Effect of Shade on Arabica Coffee Berry Disease Development: Toward an Agroforestry System to Reduce Disease Impact

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Accepted for publication 9 September 2008.

ABSTRACT

Mouen Bedimo, J. A., Njiayouom, I., Bieysse, D., Ndoumbè Nkeng, M., Cilas, C., and Nottéghem, J. L. 2008. Effect of shade on Arabica coffee berry disease development: Toward an agroforestry system to reduce disease impact. *Phytopathology* 98:1320-1325.

Coffee berry disease (CBD), caused by *Colletotrichum kahawae*, is a major constraint for Arabica coffee cultivation in Africa. The disease is specific to green berries and can lead to 60% harvest losses. In Cameroon, mixed cropping systems of coffee with other crops, such as fruit trees, are very widespread agricultural practices. Fruit trees are commonly planted at random on coffee farms, providing a heterogeneous shading pattern for coffee trees growing underneath. Based on a recent study of CBD, it is known that those plants can reduce disease incidence. To assess the

specific effect of shade, in situ and in vitro disease development was compared between coffee trees shaded artificially by a net and trees located in full sunlight. In the field, assessments confirmed a reduction in CBD on trees grown under shade compared with those grown in full sunlight. Artificial inoculations in the laboratory showed that shade did not have any effect on the intrinsic susceptibility of coffee berries to CBD. Coffee shading mainly acts on environmental parameters in limiting disease incidence. In addition to reducing yield losses, agroforestry system may also be helpful in reducing chemical control of the disease and in diversifying coffee growers' incomes.

Additional keywords: barrier effect, splash dispersal.

Plant disease epidemiology studies in complex plant communities, such as rain forest, are very few, although this topic appears crucial for developing sustainable land-use strategies (23). For example, it is suspected that plant density makes the difference for South American leaf blight (SALB) between natural Amazonian forest, where there is nearly no damage, and monospecific plantations, where the levels of damage are often very high (20); however, this hypothesis was never reinforced by appropriate studies. In the case of cocoa, coffee, or tea plantations, agroforestry systems could also modify pests and disease incidence compared with monospecific plantations, and the effect of shade trees on diseases could have several explanations (5,6,20,41). Annual crop associations are another case of complex plant communities and several studies concerned plant physiology or resource partitioning (15) but, even for these simple cases, few epidemiological studies were carried out.

The Arabica coffee tree is a shade-growing plant in its natural biotope (32). In order to ensure its adequate development in new growing zones, its domestication has often required the establishment of shade plants, such as *Leucaena*, *Albizia*, *Acacia*, or *Erythrina* spp. Shade level depends on tree species and pruning intensity and can vary widely, from 30 to 70%, but cultivation in full sunlight also exists in many regions (25,37). The percentage of shade and the species of the shade tree has an incidence on the intensity of the epidemic of some diseases such as American leaf spot epidemics in Central America, for which the level increases with shade (2). In Africa, this plant of great socioeconomic im-

portance is subject to highly destructive parasite attacks by *Colletotrichum kahawae*, which causes coffee berry disease (CBD) (47). It is a disease specific to green berries and has only been found to date in African production zones (26). It has a high incidence in highland regions (>1,600 m), where it can cause up to ~60% harvest losses (8,31). Mummified berries, twig bark, and dead branches are considered to be primary inoculum sources for the disease (31,35,45). However, it is still not clear how the pathogen survives between two production seasons (28). CBD occurs as dark necrotic, sunken spots, sometimes with orange-colored acervuli. Most infected berries fall prematurely; some remain attached to the branches, thereby forming secondary sources of inoculum capable of causing fresh contamination.

As for all anthracnose diseases, CBD development depends on climatic factors such as rainfall, temperature, and relative humidity (11,17,21,34). Rainfall is the main agent of *Colletotrichum* spp. conidium dispersal (18,28,46). Most conidia of *C. kahawae* can be effectively dispersed by an optimum rainfall of 10 mm but heavy rainfall leads more to their leaching from the coffee tree canopy to the soil (46). Relative humidity close to saturation and optimum temperatures of 20 to 22°C are conducive to their germination and appressorium formation (16,26). *Colletotrichum* spp. conidium germination can occur 24 h after conidia enter into contact with the tissues of the host plant (9,14). There then follows elongation of the germ tubes, whose apical section later differentiates into an appressorium (4,12,24,42). The infection hyphae arising from those appressoria then colonize the contaminated fruit, causing necrosis of the tissues on which new acervuli form.

