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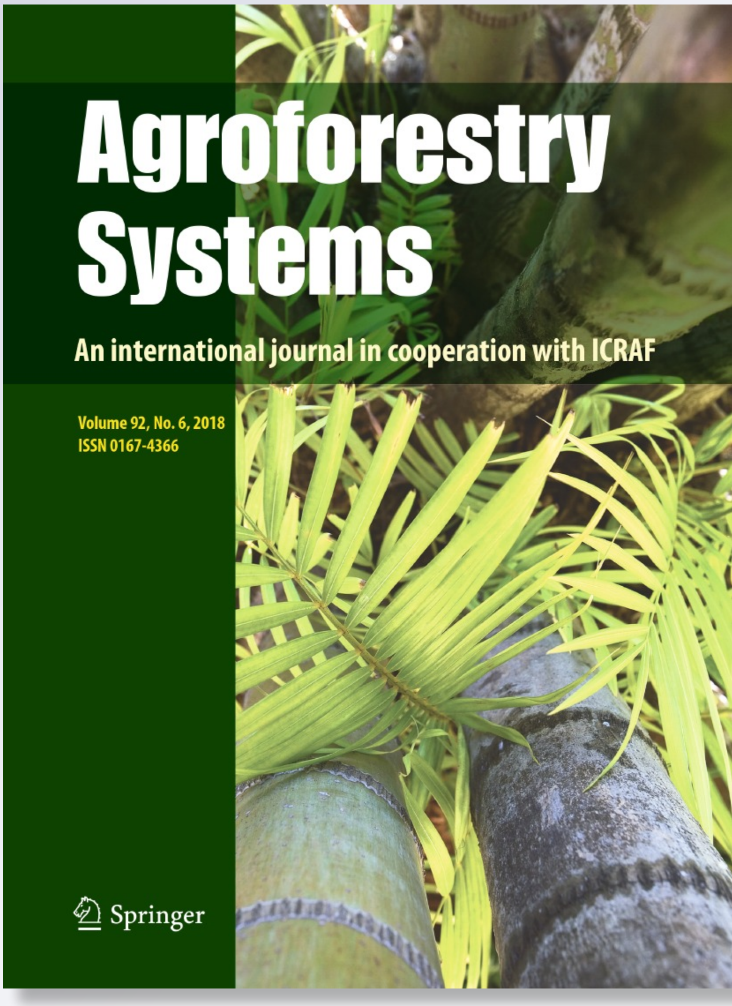

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Abstract Coffee leaf rust (CLR), caused by *Hemileia vastarix*, is one of the most serious diseases of coffee plantations and cause great losses in coffee production. We aimed to examine coffee varieties, shade, age of coffee plants, coffee plant density and soil properties in relation to CLR infection. To do this, we established a total of 75 plots in three agroforestry coffee plantations in the central Peruvian Amazon. We gathered data there in 2011 (dry season) on the presence/absence of CLR; coffee variety; age and density of coffee plants, and also took hemispherical photographs to determine canopy openness. In 2014 (wet season), we again gathered data on the same variables. In 2012, we collected soil samples from a subset of the plots. At all plantations, coffee variety had a significant effect on CLR incidence, with the Catimor variety infected less frequently than Caturra. Coffee plant age had a significant positive effect on CLR incidence. Increasing coffee density also increased CLR incidence for some of the studied plantations/seasons. Comparing those plots from which data were collected in the dry and wet seasons, we found that CLR presence was significantly higher in the wet season. The effect of shade on CLR incidence was not clear. Catimor and Caturra varieties showed opposite trends of CLR incidence in response to shade quantity in most cases (Caturra variety CLR incidence was decreasing with shading increase and Catimor CLR incidence decreasing with decreasing shading). Finally, the soil properties did not affect CLR incidence.

Keywords Coffee age · Coffee plant density · Coffee variety · Shade trees · Soil properties · Microclimate conditions

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Introduction

One of the most serious common coffee diseases is coffee leaf rust (CLR) (Kushalappa 1989; Prakash et al. 2004; Wintgens 2004), which is caused by the fungus *Hemileia vastatrix* Berk. et Br. CLR, by damaging leaves and ultimately causing them to fall, resulting in loss of physiological activity in the affected branches and thereby diminished coffee crop yield (Wintgens 2004). The disease is prevalent in the major coffee-producing countries worldwide (Wintgens 2004). In South America, CLR was first identified in Brazil in 1970 and then spread to other countries. The recent (2012–2013) outbreak of this disease lowered harvests by 10–70% in several Latin American countries, including Peru, where coffee is the key agricultural export (JNC 2014).

Catimor and Caturra are among the most popular coffee varieties in South America. The Caturra variety is well-adapted to Colombia and Central America, where it has been the subject of high-density coffee-growing practices (Wintgens 2004). However, a major problem of this variety is its susceptibility to all the main coffee diseases and pests (Wintgens 2004). Developing leaf rust-resistant varieties has been a breeding objective of the highest priority in many countries (Prakash et al. 2004; Avelino et al. 2015), and one of the results was the Catimor variety, a coffee hybrid that resulted from a cross of Caturra and the Timor hybrid, and which should be resistant to the prevailing strains of CLR (Kushalappa 1989; Wintgens 2004). Catimor is now widely distributed in the coffee-growing countries, not only in Latin America but also in Africa, Asia and Oceania (Silva et al. 2006). However in Peru the coffee varieties susceptible to CLR are still planted on approximately 95% of the area of coffee plantations (JNC 2014).

Coffee is traditionally grown under the shade of trees, forming a typical agroforestry system (Wintgens 2004). This system has many advantages compared to coffee grown in full sun, including providing a refuge for forest biota (Perfecto et al. 1996; Moguel and Toledo 1999), reducing pressure for further forest conversion to agriculture (Noponen et al. 2013), serving as a source of fuel-wood and construction material (Rice and Ward 2008), stabilizing microclimatic conditions (Lin 2007; Siles et al. 2010), and protecting soil (Siebert 2002). On the other hand, shade trees may compete with coffee for resources such as light, water and soil nutrients (Siles et al. 2010).

Influence of the tree shade on CLR is centre subject of controversy (Avelino and Rivas 2013). Increase in CLR incidence with increasing shade (Monterroso 1999) was one of the reasons for shade elimination in numerous plantations in South and Central American and Caribbean countries in the 1990s (Rice and Ward 1996). However, Eskes (1982) reported the opposite trend, i.e., CLR incidence decreasing with increasing shade. Various authors recommend intermediate levels of shading (Eskes (1982; Kushalappa 1989; Staver et al. 2001). On the other hand, Matovu et al. (2013) reported that low and medium shade intensity had the highest CLR incidence followed by high and no-shade levels. Some studies have even not detected any dependence between CLR and shade (Soto-Pinto et al. 2002; Salgado et al. 2007).

