# Influence of rubber trees on leaf-miner damage to coffee plants in an agroforestry system

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**Abstract** The coffee leaf-miner (CLM) (*Leucoptera coffeella* Guérin-Mèneville; Lepidoptera: Lyonetiidae), the main pest of coffee plants, occurs widely throughout the Neotropics where it has a significant, negative economic and quantitative impact on coffee production. This study was conducted in a rubber tree/ coffee plant interface that was influenced by the trees to a varying degrees depending on the location of the coffee plants, i.e. from beneath the rubber trees, extending through a range of distances from the edge of the tree plantation to end in a coffee monocrop field. The most severe damage inflicted on coffee plants by the CLM (number of mined leaves) from April, which marks the start of the water deficit period, until September 2003 was in the zone close to the

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M. S. Bernardes Department Crop Science, University of São Paulo, ESALQ, Av. Pádua Dias, 11, P.O. Box. 09, Piracicaba, SP 13418-900, Brazil e-mail: marcosbernardes@usp.br rubber trees, whereas the damage inflicted on plants in the monocropped field was comparable to that on coffee plants grown directly beneath the rubber trees, which received about 25–40 % of the available irradiance (I<sub>r</sub>—available irradiation at a certain position divided by the irradiation received in full sunlight, i.e. in the monocrop). From May until July damage caused by the CLM nearly doubled in each month. In midwinter (July), the damage decreased perceptibly from the tree edge toward the open field. From September onward, with the rising air temperatures CLM damage in the coffee monocrop started to increase. Based on these results, we conclude that coffee plants grown in the full sun incurred the most damage only at the end of winter, with warming air

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temperatures. Coffee plants grown in shadier locations  $(25-40 \ \% I_r)$  were less damaged by the CLM, although a higher proportion of their leaves were mined. The rubber trees probably acted as a shelter during the cold autumn and winter seasons, leading to greater CLM damage over a distance outside the rubber tree plantation that was about equal to the height of the trees. Future studies should attempt to relate leaf hydric potential to pest attack in field conditions. More rigorous measurements of shade conditions could improve our understanding of the relationship of this factor to CLM attack.

**Keywords** Leucoptera coffeella · Coffea spp. · Coffee pest · Shade · Leaf damage · *Hevea* spp. · Population dynamics

#### Introduction

The Arabian coffee plant (*Coffea arabica* L.) originates from the highlands of southern Ethiopia near the equator, where coffee plants grow under permanent shade in a tropical forest (Krug 1959; Kumar 1979). In Brazil, Kenya, Colombia and many other coffeeproducing countries, coffee plants are cultivated predominantly in full sun, mostly in extensive plantations. Even in countries with a tradition of shaded coffee cultivation, current labor shortages combined with low income levels and adverse environmental factors are leading farmers to convert to monocrop plantations, as in Puerto Rico (Borkhataria et al. 2012).

The coffee leaf-miner (CLM; *Leucoptera coffeella* Guérin-Mèneville; Lepidoptera: Lyonetiidae) also originates from Africa and feeds exclusively on palisade parenchyma cells of coffee leaves (Ramiro et al. 2004). CLM adults are nocturnally active, with a life span of 2–3 weeks. Depending on air temperature, CLM can have from four to 12 generations in a year (Parra 1985). Eggs are laid on the upper surface of the leaves, and the hatched larvae initiate mines by penetrating the leaf epidermis. CLM remain inside the leaves for about 10 days, and then the last instar leaves the mine to spin a cocoon on the underside of a coffee leaf located on the lower third of the plant (Ramiro et al. 2004). CLM larvae are minimally

exposed to the outside of the leaf (Bustillo and Villacorta 1994), which makes control of this pest more difficult.