CBD epidemics are polycyclic and recurrent from one year to the next (28,31,45). They usually coincide with the annual fruiting cycle of the coffee trees, itself highly dependent upon the

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doi:10.1094/PHYTO-98-12-1320

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rainfall pattern of infested regions. For example, in Kenya, where the bimodal rainfall pattern encourages two annual fruiting cycles, CBD epidemics develop in two main annual cycles that overlap. On the other hand, the disease only has one annual development cycle in regions where the coffee trees flower once, as in the highlands of West Cameroon, which has a monomodal rainfall pattern. In these regions, the disease develops over time following three main sequences: (i) a phase of slow progression after the first infected berries appear in the 8th to 10th week after flowering; (ii) a phase of exponential progression between the 10th and 21st week after flowering, corresponding to the period of fruit formation; and (iii) an asymptotic phase at approximately the 22nd week after flowering (i.e., at the beginning of the fruit hardening period) (29).

In Cameroon, on small family coffee farms, shade plants mostly consist of various fruit trees planted randomly among the coffee trees, thereby shading the coffee trees in a fairly heterogeneous way. Such plants can limit the development of coffee leaf rust caused by *Hemileia vastatrix* (3) or CBD (22,30,38). Based on recent epidemiological studies conducted on CBD in Cameroon (30), we put forward two main hypotheses regarding reduced disease incidence under shade plants: either they form a physical barrier to effective dispersal of the pathogen's conidia or they affect the physiology of berries and, consequently, their receptiveness to *C. kahawae*. Consequently, epidemiological monitoring of CBD was undertaken in 2005 in Cameroon on coffee trees shaded by nets to provide defined, consistent shade treatments, and trees exposed to full sunlight. This study was conducted at the same time as artificial inoculations in the laboratory on berries taken from those different coffee trees. The purpose of these experiments was to assess the specific effect of permanent, uniform shading on CBD development in zones with very strong infection pressure. They were also to determine the impact of this coffee-growing method on the intrinsic susceptibility of berries to the disease over time.

MATERIALS AND METHODS

Epidemiological monitoring in the field. Planting material. The field experiments were conducted in a smallholding in Bafou (05°33.540N, 10°04.520E, 1,820 m above sea level), located in the highlands of West Cameroon. Thirty-four coffee trees were identified inside the plantation planted with CBD-susceptible cultivars (cv. Jamaica). In order to control shading conditions so that all the coffee trees studied in the field were placed under the same expanse and density of shade, permanent artificial shade was provided by black shade netting with a regular mesh allowing 50% of the light to filter through (Tildennet EC 50%, Tilden Industries, U.K.). Half of the coffee trees were placed individually under shade netting, each paired with immediately adjacent trees in full sunlight. Epidemiological monitoring in the field was carried out using three plagiotropic branches with at least five glomerules were marked on each of the coffee trees (i.e., one branch in the upper storey, one in the middle storey, and one in the lower storey).

Weekly observations were carried out on the marked branches from the 6th to 24th week after flowering (from 27 April to 25 August 2005) (i.e., 19, observations in all). They consisted of counting (i) the total number of berries (Btot), (ii) the number of new diseased berries and their marking with small labels (Bdis), and (iii) old diseased berries (already marked) (Bmark).

For each coffee tree in the study, the different harvest losses were estimated by three methods.

(i) The percentage of total losses (Ltot) expressed all the losses due to CBD or not, recorded over a year. It was calculated by the formula $L_{tot} = [B_{tot1} - (B_{tot_n} - B_{mark_n} - B_{dis_n}) / B_{tot1}] \times 100$, where B_{tot1} indicates the total number of berries on the first inspection and the expression $(B_{tot_n} - B_{mark_n} - B_{dis_n})$ the num-

ber of healthy berries in the last week of observations. The terms B_{tot_n} , B_{mark_n} , and B_{dis_n} represent the total number of berries, the total number of marked diseased berries and the total number of newly infected berries on the final inspection.

