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Shade is conducive to coffee rust as compared to full sun exposure under standardized fruit load conditions

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ABSTRACT

Shade effects on coffee rust are controversial, possibly because shade helps to prevent high fruit loads, which decreases leaf receptivity to the pathogen but, at the same time, might provide a better microclimate for germination and colonization. These two probable antagonistic pathways are combined under natural conditions. In order to clarify their individual effects, we dissociated the two factors by manually homogenising fruit loads under two light exposure situations, under shade and in full sunlight. The trial was set up in Turrialba, Costa Rica at 600 m of elevation, in a coffee plot initially under shade provided by the tree legume *Erythrina poeppigiana*. The plot was subdivided into two subplots: one was maintained under shade, whereas shade was eliminated in the second subplot. In each subplot, we removed fruiting nodes from 40 coffee plants in order to obtain the following four levels: none, 150, 250, and 500 fruiting nodes per coffee plant. Coffee rust incidence and severity, along with plant growth and defoliation, were assessed on these coffee plants over a period of two years. Air and leaf temperatures, leaf wetness and relative humidity were also monitored. As expected, the intensity of the coffee rust epidemic increased in line with fruit load. We quantified a 28.9% increase in coffee rust incidence and a 129.2% increase in severity on plants with 500 fruiting nodes as compared to plants with no fruits. With the homogenised fruit load, the intensity of the coffee rust epidemic was greater in the shaded subplot, with a 21.5% increase in incidence and a 22.4% increase in severity. Two mechanisms were suggested. Firstly, we highlighted a dilution effect due to host growth which was 25.2% and 37.5% greater in full sunlight when considering new leaves or new leaf area respectively. Secondly, the microclimate was more conducive to coffee rust under shade, with lower intra-day temperature variations, due to lower maxima, and a higher leaf wetness frequency. We concluded that shade has antagonistic effects on coffee rust. Coffee rust is reduced by shade because shade reduces the fruit load. However, with an equivalent number of fruiting nodes, coffee rust incidence and, to a lesser extent, severity were greater under shade. The service provided by shade in controlling coffee rust is necessarily associated with a disservice that consists in reducing yield in the short term.

1. Introduction

Shade trees provide multiple services in coffee agroforestry systems and can help to naturally reduce several coffee pests and diseases via different pathways (Beer et al., 1998; Schroth et al., 2000; Staver et al., 2001; Ratnadass et al., 2011). Coffee-based agroforestry systems have a higher level of biodiversity compared to plantations in full sunlight. Shade trees, which can be very diverse and abundant in certain rustic agroforestry systems (Moguel and Toledo, 1999; Soto-Pinto et al., 2001), provide habitats for a large number of species. Some of these are directly involved in pest and disease biocontrol. Such is the case with birds (Moguel and Toledo, 1999) and ants (Philpott and Armbrecht, 2006) which are able to prey on the coffee berry borer (*Hypothenemus hampei*) (Armbrecht and Gallego, 2007; Kellermann et al., 2008). In addition, shade can help to control pests and diseases by modifying microclimate conditions. It has been suggested that shade trees reduce coffee berry disease (*Colletotrichum kahawae*) incidence by intercepting rainfall and reducing the intensity of raindrop impacts on coffee trees, thereby limiting the splash dispersal of propagules (Mouen Bedimo et al., 2008). Coffee blight (*Phoma costarricencis*)

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can be reduced by establishing windbreaks and shade trees (Muller et al., 2004). Trees intercept winds, particularly cold winds, and protect coffee leaves from mechanical injuries enabling the pathogen to penetrate. Shade also lessens coffee brown eye spot disease (*Cercospora coffeicola*) (Echandi, 1969; Staver et al., 2001). According to Echandi (1969), *C. coffeicola* has a high temperature requirement for germination (30 °C) and plant tissue colonization is favoured when soil moisture is low. These two conditions are frequently encountered at full sun exposure and can be corrected by intercropping coffee with shade trees. Microclimate modifications due to shade may also indirectly affect pests and diseases through host physiology changes. The over-bearing disease (*Colletotrichum* spp), which affects over-producing plants and causes branch die-back, can be almost completely eliminated by preventing high yields from occurring (Muller et al., 2004) with appropriate shade (Cannell, 1985; DaMatta, 2004). Shaded conditions also seem to favour the development of beneficial fungi, such as *Beauveria bassiana* and *Lecanicillium lecanii*, two biocontrol agents of *H. hampei* and *Hemileia vastatrix* respectively (Staver et al., 2001).

However, shade may provide better conditions for other coffee pests and diseases. For instance, shade is known to be conducive to *Mycena citricolor*, the causal agent of American leaf spot disease, (Avelino et al., 2007), to *Corticium koleroga*, responsible for white thread blight, and to *C. salmonicolor* (now *Erythricium salmonicolor*), the causal agent of pink disease (Schroth et al., 2000). The reason is probably because shading leads to greater wetness. Likewise, coffee berry borer seems to benefit from shade (Bosselmann et al., 2009), particularly dense shade (Feliz Matos et al., 2004), possibly in relation with higher relative humidity, which increases insect longevity and fecundity (Baker et al., 1994). Some shade trees may also be alternative hosts for several pests and diseases. The pathogens *C. salmonicolor*, *C. koleroga* and *Rosellinia* spp. affect a great number of plant species. Some of them are forestry species that might be used as shade trees in rustic systems (Benchimol et al., 2001; Roux and Coetzee, 2005). Similarly, *M. citricolor* is able to attack at least 150 plant species belonging to 45 families, including tree legumes of the genus *Inga* (Sequeira, 1958) which are commonly used as shade trees in Mesoamerica. Despite being considered specific to coffee, coffee berry borer is able to find refuge and reproduce in other fruits (Damon, 2000; Gumier-Costa, 2009).

