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The effect of light intensity on incomplete resistance of coffee to Hemileia vastatrix

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Abstract

Resistance of coffee to race II of *Hemileia vastatrix* was tested in different environments at light intensities (LI) from 17 to 100% of total outdoor radiation. Nine treatments, in which three levels of LI before inoculation were combined with three levels of LI after inoculation, were applied to seedlings of the susceptible cv. Mundo Novo. Higher LI before inoculation induced a significant increase in lesion density, whereas the opposite was observed for treatments after inoculation. Maximum differences in lesion density were threefold. The interaction between pre- and post-inoculation treatments was also significant. Necrosis of lesions occurred under extremely high LI after inoculation.

Genotypes of the Icatu population and of *Coffea canephora* cv. Kouillou, which varied in disease level in the field, were tested in different environments, constant LI being applied before and after inoculation. Most genotypes were more resistant at low LI than at high LI, paralleling the results obtained for the control cv. Mundo Novo. With cv. Kouillou, sporulating lesion density, latency period and reaction type were significantly affected by LI and genotype. The interaction between LI and genotypes was significant for sporulating lesion density and reaction type, mainly because the most resistent genotype was not affected, or affected in opposite direction, by LI.

Environment affected the expression of the resistance gene S_H4. Observations on a segregating F2 population indicated dominant gene action in the greenhouse (low LI) and incomplete dominant to nearly recessive gene action in the nursery (high LI). Incomplete dominance was expressed by heterogeneous to susceptible reaction types of heterozygote plants (S_H4s_H4), under high LI.

Some ecological and breeding aspects of the observed effect of LI on resistance to coffee leaf rust are discussed.

Additional keywords: coffee leaf rust, complete resistance, major gene resistance, temperature, heterogeneous reaction type, components of resistance.

Introduction

The influence of invironment is a common aspect of plant disease (Colhoun, 1973). Knowledge of how environment affects disease is of great importance to the plant breeder, who must choose a suitable environment for resistance screening. It is also essential for a basic understanding of the physiology and ecology of host-pathogen relationships.

Incomplete resistance is generally more affected by environment than complete,

major gene resistance. Polygenically inherited incomplete resistance, even when partially race-specific, could provide a more durable protection to diseases than complete monogenic resistance, but this idea is still being discussed in the literature (e.g. Simons, 1972; Vanderplank, 1975; Parlevliet and Zadoks, 1977). Durable resistance to orange coffee rust or coffee leaf rust *(Hemileia vastatrix* Berk. et Br.) is considered to be of great value for the perennial coffee crop.

Effects of light intensity (LI) on resistance were reported for a number of plant diseases, e.g. yellow rust of wheat and barley (Bever, 1934; Manners, 1950; Stubbs, 1967), late blight of potato (Umaerus, 1970; Schumann and Thurston, 1977) and powdery mildew of oats (Jones, 1975). These reports refer to major gene resistance as well as to 'field resistance' or 'adult plant resistance'.

Little is known about the influence of environment on resistance to coffee leaf rust. According to d'Oliveira (1957), who selected for coffee rust resistance, LI and temperature may affect symptom expression. Monaco et al. (1973) observed inhibition of lesion growth when plants were temporarily exposed to a temperature of 40 °C. Rodrigues (1975) found treatments of 45 °C during 1.5 h to cause predisposition to coffee rust. He mentioned that these treatments resulted in a higher susceptibility of compatible and of some normally incompatible combinations.

The studies reported in the present paper were undertaken following observations in the greenhouse and the field, which indicated an effect of shade on resistance to coffee leaf rust.

Materials and methods

Definitions. Complete resistance is considered here as any form of resistance in which reproduction of the pathogen is completely inhibited. Incomplete resistance allows for at least some reproduction of the pathogen. Major gene resistance is related to one or a few genes each of which has a great effect on resistance. Major gene resistance is not always complete resistance (Parlevliet, 1979).

Location. All experiments were carried out at the experimental station of the Instituto Agronômico at Campinas, S.P., Brazil.