The effects of other plant and environmental variables on susceptibility to CLR have also been examined. Avelino et al. (1991) found older coffee leaves to be more vulnerable to CLR. Additionally, CLR incidence is generally higher in high-yielding plants (Zambolim et al. 1992; Avelino and Savary 2002; Wintgens 2004; Avelino et al. 2006; López-Bravo et al. 2012) and in plantations with high coffee plant density (Kushalappa 1989).

The ideal type of soil for coffee growing is slightly acidic (4.5–6), deep, permeable, and porous (Wintgens 2004). Lamouroux et al. (1995) found that CLR was generally associated with pH values that overlap with the lower part of this range (<4.7) and also with poor soil structure (especially soils with organic matter content < 3%). Avelino et al. (1998) and Pellegrin et al. (1995) noted that a low soil pH combined with high yield can also predispose coffee shrubs to the CLR infection.

Seasonal fluctuation in temperature and rain distribution also influences the incidence of CLR. Optimum temperatures for uredospore germination and infection range from 21° to 25 °C (Nutman et al. 1960; Kushalappa et al. 1983). High temperatures are restrictive to coffee rust growth, with germination inhibited above 28–30 °C (Rayner 1961; Nutman et al. 1960; Kushalappa et al. 1983) and lesion growth suppressed after several exposures to 40 °C (Ribeiro et al. 1978). In high altitude regions, coffee rust epidemics are less intense due to lower temperatures (Bock 1962; Avelino et al. 1991, 2006). Rain contributes to the transport of urediniospores for short distance, and water (i.e., H_2O in liquid form) is necessary for germination until leaf penetration (Avelino and Rivas 2013). CLR epidemics develop during the rainy season and declines when the rainy season stops (Gálvez et al. 1980; Santacreo et al. 1983; Holguín 1985; Avelino et al. 1991). However, lack of rain does not seem to be a significant limiting factor for CLR epidemic development. Other sources of free water such as dew can facilitate the germination of spores during the absence of rain (Muller 1975).

To elucidate the above factors in relation to coffee shrub susceptibility to CLR, we performed field research in four coffee plantations in Peru. Data collection was conducted at the end of both the dry and the wet seasons. The following main questions were investigated:

(a) What is the effect of coffee variety on CLR incidence in actual farm conditions?
(b) How does shading influence the incidence of CLR?
(c) How do coffee plant age, plant density and soil properties affect CLR incidence and how do these variables interact with coffee variety?

Materials and methods

Description of study sites

This study was conducted in the Villa Rica (10°44′S; 75°16W) district, Pasco region, Peru (Fig. 1), which is located in the foothills of Peruvian Andes in the tropical humid mountain forest zone. Villa Rica district is one of the centres of coffee production in Peru (Hamlin and Salick 2003), so the landscape is shaped by coffee plantations with some cattle farming. The mean annual rainfall of the area is 1590 mm, and the average annual temperature is 17.8 °C (Ponce et al. 2008). Soils in the region are classified as dystric Cambisols (Brack 2012; Michéli et al. 2006). The majority of coffee plantations in the district are using agroforestry (Greenberg and Rice 1999). CLR is a serious problem in the Pasco region: in December 2013, about 33% of coffee shrubs were infected with it (JNC 2014).

At the end of the dry season (i.e., October) of 2011, three coffee plantations were selected for the first data collection: Ave Fénix; Santa Rosa and Carrillo. Data were collected again at the end of the wet season (February) of 2014 at Ave Fénix and Santa Rosa, and data were also collected at La Torre (instead of Carrillo). Locations of all studied plantations are shown on Table 1 and Fig. 1.

Organic farming management is used in all selected plantations. Management is relatively simple and is applied identically across all the coffee plantations at each location. Coffee is pruned systematically with one-third of the rows are pruned each year to a height of 0.4 m, the next rows pruned the following year and so on, such that each row is pruned every three years (see schematic depiction in Fig. 2). The farmers leave the organic material from pruning on the soil to decompose.

Ave Fénix plantation, shaded mainly by *Inga* spp., is located in the village of Alto Palomar. During the measurement, 7.4 ha of this plantation were shaded by *Inga* spp. and 1 ha was unshaded. Santa Rosa plantation, shaded mainly by *Pinus* spp., is located near Lake Oconal. It consists of first-generation coffee plants on former pastureland, and is one of the first coffee agroforestry plantations shaded by *Pinus* spp. in the region. Carrillo plantation also comprises first-generation coffee plants, which in this case are shaded mainly by *Eucalyptus* spp. which were planted as part of the conversion process from pastureland to plantation. It is located 4 km north of the town of Villa Rica. Data collection at this plantation was not possible in February 2014 because of the elimination of coffee shrubs from this site. La Torre plantation, located next to Lake Oconal, was also shaded mainly by *Eucalyptus* spp. planted for conversion from pastureland to plantation. Data were collected at this plantation in 2014 instead of the Carrillo plantation.

Data collection

A total of 75 circular plots (25 at each of the three original plantations), each having an area of 100 m^2, were established randomly within the studied plantations, in October 2011 (dry season). In February 2014 (wet season), data were collected again from the 50 plots at the Ave Fénix and Santa Rosa plantations and 25 new plots were established and data collected from them at the La Torre plantation. CLR presence/absence, coffee variety and coffee plant age were recorded for each coffee plant on the plots. The coffee plant density was calculated for each plot. A coffee plant would be categorized as infected by CLR if the orange chlorotic spots were observed on the upper surface of the leaves. Five age classes of coffee plants

