1967). The increase in resistance during maturation may be followed by a decrease in resistance with further ageing (Jones and Hayes, 1971; Luttrell et al., 1974; Mence and Pegg, 1971; Parlevliet, 1975; Umaerus, 1970). Padmanabhan and Ganguly (1954) observed that resistance of rice to *Helminthosporium* decreased with age but that resistance to rice blast increased with age.

For perennial crops the age of plant organs may be more important than the age of the whole plant. Reports exist on the effect of leaf age on resistance to fungal pathogens (Weinhold and English, 1964; Williams and Kuć, 1969; Sharma et al., 1980). The developmental stage of coffee berries appeared to influence resistance to coffee berry disease (Mulinge, 1970; van der Graaff, 1981). Little is known about the influence of leaf age on resistance to orange coffee rust or coffee leaf rust (Hemileia vastatrix Berk. et Br.). D'Oliveira (1957), screening for resistance to coffee rust, mentioned that mature leaves are more resistant than succulent young leaves.

Results are reported here on the effect of leaf age on incomplete resistance to coffee leaf rust at various levels.

Materials and methods

Details on resistance terminology, coffee and rust genotypes used, standard inoculation methods and observations on natural and artificial infection are described by Eskes (1982).

Location. Alle experiments were carried out at the Experimental Station of the Instituto Agronômico of Campinas (I.A.C.), S.P., Brazil.

Coffee genotypes. The coffee plants used were one-year-old seedlings or cuttings from field plants. The age of the field plants was 10 years with Icatu and with the Coffea arabica cvs Mundo Novo and Catuai, 6 years with Catimor, and about 45 years with the C. canephora cv. Kouillou. Icatu and Catimor consist of advanced breeding generations derived from crosses between C. arabica (4x = 44) and C. canephora (4x = 22) (Monaco, 1977; Rodrigues et al., 1975). Cvs Mundo Novo and Catuai are equally susceptible to the common race II of H. vastatrix. The genotypes used from cv. Kouillou and from the Icatu and Catimor populations varied in level of resistance. The cuttings of the coffee differentials used in experiment 6 belonged to the collection of differentials of the Phytopathology Department of the I.A.C. The seedlings of the Agaro C1164-4 introduction, used in the same experiment, were two years old.

Rust materials. Unless stated otherwise, race II of H. vastatrix has been employed. Isolate 2, used in experiment 5, was obtained in 1979 from an Icatu field plant with complete resistance to race II.

Inoculation dates and method. Experiments 1 to 5 were inoculated on 15 December 1976; 25 February, 27 March and 24 March 1981, and 10 November 1980, respectively. Standard inoculation was done by spraying suspensions of urediospores on the abaxial leaf surface, using densities of 0.5 to 1.5 mg urediospores per ml. The number of spores in one mg is about 1.5×10^5 . In experiment 1B dry urediospores were applied with a scalpel on the abaxial leaf surface and spread with a small brush. Subsequently the spores were wetted by spraying distilled water on the leaf. After inoculation the plants were always incubated in a humid dark room at 22 ± 2 °C during 24 to 48 hours.

Leaf age treatments. Coffee leaves can remain on the plant for more than one year. In Campinas, rapid vegetative growth occurs during the wet summer (October to

April), when 4 to 8 new leaf pairs may develop on each branch. Growth ceases during the dry winter. Natural and also rust-induced leaf fall is highest at the onset of the dry season (May, June), which coincides with harvest time.

Three stages of leaf age were considered. 'Young' leaves were just fully developed leaves which were shiny and succulent. 'Adult' leaves varied in age from a few weeks to a few months at the day of inoculation and had lost the shiny appearance. 'Old' leaves, formed in the foregoing growing season, varied in age from 6 to 12 months.

A second way of identifying leaf age was by position on the branch. Leaf position 1 generally indicated a young leaf, higher positions adult or old leaves.

Observations. Observations on the components of resistance were made every two or three days after appearance of first symptoms. Reaction type (RT) was scored between 50 and 60 days after inoculation when no further increase in sporulation occurred, using a 0 to 9 scale (Eskes and Toma-Braghini, 1981). Value 0 indicates absence of visible symptoms, values 1 to 3 variation within resistant reaction types, 4 to 7 heterogeneous reaction types with increasing sporulation intensity and percentage of spurulating lesions, and 8 and 9 susceptible reaction types with moderate (8) to high (9) sporulation intensity.