Shade effects on coffee pests and diseases are usually not so clear, as shade may be propitious to a given process in the life cycle of a noxious organism and hamper another process at the same time. The balance of these antagonistic effects is variable and often controversial, as in the case of coffee rust. A high shade percentage may reduce coffee rust attacks by regulating yields, which could partly explain the results obtained by Soto-Pinto et al. in Mexico (2002). For reasons not well understood, epidemics are more intense when fruit load is high (Zambolim et al., 1992; Silva-Acuña, 1994; de Carvalho et al., 1996, 2001; Avelino et al., 2004, 2006; Costa et al., 2006). This condition is often reached with full sun exposure. As a consequence, a high degree of shade may negatively affect the development of this disease through the effects of shade on fruit load (Avelino et al., 2004, 2006). However, shade also buffers temperatures, intercepts light and probably increases moisture in the plantation. These effects are all conducive to the infection process (Avelino et al., 2004), which may explain the opposite results observed in Central America (Staver et al., 2001; Avelino et al., 2006).

These two pathways are combined under natural conditions. As a consequence, their individual effects cannot usually be studied separately. In our study, we dissociated the two factors by manually homogenising fruit loads in two light exposure situations, under shade and in full sunlight. This research, which has apparently never been undertaken before, will help to clarify the effects of shade on coffee rust.

2. Materials and methods

2.1. Climatic characteristics of the study location

A field experiment was carried out in 2008 and 2009 at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) experimental station (Turrialba, Costa Rica; 9°53′ N, 83°38′ W). This location has climatic characteristics conducive to coffee rust development. Rainfall is abundant, 2700 mm 69-year average annual rainfall; 3029 mm and 2835 mm in 2008 and 2009 respectively. Rainfall is also almost evenly distributed throughout the year due to a strong Caribbean influence. However, rainfall usually decreases between February and April, with 365 mm of rainfall on average over those three months. In 2008, the minimum monthly rainfall was reached in March with 43 mm. In 2009, the minimum was recorded in April with 39 mm. The CATIE experimental station is located 600 m above sea level, close to the lowest altitude at which coffee is cultivated in Costa Rica. The mean annual temperature is 22 °C (53-year average) with very little variation. The monthly averages varied from 20 to 23 °C in 2008, and from 21 to 23 °C in 2009.

2.2. Coffee plot characteristics and shade management

We used a uniform flat coffee plot measuring 1800 m^2, previously managed under shade. The shade was provided by a tree legume (*Erythrina poeppigiana*) planted at a density of 417 trees ha^{-1}. The coffee plot was planted in 1999 with the dwarf cultivar Caturra at low plant spacing (2 m × 1 m) resulting in high densities (5000 coffee bushes ha^{-1}). In addition, when the plantation was being set up, two coffee plants were planted in each hole. The Caturra variety, which is commonly used in Costa Rica, is susceptible to all the known coffee rust races. This coffee plot was managed intensively, using high levels of inputs, particularly fertilisers, herbicides, insecticides (against coffee berry borers) and fungicides (against coffee rust). The shade trees used to be pruned twice a year, as in most coffee plantations in Turrialba. Severe pruning is carried out in January–February to stimulate flowering. The shade trees are then pruned a second time in July before the beginning of the harvest.

For the purposes of the trial, the coffee plot was subdivided into two subplots. One was maintained with shade, managed almost as before, the only difference being that pruning of the shade trees in July 2009 was less severe than in previous years at the same period. The shade percentage was assessed each month, or each month and a half, during the rainy season in four places at the centre of the shaded subplot. We did this using a spherical densiometer used to measure forest overstorey density (Lemmon, 1957). We obtained an average shade cover of 23% and 57% in the last five months of 2008 and 2009 respectively. In 2009, shade cover was closer to the shade level recommended for coffee production in warm low altitude regions (Beer et al., 1998; Staver et al., 2001). In the second subplot, shade was eliminated at the beginning of 2008. As a consequence, this subplot was subjected to full sun exposure. No fungicide was used during the trial. Other input applications and cropping practices remained unchanged.

2.3. Fruit load regulation and levels obtained

In each study year, we selected 20 high-yielding coffee bushes (40 coffee plants) from 50 coffee bushes (5 rows of 10 coffee bushes) located in the centre of each subplot. We then counted the number of fruiting nodes on each of these 40 coffee plants. By uniformly removing excess of fruiting nodes (FN), we obtained four levels of FN per coffee plant: 0, 150, 250, and 500. We obtained 10 coffee plants with 0 FN, 11 with 150 FN and 250 FN, and only eight with 500 FN, as coffee plants with more than 500 FN were rare in the plot. Each coffee bush comprised a combination of two FN levels (one per coffee plant). All the possible combinations were represented two or three times in each subplot, except the combination of two coffee plants with 500 FN which was absent. Fruiting nodes were removed in July 2008 for the first study year and in May 2009 for the second year.

The number of fruiting nodes is the most important predictor of fruit load, hence of yield (Upreti et al., 1992). By homogenising the number of fruiting nodes, we assumed that yield was homogenised. Avelino et al. (2006) found a threshold value of 230 FN above which coffee rust seemed to be favoured under shade. Two of the studied levels were below this threshold and two above.