Coffee genotypes. One year old seedlings of *Coffea arabica* cv. Mundo Novo, cv. Catuai and of the F2 population of cross H 7317 (Agaro C 1164-19 × cv. Catuai) were used in experiments 1 to 4. Cv. Mundo Novo and cv. Catuai are genetically related cultivars both susceptible to race II of *H. vastatrix.* The Agaro C 1164-19 plant is homozygous for the S_H4 resistance gene. In experiments 5 and 6 cuttings from field plants of *C. canephora* cv. Kouillou and of Icatu were used. Icatu consists of tetraploid plants of advanced breeding generations of an artificial hybrid between *C. canephora* (2x = 22) and *C. arabica* (4x = 44). Cv. Kouillou is commercially grown under the name of 'Conilon' in the state of Espirito Santo, Brazil. All the 'Kouillou' and Icatu genotypes showed at least some infection in the field.

Rust material. In all experiments isolates of race II of *H. vastatrix,* which has the v5 virulence factor, were used. The isolates were maintained in the greenhouse on susceptible coffee plants and spores were stored in the refrigerator at 52% relative humidity.

Racial purity was regularly controlled by inoculation on the coffee differentials for S_H1, S_H2, S_H3 and S_H4. Before each experiment, the germination percentage of the urediospores in distilled water was determined. Spore batches with less than 10% germination were not used. According to the germination percentage of the spore batch, the urediospore densities applied in the experiments varied from 0.5 to 1.5 mg ml^{-1} (75×10^3 to 225×10^3 spores per ml).

Standard inoculation method. Uniform dilution of the urediospores in distilled water was obtained by shaking and stirring the suspension during 10 min. Inoculations were carried out by spraying the suspension on the abaxial surface of the coffee leaves with a Steula I paint sprayer pressurized by a small pump. The whole leaf surface was uniformly covered with small droplets, at a rate of about 0.3 ml per 10 cm^2 leaf area. The coefficient of variation of the spore deposite as determined on glass slides was 23%. The number of inoculated leaves per plant varied from 3 to 5, for seedlings, and from 8 to 36 for cuttings. After inoculation the plants were placed in a humid dark room at 22 ± 2 °C for 24 tot 48 h.

Inoculation dates. Inoculations of experiments 1 and 2 were done in September, and of experiment 3 in November, 1979. Inoculations of experiments 5 and 6 were made in January and March, 1981.

Light intensity treatments. Different LI were applied by placing the plants in the greenhouse, in the nursery, or in two different screenhouses. In these environments radiation was respectively 17, 66, 24 and 43% of total radiation, as determined with an Epplin radiometer on a bright day, when the total radiation was 2200 $J.cm^{-2}$. Average radiation in Campinas during the summer months is about 1900 tot 2500, and during the winter months 1000 to 1500 J. cm^{-2}. Shade was provided by chalk on the window panes of the greenhouse, by wooden lating in the nursery, and by black nylon 'Sombrite' net of different mesh sizes in the screenhouses. Differences in air temperature between the four environments did not exceed 2 °C.

LI treatments started 1.5 month before inoculation (exps 3,5 and 6) or after inoculation (exps 2 and 3) and were prolonged till the end of the observation period (45 to 60 days after inoculation).

Observations. To determine the components of resistance, observations were made every two or three days after appearance of the first symptoms. Lesion density (LD = number of lesions per leaf area unit) was determined at the onset of sporulation and sporulating lesion density (SLD = number of sporulating lesions per leaf area unit) at the moment that no further increase in the number of sporulating lesions occurred. Latency period (LP) is the time in days from inoculation till 50% of all finally sporulating lesions have come to sporulation. The reaction type (RT) was scored, between 50 and 60 days after inoculation, using a 0 to 9 scale (Eskes and Toma-Braghini, 1981). Scale value 0 indicates absence of visible symptoms, values 1 to 3 variation within resistant reaction types, values 4 to 7 heterogeneous reaction types with increasing sporulation intensity and % of sporulating lesions, and values 8 and 9 indicate highly susceptible reaction types, with some variation in sporulation intensity. RT scores were applied to individual leaves or to a whole plant or genotype. Natural infection in

the field was assessed by means of a 1 to 5 scale adapted from Costa and Ribeiro (1975). Value 1 indicates absence of sporulating lesions, values 2 to 5 increasing incidence of sporulating lesions, associated with an increase in reaction type. These observations were made annually for Icatu plants and every 6 months for 'Kouillou' plants. Data on field infection are means of these observations over the period 1976 to 1981.