(ii) The percentage of diseased berries (Pdis) was the ratio between the sum of newly diseased berries counted over all the weeks of observations (ΣB_{dis1-n}) and the initial number of berries (B_{tot1}): $P_{dis} = (\Sigma B_{dis1-n} / B_{tot1}) \times 100$.

(iii) The percentage of losses not due to CBD (Pfall) was expressed by the difference between total losses and losses due to CBD ($P_{loss} - P_{dis}$). These losses were called "physiological fall" because they were mainly due to the falling of apparently healthy berries.

Experimental design and observations. This study was conducted in a split-plot (two-way) factorial experimental design which comprised 16 replicates. The main factor was shade (full sun or 50% shade) and the secondary factor was the different storeys in the coffee trees (upper, intermediate, and lower storey). Each coffee tree amounted to one replicate.

Artificial inoculations in the laboratory. Plant material. Green coffee berries were sampled from the shade and in full-sunlight treatments, using trees that had been especially reserved for green berry sampling, for artificial inoculations in the laboratory. The samples were taken from three storeys of the coffee trees (upper, middle, and lower) in the 12th, 16th, 18th, and 22nd weeks after flowering. On each sampling operation, 125 berries were taken per storey (i.e., 375 berries per tree). Susceptible and tolerant controls were introduced to check inoculation validity. Berries were taken from the field-tolerant cv. Java and the highly susceptible cv. Caturra. The samples were taken from plants grown in full sunlight in the varietal collection at IRAD's Santa station in Northwest Cameroon.

The berries taken from each storey of the four coffee trees in the study were divided between five petri dishes lined with blotting paper imbibed with sterile distilled water at a rate of 25 berries per dish (i.e., five replicates of 25 berries per storey).

Plant pathogen and inoculation technique. The isolate of *C. kahawae* was obtained from infected berries of a coffee tree in the Bafou plot. It was purified by monoconidial culturing in a petri dish on potato-dextrose-agar (PDA) medium. The isolate arising from the culture displayed relatively slow radial growth and a woolly, dark-gray mycelium after 10 days of storage at 22°C with a 12-h photoperiod. Its pathogenicity was tested beforehand on detached berries before its routine use in actual artificial inoculations. The inoculum consisted of a filtrate of the conidial suspension obtained by scraping pure cultures of the isolate imbibed with sterile distilled water. It was calibrated at 10^6 conidia/ml prior to inoculation. A 10- μ l droplet was then deposited on each of the berries using a micropipette. After inoculation, the berries were incubated in a climatic chamber (phytotron) regulated to a temperature of 21°C with a 12-h photoperiod.

Experimental design and observations. Three main factors were studied during this experiment: (i) origin of the artificially inoculated berries (shaded coffee tree, coffee tree in full sunlight, Java coffee tree [tolerant control], and Caturra coffee tree [susceptible control]); (ii) coffee tree storey (upper, middle, and lower); and (iii) berry age at the time of artificial inoculation.

Observations began 24 h after inoculation and continued for 10 successive days. The 10-day observation period limited the risk of confusing CBD symptoms with infections by opportunistic fungi such as *Pestalotia* spp. Thus, daily observations consisted in counting the total number of diseased berries in each petri dish.

Evaluation of berry susceptibility in vitro. The data gathered enabled us to calculate the berry infection rate (R_{inf}) and the index of infection precocity (Ind_p) per petri dish. The infection rate corresponded to the percentage of successful inoculations on the tenth day of observations. It was obtained by formula $R_{inf} =$

$(Bdis_{10} \times 100)/N$, where $Bdis_{10}$ was the total number of diseased berries counted in the petri dish on the 10th day of observations and N was the total number of inoculated berries ($N = 25$).