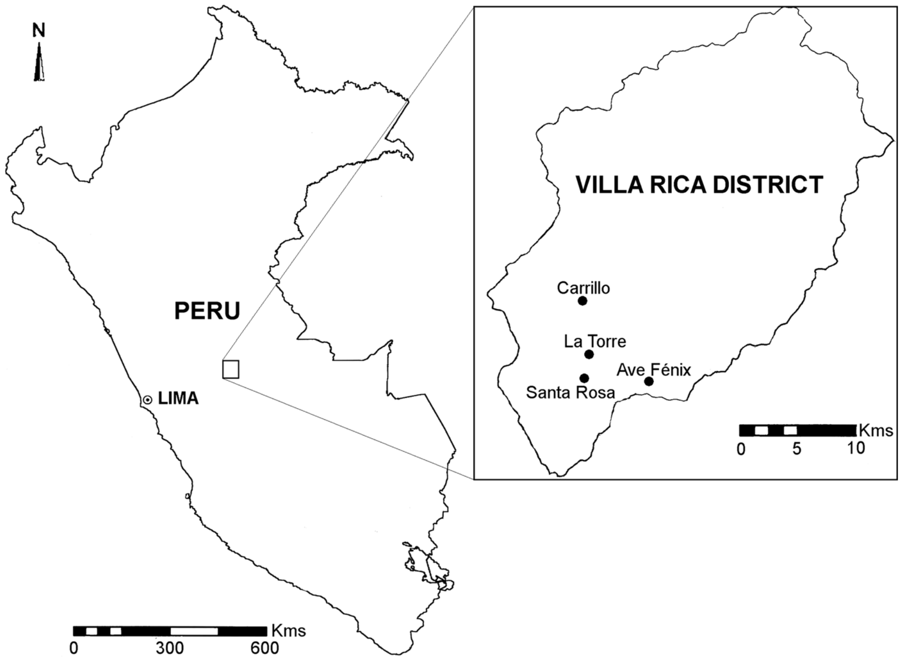

Fig. 1 Locations of studied plantations

Table 1 Descriptions of studied coffee plantations in terms of location, area, mean altitude, dominant tree species and average age

Plantation	X (UTM)	Y (UTM)	Area (ha)	Altitude (m.a.s.l.)	Dominant species	Average age (years)	Coffee varieties
Santa Rosa	471,531	8,809,929	3.98	1540	*Pinus* spp.	15	Cati, Catu, Cata
La Torre	469,052	8,811,679	0.85	1530	*Eucalyptus* spp.	11	Cati, Catu, T, B
Ave Fénix	475,784	8,808,864	7.37	1550	*Inga* spp.	15	Cati, Catu, Cata, T, P
Carrillo	471,882	8,816,212	0.96	1660	*Eucalyptus* spp.	7	Cati, Catu

UTM Universal Transverse Mercator, *m.a.s.l.* meters above sea level, *Cati* catimor, *Catu* caturra, *Cata* catuai, *T* typical, *B* bourbon, *P* pache

were distinguished: (1) from 1 to 5 years old; (2) from 6 to 10 years old; (3) from 11 to 15 years old; (4) from 16 to 25 years old; and (5) more than 25 years old. These age classes reflected the age of the whole plant (and thus did not take into account shoot ages as affected by pruning).

Hemispherical photographs to asses canopy openness were taken looking upwards from the centre of each coffee measurement plot, above coffee plant at the height of 1.6 m (using a Canon EOS 550D camera with Sigma 4.5 mm f/2.8 EX DC lens) at the same times that data were collected. The photographs were intentionally underexposed by two stops (−2EVs) as shown by Beckschäfer et al. (2013) to be the minimum required underexposure for hemispherical photographs for the purposes of forest canopy openness estimation. They were pre-processed in Lightroom 4 (Adobe Corporation), where image contrast was increased to make canopy/sky classification easier and each entire image was checked for bright areas (from direct or reflected sunlight) on stems, branches and the ground. These areas were darkened manually to ensure they were not misclassified as sky during automatic image classification. Photographs were then classified using the IsoData method in ImageJ vers. 1.48v. Finally, two canopy openness values were

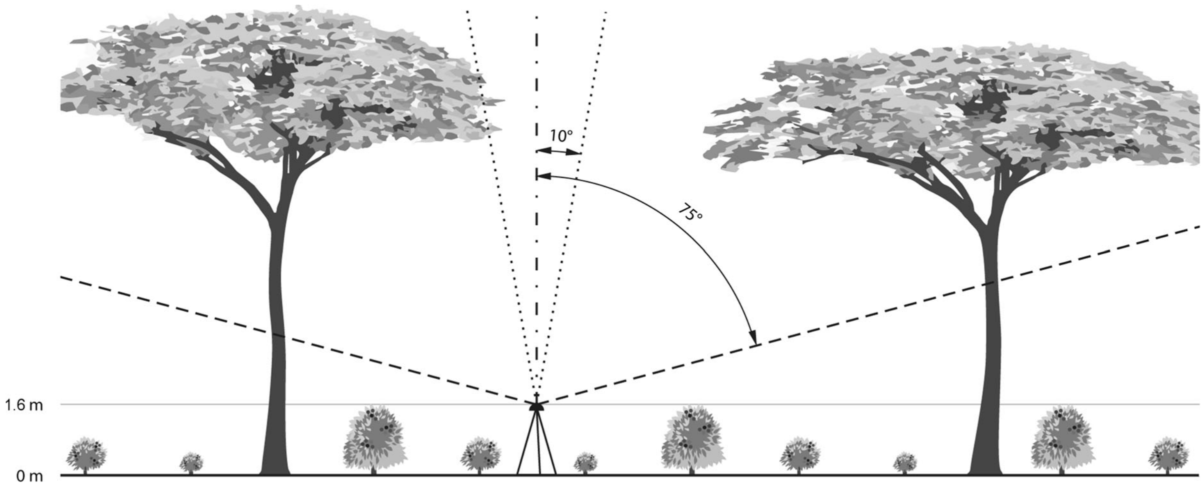

Fig. 2 Location of camera for the hemispherical photographs, showing marked zenith angles of 10° and 75°. The depiction of coffee plants (below the trees) also illustrates the systematic coffee pruning described in the text

calculated from each photograph, bot employing CIMES vers. 9 (Gonsamo et al. 2011) The first, with a 10° zenith angle, was calculated to assess the openness directly above the coffee plant, while the second, with a 75° zenith angle, was intended to characterize the overall situation (Fig. 2).

Soil samples were collected in 2012 from a total of 24 of the coffee survey plots at the Ave Fénix, Santa Rosa and Carrillo plantations (three of these plots at each plantation). All soil sampling plots were selected in similar slope (approximately 15°). From each soil sampling plot, three soil samples were taken from the depth of 0–10 cm, and were mixed together to get a mixed soil sample used for further analysis. Soil water content (denoted as moisture) was assessed by oven-drying at 105 °C; texture (sand 0.05–2 mm, silt 0.002–0.05 mm and clay <0.002 mm percentage) was assessed using a hydrometer (Bouyoucos 1962); soil reaction (pH/KCl or pH/H_2O) was assessed from suspension of soil sample:1 M KCl or H_2O, respectively at a 1:1 ratio (v:w); aluminium content (Al) was assessed according to Yuan (1958); total organic carbon (TOC) was assessed according to Walkley and Black (1934); nutrient content (K_2O in kg ha^{-1}, Ca and Mg in Cmol kg^{-1}) was assessed from suspension of soil sample:1 N ammonium acetate at a 1:10 ratio (v:w) using atomic adsorption spectrophotometry from a solution of 1 N ammonium acetate at pH 7; cation exchange capacity (CEC) was assessed as effective in 1 N KCl when soil sample:eluent ratio was 1:10 (v:w); and base saturation (BS) was expressed as the base cation percentage of CEC. All soil samples were processed at the laboratory of the Universidad Agraria Nacional de la Selva, Tingo Maria, Peru.