Results

In the first three experiments the effect of LI on the susceptible coffee cultivars Mundo Novo and Catuai was investigated. Experiment 1 showed that different LI, applied during some hours immediately before inoculation, did not significantly affect the lesion density and latency period of seedlings of cv. Mundo Novo in the greenhouse (Table 1).

Table 1. Lesion density (LD = number of lesion per leaf) and latency period (LP, in days) of *C. arabica* cv. Mundo Novo seedlings, grown in the greenhouse, treated at different light intensities immediately before inoculation.

Treatment before inoculation	LD	LP
Darkness for 6 h	17.2	38
Shade of the greenhouse	10.4	37
Full sunlight for 1 h	8.9	37
Full sunlight for 6 h	9.2	38

Tabel 1. Lesiedichtheid (LD = aantal lesies per blad) en latentieperiode (LP, in dagen) van zaailingen van het C. arabica ras Mundo Novo, opgegroeid in de kas, geplaatst bij verschillende lichtintensiteiten vlak voor inoculatie.

In experiment 2, different levels of LI after inoculation were applied to cv. Catuai. The number of lesions per leaf and the percentage of necrotic lesions were affected significantly, but not so the latency period (Table 2). At 100% LI most lesions became

Table 2. Infection of seedlings of *C. arabica* cv. Catuai placed after inoculation, at different light intensities, expressed as % of total radiation. Different letters indicate significant differences according to the Scheffé test at P = 0.05.

Parameters of infection	Light intensity (%)		
	24	43	100
Number of lesions per leaf	36 a	22 a	13 b
Percentage of necrotic lesions	30 a	28 a	94 b
Latency period	43 a	48 a	41 a

Tabel 2. Infectie van zaailingen van het C. arabica ras Catuai geplaatst, na inoculatie, bij verschillende lichtintensiteiten, uitgedrukt als % van de totale instraling. Verschillende letters duiden significantie van verschillen aan voor iedere parameter, getoetst volgens de Scheffé test bij P = 0.05.

necrotic before sporulation began. Only those lesions that were not directly exposed to sunlight came to normal sporulation. Therefore, the 100% LI treatment after inoculation was replaced by the 66% LI treatment in following experiments.

Table 3. Lesion density (LD = number of lesions per leaf) and latency period (LP, in days) of *C. arabica* cv. Mundo Novo seedlings placed at three different light intensities (LI = percentage of total radiation) before and after inoculation.

LI before inoculation	LD				LP			
	LI after inoculation				LI after inoculation			
	24	43	66	mean	24	43	66	mean
24	16	19	15	17	36	36	39	37
43	32	21	11	21	35	36	39	37
100	49	37	20	35	31	34	38	34
Mean	33	26	15	25	34	35	39	36

Analysis of variance:

	LD				LP			
Source	DF	MS	F	P≤	DF	MS	F	P≤
LI before inoculation	2	12033	38.6	0.001	2	296.2	17.6	0.001
LI after inoculation	2	8741	28.0	0.001	2	595.5	35.5	0.001
Interaction	4	2011	6.5	0.001	4	42.9	2.6	0.05
Residual	357	312			341	16.8		
Total	365				349			

Tabel 3. Lesiedichtheid (LD = aantal lesies per blad) en latentieperiode (LP, in dagen) van zaailingen van het C. arabica ras Mundo Novo geplaatst bij drie verschillende lichtintensiteiten (LI) vóór en ná inoculatie.

The effects of LI before as well as after inoculation were studied together in experiment 3 for cv. Mundo Novo. LI treatments were initiated 1.5 month before inoculation. The results (Table 3) showed significant but opposite effects of LI before and after inoculation on lesion density and latency period. Also, the interaction between treatments was significant. In general latency period was not greatly affected and the differences could partly be explained by the observed negative correlation with lesion density (see Table 3). In this experiment, three leaves of each seedling were inoculated. The youngest leaf was formed during the pre-inoculation treatments. For this leaf, the greatest difference in lesion density between the treatments was about a tenfold, which was much more than for the other two leaves, where these differences were about a fivefold (second leaf) and a twofold (third leaf). This may be explained by shading of the lower leaves by the higher ones. The necrosis of lesions seen in experiment 2 was hardly noticed in experiment 3.