2.4. Coffee rust and host growth assessments and their descriptors

On each of the selected coffee plants, four branches were identified in two different storeys (two in the middle of the coffee plant, and two in the upper storey). Coffee rust progress was monitored by inspecting young leaves on these branches. The criterion used to define the age of the leaves was a very short internode that normally forms during the dry season. Old leaves are located between the base of the branch and this short internode. Young leaves are located between the short internode and the tip of the shoot. Old leaves bear the residual inoculum of the earlier epidemic. That inoculum helps to trigger the subsequent epidemic on young leaves (Avelino et al., 1991). For the inspections, we followed the methodology proposed by Kushalappa and Ludwig (1982). Each leaf was first individually mapped. On each inspection, we recorded the presence or absence of the leaf and its area, when present, using a diagrammatic scale. We also scored the presence or absence of coffee rust and the proportion of diseased leaf area using the scale proposed by Kushalappa and Chaves (1978). This non-destructive method enabled us to identify different changes between subsequent dates such as: new infected leaves and new infected area, new leaves and new leaf area, fallen leaves and lost area, loss of inoculum in terms of infected leaves and infected area. Inspections were carried out every three weeks during the rainy season, from August to January 2009 and from May to December 2009. Leaf area assessments began one month later in 2008.

Three kinds of variables were calculated from the collected data for each coffee plant:

(i) We calculated the cumulative percentage of diseased leaves or leaf area on each assessment date as a measurement of the incidence or of severity respectively: CR_t

On the first assessment date, $t = 1$, $CR_1 = 100 \times (R_1/L_1)$ where R is the number of rusted leaves or rusted area and L is the total number of leaves or total leaf area. From the second assessment date, $t = 2$ to n, $CR_t = 100 \times (R_1 + \sum_2^n NR_{t,t-1})/(L_1 + \sum_2^n NL_{t,t-1})$ where $NR_{t,t-1}$ is the number of newly rusted leaves or newly rusted area between $t-1$ and t and $NL_{t,t-1}$ is the number of new leaves or new area. Two disease progress curves were obtained by plotting the CR_t values, expressed as the proportion of leaf area or proportion of leaves, over time. Then we calculated the Area Under these Disease Progress Curves: *AUDPC* (in days.%).

(ii) As a descriptor of host growth, we calculated the percentage of new leaves or new area produced during the year (from $t = 2$ to $t = n$) with respect to the number of leaves or the leaf area of the first assessment date: HG.

$$HG = 100 \times \frac{\sum_2^n NL_{t,t-1}}{L_1}$$

(iii) As a descriptor of host defoliation, we calculated the percentage of fallen leaves or lost leaf area with respect to the total number of leaves or leaf area observed during the year: HD.

$$HD = 100 \times \left(1 - \frac{L_n}{L_1 + \sum_2^n NL_{t,t-1}}\right)$$

2.5. Microclimate recording

A Hobo H21-001 weather station (Onset Computer Corporation, Bourne, MA, USA) with nine sensors was positioned at the centre of each subplot: five rigid leaf wetness sensors (S-LWA-M003), three air temperature sensors (S-TMB-M0XX) and one air temperature-relative humidity sensor (S-THB-M00x) were located at different heights and places in the same way in both subplots as shown in Fig. 1. Sampling occurred every minute and the means of 30 data were recorded every 30 min. These microclimate variables were monitored from August 2008 to December 2009. Leaf temperature was monitored from August to October 2009 only. For that purpose, in each subplot, we used a Campbell CR23X station (Campbell Scientific, Inc., Logan, UT, USA) with four thermocouples sensors (copper-constantan) placed on the underside of four leaves located close to the air temperature sensors. Sampling occurred every 10 seconds and the means of 180 data were recorded every 30 min. Temperature and relative humidity sensors were previously calibrated and corrections were applied to homogenise the data. In addition, wetness sensors were field calibrated to determine the wet/dry transition point. Rainfall was recorded by a rain gauge located near the study site.

2.6. Analysis methods

In order to test the effects of the number of fruiting nodes and plot conditions (mainly light exposure conditions) on coffee rust and host growth, we performed analyses of variance using the mixed model. Fixed effects were assigned to the number of fruiting nodes and plot conditions, and random effects to the study year. The response variables were the host and coffee rust descriptors described earlier. Each coffee plant was considered as a replicate. Mean comparisons were carried out using the Least Significant Difference (LSD) test.

Microclimate data were analysed by comparing intra-day variations for the two plot conditions. We plotted (i) the means of four sensors for air temperature (ii) leaf wetness frequency, which was deduced from the five leaf wetness sensors (iii) relative humidity (only one sensor per plot) and (iv) the means of four thermocouples for leaf temperature. For all these comparisons, data were processed separately according to the daily rainfall amount: no rain, 0–5 mm, >5 mm. Standard errors were calculated at each time. Days with any missing data due to stations malfunctioning were discarded. For the leaf temperature data, the number of days considered for comparisons in each of the rainfall categories, no rain, 0–5 mm and >5 mm were respectively 11, 25 and 14, in the period from 18 August to 30 October 2009. For other microclimatic data, the number of days was respectively 14, 67 and 58, between 11 September 2008 and 28 January 2009