Air temperature and air humidity at the Ave Fénix plantation were measured continuously at the shaded and non-shaded sites at a height of 2 m using a Minikin RTD (EMS, Brno, Czech Republic) with sensor accuracy ±0.2 °C and ±2%, respectively. The microclimatic measurements were conducted from February 2011 to January 2014.

Statistical analysis

We used boxplots to show the distributions of age, plant density and openness of all studied plantations from the data collected in 2011 and 2014. Next, we analysed whether there were differences in CLR infection probabilities on different plantations using generalised linear mixed effect models (GLMM) with binomial distribution of errors, logit link function and treating plot ID as a random effect.

Our main goal in statistical analysis was to reveal the main factors influencing CLR infection probability. Because we found in the preliminary analysis that plantations were fairly distinct in their ranges of explanatory variable values and that the overall dataset was rather unbalanced, we decided to conduct separate analyses for each plantation/season. We again used GLMM with plot ID as a random effect, binomial distribution of errors and logit link function. Our response variable was coffee plant infection probability and explanatory variables (fixed effects) were coffee variety, age, canopy openness and density. We chose to examine only the most important coffee varieties, Caturra and Catimor, as the other varieties were often missing, making analysis difficult to perform. First, we calculated simple models with only one fixed effect and then we combined several variables to find the overall best model and its alternatives. We also included interactions of age, canopy openness and density with coffee variety because we expected that the responses of these variables could be different for resistant and susceptible varieties. We reported final models with all significant combinations of variables, along with the values for their AIC (Akaike Information Criterion) and marginal and conditional pseudo R^2 (Nakagawa and Schielzeth 2013).

We simplified the analyses of soil variables because we had a relatively small sample size—a total of 24 samples from all plantations. Therefore, we analysed all plantations together instead of doing separate analyses for each plantation. Additionally, because we had just one value for each soil variable for each sample plot, we used a generalized linear model (GLM) approach with quasibinomial distribution of errors and link function logit instead of the more sophisticated GLMM. In the first model (M1), each soil variable was used as the only fixed effect variable. Because we found coffee plant age and variety to be the most important variables, we also fitted one model (M2) with the interaction of the particular soil variable and the mean coffee plant age on the plot and one model (M3) with the interaction of the particular soil variable and percentage of resistant Catimor variety on the soil sampling plot. Next, to have a general overview of all soil variables, we generated ordination plots using principal component analysis (PCA).

Statistical analyses were carried out in the software environment of R version 3.2.3 (R Core Team 2015), GLMM in lme4 package version 1.1-11 (Bates et al. 2014), conditional and marginal pseudo R^2 in MuMIn package version 1.15.6 (Bartoń 2015), and PCA in vegan package version 2.3-5 (Oksanen et al. 2016).

Results

Basic characteristics of coffee plantations

Data distribution for age, coffee plant density and canopy openness is shown in box plots (Fig. 3). We divided the studied plantations into two groups regarding coffee plant age: even-aged (Carrillo and La Torre) and uneven-aged coffee plantations (Ave Fénix and Santa Rosa). The lowest coffee plant density was at the Carillo plantation and the highest at the Ave Fénix plantation. Canopy openness 75 was lower in 2014 than in 2011 and its variability was low in all plantations. Canopy openness 10 also decreased between the years 2011 and 2014, but had greater variability in all plantations.

According to the results of the soil analyses, (Table 2; Fig. 4) the plantations are generally characterized by loamy texture, having strongly acidic pH/KCl, high to very high TOC content, medium to high content of Mg, low (Santa Rosa) to moderately low CEC and high to very high BS. The soil parameters were well-grouped at Santa Rosa, especially compared with Ave Fénix, which has a larger area with more varied conditions.

Average daily temperature in October 2011 (dry season) at the shaded site was 18.6 ± 0.5 °C and at unshaded site it was 19.0 ± 0.5 °C. Average daily temperature in February 2014 (wet season) was 18.4 ± 0.3 °C at the shaded site and 18.9 ± 0.4 °C at the non-shaded site. Average daily humidity on October 2011 was 87.7 ± 3.17% at shaded site and 82.5 ± 3.24% at the non-shaded site; in February 2012 it was 97.4 ± 1.12% at shaded site and 96.4 ± 1.47% at the non-shaded site. All standard deviations were calculated from daily means. In the dry season, October 2011, temperatures were optimal for CLR from 12:00 to 17:00 at the shaded site and from 11:00 to 17:00 at the non-shaded site. In the wet season, February 2014, it was from 14:00 to 16:00 at the shaded site and from 12:00 to 17:00 at the non-shaded site. The difference between the shaded and non-shaded sites was higher in the wet season (Fig. 5).

Influence of coffee variety, shade, age and plant density on CLR incidence

The most important factors influencing CLR incidence were coffee variety and the age of the coffee