Assessment of natural infection in the field was by scoring on a 1 to 5 scale. Value 1 indicates absence of symptoms and values 2 to 5 increasing numbers of sporulating lesions, associated with an increase in reaction type. These observations were made annually with Icatu plants and every 6 months with cv. Kouillou plants. Data on field infection represent means over the years 1976 to 1981.

Statistics. For elaboration of the results, SPSS (Statistical Package for the Social sciences) has been applied. The Friedman test (Siegel, 1956) has been used when the distribution of the data deviated from the normal distribution.

Results

In experiment 1A and 1B, the effect of leaf position on the branch on susceptibility of cv. Mundo Novo was studied with two inoculation methods. Four or five leaf pairs of six branches were inoculated. With the standard suspension inoculation method only leaves of position 5 showed a significantly lower lesion density (LD) than the other leaves, whereas latency period (LP) was only slightly affected (Table 1). Results were somewhat different when the inoculation was done with dry urediospores and subsequent wetting by spraying. Then, the youngest leaf had the highest LD value and LD declined more rapidly with increasing leaf position than with the suspension method. The variation in LP was small but significant, due to the low coefficient of variation (CV) for this component. The average CV values for LD and LP in the experiments were 88 and 6%, respectively.

In experiment 2 the effect of leaf age was studied with cv. Kouillou genotypes and cv. Mundo Novo under field conditions. Of each genotype all leaves of four branches were inoculated. All five genotypes of cv. Kouillou showed a significantly higher level of resistance in adult than in old leaves (Table 2). Differences with genotypes C67-12 were smallest and least significant. With cv. Mundo Novo no significant differences were observed for the resistance components. With both cultivars no difference was

Table 1. Lesion density (LD = number of lesions per leaf) and latency period (LP, in days) of leaves of cv. Mundo Novo at different positions on the branch inoculated in the greenhouse by two methods.

Experiment	Method of inoculation	Component of resistance	Leaf position ¹					
	moculation	of resistance	1	2	3	4	5	
1A	Spraying of a	LD	27 ^{a2}	33a	37ª	29ª	11 ^b	
	suspension (stan- dard method)	LP	35^{a^2}	35ª	35ª	35ª	36 ^b	
1B	Applying dry ure-	LD	38a	19 ^{ab}	20 ^{ab}	20 ^b	_	
	diospores with sub- sequent wetting	LP	32ª	34 ^b	33ab	34 ^b	_	

¹ The age of leaves of position 1 to 4 increased from a few weeks to 3 months, respectively, while leaves of position 5 were about 7 months old on the inoculation date.

Tabel 1. Lesiedichtheid (LD = aantal lesies per blad) en latentieperiode (LP, in dagen) van bladeren van cv. Mundo Novo met verschillende positie aan de tak geïnoculeerd in de kas op twee verschillende manieren.

observed between leaves of similar age group but with different positions on the branches. The percentage of infected leaves that dropped from the branch before 70 days after inoculation varied from 0 to 26 and from 57 to 100 with adult and old leaves, respectively (Table 2). Leaf fall of symptomless leaves, from the same experiment, was about 0 and 20 percent for adult and old leaves, respectively. Therefore, the pronounced leaf fall of old leaves was apparently induced by the rust infections.

Six leaves used in this experiment were considered as young leaves, because they still has a shiny appearance on the day of inoculation. Average lesion density of these leaves was about 2 to 4 times higher than of adult leaves, which is in agreement with the higher susceptibility of young leaves observed in the following experiment.

In experiment 3, one-year-old cuttings of the same plants of cv. Kouillou as used in experiment 2 were inoculated in the greenhouse. The cuttings had grown vigorously during the two months prior to inoculation. Four to ten cuttings were inoculated per genotype, using one branch per cutting with three leaf pairs each. The leaves of the first or top pair were called young and of the second and third pairs were called adult. Generally, differences between leaf ages within genotypes were not statistically significant (Table 3), but the differences between the means were significant, except for RT, which indicates a tendency. The difference in susceptibility was most expressed by lesion density, which in average was 53 for young leaves and 21 for adult ones.