The infection precocity index was an estimation of the speed with which symptoms occurred after inoculation. It was calculated from the following formula, based on that used by (40), to calculate the production precocity index for mango: $Ind_p = (6X_5 + 5X_6 + 4X_7 + 3X_8 + 2X_9 + X_{10})/6(\Sigma Nmal)$.

The variables X_5 , X_6 , X_7 , X_8 , X_9 , and X_{10} represented the number of new berries displaying symptoms on the 5th, 6th, 7th, 8th, 9th, and 10th day after inoculation, respectively, because the first symptoms on the most susceptible berries occurred on the fifth day of observations. The coefficients 6, 5, 4, 3, 2, and 1, which corresponded to an arithmetic progression of reason -1 (minus one), were attributed in that order to each variable X_{i+1} , in order to give greater weight to berries attacked early. The term $\Sigma Ndis$ was the sum of new diseased berries counted between the 5th and 10th day of observations. In reality, that term was equivalent to variable $Bdis_{10}$ used to calculate the infection rate. The infection precocity index (Ind_p) was 1 (one) if all the infected berries were counted on the fifth day of observations. It was 0.16667, a 6th, if all the inoculated berries did not display symptoms until the 10th day of observations.

Statistical analyses. In order to comply with conditions for applying an analysis of variance, all the data expressed as percentages, after analysis of the residuals, were arcsin $\sqrt{x}$ transformed. The analysis of variance was performed with the general linear model (GLM) procedure of the Statistical Analysis System (SAS) software (version 9.1). Means between the factors studied were studied by the Student-Newman-Keuls test at 5%.

RESULTS

Characterization of harvest losses. Losses due to CBD varied very significantly ($P < 0.0001$) depending on coffee tree shading. Likewise, those losses differed significantly ($P = 0.0499$) depending on the storeys, whatever the coffee tree shading. On the other hand, no significant difference was found between the factors studied for losses due to physiological fall (Table 1). The infection rate for coffee trees under artificial shade, estimated at 30% of diseased berries, was well below that for the coffee trees without shade, which had $\approx 50\%$ of diseased berries (Table 2). In addition, berries from the lower branches of the coffee trees were significantly less attacked than those from the middle and upper branches, which were part of the same uniform group of means (Table 2).

The first diseased berries were seen in the ninth week after flowering, whatever the coffee tree shading (Fig. 1). Then, the new infection rate progressed in the same way in shade and sunlight up to the 11th week, when $\approx 3\%$ of new infections were recorded on all the coffee trees. Between the 12th and 16th week after flowering, the weekly rate of newly infected berries on coffee trees in full sunlight was clearly greater than for the trees under the shade netting. The disease peak was reached in the 14th week, with $\approx 11\%$ of new diseased berries found on the coffee trees exposed to full sunlight. That disease rate corresponded to double that recorded on shaded coffee trees. All the coffee trees displayed the same new infection rate between the 17th and 24th

week, whatever the shade. New infections decreased considerably (under 1%) from the 20th week after flowering onward.

Disease development on berries inoculated artificially in the laboratory. The analysis of variance results (Table 3) show that all the main factors studied (coffee tree cultivars, branch storey, and berry age) had a highly significant effect ($P < 0.0001$) on the infection rate and on the disease precocity index. The same applied for the different interactions between those factors. However, the effect of the main factors remained highly preponderant, given the large values of the F test, which were sometimes more than 10 times those of the interactions. According to the Student-Newman-Keuls test, the disease was significantly more severe and occurred earlier on berries of the Caturra coffee tree (susceptible control) than on berries of the other coffee trees. The lowest infection rate (41.7%) and precocity index (0.36) were found for berries from the Java coffee tree (tolerant control). Berries from coffee trees under artificial shade displayed an intermediate disease level and precocity index which were statistically equivalent to those of berries from trees exposed to sunlight. This means separation test also brought out rising severity and precocity gradients for the disease depending on the coffee tree storeys.