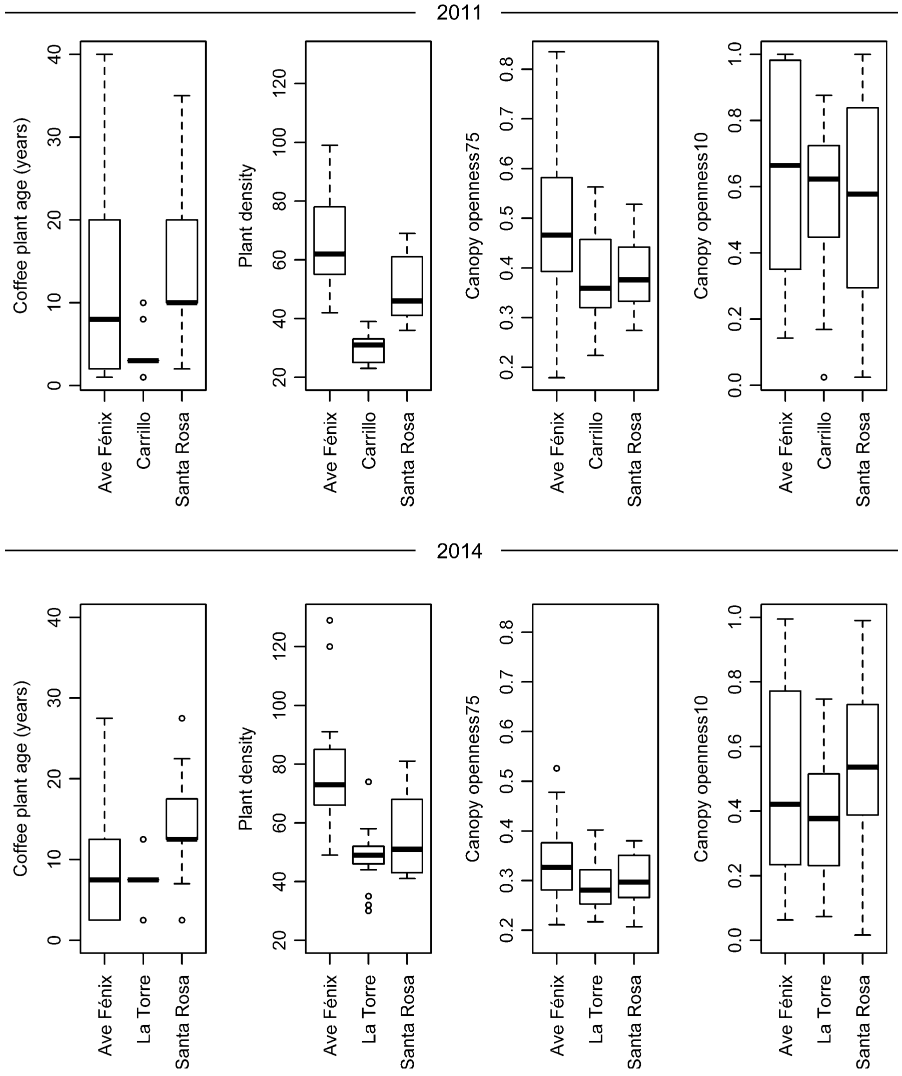

Fig. 3 *Boxplots* showing distributions of age, plant density and canopy openness (10° and 75°) of all studied plantations from 2011 and 2014. The *horizontal line* in each *box* represents the median; the *hinges* represent the 25th and 75th percentiles; the *whiskers* represent 1.5 times the interquartile range and *open circles* represent values outside this interval

plants. Catimor had less CLR incidence than the Caturra variety at all plantations in both 2011 and 2014 ($p < 0.001$, at the Carrillo plantation $p = 0.004$, Fig. 6). Coffee plant age was the second-most important factor: with increasing age the probability of CLR infection increased at the majority of plantations ($p < 0.001$, for Ave Fénix 2014 $p = 0.027$, Carrillo and La Torre – not significant, Table 3; Fig. 6a–d).

The effect of shade (here characterised in terms of canopy openness) on CLR incidence was not very clear. Canopy openness measured using a 10° angle significantly influenced CLR incidence in the wet season (p-values from 0.002 to 0.037), but it was not significant in the dry season. On the other hand, canopy openness measured using a 75° angle significantly influenced CLR incidence in the dry season (p-values from 0.001 to 0.026) but it was not significant in the wet season (with the exception of the Caturra variety at Ave Fénix).

Coffee plant density influenced the CLR incidence at just half of the studied plantations/seasons, and it had mostly a positive effect on CLR incidence with the exception of Caturra at Ave Fénix and Catimor at Santa Rosa ($p < 0.001$ for Santa Rosa 2011, interaction of density and variety p-values ranged from 0.004 to 0.038 for La Torre, Ave Fénix 2011 and Santa Rosa 2014, Table 3; Fig. 6c, f). Soil characteristics were not

Table 2 Basic soil properties—means and standard deviations (SD) in first 10 cm layer of soil in each plantation and p-values reported from analysis of the effects of soil variables on CLR incidence

Soil property	Ave Fénix	Carillo	Santa Rosa	M1 p value	M2 p-value	M3 p-value
Soil texture						
Sand content (%)	42.7 ± 11.9	47.7 ± 8.3	48.0 ± 6.3	0.333	0.425	0.952
Clay content (%)	24.9 ± 7.6	19.0 ± 2.6	15.0 ± 2.3	0.404	0.543	0.109
Silt content (%)	32.4 ± 5.9	33.3 ± 6.3	36.9 ± 5.2	0.512	0.487	0.140
Soil reaction						
Potential soil reaction pH/KCl	3.8 ± 0.5	4.4 ± 0.3	4.1 ± 0.3	0.590	0.140	0.289
Active soil reaction pH/H_2O	4.1 ± 0.41	4.7 ± 0.2	4.3 ± 0.3	0.525	0.167	0.242
Total organic carbon (%)	2.0 ± 1.1	1.8 ± 0.7	2.4 ± 0.5	0.435	0.166	0.463
Nutrient content in total amount K_2O [kg/ha]	459.6 ± 112	315.4 ± 143.5	330.6 ± 84.2	0.431	0.342	0.189
Ca exchangeable (Cmol/kg)	6.8 ± 4.5	12.2 ± 3.1	5.1 ± 1.1	0.359	0.342	0.677
Mg exchangeable (Cmol/kg)	1.6 ± 0.6	1.8 ± 0.6	1.1 ± 0.2	0.396	0.296	0.148
Cation exchange capacity (Cmol/kg)	11.5 ± 4.6	15.1 ± 3.2	7.5 ± 1.1	0.720	0.245	0.163
Base saturation (%)	70.4 ± 16.9	92.6 ± 3.4	81.8 ± 6.4	0.837	0.320	0.117

M1 simple model with soil characteristic only, *M2* model with soil characteristic, mean plot age and their interaction; *M3* model with soil characteristic, plot Catimor plant representation (as percentage of all coffee plants on plot) and their interaction; p-value of interaction term is reported

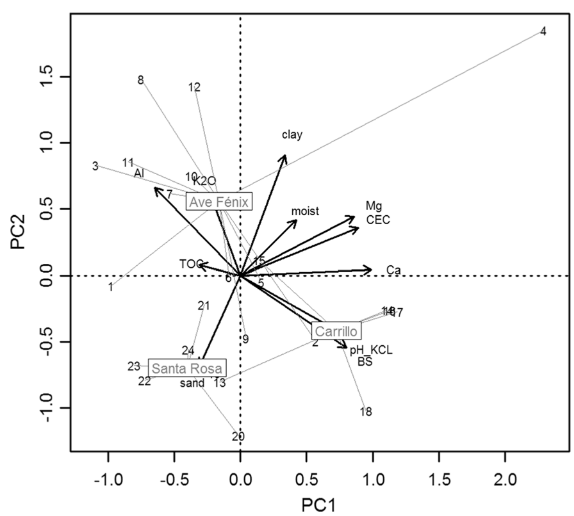

Fig. 4 Ordination of studied soil properties showing interactions among them and individual plantations obtained by principal component analysis. Plots within the same plantation are distinguished using a spider plot

significant either when considered by itself or in interaction with coffee variety or age.

