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Shade tree traits and microclimate modifications: Implications for pathogen management in biodiverse coffee agroforests

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Shade tree traits and microclimate modifications: Implications for pathogen management in biodiverse coffee agroforests

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Abstract

Diversified coffee agroforests modify microclimate conditions in comparison to monocultures, impacting the success of significant plant pathogens, such as *Hemileia vastatrix*, which causes coffee leaf rust (CLR). However, research is often limited to the dichotomous analysis of shaded agroforestry systems or unshaded monocultures, often overlooking the nuanced effect of shade tree trait diversity. Our study aims to determine the cumulative effects of shade tree canopy architectural characteristics and leaf functional traits in biodiverse agroforests on microclimate modifications and CLR incidence. We measured plot-level microclimate conditions (air temperature, relative humidity, leaf wetness duration, throughfall kinetic energy) in three single-stratum and two double-strata shade tree canopy treatments, including *Erythrina poeppigiana, Terminalia amazonia,* and *Chloroleucon eurycyclum*. Commonly reported canopy characteristics and leaf traits were compared to average microclimate conditions and CLR incidence levels. We found that shade tree trait expression significantly explained most microclimate conditions, and that two key shade tree traits (canopy openness, leaf area) significantly explain CLR incidence levels ($R^2 = 0.211$, $p = 0.036$). Our results highlight the differences in microclimate conditions and CLR incidence among biodiverse agroforests, as well as the important explanatory power of shade tree traits. Specific effects of shade tree traits on pathogen dynamics can directly inform agroforestry system design (i.e. shade tree species selection) and sustainable coffee farm management practices (i.e. pruning practices).

Keywords: agroforestry, *Coffea arabica*, Costa Rica, diversity, *Hemileia vastatrix,* leaf functional traits, shade tree architecture

1. INTRODUCTION

Diversified agroforestry systems are characterized by the deliberate planting and retention of

both native and non-native tree species. This enhanced diversity contributes many important

ecosystem features (e.g. habitat; Perfecto, Rice, Greenberg, & Van Der Voort, 1996) and

processes (e.g. nutrient cycling; Isaac & Borden, 2019). However, one often overlooked but

important modification in biodiverse agroforests is the modification of microclimate conditions

(Lin, 2007; Siles, Harmand, & Vaast, 2010), including relative humidity and air temperature (e.g.

Vaast, Kanten, Siles, & Angrand, 2008), rainfall characteristics (e.g. Avelino et al., 2020), and

leaf wetness dynamics (e.g. López-Bravo, Virginio-Filho, & Avelino, 2012). These shifts in

microclimate conditions can lead to expanded growing regions (DaMatta & Ramalho, 2006) and

greater resiliency to climate change (Lin, Perfecto, & Vandermeer, 2008). They can also lead to

changes in pathogen incidence in the understory plant community (Koech & Whitbread, 2000;

Schroth, Balle, & Peltier, 1995).

However, these effects are complex and results in the literature are often contradictory (e.g.

Mortimer, Saj, & David, 2018), including in coffee agroforestry systems (Avelino, Allinne,

Cerda, Willocquet, & Savary, 2018). A dominant coffee pathogen is *Hemileia vastatrix*, which

causes the foliar disease coffee leaf rust (CLR), the only important coffee disease with global

distribution (Avelino et al., 2018). This obligate biotrophic fungus infects coffee leaves via

dispersed uredospores that penetrate through coffee leaves' stomata with appressoria.

Microclimate conditions largely determine the success of various lifecycle stages of the *H.*

vastatrix fungus at a fine temporal scale (Merle, Tixier, Virginio Filho, Cilas, & Avelino, 2020).

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More specifically, uredospore dispersal is encouraged by high wind speeds and rainfall energy (Kushalappa & Eskes, 1989; Rayner, 1961b; Waller, 1982); uredospore germination requires wet leaves (Rayner, 1961a); and uredospore germination, penetration, and colonization excel within specific air temperature ranges and low light conditions (Avelino, Willocquet, & Savary, 2004).