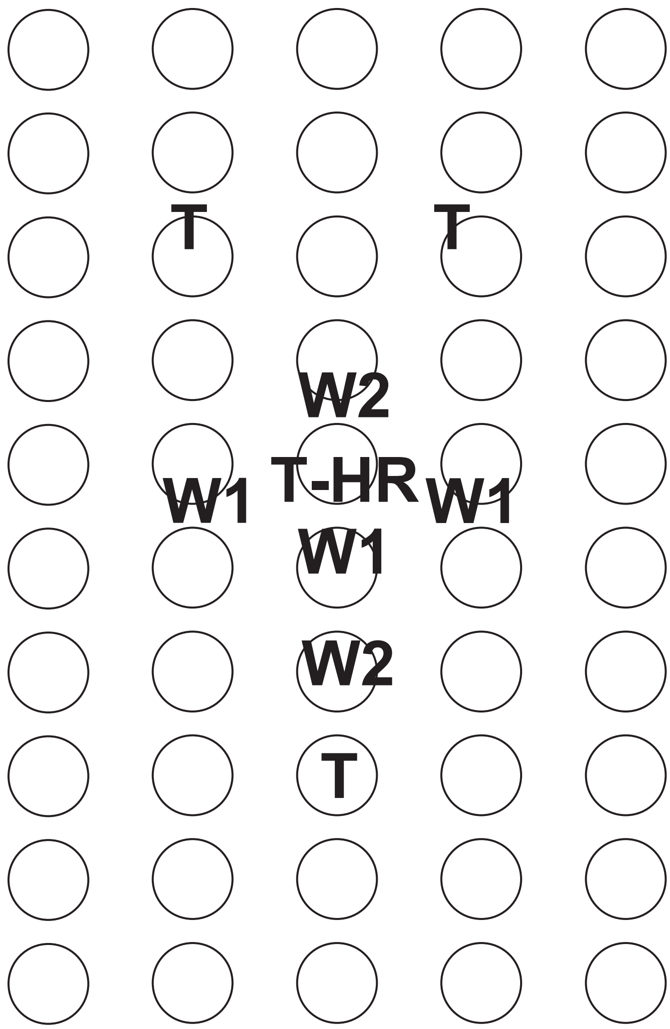

Fig. 1. Sensors distribution in each subplot. *T*: air and leaf temperature sensors at a height of 1.5 m; T-HR: relative humidity; air and leaf temperature sensors at a height of 1.2 m; W: leaf wetness sensors at heights of 0.8 m (1) and 0.5 m (2). The circles indicate the coffee bushes (five rows of 10 coffee bushes, 2 m between rows and 1 m between coffee bushes within the row).

(2008), and 32, 74 and 69, between 3 June and 8 December 2009 (2009).

3. Results

3.1. Coffee rust and host growth depending on light exposure conditions and the number of fruiting nodes per plant

As shown in Table 1, coffee rust epidemics were more intense in the shaded plot as compared to the full sunlight plot: $AUDPC_l$ (for the proportion of leaves) and $AUDPC_a$ (for the proportion of leaf area) were respectively 21.5% and 22.4% higher under shade. However, $AUDPC_a$ under shade was not significantly different from that at full sun exposure at $P < 0.05$ but at $P < 0.15$. Coffee rust epidemics were also more intense in high-yielding coffee plants: $AUDPC_l$ and $AUDPC_a$ were respectively 28.9% and 129.2% higher in coffee plants with 500 FN as compared to coffee plants with no fruits. Intermediate severity levels were found with 150 FN and 250 FN. No interaction was found between plot conditions and the number of fruiting nodes per coffee plant. Fig. 2 shows the behaviour of coffee rust depending on light exposure conditions and on the number of fruiting nodes per coffee plant over the two years of the study. The epidemic appeared to be much more severe in 2008 than in 2009. In addition, the shade effects seemed more consistent over the two years when considering the proportion of infected leaves than when considering the proportion of leaf area infected. For instance, for the 500 FN level, the cumulative percentage of leaf area infected reached higher levels with full sun exposure as compared to shaded condition in 2008, whereas the reverse was observed in 2009 (Fig. 2; Table 2).

Table 1
Light exposure and fruit load effects on coffee rust.

Studied factor	Treatment	$AUDPC_l$ (days.%)	$AUDPC_a$ (days.%)
Light exposure condition	Full sunlight	8656a	684a
	Shade	10515b	837a
Number of fruiting nodes per coffee plant	0	8178a	473a
	150	9710b	714ab
	250	9914b	771b
	500	10540b	1084c

AUDPC: Area under the progress curve of coffee rust expressed as cumulative percentage of leaves ($AUDPC_l$) or infected leaf area ($AUDPC_a$).
Data followed by the same letter are not significantly different according to the LSD test ($P < 0.05$).

As a result of different rust attacks, the rate of defoliation appeared to be higher under the shaded condition as compared to full sun exposure. We found differences between the two light exposure conditions of 5.3%, when considering the number of leaves, and 7.6% (significant at $P < 0.07$), when considering the leaf area (Table 2). Similarly, the rate of defoliation was 16.4% higher when considering the number of leaves and 14.9% higher when considering the leaf area, under the 500 FN conditions as compared to the 0 FN conditions (Table 2). No differences were found between different FN levels for growth. However, the growth rate was much higher with full sun exposure than for shaded condition: differences of 25.2% and 37.5% were observed between the two light exposure conditions when considering the number of leaves and the leaf area respectively.