In experiment 4, leaves of different positions on one year old seedlings of Catimor families were used. The families segregated for complete as well as incomplete resistance. Only seedlings with incomplete resistance were considered, 6 to 12 per family. Table 4 shows that the effect of leaf position on reaction type varied according to the family. The most remarkable effect was observed for the C2502 family, which showed nearly complete resistance in the younger leaves whereas older leaves were nor-

² Different letters indicate significant differences within rows according to the LSD 0.05 values.

reaction type (RT) and leaf fall (LF, in percentage observed 70 days after inoculation) of adult and old leaves of cv. Kouillou genotypes and Table 2. Latency period (LP, in days), lesion density (LD = number of lesion per 10 cm² leaf surface), sporulating lesion density (SLD), of cv. Mundo Novo, inoculated in the field.

Genotype	Disease score	LP		CI		SLD	D	RT		LF	ſr.
	(1-5 scale)	leaf age	geı	leaf age	age	leaf age	age	leaf age	age	leaf age	age
		adult	plo	adult	old	adult	plo	adult	old	adult	old
Cv. Kouillou:											
C66- 1	1.6	ı	59	0.32^{a^2}	3.70^{b}	0.00^a	0.95^{b}	2.3^{a}	5.3^{b}	0a	$2e_{ m p}$
C70-11	1.8	ı	20	0.09^{a}	1.15^{6}	0.00^{a}	0.60^{6}	3.0^{a}	4.3^{b}	e O	100 ^b
C60- 3	2.2	61a	48^a	0.04^{a}	1.50^{b}	0.04^{a}	1.50^{b}	4.3^{8}	6.5 ^b	Oa	57^a
C67-12	3.0	e99	43^a	1.50^{a}	1.75^{a}	0.48^{a}	1.19^{a}	4.0^{a}	5.8^{b}	Oa	47ª
C68-15	4.3	53^{a}	41 ^b	3.73^{a}	7.48^{b}	2.70^{a}	$7.48^{\rm b}$	5.8^{a}	8.0^{b}	17a	100 ^b
Mean	ı	ı	ı	1.14^{a}	3.12b	0.64^{a}	2.35^{b}	3.9ª	6.0 ^b	За	72 ^b
Cv. Mundo Novo	4.5	34ª	34ª	10.10 ^a 12.80 ^a	12.80ª	10.10 ^a 12.80 ^a	12.80ª	8.5a	8.5ª	26ª	94 ^b

¹ Adult leaves varied in age from 1 to 3 months, old leaves were over 8 months old.

² Different letters indicate significant differences between leaf ages, within genotypes, according to the analysis of Friedman at P = 0.05.

Tabel 2. Latentieperiode (LP, in dagen), lesiedichtheid (LD = aantal lesies per 10 cm² bladoppervlak), dichtheid van sporulerende lesies (SLD), reactietype (RT) en bladval (LF, in percentage waargenomen 70 dagen na inoculatie) van volwassen en oude bladeren bij cv. Kouillou genotypen en bij cv. Mundo Novo, geïnoculeerd in het veld.

Table 3. Latency period (LP, in days), lesion density (LD = number of lesions per 15 cm² leaf surface), sporulating lesion density (SLD), and reaction type (RT) of young and adult leaves with five genotypes of cv. Kouillou observed in the greenhouse.

Genotype	Disease score In the field	L	P	L	D	SLD leaf age		R	Т
	(1-5 scale)	leaf	age ¹	leaf	age			leaf	age
		young	adult	young	adult	young	adult	young	adult
C66- 1	1.6	61 ^{a2}	64 ^a	52a	16 ^b	2 ^a	2ª	2.8ª	1.7a
C70-11	1.8	51a	56a	72ª	22 ^b	40a	12 ^b	6.0^{a}	5.3a
C66- 3	2.2	53a	60 ^b	46a	14ª	13 ^a	7 ^a	4.5a	3.8a
C67-12	3.0	47a	51a	41 ^a	23a	31a	17 ^a	5.7a	4.8a
C68-15	4.3	35a	43 ^b	52 ^a	32 ^a	50 ^a	30^{a}	8.3a	8.2a
Means		50 ^a	55 ^b	53 ^a	21 ^b	27 ^a	13 ^b	5.5a	4.8a

¹ 'Young' leaves were generally leaves which had just expanded and 'adult' leaves varied in age from about one to three months on the day of inoculation.