The CLM is the main pest of coffee plants only in the Neotropics, where it can cause productivity losses of >50 % due to premature drop of the leaves and consequent reduction of photosynthesis area (Reis and Souza 1996; Souza et al. 1998; Ramiro et al. 2004). Given the need to produce new leaves after an infestation, the sink-source relationship is negatively affected, with a resultant drop in productivity because of the necessary competition for the photoassimilates needed to regenerate the photosynthetic tissue (Souza et al. 1998). Farmers' general lack of knowledge of the coffee entomofauna has led to extensive and indiscriminate application of chemical products. As a result, a series of disastrous environmental disturbances have aggravated many entomological problems due to the reduction of natural control agents (Parra 1985; Souza et al. 1998, Mendonça et al. 2006). The demand for organic products and public pressure for less aggressive crop-management practices are obligating farmers to employ new products and methods, despite the lack of information on their efficiency (Leroy et al. 2000; Venzon et al. 2005). Combined use of cultural, biological and chemical methods seems to be the most favorable alternative approach to control the spread of CLM infestation (Oliveira et al. 2008).

The population dynamics of the CLM are affected by environmental factors, phytosanitation practices and nutritional conditions of the crop, and by the presence of natural enemies (Moraes 1998; Vega et al. 2006; Cornelissen and Stiling 2008; Teodoro et al. 2008). Temperature is positively correlated with increases in damage, whereas high precipitation and lower air relative humidity have negative effects (Parra 1985; Nestel et al. 1994). Understanding the impact of weather can be highly useful for the management of CLM (Pereira et al. 2007; Lomelí-Flores et al. 2009, 2010).

The presence of trees in a crop production system modifies both the radiation balance and the wind behavior in the area under their influence. The combined effects of these changes in the microclimate alter the balance of available energy, leading to modifications in water use, productivity and phenology of the plants (Monteith et al. 1991; Brenner 1996). Modification of the management system leads to intrinsic physiological changes as the crop adapts, which in turn make it necessary to develop new management and sanitation practices (Meireles et al. 2001). Coffee plants are recommended as being potentially suitable plants for agroforestry systems (AFS) (Beer et al. 1998; Muschler 2001) because of their ability, under conditions of severely reduced radiation availability, to adapt morphologically by changing their canopy characteristics (Righi 2005) and their ability to sustain the same phytomass (Righi et al. 2008). Rubber trees (Hevea spp.) are especially suited for this combination, as the yield per plant in AFS increases by about 50 % compared to a monoculture, with a potential for further increases through changes in the tap system (Righi and Bernardes 2008). Reis et al. (2002) pointed out that the use of trees, such as rubber trees, would help to control the CLM, as the trees would act as a refugium for this pest's natural enemies (Thomaziello et al. 2000). The increase in complexity of a production system, as in a coffeebased AFS, may enhance predation on arthropods by vertebrates, such as birds, lizards, bats, among others (Perfecto et al. 2007), and invertebrates (Cardinale et al. 2003). Ants can be important agents of biological control (Philpott and Armbrecht 2006; De la Mora et al. 2008), with different species feeding on different CLM life stages (Lomelí-Flores et al. 2009, 2010).

There is a lack of field experiments with CLM, especially in complex agroecosystems, that aim to determine which factors affect infestations. No attempt has been made to systematically examine microenvironmental conditions and to relate them to CLM damage under field conditions. The main aim of our study was to investigate the influence of trees on the damage inflicted by CLM to coffee plants planted beneath and adjacent to a rubber tree plantation (interface) and in a monocrop.