3.2. Microclimate characterisation

Microclimate differences between the two light exposure conditions were only recorded during the day (6:00 am–6:00 pm, Fig. 3). The air temperature was globally higher with full sun exposure as compared to shaded condition. Conversely, the leaf wetness frequency and relative humidity were higher under shade. The differences were usually more visible around noon on dry days, particularly in 2009, when greater shade cover was maintained. At noon, in 2008, the air temperature was 2.2, 1.9, and 1.3 °C higher on average with full sun exposure as compared to shaded condition, on dry, low rainfall ($\leq$5 mm), and high rainfall days (>5 mm) respectively. In 2009, the differences between the two light exposure conditions were 2.9, 3.0 and 2.0 °C respectively (Table 3). At noon, the leaf wetness frequency was very similar in 2008 in the two study plots. The differences were clearer in 2009, where the leaf wetness frequency was 36.3, 45.9 and 31.5% higher under shade than in full sunlight, on dry, low rainfall and high rainfall days respectively (Table 3). Similarly, the relative humidity was 9.1, 6.8 and 4.0% higher in 2008, and 8.8, 9.0 and 6.5% in 2009, in the shaded plot as compared to full sun exposure, under the same rainfall conditions as before (Table 3).

Leaf and air temperature intra-day variations followed the same pattern (Figs. 3 and 4). However, during the day, leaf temperatures were normally higher than air temperatures. In addition, differences between leaf and air temperatures were greater with full sun exposure than under shade. For instance, at noon, on dry days, with full sun exposure, the leaf temperature was 7.1 °C higher on average

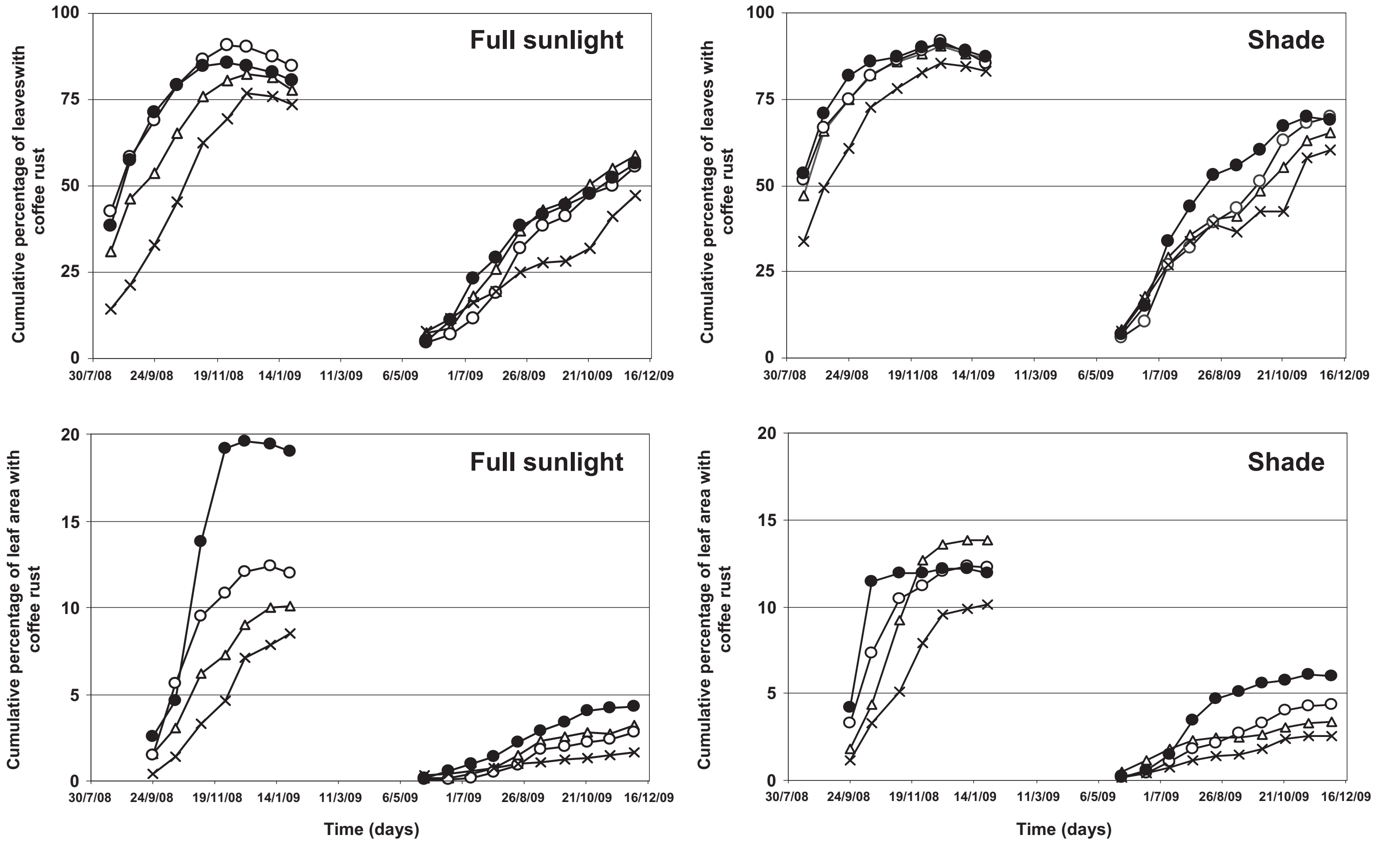

Fig. 2. Coffee rust progress curves expressed as cumulative percentages of infected leaves or infected leaf area, as a function of the number of fruiting nodes per coffee plant and light exposure. Number of fruiting nodes per coffee plant: 0 (×), 150 (△), 250 (○), 500 (●).

than the air temperature, and only 3.8 °C higher under shade. As a consequence, the leaf temperature was 6.4 °C higher with full sun exposure than under shade (Table 4). From 18 August to 30 October 2009, the period used for comparison, average leaf temperatures never exceeded 30 °C under shade. Conversely, this temperature was usually reached with full sun exposure, between 9:00 and 10:00 am, under the three studied rainfall conditions (Fig. 4).