Tabel 3. Latentieperiode (LP, in dagen), lesiedichtheid (LD = aantal lesies per 15 cm² bladoppervlak), dichtheid van sporulerende lesies (SLD) en reactietype (RT) van jonge en volwassen bladeren bij vijf genotypen van het ras Kouillou waargenomen in de kas.

Table 4. Reaction type of leaves of different age of seedlings with incomplete resistance to coffee leaf rust for five families derived from the cv. Caturra × Hybrid of Timor cross (Catimor) and of cv. Catuai observed in the greenhouse.

Origin	Leaf position ¹						
of family	1	2	3	4	5		
Catimor:							
UFV386-19	8.5^{a^2}	8.3a	8.4a	8.7a	8.8a	8.5	
C2502	4.0 ^a	6.5 ^b	7.9°	8.3°	8.4c	7.0	
UFV386-C798-A	5.2a	5.9ab	6.1ab	6.6ab	6.7 ^b	6.1	
UFV386-C798-B	3.7ª	4.3ab	4.3ab	4.7 ^b	5.4 ^b	4.5	
C2501	2.9 ^a	3.2a	3.6 ^a	3.3 ^a	3.0^a	3.2	
Cv. Catuai	8.5 ^a	8.4a	8.5a	8.5a	8.9a	8.6	

¹ The age of the leaves of position 1 to 5 ranged from a few weeks to about 5 months on the day of inoculation, respectively.

 $^{^2}$ Different letters indicate significant differences, between leaf ages, within genotypes, according to the Friedman test at P = 0.05.

² Different letters indicate significant differences between leaf positions within families, according to the LSd 0.05 value.

Tabel 4. Reactietype van bladeren van verschillende leeftijd bij zaailingen van vijf families die afstammen van de kruising tussen cv. Caturra \times hybrid of Timor (Catimor) en van cv. Catuai, waargenomen in de kas.

Table 5. Latency period (LP, in days), percentage of sporulating lesions (PSL) and reaction type (RT) of adult and old leaves for four coffee genotypes inoculated in the field with *H. vastatrix*, race II and isolate 2.

Genotype	Race or	LP		PS	PSL		Т
	isolate	leaf a	age ¹	leaf	age	leaf	age
		adult	old	adult	old	adult	old
Icatu:	Race II	-	50	1	80	3	7
H 4782-10-203	Isolate 2	45	39	75	98	7	8
Icatu:	Race II	39	39	75	100	8	9
H 3851- 2-689	Isolate 2	36	35	94	100	9	9
Catimor:	Race II	_	54	0	63	2	5
C 2012-19	Isolate 2	45	46	44	73	6	7
Cv. Mundo Novo	Race II	38	35	97	98	9	9
	Isolate 2	48	38	59	92	6	8

¹ The age of the adult leaves was 1 to 2 months and that of old leaves over 6 months on the day of inoculation.

Table 6. Variation in reaction type observed on adult and old leaves of three coffee differentials and of the Agaro C1164-4 introduction, inoculated with two races of *H. vastatrix* in the greenhouse. Each entry is based on 6 to 12 leaves.

Differential or introduction	Genotype	Race I (Race XV (V2v4): leaf age	
		adult	old	adult	old
CIFC 32/1	$S_H 2S_H 2 s_H 4 s_H 4$	8-9	8-9	0-1	0-1
CIFC H152/3	$S_H 2s_H 2 S_H 4s_H 4$	2-4	4-7	0-1	0-1
CIFC 110/5	$s_H 2 s_H 2 S_H 4 S_H 4$	2-3	2-3	4-8	7-9
Agaro C1164-4	$s_H 2 s_H 2 S_H 4 S_H 4$	2-4	2-3	8-9	8-9

Tabel 6. Variatie in reactietype waargenomen aan volwassen en oude bladeren van drie differentiërende koffieplanten en van de Agaro C1164-4 introductie, geïnoculeerd met twee fysio's van H. vastatrix in de kas. Ieder gegeven is gebaseerd op 6 à 12 bladeren.

Tabel 5. Latentieperiode (LP, in dagen), percentage sporulerende lesies (PSL) en reactietype (RT) van volwassen en oude bladeren bij vier koffiegenotypen geïnoculeerd met twee isolaten van H. vastatrix in het veld (race II en isolate 2).

mally susceptible. The difference in response between families is probably not due to a difference in age of the leaves of similar positions, because growth rate of the seedlings was about equal with all families. The control cv. Catuai did not show a significant effect of leaf position on reaction type.