## Materials and methods

The study was conducted in a rubber tree/coffee plant interface, with varying influence of the rubber trees on the coffee plants depending on the location of the coffee plants, i.e., beneath or at different distances from the edge of the tree plantation. This experiment was carried out on the experimental campus of the Department of Crop Science, Escola Superior de Agricultura "Luiz de Queiroz", University of São Paulo (ESALQ/USP) in Piracicaba, São Paulo, Brazil (22°42′30″S, 47°38′00″W; altitude 554 m a.s.l.) from February 2003 until January 2004. The climate in this region is subtropical and humid, with rainy summers and dry winters (Sentelhas et al. 1998), corresponding to Cwa in the Köppen (1948) classification. The mean annual temperature is 21.4 °C; the monthly mean temperature is 24.8 °C in the summer and 17.1 °C in winter. The mean annual precipitation is 1,278 mm, with 1,000 mm falling from October through March and 278 mm from April through September. Unusually, the dry period in the year of the study began in the autumn and continued through mid-spring (period from April to November). The hydric balance showed a water shortage of 213 mm and an excess of 234 mm over the course of the year. However, it still fell within the suggested climate requirements for the coffee plant as described by Camargo (1985). The lowest monthly mean air temperature was 15.6 °C in July 2003, and the highest temperature recorded was 27.2 °C at the end of February of the same year. The study year had an unusually long dry period (8 months) and higher temperatures, both well above historical averages. The real evapotranspiration (ET<sub>R</sub>) and potential evapotranspiration  $(ET_P)$  were about the same most of the year, meeting the largest part of the water demand. From the end of June until the middle of November a significant difference between the curves occurred, indicating the period of highest water deficit (Fig. 1).

The soil, with a slope varying from 0 to 15 %, is a red eutroferric Nitosol, which is a structured eutrophic soil with a moderate A-horizon and clay-textured (American classification Kandiudalfic Eutrodox). The soil fertility, mineral fertilization and the irrigation drip system installed at the experimental site were intended to prevent limitations and any hindrance to the growth and development of the plants. Fertilizers and limestone were applied based on the soil analysis.

*Coffea arabica* cv. Obatã (IAC-1669-20) is a variety of coffee well known for its leaf retention (Conceição et al. 2005). In our study, plants of this variety were planted in rows of 3.4 m wide with 0.9 m between-plants, during the first 15 days of January 2002. The coffee plant seedlings were planted in a continuous strip starting from beneath the rubber tree plantation, continuing outside to the interface with the trees and ending with a monoculture far from the influence of trees. At the time of planting, the seedlings were 9 months old and were obtained from

**Fig. 1** a Mean air temperature (10-day intervals) and precipitation (mm), b hydric balance, potential and real evapotranspiration (*ETP*, *ETR*, respectively) according to Thornthwaite (1948) during 2003 at Piracicaba, São Paulo, Brazil. *Def.* water deficit, *Exc* water excess



seeds sown directly in plastic bags. The rubber trees (*Hevea* spp.) had been planted in 1991 in rows 8m wide with a between-plant spacing of 2.5 m; seed-lings were grafted in plastic bags with two mature leaves projecting onto the graft. The entire experimental field was composed of the same clone, PB-235.

The damage caused to the coffee plants by the CLM was evaluated as a function of the distance from the edge of the rubber trees (distance zero), which mediates the intensity of crop interactions. Negative values were assigned to the rows located inside the rubber tree plantation, and opposite positive values were assigned for those plants located outside at increasing distances. The distances evaluated were: (1) inside distances of -13.7, -10.3, -5.7, -2.3 m; (2) outside distances of 1.5, 4.9, 8.3, 11.7, 15.1, 18.5 m; (3) the monoculture (Fig. 2).

The damage inflicted by the CLM was quantified directly by counting all of the mined leaves on a whole plant, as described by Souza et al. (1998). At each



Fig. 2 Cross-section of the experimental field showing the arrangement of rubber trees (*Hevea* spp.) and coffee plants (*Coffea arabica* L.). The *first line* of rubber trees facing the coffee crop represents trees in the agroforestry system (AFS) in

distance, ten coffee plants were evaluated monthly during a 1-year period. The plants were identified by row and their sequential number in the row, and the evolution of damage was noted on the same plant throughout the experimental period. At the end of the experiment, the total foliage area of each plant was measured by counting the number of leaves per plant multiplied by the corrected mean leaf size. Righi (2005) found that the area of an average coffee leaf is equivalent to 68 % of the rectangle calculated based on its size measurement (length × width).