For the two plots (at Ave Fénix and Santa Rosa plantations) from which data were collected in both October 2011 and February 2014, we found that CLR incidence was significantly higher ($p < 0.001$) in 2014. The increase in CLR infection was more pronounced in the Santa Rosa plantation (from 51 to 60%) than in Ave Fénix (52–53%). Figure 7 shows CLR incidence in studied plantations/seasons. Final models are provided in the Table 4.

Discussion

Average CLR incidence for each plantation ranged from 10 to 51% in the dry season (October 2011) and from 16 to 60% in the wet season (February 2014). This is in the range of CLR infection reported in Peru (10–70%) (JNC 2014), but higher than other authors have found elsewhere: on plots in Mexico, Soto-Pinto et al. (2002) found the percentage of CLR ranged from 5.1 to 20.2%; Avelino et al. (1991) reported 24% CLR in Mexico; and Brown et al. (1995) found an 18% incidence of CLR in Papua New Guinea.

Our study found coffee variety to have an important effect on CLR incidence. In particular, the Caturra was the susceptible variety and Catimor the resistant one as others have also found (Wintgens 2004; Silva et al. 2006). Moreover, we found that the effect of other factors—especially canopy openness and coffee plant

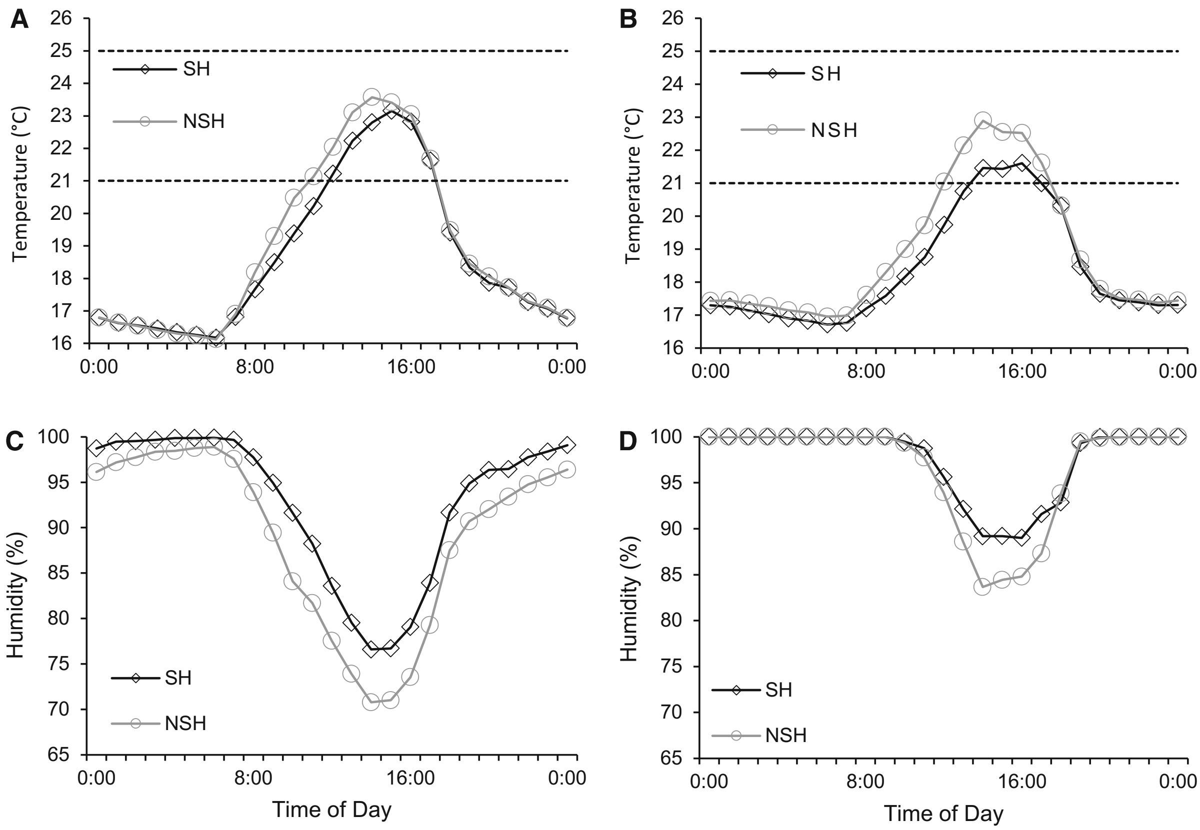

Fig. 5 Average hourly air temperature (**a**, **b**) and air humidity (**c**, **d**) in the dry season, October 2011 (**a c**) and in the wet season, February 2014 (**b d**). *SH* shaded site, *NSH* non-shaded site. Temperatures between the *dotted lines* are optimal for CLR development

density differed for the Catimor and Caturra varieties (significant interaction of these variables and variety) (Table 2; Fig. 3).

The second-most important factor influencing CLR incidence was age. With increasing age, CLR incidence increased for both studied varieties. We did not find other studies examining the effect of plant age on CLR presence. However, Eskes and Toma-Braghini (1982) studied the influence of leaf age on incomplete resistance to CLR in Brazil and found that for the susceptible variety Catuai there was no effect of leaf age on the latency period, but for Catimor, the resistance to CLR decreased with increasing leave age. Additionally, the results of Coutinho et al. (1994) indicated that Caturra showed increased resistance with increasing leaf age. However, our results cannot be directly compared with the results of Eskes and Toma-Braghini (1982) or Coutinho et al. (1994), because the age of whole plants does not reflect the age of leaves, mainly because plants in plantations such as those studied are pruned regularly. In the context of our study, it is important to mention that approximately 70% of the coffee plantations in Peru are older than 20 years (JNC 2014) and hence the risk of CLR epidemic is large. In particular, we found that the critical age at which CLR infection increases substantially even for the resistant Catimor variety seems to be between 15 and 20 years. Therefore, when coffee plants reach this threshold, they should be replaced with new ones.