Experiment 5 was carried out in the field and included four coffee plants with differential reactions to two races of *H. vastatrix* (Table 5). For each genotype/race combination all leaves of two branches, growing in the shade, were inoculated. The resistance to race II of adult leaves of the genotypes H 4782-10-203 and C2012-19 was nearly complete, whereas old leaves were quite susceptible. Similar but smaller effects of leaf age were observed with other combinations. The differences in pathogenicity between race II and isolate 2 were more expressed in adult than in old leaves.

Table 6 shows the results of inocultions, carried out in different months and different years, of three differential clones with the resistance genes S_H2 and S_H4 and of seedling progeny of the Agaro C1164-4 introduction. Adult leaves of the differential CIFC 110/5 were not always susceptible when inoculated with the 'compatible' race XV; with one inoculation predominantly flecks and chlorotic lesions developed and sometimes early necrosis of apparently susceptible lesions occurred. These reactions were not observed with the progeny of the Agaro C1164-4 introduction, which is also homozygous for the dominant allele S_H4 . Therefore, the unstable adult leaf resistance of the 110/5 differential must be due to a resistance factor other than S_H4 . Table 6 also shows the relative susceptibility to race I of old leaves in relation to young leaves of differential H152/3, which is heterozygous for S_H4 . Resistance due to gene S_H2 was not affected by leaf age or heterozygozity.

Discussion

C. arabica cultivars. Leaf age or position did not greatly influence the susceptibility of cvs Mundo Novo and Catuai (Tables 1,2, and 4). Only lesion density was affected to some extent by leaf position (Table 1). The decrease in lesion density of leaves at position 4 and 5 may be partly due to the effect of light intensity (see below). The two inoculation methods applied in experiment 1 appeared to interact with the effect of leaf position. This interaction might be related to differences in leaf surface characteristics. Urediospores may adhere better to the waxy surface of young leaves than to the harder and drier surface of older leaves. Besides, water droplets coalesce and runn off more easily from young than from older leaves.

Other coffee genotypes. Tables 2 and 3 suggest the existence of three phases of susceptibility during the development of leaves of *C. canephora* cv. Kouillou. Adult leaves were relatively more resistant than young or old leaves. Results with Icatu and Catimor genotypes (Tables 4 and 5) showed higher resistance of young or adult leaves than of old leaves. With some genotypes resistance was only expressed in young leaves, older ones being normally susceptible, a combination which was never observed with the cv. Kouillou genotypes.

Types of incomplete resistance involved. Complete monogenic resistance is often race-specific resistance, as is also the case with coffee leaf rust (Rodrigues et al., 1975). Tables 5 and 6 show how certain types of incomplete resistance to coffee leaf rust may

also be race-specific. Nothing is known about the specificity of the resistance of the Catimor families shown in Table 4.

Within Catimor families quite distinct phenotypes were observed with either complete resistance, intermediate resistance or high susceptibility. Therefore, these families could have mono- or oligogenic resistance with incomplete dominance, as observed with the $S_{\rm H}4$ resistance gene (Table 6).

The genetic base of the resistance shown by most genotypes of cv. Kouillou seems complex (personal observations). Some specificity of resistance has been observed with genotype C67-12, which was more susceptible to a rust race detected in the 'Kouillou' population in 1980 than to race II. The other genotypes have maintained their resistance in the field from 1976 to 1981. Any inference about the durability of this resistance is speculative. However, the pecularities of the resistance of these genotypes of cv. Kouillou resemble those of other reportedly stable pathosystems (Jones and Hayes, 1971; Parlevliet, 1975; Umaerus, 1970). Therefore, the resistance of certain 'Kouillou' plants could be of great value in obtaining durable resistance to coffee rust.

Effect of leaf age on complete resistance. Most results shown in this paper relate to incomplete resistance, though also genotypes with complete resistance were included in the experiments. Complete resistance is common in the Icatu and Catimor populations, but is less frequent in cv. Kouillou. As far as observed, leaf age does not much affect the expression of complete resistance. However, certain genotypes with complete resistance showed symptoms on young leaves (flecks and tumefactions), while adult leaves were symptomless.