TABLE 2. Comparison of harvest loss means depending on coffee tree shading and the position of their branches (field monitoring)

Parameters studied ^z	Losses caused by coffee berry disease (%)	Physiological fall (%)
Lighting		
Trees under shade netting	29.56 b	32.56 a
Trees in full sunlight	49.89 a	35.37 a
Position		
Upper branches	44.22 a	34.51 a
Middle branches	42.34 a	36.80 a
Lower branches	32.61 b	30.59 a

^z Coffee tree lighting and position of coffee tree branches.

Fig. 1. Appearance of new diseased berries over time depending on coffee tree shading (in 2005).

TABLE 1. Analysis of variance for losses caused by coffee berry disease (CBD) and those due to physiological fall (field monitoring)

Source of variation	df	Losses caused by CBD		Physiological fall	
		F test	P > F	F test	P > F
Coffee tree lighting	1	17.31	<0.0001	0.25	0.6183
Position of branches	2	3.10	0.0499	0.46	0.6327
Lighting $\times$ position	2	1.45	0.2402	0.77	0.4674
Error	90	...	...	...	...

However, berry susceptibility varied greatly over time, with the lowest infection rate and precocity index being observed in the 22nd week after flowering (Table 4).

During the first three series of artificial inoculations (Fig. 2), berries from coffee trees exposed to sunlight displayed the same infection rates as those from shaded coffee trees. However, in the 22nd week after flowering, berries from coffee trees exposed to sunlight proved to be more susceptible to CBD than those from shaded coffee trees. Berries from the CBD-susceptible control (Caturra) were more attacked than those from all the other coffee trees in the 16th and 22nd week. They displayed the same infection rate as berries from trees under shade and in full sunlight in the 12th and 18th week after flowering. The lowest infection rates were always found on berries from the disease-tolerant control (Java), regardless of the series of artificial inoculations considered. Yet the berries of that control, and those of shaded coffee trees, had the same infection rate after inoculation in the 22nd week after flowering (Fig. 2). Regardless of their age, berries taken from coffee trees in full sunlight displayed varying susceptibility to the disease following a rising gradient depending on the position of the branches in the coffee tree (Fig. 3B). That susceptibility gradient was also seen for berries from shaded coffee trees, except for those of the 12th week taken from upper and middle branches, which had the same degree of susceptibility to the disease (Fig. 3A). All the berries from upper branches of unshaded coffee trees were attacked after artificial inoculation in the 12th week after flowering.

DISCUSSION

Artificial shade placed over the coffee trees considerably reduced CBD development. Epidemiological monitoring showed that coffee trees in full sunlight were more severely attacked than coffee trees covered with shade netting. On the other hand, artificial inoculations of detached berries showed that, under our experimental conditions, the intrinsic susceptibility of berries to the disease was not significantly different between shaded and unshaded coffee trees (Fig. 2). The shade effect can work in various manners (41): shade reduces sunlight and particularly UV-B, which plays an important role on some plant diseases such as blister blight of tea (19); shade modifies the microenvironmental conditions (reduced temperature, reduced temperature fluctuations, reduced air movements, and increased humidity) and creates a “phylloclimate” able to perturb interactions between pathogens and target organs (10); and shade can also work as a barrier and can limit the splash dispersal of the pathogen (33). With our results, we conclude that the preponderant influence of shade netting is on the epidemic parameters in the *C. kahawae*–*Coffea arabica* pathosystem, which tallies with the “barrier effect” hypothesis whereby shade plants limit CBD dispersal (30, 38). In fact, in our study, shade did not induce any change in the intrinsic susceptibility of berries to CBD by artificial inoculations of detached berries. Actually, shade could limit the rain intensity and, consequently, the splash dispersal of *Colletotrichum kahawae*, as has been already mentioned in other studies for several pathogens and, particularly, *Colletotrichum* spp. (13,33,34,48,49).