At the same positions, the solar radiation available to the coffee plants was measured continuously at their tops by using solarimeter tubes (TS-UM-3; Eijkelkamp, Giesbeek, The Netherlands) connected to a data acquisition system (DL2e; Delta-T Devices, Cambridge, UK) installed in the experimental field. The environmental conditions for the monocropped plants were measured by the Main Meteorological Station of the Department of Exact Sciences, ESALQ-USP, located next to the experiment. The available irradiation for each position was integrated for each day. This value was divided by the available radiation without tree interference (full sun), giving the irradiation fraction ( $I_r$ ) available in each row (distance from the trees).

a half alley of double rows. The *second line* represents trees in the AFS planted with the same spacing (row width 8 m; between-plant spacing 2.5 m)

The experimental field proved to be quite homogeneous when the CLM damage was evaluated as a function of distance from the trees, as mentioned above. The regression between CLM damage (number of mined leaves per plant) and tree distance (m) for each month was calculated based on the coefficient of determination.

## Results

Solar radiation and plant plasticity

The available irradiation (%  $I_r$ ), total leaf number, foliage area and percentage of mined leaves for the coffee plants at the end of the experiment are presented in Table 1. The available irradiation increased abruptly at the second row (4.9 m) outside the rubber tree plantation. At the end of the experiment, the coffee plants showed clear adaptations to the different environments. The mean total leaf number per plant in each position increased with the amount of sunlight, i.e. in the direction of the full sun, as did the total foliage area. Plants receiving available irradiation ranging from <25 to 40 %  $I_r$  had about one-third to one-half the number of leaves as monocropped plants. In plants receiving from 45 to 100 %  $I_r$  (full

| as a percentage (7, 1, or that reaching the open field. I nacleaba, 51, Blazh - January 2004 |                         |       |      |      |                          |      |      |      |      |      |          |
|--|-------------------------|-------|------|------|--------------------------|------|------|------|------|------|----------|
| Distance (m)   | Inside (m) <sup>a</sup> |       |      |      | Outside (m) <sup>a</sup> |      |      |      |      |      |          |
|  | -13.7                   | -10.3 | -5.7 | -2.3 | 1.5                      | 4.9  | 8.3  | 11.7 | 15.1 | 18.5 | Monocrop |
| Available irradiation (% Ir)   | 25                      | 30    | 35   | 40   | 45                       | 80   | 90   | 95   | 100  | 100  | 100      |
| Total leaf number  | 133                     | 148   | 168  | 219  | 359                      | 365  | 361  | 382  | 343  | 409  | 393      |
| Foliage area (m <sup>2</sup> )   | 0.81                    | 0.88  | 0.87 | 0.99 | 1.80                     | 2.26 | 1.52 | 1.50 | 1.56 | 2.13 | 1.69     |
| Percentage of mined leaves   | 43                      | 44    | 37   | 29   | 19                       | 19   | 24   | 25   | 23   | 23   | 19       |

**Table 1** Total leaf number, foliage area and percentage of mined leaves observed at the end of the experimental period, according to the distance of the coffee plants from the edge of the rubber trees. Available solar radiation to coffee plants at each distance is given as a percentage (% I<sub>r</sub>) of that reaching the open field. Piracicaba, SP, Brazil - January 2004

<sup>a</sup> Negative values were assigned to the rows located inside the rubber tree plantation, and opposite positive values were assigned for those located outside at increasing distances

sum—monocrop), the number of leaves was similar, with the relatively more shaded plants having 92 % of the number of leaves as the plants located in the full sun. In other words, plants receiving from <25 to 40 % I<sub>r</sub> had about half the foliage area (m<sup>2</sup>) as the monocrop plants. From 45 % I<sub>r</sub> upward, the foliage area was quite similar, ranging within the maximum values.

## Influence of rubber trees on CLM damage

The evolution of the mean CLM damage (number of mined leaves per plant) throughout the year showed clearly different patterns for each position evaluated. Figure 3 shows the progression of CLM damage month by month as a function of tree distance. At the beginning of the experiment, the coffee plants at all distances did not show significant CLM damage. However, after only a few months, the CLM damage increased sharply.