Our study, like previous research (Avelino and Rivas 2013), shows that the influence of shade on CLR is not straightforward. Although Eskes (1982) found that increased shading was associated with increased *Coffea arabica* resistance to CLR, that study's methodology incorporated artificial inoculation of leaves, making a direct comparison with our study difficult. Monterroso's (1999) comparative study of shaded (80%) and open-sun coffee fields in the uplands of southern Nicaragua showed rust levels to

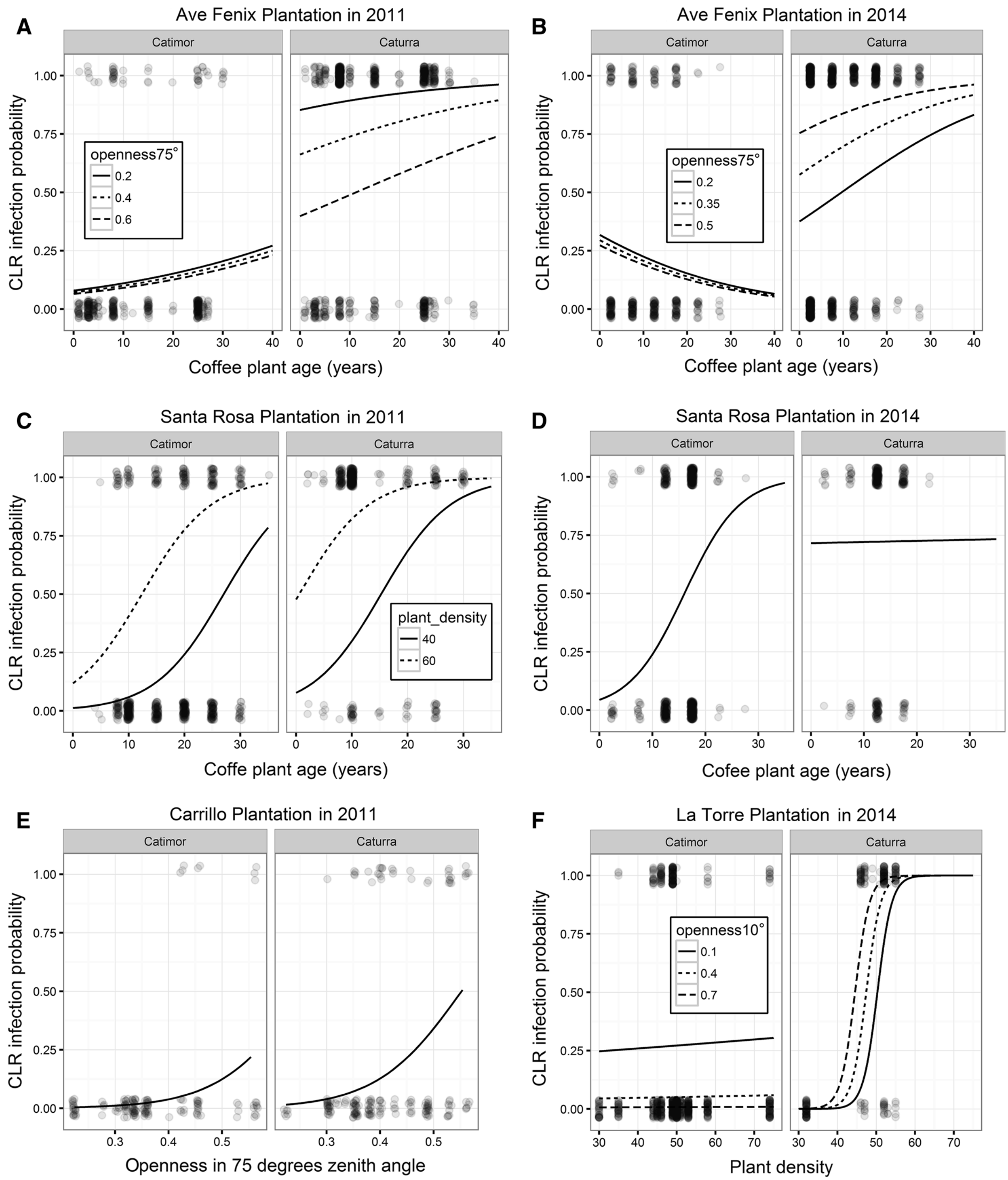

Fig. 6 The probability of CLR infection in relation to the most important variables (separately for plantations and seasons: **a**, **b**—Ave Fenix; **c**, **d**—Santa Rosa; **e**—Carrillo, **f**—La Torre). *Dots* represent observed values jittered around the *x* and *y* axes and semi-transparent to be more informative because there were just two possible values 1 and 0 (CLR present/not present)

be higher in the shade; this was attributed primarily to increased humidity. Although our findings regarding shade differed from those of Monterroso (1999), we also suggested increased humidity to be associated with higher CLR incidence during the wet season.

Our results regarding effects of shade (in terms of canopy openness) differed when assessed for the angles 10° and 75° (canopy openness 10° and canopy openness 75°, respectively). Interestingly, canopy openness 10° had an effect on CLR incidence only in the wet season, whereas canopy openness 75° had an effect on CLR incidence in the dry season (except for the Caturra variety at Ave Fénix). The importance of canopy openness 10° during the wet season could be explained by the effect of shade trees growing directly over the coffee in decreasing the amount of rain that falls on coffee plants (interception effect). In contrast, canopy openness 75° is more representative of lateral light, which is likely more important in the dry season when the shade from neighbouring is important in the morning and afternoon. Particularly interesting is that the Catimor and Caturra varieties showed opposite trends in response to canopy openness in most cases. For Caturra, increasing canopy openness results in increasing CLR incidence in the majority of plantations/seasons, whereas for Catimor, increasing canopy openness was associated with decrease CLR incidence in most of the plantations/seasons.