In the field or in the laboratory, berry susceptibility over time varied in the same way regardless of shade treatment (Figs. 1 and 2). Other studies suggest that berry ripening may occur faster in coffee trees exposed to full sunlight than in shaded trees (44) but the effect of shading on berry development did not appear to affect their receptiveness to *C. kahawae* susceptibility. Furthermore, the peak of the CBD epidemic in the field (14th week after flowering) did not coincide with the maximum berry susceptibility period (18th week after flowering). The peak in new CBD infections appeared to coincide with the period of maximum inoculum pressure and suitable climatic conditions. In the case of polycyclic epidemics such as CBD, the inoculum pressure in plantations increases in line with the appearance of new receptive organs, especially when the fruiting and pathogen dispersal parameters are optimum (39,50). Thus, inoculum pressure re-

TABLE 4. Means for the infection level and precocity index per type of coffee tree, by storey and by berry age (artificial inoculations)

Parameters studied	Infection rate (%)	Infection precocity
Type of coffee trees		
Cv. Caturra (control)	75.800 a	0.588 a
Cv. Jamaica under shade	59.923 b	0.471 b
Cv. Jamaica in sunlight	58.305 b	0.470 b
Cv. Java (témoin)	41.695 c	0.358 c
Position of coffee tree branches		
Upper branches	74.880 a	0.517 a
Middle branches	59.117 b	0.467 b
Lower branches	43.538 c	0.434 c
Berry age		
12th week	59.649 b	0.463 c
16th week	67.579 b	0.473 b
18th week	74.596 a	0.560 a
22nd week	34.915 c	0.395 d

Fig. 2. Berry infection rate, depending on the coffee trees, on different artificial inoculation dates.

TABLE 3. Analysis of variance for the infection level and disease precocity index (artificial inoculations)^z

Source of variation	df	Infection rate		Infection precocity	
		F test	P > F	F test	P > F
Type of coffee trees	3	109.74	<0.0001	123.64	<0.0001
Coffee tree storey	2	218.90	<0.0001	35.31	<0.0001
Berry age	3	162.00	<0.0001	65.29	<0.0001
Trees × storey	6	10.41	<0.0001	8.61	<0.0001
Trees × berry age	9	11.96	<0.0001	22.82	<0.0001
Storey × berry age	6	2.17	0.479	6.38	<0.0001

^z Coefficient of variation = 13.79 and 13.86% for infection rate and precocity, respectively.

mains highly dependent upon climatic factors, such as the temperature, relative humidity and rainfall (1,27,36,43).

Field observations revealed that there was a rising gradient of disease severity regardless of coffee tree shading. That gradient appeared to be due to more efficient *C. kahawae* conidium dispersal on berries in the canopy compared with those in the lower storeys (30). The same type of gradient was found for intrinsic berry susceptibility, following the artificial inoculations carried out in vitro. This result confirmed disease distribution on a coffee tree scale, as revealed by observations in the field. However, it also indicated that berries on the upper branches are apparently naturally more receptive to *C. kahawae* aggression than on the lower branches. For other fruit diseases, often there also are differences between trunk and canopy in term of severity but it is more common that the fruit on the canopy are less attacked than the fruit on the trunk or on the lower storeys, such as for *Phytophthora* disease on cacao (7), because of the microclimate being dryer on the canopy.

This study confirmed that shade plants grown with coffee trees could considerably reduce losses due to CBD. They probably act as a physical barrier to efficient pathogen dispersal on coffee trees. However, shade plants do not appear to have any effect on the intrinsic susceptibility of berries to CBD. Reducing losses caused by the disease through the use of shade plants is an original prospect for reducing CBD impact, because the incidence of fungal diseases is often greater under shade (2). However, it would be worth confirming our results under other agroecological conditions where CBD thrives. Interactions with interplanted perennial plants should also be studied, in terms of both agroecological relations and health (23), in order to optimize agro-

forestry systems (choice of species and planting designs). This study suggests that an agroforestry system could be established to assess how such a system might reduce CBD incidence in areas where the disease has a strong impact.

ACKNOWLEDGMENTS

This study was funded by the European Union (Inco-Dev/CBD-Resist project). We thank J. P. Deumeni and the observation teams at the IRAD stations at Santa and Foubot (Cameroon) for data gathering and P. F. Mouen Bedimo for data entry and verification.

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Fig. 3. Berry infection rate, depending on the storeys, on different artificial inoculation dates for **A**, trees under shade and **B**, trees in full sunlight.

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