Other factors influencing incomplete resistance. As reported earlier high light intensities may predispose coffee plants to coffee leaf rust (Eskes, 1982). Leaves of different positions on the branch will receive different light intensities. Therefore the results of Tables 1, 3, and 4 may be confounded with an effect of light intensity, though shading of leaves was avoided as much as possible by suitable spacing of the plants.

Seasonal effects on resistance, which could not be explained by differences in leaf age, have been observed with the genotypes of Icatu mentioned in Table 5. Resistance of these genotypes to race II was higher in winter and spring than in summer and autumn. The same was observed for the relative resistance of cv. Mundo Novo to isolate 2. The resistance of the genotypes of cv. Kouillou in experiment 2 was higher than in other field inoculations of these genotypes. It is supposed that the relatively hot and dry weather, which prevailed during experiment 2, may have increased resistance of the plants in the field.

Epidemiological aspects. Rust epidemics in cv. Kouillou usually start early in the season but subsequent development is slower than in cv. Mundo Novo and Catuai (Cadena-Gomez and Buritića-Céspedes, 1980; personal observations). This can be explained, at least in part, by the difference in effect of leaf age between these cultivars (Tables 1, 2, 3 and 4).

The high pathogen-induced leaf fall of old leaves also has epidemiological connotations. Leaf rust in Brazil has to overwinter on old leaves which drop easily upon infection (Table 2), thereby decreasing the carry-over of inoculum to the next growing season.

Breeding aspects. Screening for resistance to coffee leaf rust is often done by inoculating young, recently expanded leaves (e.g. D'Oliveira, 1957). The results of the present paper suggest that, with certain coffee genotypes, this inoculation method may under- or overestimate the real level of resistance of the entire plant. The breeder who is interested in measuring incomplete resistance with precision will have to inoculate leaves of different ages.

The coffee differential heterozygous for S_H4 (Table 6) was incompletely resistant when inoculated with the 'incompatible' race I. Therefore, this differential should be used with care in race identification studies.

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Samenvatting

Het effect van bladleeftijd op incomplete resistentie van koffie tegen Hemileia vastatrix

Het effect van bladleeftijd op incomplete resistentie van koffie tegen fysio II van koffieroest (Hemileia vastatrix), het algemeen voorkomende fysio in Brazilië, werd getoetst in de kas en in het veld. Drie stadia in de bladleeftijd werden onderscheiden: 'jong' blad dat net volgroeid was en nog glansde op de dag van inoculatie, 'volwassen' blad van 1 tot 4 maanden oud en 'oud' blad van 6 tot 12 maanden oud dat gevormd was in het voorafgaande groeiseizoen.

Het effect van bladleeftijd varieërde met het koffiegenotype. Bij de vatbare *Coffea arabica* rassen Mundo Novo en Catuai werd geen belangrijke invloed waargenomen van bladleeftijd op latentieperiode en reactietype. Lesiedichtheid werd, afhankelijk van de inoculatiemethode, wel enigszins beïnvloed. Bij vijf genotypen van het *C. canephora* ras Kouillou, die varieerden in niveau van incomplete resistentie, bleek volwassen blad veelal resistenter dan jong en oud blad. Deze resistentie uitte zich voornamelijk door een lagere lesiedichtheid maar ook door een langere latente periode en een lager reactietype.

Van de hybride populaties Icatu en Catimor werden enkele genotypen met fysiospecifieke incomplete resistentie getoets alsmede genotypen waarvan de specificiteit van de resistentie onbekend was. Verschillen in resistentie uitten zich voornamelijk door verschillen in reactietype. Over het algemeen nam de resistentie af bij toenemende bladouderdom. Anders dan bij de cv. Kouillou werd bij Icatu en Catimor geen grotere vatbaarheid van jong ten opzichte van volwassen blad waargenomen. Bij sommige

genotypen kwam resistantie zelfs alleen maar tot uiting in het jonge blad, terwijl het volwassen blad normaal vatbaar was. Een soortgelijk effect van bladleeftijd werd waargenomen bij inoculatie van de koffiedifferentieel CIFC H153/3, die heterozygoot is voor het resistentiegen S_H4, met het incompatibele fysio I.