In 2008 and 2009, there were respectively 83 and 93 dry days, 145 and 152 days with rainfall ≤5 mm, and 138 and 120 days with rainfall >5 mm.

4. Discussion

We did not find any interaction between fruit load and shade, indicating that shade was conducive to coffee rust at the low altitude and under the rainy conditions in Turrialba, independently of the fruit load. In addition, we highlighted a positive relationship between the number of fruiting nodes and coffee rust incidence and severity, which is consistent with previous results obtained in Latin America (Zambolim et al., 1992; Silva-Acuña, 1994; de Carvalho et al., 1996, 2001; Avelino et al., 2004, 2006; Costa et al., 2006). These two relationships help to explain the apparently contradictory results for shade effects found in the literature (Staver et al., 2001; Soto-Pinto et al., 2002; Avelino et al., 2006). Coffee rust is reduced by shade because shade reduces the number of fruiting nodes and the number of fruits per node (Cannell, 1985; DaMatta, 2004). It is possible to find higher coffee rust severities and incidences with full sun exposure when the fruit load is heavy, than under shade when the fruit load is lower. However, with an equivalent number of fruiting nodes, coffee rust incidence and, to a lesser extent, severity were greater under shade, suggesting that mechanisms other than fruit load are involved in disease expression.

Firstly, the dilution effect due to host growth had to be higher with full sun exposure than under shade, as the host grew more under the former condition than under the latter, as expected (Cannell, 1985). This dilution effect is due to the introduction of new healthy leaves or leaf area over time, which reduces the apparent infection rate (Ferrandino, 2008). This effect has already been proposed for coffee diseases, and especially coffee rust. Kushalappa and Ludwig (1982) demonstrated that negative values of the apparent infection rate could be found during periods when coffee growth, expressed as new leaves or new area, was faster than the increase in diseased leaves or diseased area, resulting in a dilution of coffee rust proportions. This effect has also been proposed for explaining the negative relationship between coffee rust incidence and the number of fertilizer applications (Avelino

Table 2
Light exposure and fruit load effects on coffee growth and defoliation.

Studied factor	Treatment	HG_l	HG_a	HD_l	HD_a
Light exposure condition	Full sunlight	83.6a	110.5a	68.4a	68.1a
	Shade	58.4b	73.0b	73.7b	75.7a
Number of fruiting nodes per coffee plant	0	77.1a	86.1a	59.9a	61.4a
	150	74.0a	86.1a	73.6b	75.1b
	250	68.6a	100.5a	74.4b	74.8b
	500	64.3a	94.4a	76.3b	76.3b

HG: Host growth expressed as the percentage of new leaves (HG_l) or new area (HG_a) produced during the year with respect to the number of leaves or the leaf area of the first assessment date.
HD: percentage of fallen leaves (HD_l) or lost leaf area (HD_a) with respect to the total number of leaves or leaf area observed during the year.
Data followed by the same letter are not significantly different according to the LSD test ($P < 0.05$).

Table 3
Light exposure effects on microclimate at noon (means and standard errors).[a]

Year	Daily rainfall condition (mm)	Air temperature °C (standard error)		Wetness frequency % (standard error)		Relative humidty % (standard error)	
		Full sunlight	Shade	Full sunlight	Shade	Full sunlight	Shade
2008	0	32.1 (0.6)	29.9 (0.6)	2.9 (1.9)	7.1 (4.0)	59.7 (1.4)	68.8 (1.0)
	0–5	29.3 (0.4)	27.4 (0.4)	16.7 (4.3)	23.0 (4.5)	69.3 (1.4)	76.1 (1.1)
	>5	26.9 (0.6)	25.6 (0.5)	45.9 (6.3)	53.5 (6.1)	80.1 (1.8)	84.1 (1.4)
2009	0	31.1 (0.5)	28.2 (0.4)	3.1 (3.1)	39.4 (6.1)	66.5 (1.7)	75.3 (1.3)
	0–5	30.6 (0.3)	27.6 (0.3)	11.2 (3.3)	57.1 (4.3)	69.0 (1.1)	78.0 (1.0)
	>5	28.1 (0.4)	26.1 (0.4)	34.1 (5.5)	65.6 (4.6)	75.7 (1.5)	82.2 (1.2)

[a] Days with missing data were not included in the calculations. See text for shade cover, studied periods and number of days in each daily rainfall category.