From February to April 2003, CLM damage was very low, with only a few mined leaves. From April onward, the slope of the regression line changed significantly, with an accentuated upward inflection near the rubber tree edge. CLM damage from April to September 2003 was much more severe in the zone from near the trees to 18.5 m distant (which was receiving 100 %  $I_r$ ), while in the monocropped coffee (arbitrarily represented at 50 m for graphical purposes only) it remained at about the same level as on coffee plants in shadier positions (inside the rubber tree plantation, with 25-40 % Ir). In July (midwinter; the mean air temperature of the coldest day of the year being 15.6 °C) the coffee plants near the rubber trees were much more damaged, and the degree of damage decreased from 4.9 m distant from the rubber trees to the open field. From September onward, with the warming air temperature, CLM damage to the monocrop began to increase. Monocropped plants sustained the same level of damage as the plants in the other positions near the trees only from October onwards, maintaining this level until December. In January the CLM damage appeared to begin to equalize at all the locations, with plants near the trees (mainly those from 8.3 to 18.5 m in the range of 90–100 %  $I_r$ ) still being the most damaged.

In order to assess the severity of the CLM damage at each distance from the trees, at the end of the experiment we divided the number of mined leaves per plant by its total leaf number to obtain the percentage of mined leaves per plant (Table 1). In addition to their lower figures for the total damage throughout the year, the coffee plants located beneath the rubber trees (receiving 25–40 %  $I_r$ ) showed the highest proportion of mined leaves per plant. This indicated that a large part of their fewer leaves were damaged, reducing the photosynthetic apparatus even further. The severity of the damage decreased sharply just outside the edge of the rubber tree plantation. On average, coffee plants well inside the rubber tree plantation had roughly 40 % of their leaves mined, whereas outside the severity of the damage was about half of that (circa 20 %).

## Discussion

Solar radiation and plant plasticity

The use of shade trees on coffee farms reduces the total radiation incidence (as also observed in this study) and



**Fig. 3** Mean damage (number of mined leaves per plant) of coffee leaf-miners (*Leucoptera coffeella*) on coffee plants at each distance from the rubber tree plantation edge, from February 2003 through January 2004 at Piracicaba, São Paulo, Brazil. The regression *line* is provided for each month so that the

trend for damage can be perceived. The *y*-axis was set at distance zero, marking the interface of the rubber trees  $\times$  coffee plants. Coffee plants in the monocrop are arbitrarily represented at 50 m for the purpose of graphing only. Note the use of different scales (*y*-axis) in order to show the lower values

restricts wind speed, thus reducing the fluctuations in daily temperature and the evapotranspiration of the crop (Barradas and Fanjul 1986; Velasco et al. 2001). The reduction of wind speed restricts CLM dissemination, which occurs mostly via the airstream (Parra 1985; Souza et al. 1998). The influence of trees on the microclimate conditions around coffee plants depends on plant density and season of the year (Beer et al. 1998; Muschler 2001; Righi 2005). Modifications to the microclimate alter plant responses, leading to changes in the plants themselves (Righi 2005), in productivity and in the life cycle (Monteith et al. 1991; Brenner 1996). The irradiation fraction of 45 % (1.5 m distance) seems to be a tipping point in plant performance, with an abrupt change in many characteristics, including trunk diameter, total plant height, trunk height, canopy height, leaf number, foliage area, leaf area index (LAI) and canopy volume. The massive investment of coffee plants in canopy structure from 45 %  $I_r$  onwards is a clear response to available irradiation, increasing the area available to capture solar radiation (see detailed discussion by Righi et al. 2008).