Our results also indicate that increasing coffee plant density generally increased the incidence of CLR. This is in accordance with Avelino and Rivas (2013), who reported that the practice of planting coffee at high densities favoured CLR incidence in standardized fruit

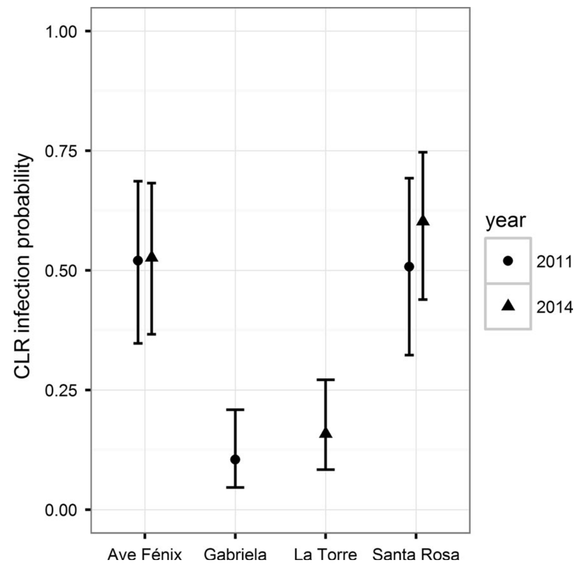

Fig. 7 Probability of CLR infection by plantation and season (October 2011 and February 2014). Mean values for plantations and seasons were calculated using GLMM and their 95% confidence intervals are shown. Pairwise comparisons of plots in Ave Fénix and Santa Rosa plantations (using GLMM) showed significant differences between the two seasons ($p < 0.001$)

Table 3 Overview of the effects of studied variables on CLR incidence shown for traditional Caturra and resistant Catimor coffee varieties and for different plantations and seasons

Season	Plantation	Age		Openness10		Openness75		Density	
		Catimor	Caturra	Catimor	Caturra	Catimor	Caturra	Catimor	Caturra
2011	Ave Fenix	+	+	.	.	-	--	+	-
2014	Ave Fenix	-	+	-	+	.	+	.	.
2011	Santa Rosa	++	++	.	.	-	+	+	+
2014	Santa Rosa	++	.	+	-	.	.	(-)	+
2011	Carrillo	.	.	.	.	+	+	.	.
2014	La Tore	.	.	-	+	.	.	.	+

'++' strong positive effect (i.e., CLR incidence increase); '+' positive effect; '.' non-significant effect; '(−)' negative effect (i.e., CLR incidence decrease); '--' strong negative effect. Plantations with very narrow gradient for the particular variable and variety are indicated by a grey background

Table 4 Overview of final models estimating CLR infection probability for studied plantations and seasons

Model specification	ΔAIC	Marginal pseudo R^2	Conditional pseudo R^2
2011			
Ave Fenix			
Sort × Plant density + Sort × Openness 75 + Age	–	0.484	0.707
Sort × Openness 75 + Age	1.1	0.465	0.696
Carrillo			
Sort + Openness 75	–	0.350	0.451
Santa Rosa			
Sort × Openness 75 + Age + Plant density	–	0.350	0.570
Sort + Age + Plant density	4.7	0.303	0.550
Sort × Openness 75 + Age	9.3	0.201	0.589
2014			
Ave Fenix			
Sort × Age + Sort × Openness 75	–	0.209	0.412
Sort × Openness 75	12.3	0.199	0.422
Sort × Openness 10	22.6	0.173	0.432
La Torre			
Sort × Plant density + Sort × Openness 10	–	0.449	0.775
Santa Rosa			
Sort × Age + Sort × Openness 10	–	0.160	0.439
Sort × Plant density + Sort × Openness 10	16.5	0.169	0.434

Models were fitted using generalised linear mixed models with binomial distributions. AIC differences (ΔAIC) from the best model for particular plantations, and marginal and conditional pseudo R^2 values are shown. Marginal pseudo R^2 values are associated with fixed effects only, whereas conditional pseudo R^2 values are associated with both fixed and random effects

ripening conditions (i.e., same quantity of ripe fruit per branch). Moreover, high coffee plant density increases the leaf area index (Arcila-Pulgarín and Chaves-Córdoba 1995; Cannell 1975), which favours urediniospore interception (Avelino et al. 2004). High densities can also favour the spread of the disease from plant to plant by increasing contact between plants (Burdon and Chilvers 1982). However, on Caturra plants at Ave Fénix in 2011 the CLR incidence decreased with increasing coffee shrub density. This might best be understood in terms of increased coffee planting density implying greater self-shading between coffee plants (Avelino et al. 2004), which, therefore, would produce similar effects to those of increased shade, which mostly resulted in decreased CLR incidence for Caturra in our study.

Soils at all the plantations had pH values near or below the lower limit favourable for coffee growing, with the pH/KCl in particular not in the range of appropriate values for this activity (Wintgens 2012). Moreover, these values were in the range that increases susceptibility to CLR (Lamouroux et al. 1995; Avelino et al. 1998; Pellegrin et al. 1995). In contrast, the soil structure we found does not favour CLR presence (Lamouroux et al. 1995), and the soil nutrient status (Ca, Mg and K content evaluated according to the criterion of Costantini 2009) did not limit coffee growth at any of the studied plantations. Finally, we did not find any soil variable to have a significant effect on CLR incidence. However, the range of soil properties in our study was relatively narrow, which resulted in low potential to detect significant trends.

It is known that incidence of CLR is influenced by microclimate conditions (Avelino and Rivas 2013; Avelino et al. 2007; Carvalho et al. 1961; Smith 1981). In our case, CLR optimal temperatures were observed for a longer time in October 2011 (dry season) than in February 2014 (wet season) at Ave Fénix, at both the shaded and non-shaded sites. This would suggest that we would find a higher CLR incidence in October

2011. However, we found the opposite, i.e., a higher CLR incidence in February 2014. We suppose that in February 2014 the determining factor was the wetter climate rather than temperatures. Other authors have also reported similar results (Gálvez et al. 1980; Santacreo et al. 1983; Holguín 1985; Avelino et al. 1991), showing that CLR epidemics develop during the rainy season and decline when the rainy season ends.

Conclusions

Our study showed that, of the factors we considered, the ones with the most important influence on CLR incidence are coffee variety and the age of the coffee plants. The importance of coffee plant age is an especially important finding because of the overall lack of studies focused on this factor. The effect of canopy openness on CLR incidence differed between the different zenit angles used for openness assessment, and among varieties and plantations. Canopy openness 10° had effect on CLR incidence only in the wet season, and canopy openness 75° had effect on CLR incidence in the dry season. Especially noteworthy is the fact that Catimor and Caturra varieties showed opposite trends in response to canopy openness in most cases. These results indicate the need of study the influence of shade effects in concert with other factors influencing CLR incidence.

Our general recommendation for coffee growers is to use resistant coffee varieties and to replace coffee plants when they become too old to be resistant to CLR infection. On the other hand, conversion of agroforestry to monoculture plantations is not recommended as a way to reduce the CLR presence, as the relationship between the amount of shade and the CLR presence remains unclear, and, moreover, such a transition would result in loss of the various benefits provided by agroforestry.

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