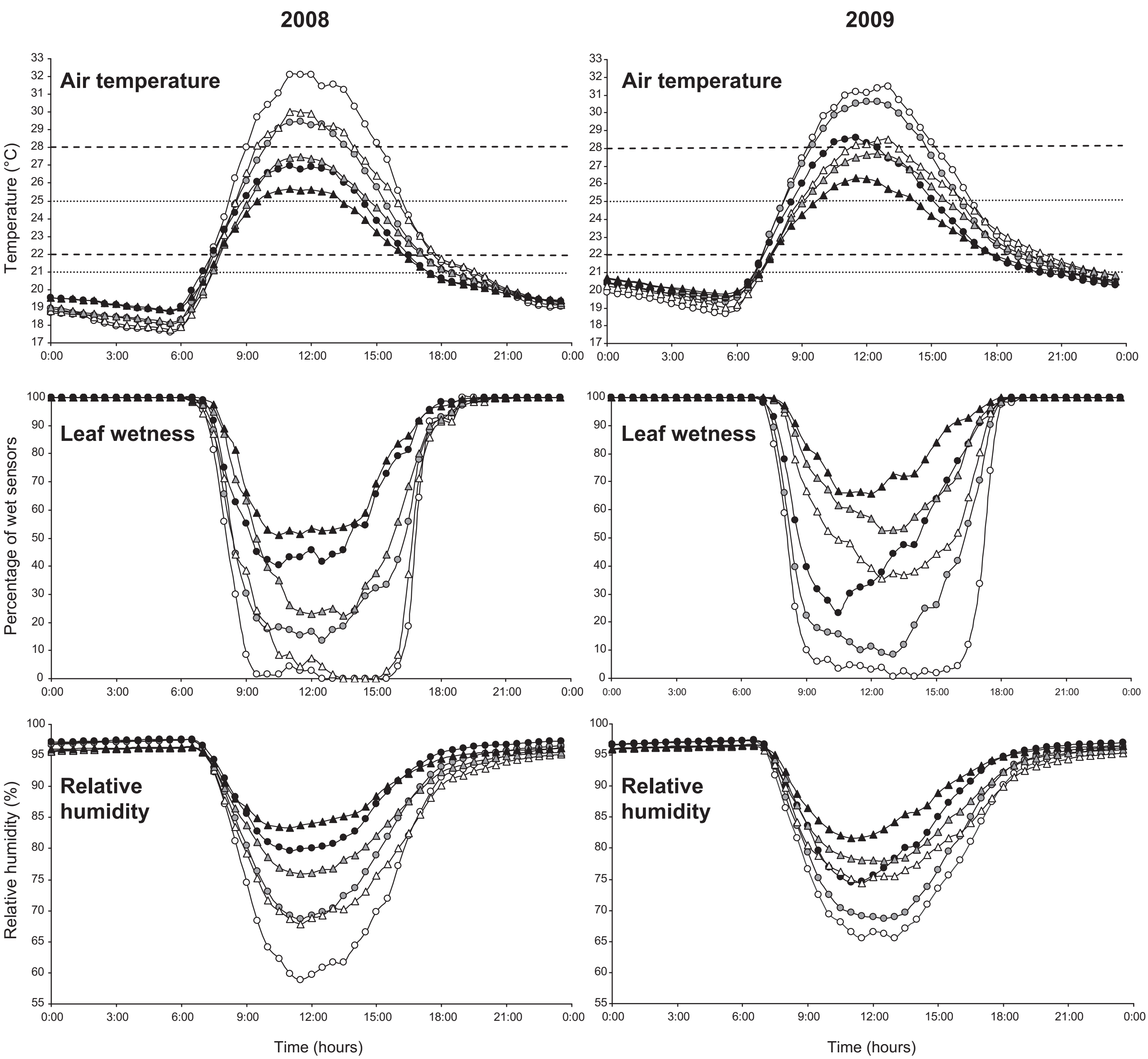

Fig. 3. Intra-day variations in air temperature, leaf wetness, relative humidity during the rainy season, under different daily rainfall conditions (no rainfall: white, ≤5 mm: grey, >5 mm: black) with full sun exposure (○) and under shaded conditions (Δ) over two consecutive years. Days with missing data were not included in the calculations. Optimum temperature range for germination and infection (continuous lines) and for the latent period (dotted lines) according to Waller (1982). See text for shade cover, studied periods, and number of days in each daily rainfall category.

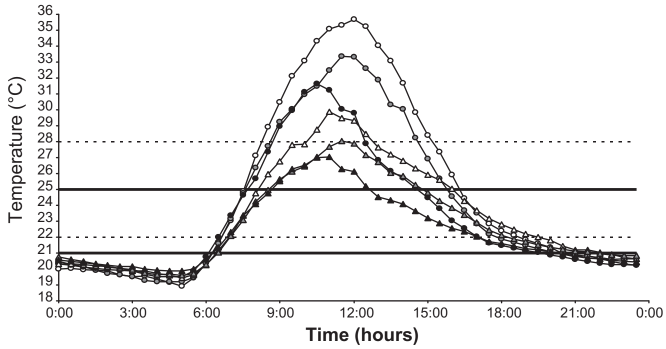

Fig. 4. Intra-day variations in leaf temperature during the 2009 rainy season, under different rainfall conditions (no rainfall: white, ≤5 mm: grey, >5 mm: black) with full sun exposure (○) and under shaded conditions (Δ). Days with missing data were not included in the calculations. Optimum temperature range for germination and infection (continuous lines) and for the latent period (dotted lines) according to Waller (1982). See text for shade cover, studied period, and number of days in each daily rainfall category.

et al., 2006). Fertilizer applications probably promote a good host growth and thereby a decrease in disease proportions. A similar effect has been suggested for American leaf spot disease caused by *M. citricolor* (Avelino et al., 2007).