Whereas in a monocrop situation the number of mined leaves may be related to minimum air temperature, as observed by Lomelí-Flores et al. (2010), this does not satisfactorily explain the less intense CLM damage to the relatively more shaded plants (25-40 % I<sub>r</sub>) immediately adjacent to the most intensely damaged plants. Coffee plants in shadier positions showed a perceptible decrease in the number of leaves and foliage area; the observed values were less than half of those found in sunnier positions. Cardenas (1981) found no correlation between several morphological characteristics of leaves from different coffee varieties and the degree of susceptibility to the attack of CLM, which feeds solely on the palisade tissue. Thus, the morphological adaptations themselves, including the larger specific leaf area  $(m^2 \text{ leaf } \text{kg}^{-1})$  under shade conditions (with thinner leaves and a larger surface) and the inverse in full sun (Righi 2005), are not correlated to the intensity of the pest attack.

#### Influence of rubber trees on CLM damage

Once inflicted, the damage will persist for several months, as the leaves do not drop easily. Thus, the increase in the number of mined leaves indicates the growth of a population at a specific location. The rubber trees might have had a shelter effect during the cold season, which in our study favored higher CLM damage in the zone between 1.5 and 18.5 m from the trees, with a perceptible decrease in damage toward the open field (monocrop). This protective effect more or less matched the height of the rubber trees (1 H), which was about 15 m (Fig. 3). It is impossible to relate the CLM damage from May to August to the available irradiance because the latter it reached 100 %  $I_r$ .

In April and May, when the period of water shortage began (Fig. 1), CLM damage increased steadily, and from May until July the damage almost doubled in each month. Interestingly, CLM damage to the monocrop was still low compared to the damage to the plants located beneath the rubber trees. From July onwards, CLM damage occurred more steadily, increasing more slowly and reaching its peak in October. In contrast to plants in other positions, coffee plants in the monocrop showed a continuous increase of mined leaves, which equaled the damage near the trees only in October. The largest difference between  $ET_P$  and the  $ET_R$ , as well as the highest water deficit in the soil occurred in this month (Fig. 1). These observations are in agreement with the findings of Carracedo et al. (1991), Nestel et al. (1994) and Meireles et al. (2001), all of whom observed the largest CLM occurrence in plants under conditions of more intense water shortage. Leaves under hydric stress are 2° to 4° C warmer than those of wellwatered plants and, consequently, provide almost ideal conditions for pest development (Mattson and Haak 1987). Righi et al. (2011) evaluated the instantaneous soil water content in this experimental field at the end of the same dry season and observed that plants located farther from the tree border (from 1.5 m to the beginning of the monocrop) were in a similar dry condition. The soil moisture content rose inside the rubber tree plantation. These authors attributed this effect to rainfall interception by the trees, better water infiltration and less water evaporation from the soil. Thus, plants beneath rubber trees would be subject to a lower degree of water deficiency.

With the beginning of the rains and the lessened severity of the drought in October/November, CLM damage declined until January 2004. This change in the damage level seems to be in agreement with the reports of other researchers on the incidence of this pest in the Neotropics (Villacorta 1980; Nestel et al.

1994; Souza et al. 1998; Pereira et al. 2007), who found that rain acts as a mortality factor. Conversely, Lomelí-Flores et al. (2010), in a study in Chiapas, Mexico, found a higher percentage of mined leaves in the rainy season. Weather conditions would not only affect CLM mortality rates but would also affect the reproductive potential of the pest and, therefore, significantly alter the population dynamics (Pereira et al. 2007). On the other hand, the decrease we observed in CLM damage may have been due to the senescence and the natural leaf fall. It is not possible to determine the turnover attack, as the leaves were not marked.