In experiment 4, seedlings of an F2 population, segregating for resistance gene S_H4,

Table 4. Segregation for resistance to race II (v5) of *H. vastatrix* among F2 seedlings derived from *C. arabica* cross H 7317 ($S_H4S_H4 \times s_Hs_H4$) in nursery and greenhouse environments. Resistance groups are indicated by: S (susceptible, sporulating lesions only), MR (moderately resistant, a mixture of resistant type lesions and sporulating lesions), and R (resistant, no sporulating lesions).

Environment	Light intensity (% of total radiation)	Inoculation date	Observation period (number of days after inoculation)	Number of seedlings observed	Frequency of seedlings (%)		
					S	MR	R
Nursery	66	8-2-79	50	197	28.4	33.5	38.1
		8-2-79	80	192	57.8	14.6	27.6
		2-5-79	64	409	26.2	36.2	37.7
Greenhouse	17	25-4-79	60	250	26.6	0	73.4

Tabel 4. Uitsplitsing voor resistentie tegen fysio II (v5) van H. vaststrix bij F2 zaailingen van C. arabica kruising H 7317 ($S_H4S_H4 \times s_Hs_H4$) in de kwekerij en in de kas. Resistentiegroepen zijn aangeduid met: S (vatbare planten met alleen sporulerende lesies), MR (matig resistente planten met zowel lesies van het resistente type als sporulerende lesies) en R (resistente planten zonder sporulerende lesies).

Table 5. Lesion density (LD = number of lesions per leaf) and reaction type (RT) of cuttings of eight coffee genotypes with varying disease scores in the field placed at three different light intensities (LI, in percentage of total radiation). Each figure is based on one or two cuttings, with 10 to 36 inoculated leaves each.

Genotype	Disease score in the field (1-5 scale)	LD			RT		
		LI before/after inoculation			LI before/after inoculation		
		24/24	43/43	100/66	24/24	43/43	100/66
C. canephora cv. Kouillou:							
C 69-14	2.1	4	8	26	5.0	6.5	8.0
C 67- 5	3.5	11	9	53	6.5	7.5	7.5
Icatu:							
H 3851- 2-437	2.0	10	28	33	3.0	4.0	5.0
H 3849- 9- 27	3.4	4	31	52	4.0	6.0	7.0
H 4782-13- 72	4.2	56	44	108	8.5	8.0	8.0
H 3851- 2-513	5.0	112	152	135	8.0	9.0	9.0
C. arabica cv. Mundo Novo	4.4	38	68	77	8.0	8.0	9.0
H 7317 (S_H4s_H4)	–	10	–	73	1.0	–	6.0

Tabel 5. Lesiedichtheid (LD, in aantallen per blad) en reactietype (RT) van stekken van acht koffiegenotypen, met een variërende ziektescore in het veld, geplaatst bij drie verschillende lichtintensiteiten (LI, in percentage van de totale instraling). Ieder getal is gebaseerd op 1 of 2 stekken. Per stek werden 10 tot 36 bladeren geïnoculeerd.

were inoculated in the nursery and in the greenhouse. In the greenhouse the expected 1S : 3R ratio was obtained (Table 4). However, in the nursery no clear distinction of the plants into S and R could me made. Many plants had an intermediate reaction type (MR), characterized by a mixture of sporulating and non-sporulating lesions. At 80 days after inoculation more plants were classified as S than at 50 days after inoculation. At both observation dates all plants of the susceptible parent cv. Catuai (s_H4s_H4) were of the S type and all plants of the resistant parent Agaro (S_H4S_H4) were of the R type. For this reason, and because of the observed segregation ratio, it was concluded that the plants heterozygous for S_H4 were incompletely resistant in the nursery and completely resistant in the greenhouse. The difference between the two environments was probably due to differences in LI because air temperatures were very similar in both environments. This conclusion was further confirmed by results of the inoculation of two cuttings of the F1 plant of the Agaro × cv. Catuai cross, which was heterozygous for S_H4, at high and low LI (Table 5). A heterogeneous reaction type was observed under high LI and a completely resistant reaction type under low LI.