Secondly, shade improved the microclimate for coffee rust development. In the warm region of the study, high air and leaf temperatures were reduced by shade, as expected (Barradas and Fanjul, 1986; Jaramillo-Robledo and Gómez-Gómez, 1989; Siles et al., 2010). This was especially true in 2009 when greater shade cover was maintained. The temperature requirements of coffee rust are well documented. Optimum temperatures for uredospore germination and infection range from 21 to 25 °C at constant temperatures and in the presence of free water (Nutman et al., 1963; Waller, 1982; Kushalappa et al., 1983). The latent period is shorter between 22 °C and 28 °C (Waller, 1982). High temperatures are very restrictive to coffee rust growth: germination is inhibited above 28–30 °C (Rayner, 1961; Nutman et al., 1963; Kushalappa et al., 1983; de Jong et al., 1987) and lesion growth is suppressed after several exposures to 40 °C (Ribeiro et al., 1978). As a result, it can be concluded that temperatures under shade were frequently closer to the optimum temperatures for coffee rust growth. Actually, on rainy days, when moisture conditions for infection were favourable, we found that mean daytime air temperatures were below 28 °C on average under shade. Conversely, mean daytime air temperatures exceeded 28 °C with full sun exposure on low rainfall days (≤5 mm) in the two study years, and on very wet days (>5 mm) in 2009. The differences were even larger when considering leaf temperatures, with maxima between 32 and 36 °C on average with full sun exposure depending on daily rainfall amounts, whereas the maxima did not exceed 30 °C under shade. Moisture also seemed to be more conducive to coffee rust under shade. Free water is essential for uredospore germination up to penetration (Rayner, 1961; Nutman et al., 1963; Waller, 1982; Kushalappa et al., 1983). In our trial, the wetness frequency was always close to 100% during the night under all the studied light and rainfall conditions. However infection can be successful with only six hours of free water at 21 ± 2 °C, around 20 hours of continuous wetness are necessary to obtain an infection rate of 80% with respect to maximum infection (Kushalappa et al., 1983). de Jong et al. (1987) demonstrated that penetration was faster if wetted spores were exposed to 22–26 °C for some hours, favouring germination, and then to 15–18 °C, favouring appressorium formation. They suggested these conditions could be normally found at the beginning of the night. However, the low temperatures were rarely reached in our trial at that time. They were mostly found at the end of the night. These elements indicate infection was probably not so fast during the night and extended wetness duration during the day might have been necessary for completing infection in most cases. On very wet days (>5 mm), meaning 35% of the days on average, the leaf wetness frequency never decreased to very low levels under shade. The leaf wetness frequency was always above 50% on average, and even above 65% in 2009, with the shade cover recommended for low altitude and warm regions, almost permanently providing good conditions for infection. To our knowledge, this comparison of coffee leaf wetness under shade and in full sunlight has never been so clearly documented before. The intra-day variation in relative humidity followed almost the same pattern as the leaf wetness frequency, as expected (Sentelhas et al., 2008). Uredospores can be dispersed by wind when relative humidity is low (Waller, 1982). Lower levels of relative humidity were obtained with full sun exposure. In addition, the wind speed was probably higher in absence of shade, as shade is known to intercept wind (Jaramillo-Robledo and Gómez-Gómez, 1989). Both effects provided better conditions for dispersal in full sunlight condition. However, considering the long distances over which uredospores can be dispersed (Bowden et al., 1971; Waller, 1982) and as the study plots were adjacent, differences in the dispersal rates were probably not relevant.

Incidence and severity, though normally well correlated (Silva-Acuña et al., 1999), are not equivalent measurements. Severity is a function of the number of successful infections and of lesion expansion. Incidence is dependent on the number of successful infections only. Variations in incidence are therefore a reflection of variations in the conditions affecting germination up to penetration, whereas variations in severity can indicate variations in the conditions affecting leaf colonization too. It is interesting to note, that shade effects on coffee rust progress were more obvious when considering incidence, whereas fruit load effects were clearer when considering severity. Shade probably favoured pre-infection processes, as previously discussed, and not so much colonization, whereas the fruit load, through plant physiology, logically favoured colonization to a greater extent. However, our results also indicate that pre-infectious events, probably at the penetration stage, could be affected by the fruit load, as lower incidences were found on coffee plants with no fruits. To our knowledge, there is no other similar positive relationship between a leaf disease, caused by a biotrophic pathogen, and fruit load. We believe this relationship is not likely to be related to a decrease in leaf nutrient contents, as good nutrition has often been reported to increase the severity of diseases caused by biotrophic fungi (Jensen and Munk, 1997;

Table 4
Light exposure effects on air and leaf temperatures at noon (means and standard errors).[a]

Daily rainfall condition (mm)	Air temperature °C (standard error)		Leaf temperature °C (standard error)	
	Full sunlight	Shade	Full sunlight	Shade
0	28.6 (1.4)	25.5 (1.2)	35.7 (1.1)	29.3 (0.7)
0–5	29.1 (0.8)	26.1 (0.6)	33.0 (0.7)	27.9 (0.5)
>5	26.3 (1.4)	24.0 (1.1)	30.0 (1.5)	26.2 (0.8)

[a] Days with missing data were not included in the calculations. See text for shade cover, studied period and number of days in each daily rainfall category.

Neumann et al., 2004). Other mechanisms are probably involved, possibly through defence compounds (de Carvalho et al., 2001), or even physiological aspects related to stomatal conductance, as *H. vastatrix* penetrates and sporulates through stomata.

Under the low altitude and warm conditions of this study, high temperatures were reduced by shade. In high altitude regions, coffee rust epidemics are less intense due to low temperatures (Bock, 1962; Avelino et al., 1991, 2006; Brown et al., 1995). We believe shade at these altitudes still buffers temperatures, though probably with a greater effect on low temperatures (Caramori et al., 1996). The expected result is the same. Temperatures under shade will remain closer to the optima for coffee rust life cycle completion even under these cool conditions.

Shade has antagonistic effects on coffee rust. It reduces coffee rust attacks only because it regulates yield. The service provided by shade in controlling coffee rust is therefore necessarily accompanied by a disservice which consists of a reduction in yields in the short term. However, this trade-off possibly vanishes over time. Shade has the ability to stabilize coffee yields over the years by limiting interanual variations, which provides a more stable income to growers (Cannell, 1985; DaMatta, 2004), while also increasing the lifespan of the coffee plants. In addition, shade provides other agronomic services such as better coffee quality, weed control, or a reduction in fertilizer and herbicide use (Fernández and Muschler, 1999).

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