Er wordt geconcludeerd dat voor het bepalen van incomplete resistentie tegen koffieroest bladeren van verschillende ouderdom getoetst dienen te worden.

References

- Cadena-Gomez, G. & Buriticá-Céspedes, P., 1980. Expresión de resistencia horizontal a la roya (*Hemileia vastatrix* Berk. et Br.) en *Coffea canephora* variedad Conilon. Cenicafé 31: 3-28.
- Dickinson, C.H. & Crute, I.R., 1974. The influence of seedling age and development on the infection of lettuce by *Bremia lactucae*. Ann. appl. Biol. 76: 47-61.
- D'Oliveira, B., 1957. As ferrugens do cafeeiro (Coffee rusts). Revta do Café port. Separata no. 3. 1957. 61 pp.
- Eskes, A.B., 1982. The effect of light intensity on incomplete resistance of coffee to *Hemileia* vastatrix. Neth. J. Pl. Path. 88: 191-202.
- Eskes, A.B. and Toma-Braghini, M., 1981. Assessment methods for resistance to coffee leaf rust (*Hemileia vastatrix* Berk. et Br.). Pl. Prot. Bull. FAO 29: 56-66.
- Graaf, N.A. van der, 1981. Selection of Arabica coffee types resistant to coffee berry disease in Ethiopia. Thesis. Communications 81-11 of the Agricultural University Wageningen, the Netherlands. 111 pp.
- Hooker, A.L., 1967. The genetics and expression of resistance in plants to rusts of the genus *Puccinia*. A. Rev. Phytopath. 5: 163-182.
- Hyde, P.M., 1977. The effect of leaf age on infection of wheat seedlings by *Erysiphe graminis* on subsequent colony development. Phytopath. Z. 88: 299-305.
- Jones, I.T. & Hayes, J.D., 1971. The effect of sowing date on adult plant resistance to *Erysiphe graminis f. sp. avenae* in oats. Ann. appl. Biol. 68: 31-39.
- Luttrell, E.S., Harris, H.B. & Wells, H.D., 1974. *Bipolaris* leaf blight of *Panicum fasciculatum:* Effects of host age and photoperiod on susceptibility. Phytopathology 64: 467-480.
- Mence, M.J. & Pegg, G.F., 1971. The biology of *Peronospora viciae* on pea: factors affecting the sucepptibility of plants to local infection and systemic colonization. Ann. Appl. Biol. 67: 297-308.
- Monaco, L.C., 1977. Consequences of the introduction of coffee rust into Brazil. Ann. N.Y. Acad. Sci. 287: 57-71.
- Mulinge, S.K., 1970. Development of coffee berry disease in relation to the stage of the berry growth. Ann. appl. Biol. 65: 269-276.
- Padmanabhan, S.Y. & Ganguly, D., 1954. Relation between the age of rice plants and its susceptibility to *Helminthosporium* and blast diseases. Proc. Indian Acad. Sci. 49, sec B.: 44-50.
- Parlevliet, E.J., 1975. Partial resistance of barley to leaf rust *Puccinia hordei* I: Effect of cultivar and development stage on latent period. Euphytica 24: 21-27.
- Rodrigues, C.J., Bettencourt, A.J. & Rijo, L., 1975. Races of the pathogen and resistance to coffee rust. A. Rev. Phytopath. 13: 49-70.
- Sharma, J.K., Heather, W.A. & Winer, P., 1980. Effect of leaf maturity and shoot age of clones of *Populus* species on susceptibility to *Melampsora larici-populina*. Phytophathology 70: 548-554.
- Siegel, S., 1956. Nonparametric statistics for the behavorial sciences. McGraw-Hill. 312 pp. Umaerus, V., 1970. Studies on field resistance to *Phytophtora infestans*. 5. Mechanisms of resistance and application to potato breeding. Z. PfIZücht. 63: 1-23.
- Weinhold, A.R. & English, H., 1964. Significance of morphological barriers and osmotic pressure in resistance of mature peach leaves to powdery mildew. Phytopathology 54: 1409-1414.

Williams, E.B. & Kuć, J., 1969. Resistance in *Malus* to *Venturia inaequalis*. A. Rev. Phytopath. 7: 223-246.

Zadoks, J.C., 1961. Yellow rust on wheat, studies on epidemiology and physiologic specialization. Tijdschr. PlZiekt. 67: 69-256.

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