Table 6. Sporulating lesion density (SLD = number of sporulating lesions per 15 cm² leaf surface), latency period (LP, in days), mean reaction type (RT), and ranges for RT of seven coffee genotypes observed in the greenhouse (Gre) and nursery (Nur).

Genotype	Disease score in the field (1-5 scale)	SLD		LP		RT(means)		RT (ranges)	
		Gre	Nur	Gre	Nur	Gre	Nur	Gre	Nur
C. canephora cv. Kouillou:									
C 67- 7	1.3	16	3	56	52	3.5	3.1	2.1-4.5	2.0-3.4
C 66- 1	1.6	2	19	60	54	2.0	5.2	1.0-4.0	4.0-6.4
C 70-11	1.8	18	34	52	38	5.6	8.4	3.6-7.0	8.3-8.5
C 66- 3	2.2	9	13	52	50	4.7	5.9	3.8-5.4	4.9-7.3
C 68- 4	3.1	23	45	45	39	6.6	9.0	5.3-8.1	8.9-9.0
C 68-15	4.3	35	43	41	37	8.1	9.0	7.9-8.8	8.6-8.9
C. arabica cv. Mundo Novo:	4.4	1	7	44	38	8.3	9.0	8.0-9.0	8.6-9.0
Means		15	23	50	44	5.5	7.1		

Analysis of variance; significance of F (P values ≤):

Source	*SLD*	*LP*	*RT*
Environment	0.001	0.001	0.001
Genotype	0.001	0.001	0.001
Interaction	0.035	0.199	0.001
Coefficient of variation (%)	59	8	11

Tabel 6. Dichtheid van sporulerende lesies (SLD = aantal sporulerende lesies per 15 cm² bladoppervlakte), latentieperiode (LP, in dagen), gemiddeld reactietype (RT) en variatiebreedte voor RT van zeven koffiegenotypen waargenomen in de kas (Gre) en in de kwekerij (Nur).

In experiment 5, two-year-old cuttings of field plants of cv. Kouillou and of Icatu were inoculated under three light regimes. The cuttings were adapted to the environments 1.5 month prior to inoculation. The results show increased susceptibility with increased LI (Table 5). The relative increase was greater for the more resistant plants for the more susceptible ones. No statistical analysis was performed because only one or two cuttings were used per treatment. The differences in disease score of the plants in the field appeared to be well related to the number of lesions per leaf in all three environments, but this relation was less clear for reaction type.

Experiment 6 consisted of inoculations of cuttings from six genotypes of cv. Kouillou and of seedlings of cv. Mundo Novo in the greenhouse and nursery. The cuttings were placed in these environments 6 weeks prior to inoculation. The age of the inoculated leaves varied from a few weeks to a few months. The results (Table 6) indicated a significant environment and genotype effect on SLD, LP and RT. Most genotypes were considerably more susceptible in the nursery environment. Interaction between environment and genotype, significant for SLD and RT, was mainly due to the different response of the C 67-7 genotype of cv. Kouillou. The reaction of this genotype was characterized by flecks and large chlorotic areas, which mostly became necrotic before sporulation started. The residual variance was large for SLD and relatively low for LP and RT, as indicated by the coefficients of variation (CV) of these components (Table 6). However, the CV values for LP and RT may have been underestimated, because more cuttings were used of the genotypes with relatively stable LP and RT (C 68-15 and cv. Mundo Novo) than of the genotypes with a more variable reaction. In this experiment the number of lesions of cv. Mundo Novo was abnormally low in relation to the 'Kouillou' genotypes. A possible explanation for this unexpected result is that the seedlings of cv. Mundo Novo were transplanted 1.5 month prior to inoculation and the cuttings of cv. Kouillou were not.