The degree of CLM damage on the plants located beneath the rubber trees (positions from -13.7 to -2.3 m, receiving 25–40 % I<sub>r</sub>) remained more stable with the increase in air temperature from July onwards (Figs. 1a, 3). From July onward, the damage was very low, with few mined leaves per plant; in contrast, CLM damage oscillated widely in plants located farther from the rubber trees. The coffee plants with 45 % Ir (1.5 m) showed a sudden decrease in CLM damage from August through October, and from then on all values were similar to those found in shadier areas (25–40 %  $I_r$ , from -13.7 to -2.3 m). These latter plants, from September onward, showed a slightly lower level of damage until the end of the experiment (Fig. 3). These observations partially contradict the conclusions drawn by a number of other investigators (Reis et al. 1975; Machado et al. 1978; Reis and Souza 1979, 1986; Villacorta 1980; Paulini 1990). Although the incidence of this pest usually increases during the dry season, this was not always the case in sunnier locations in this experiment. Our results directly contradict other reports from the Neotropics of CLM outbreaks following the reduction of shade and the coincidental use of pesticides on coffee farms (Monterrey et al. 2001; Fragoso et al. 2002; Carvalho et al. 2005; Lomelí-Flores et al. 2010).

In this experiment, no significant changes in the water vapor-pressure deficit between the two environments (inside and outside the rubber tree plantation), were expected. Sampaio (2003), in a similar experiment with açaí (*Eutherpe oleracea* Mart.) and rubber trees, observed a decrease of up to 1 °C in air temperature in the AFS in comparison with the monoculture, during the hottest hours of the day. Shade can raise the hydric status by lowering the temperature of the leaves on plants under hydric stress

(Ludlow and Powles 1988), and as observed by Righi (2005), coffee plants under an irradiance of  $<45 \% I_r$ are able to transpire freely. Avilés (1991) observed that the mortality rate of CLM larvae inside mined leaves increased when the water content rose, and Fonseca (1949) observed that abundant sap in leaves retards the growth of the larvae. In agreement with this idea, Bigger (1969 in: Parra 1985) found a higher larval mortality rate in younger leaves (53 %) than in older ones (15 %). In addition, Bigger came to the conclusion that rain did not cause mortality of the larvae in the field. According to Tapley (1961), high air relative humidity is not sufficient to kill the larvae inside the leaves, and the water must reach the plants directly to raise mortality rates. Therefore, it appears that water status and, consequently, the lower hydric potential could provide a clue to a reasonable explanation for the smaller degree of CLM damage in relatively more shaded coffee plants (25-40 % Ir), even though these were located in better protected areas.

## Complementary discussion

A better understanding of the eco-physiological interaction in an AFS will likely suggest new lines of scientific inquiry, in addition to improving crop management. Management of solar radiation and microclimate in an AFS by pruning shade trees during colder periods may be one way to control CLM damage in coffee. Most studies of CLM incidence fail to adequately characterize the plant microclimate. There is a lack of rigorous measurement of radiation intensity in relation to CLM incidence. It is therefore necessary to quantify the radiation intensity precisely—and not merely to state the conditions as "shade" or "sun".

Shade increases the foliar water content by reducing the temperature and vapor-pressure deficit, resulting in abundant water in leaves, which is less suitable for the development of CLM larvae. We suggest that the smaller degree of CLM damage in shadier areas is most likely due to asphyxiation of the larvae inside the leaf, as previously observed by Fonseca (1949) and Avilés (1991). This seems to be the main reason for the wider distribution and increased severity of damage of this pest during the dry season in many areas, which would occur in sunnier areas and with high air temperatures, as reported by several investigators

## Conclusions

conditions.

In our study, the rubber trees acted as a shelter during the colder autumn and winter seasons, leading to a higher incidence of CLM damage to coffee plants that extended to a distance about equal to the height of the trees (1 H).

The coffee plants adapted to the different situations (number of leaves, foliage area, etc.) and were damaged to different degrees throughout the year. Plants in full sun suffered the highest CLM damage only at the end of winter, with the increase in air temperature and hydric deficit. They showed similar damage levels to those in shadier positions (25–40 %  $I_r$ ) until the end of winter (August). Coffee plants grown beneath the rubber-tree canopy in shadier positions (25–40 %  $I_r$ ) were less damaged by CLM throughout the year. However, they showed the largest fraction of mined leaves, which can further compromise plant growth because of the naturally reduced foliage area.

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