Discussion

C. arabica cultivars. The susceptibility to coffee leaf rust of the Brazilian cultivars Mundo Novo and Catuai appeared to be significantly affected by LI. Treatments of high LI during 6 weeks before inoculation increased lesion density of cv. Mundo Novo threefold (Table 3) in comparison to low LI treatments. This effect was not found when high LI was applied only a few hours immediately before inoculation (Table 1). Therefore physiological differences which are induced by a more long term adaptation of the plants to the environments may have been involved.

High LI after inoculation had effects opposite to those to high LI before inoculation (Tables 2 and 3). Different treatments with an equal LI before and after inoculation were applied to cv. Mundo Novo in experiments 3, 5 and 6. In experiment 3 no significant differences were observed between these treatments (Table 3), but in experiments 5 and 6 more lesions developed in environments with a higher LI than with a lower LI. This indicates that the pre-inoculation effect was more important than the post-inoculation effect in experiments 5 and 6. The balance resulting from the two opposing effects is expected to vary according to the intensity of the treatments applied.

The S_H4 resistance gene. This resistance gene has been reported to be a dominent gene (Rodrigues et al., 1975). The present results indicate that the action of this gene may

depend on environment. In environments with low LI it was dominant indeed, but at high LI incomplete dominance was observed (Tables 4 and 5). The incomplete dominance was expressed by a heterogeneous reaction type which, as time evolved, became rather a susceptible reaction type.

C. canephora cv. Kouillou and Icatu. The resistance of most genotypes was better expressed in environments with low LI. Genotypes with intermediate levels of resistance appeared to be most affected by environment and also displayed the greatest residual variance (Tables 5 and 6). Only one genotype of cv. Kouillou, with the highest level of incomplete resistance, was not affected by environment, and caused a significant environment × genotype interaction for SLD and RT.

Relation between LI and temperature. The observed effect of LI may be confounded with an effect of temperature. Although the difference in average air temperature between the environments was not greater than 2 °C, the leaf temperatures in environments with a high LI must have been higher than in environments with low LI. Gomez and Jaramillo (1974) observed that the average temperature of sun exposed leaves of coffee was 3 to 5 °C higher than that of shaded leaves. In one case, a difference of 10 °C was observed. As reported by Monaco et al. (1973), lesion growth of *H. vastatrix* was completely inhibited when coffee plants were treated at 40 °C during 4 h on five successive days. Leaf temperatures nearly as high as 40 °C may occur in Campinas, Brazil, during the summer months, when the air temperature frequently reaches 30 to 35 °C. Therefore, the depressive effect of high post-inoculation LI on lesion development (Table 2 and 3) might be explained by the effect of temperature.

High temperature prior to inoculation may induce a higher susceptibility of plants to several rust fungi (Heath, 1979; Vanderplank, 1978). Rodrigues (1975) reported an increased susceptibility of compatible and incompatible coffee/*H. vastatrix* combinations when leaves were exposed to 45 °C during 1.5 h prior to inoculation. Therefore, the increased susceptibility induced by high LI before inoculation (Table 3), may, at least in part, be due to a temperature effect.

Types of resistance involved. The coffee genotypes used in this study had either incomplete resistance, the genetic base of which is unknown (Tables 1, 2, 3, 5, and 6), or major gene resistance provided by S_H4, which is race-specific (Table 4). The incomplete resistance of two plants of Icatu shown in Table 5 (H 3851-2-437 and H 3851-2-513) is known to be race-specific. This resistance was lost by the appearance of a new and more compatible race in the Icatu population in 1978. The other Icatu and 'Kouillou' genotypes were not affected by this race and they did not change their level of disease in the field during the years 1976 to 1981 (personal observations). Therefore, it appears that LI may affect various forms of resistance, which probably depend on different genetic mechanisms.

Ecological considerations. Field resistance of potatoes to late blight (Umaerus, 1970; Schumann and Thurston, 1977) and partial adult plant resistance of oats to powdery mildew (Jones, 1975) are reduced when lower LI are applied. Resistance of wheat to yellow rust also may decrease at lower LI, although Stubbs (1967) classified some differentials as photolabile and others as photostable. With coffee leaf rust the

tendency appears to be opposite: an increase in resistance was observed at lower LI. It could be argued that this discrepancy is caused by the different conditions under which these species normally grow in the wild. Both *C. arabica* and *C. canephora* are forest species, whereas potatoes and, certainly, cereals normally grow in the open. As observed by Sylvain (1955) 'coffee rust is rare under natural forest conditions in Ethiopia, but in cases where the upper story of the forest has been removed, leaf rust and *Cercospora coffeicola* may spread quite rapidly'. This is in agreement with the present results showing that coffee plants at high LI tend to become more susceptible. It seems plausible that resistance of plants to diseases will be optimal under conditions representing the natural environment of the species.

However, it should not be concluded that shading of susceptible *C. arabica* cultivars would help to control coffee rust. The results of Tables 2 and 3 show that pre-and post-inoculation LI treatments had opposite effects, thus suggesting that intermediate levels of LI may be optimal for rust development. These intermediate levels may predominate in the leaf canopy of coffee trees, when medium levels of shade are applied. Shading of coffee plantations will also change other environmental factors, among which relative humidity, and these may favour disease development in stead of controlling it.

Practical implications for the coffee breeder. The observed incomplete dominance of the SH4 resistance gene under nursery conditions may have practical implications for resistance screening and race identification. Coffee differentials heterozygous for S_H4 are available for detection of rust races with complex virulence (Rodrigues, et al., 1975). Care should be taken in using these differentials, because their resistance will not be complete in all environments.

The coffee breeder interested in screening for incomplete resistance may prefer to work under relatively low LI, which make this type of resistance more easily detectable. Similar LI should be applied to all plants in order to decrease the residual error of experiments.

Other environmental factors. In experiments not reported here a seasonal influence on resistance to coffee leaf rust was observed. For example, inoculations of certain Icatu plants were much more successful in summer than in winter. In addition, some races of coffee leaf rust were more difficult to grow during winter than in summer. Seasonal effects may be explained by separate or combined effects of LI, temperature, relative humidity, and leaf age. These factors deserve further investigation.

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Samenvatting

Effect van lichtintensiteit op incomplete resistentie van koffie tegen Hemileia vastatrix

Resistentie van koffie tegen fysio II van *Hemileia vastatrix* werd getoetst in milieus bij lichtintensiteiten (LI), die varieerden van 17 tot 100% van de totale instraling. Negen behandelingen, bestaande uit de combinaties van drie niveaus van LI vóór inoculatie en drie ná inoculatie, werden toegepast op zaailingen van het vatbare *Coffea arabica* ras Mundo Novo. Toenemende LI vóór inoculatie veroorzaakte een significante toename in lesiedichtheid, terwijl het tegenovergestelde werd waargenomen bij de behandeling na inoculatie. Maximale verschillen in lesiedichtheid waren drievoudig. De interactie tussen behandelingen vóór en ná inoculatie was ook significant. Bij extreem hoge LI ná inocultie trad necrose van de lesies op.

Genotypen van de Icatu populatie en van het *C. canephora* ras Kouillou, met verschillende ziektescores in het veld, werden beproefd in verschillende milieus, waarbij een constante LI voor en na inoculatie werd toegepast. De resistentie van de meeste genotypen kwam beter tot uiting bij lage LI dan bij hoge LI, wat ook waargenomen werd voor het controle ras Mundo Novo. Bij het ras Kouillou werden de dichtheid van sporulerende lesies, de latentieperiode en het reactietype significant beïnvloed door LI en genotype. De interactie tussen LI en genotype was ook significant voor dichtheid van sporulerende lesies en voor reactietype, voornamelijk doordat het meest resistente genotype niet, of in de omgekeerde richting, beïnvloed werd door LI.

De expressie van het resistentiegen S_h4 bleek ook afhankelijk van het milieu. Waarnemingen aan een uitsplitsende F2-populatie duidden op een dominante genwerking in de kas (lage LI) en een incompleet dominante, of bijna recessieve, genewerking in de kwekerij (hoge LI). Deze incomplete dominantie uitte zich d.m.v. heterogene tot vatbare reactietypes van heterozygote planten (S_H4s_H4) onder hoge LI.

Enkele ecologische en veredelingstechnische aspecten van de waargenomen invloed van LI worden besproken.

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