The microclimate modifications possible in biodiverse agroforestry systems largely depend on shade tree selection (van Oijen, Dauzat, Harmand, Lawson, & Vaast, 2010), due to large differences in shade tree architectural characteristics and leaf functional traits, both interspecifically (Hallé, Oldeman, & Tomlinson, 1978) and intraspecifically (Gagliardi, Avelino, Beilhe, & Isaac, 2020). Investigating the variability in these traits allows us to understand the mechanistic underpinnings of plant responses to and plant effects on other species (e.g. Fulthorpe, Martin, & Isaac, 2020). This approach has furthered our understanding of biodiverse agroforestry systems, specifically in relation to nutrient cycling (Blesh, 2018), litter decomposition (García-Palacios, Maestre, Kattge, & Wall, 2013), crop yield (Gagliardi, Martin, Virginio-Filho, Rapidel, & Isaac, 2015), and wind-borne pathogen dispersal patterns (Gagliardi et al., 2020). Shade tree architectural characteristics and leaf traits, such as canopy shape and leaf area, are regularly considered by farmers during agroforestry farm design, because of their perceived influence on coffee production and pest incidence (Cerdán, Rebolledo, Soto, Rapidel, & Sinclair, 2012; Isaac et al., 2018; Valencia, West, Sterling, García-Barrios, & Naeem, 2015). While there are some studies that incorporate shade tree species descriptions in their analyses (e.g. Van Kanten & Vaast, 2006), and there is growing acknowledgement of shade tree traits on urban microclimate conditions (e.g. Rahman et al., 2020), it is commonplace for research on coffee to focus on the dichotomy of shaded coffee agroforestry systems versus unshaded

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monocultures, overlooking the inevitable variability among agroforestry systems and constraining the applicability of results to on-farm practices.

Our study, along a gradient of shade tree trait diversity, aims to determine the cumulative effects of shade tree architectural characteristics and leaf functional traits in biodiverse agroforestry systems on important understory microclimate modifications and CLR incidence levels. We hypothesize that: (1) microclimate conditions that are key to the *H. vastatrix* lifecycle will significantly change under different shade tree canopies; (2) these changes will be partially explained by canopy characteristics and shade tree leaf traits; and (3) patterns of CLR incidence will correspond to key shade tree traits. Our findings will complement detailed phytopathology research that describe pathogen micro-processes at the leaf-level (see Merle et al., 2020), by exploring the role of shade tree traits on microclimate variability and pathogen dynamics.

2. MATERIALS AND METHODS

2.1. Site description

This study was conducted at the international coffee agroforestry research trial by the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), in Turrialba, Costa Rica located at 09°53´44" N and 83°40´7" W, at 685 m a.s.l. Measurements took place from May to July 2017, during the rainy season in this region, which averages 3200 mm of annual rainfall (Haggar et al., 2011). All leaf sampling took place in July 2017 during that year's peak CLR incidence, which varies annually (Avelino et al., 2020; Boudrot et al., 2016; López-Bravo et al., 2012). Within the site, *Coffea arabica* cv. Caturra (herein referred to as coffee), a variety susceptible to CLR, is

planted in agroforestry systems at a density of 5000 plants ha^{-1} with 1 m spacing between plants within coffee rows and 2 m between rows.

We included five distinct types of shade tree treatments in our study, including three single-stratum and two double-strata canopies: *Erythrina poeppigiana* (E), *Terminalia amazonia* (T), *Chloroleucon eurycyclum* (C)*, E. poeppigiana + T. amazonia* (ET) and *E. poeppigiana + C. eurycyclum* (EC) (Figure 1). Both *E. poeppigiana* and *C. eurycyclum* are leguminous tree species. These shade tree treatments were selected due to the substantial differences in canopy and leaf characteristics (Table 1), as well as to reflect common agroforestry practices in the region. *Erythrina poeppigiana* is the most commonly used shade tree species in the study region (Russo & Budowski, 1986), where it often undergoes pruning twice a year and is planted as the single shade tree species within a coffee plantation or in combination with taller shade trees.

All shade tree treatments were repeated in two amendment regimes: (1) moderate conventional, including chemical fertilizers with 150 kg N ha^{-1}, 10 kg P ha^{-1}, 75 kg K ha^{-1}, foliar mineral applications, and copper-based fungicide with cyproconazole applied to foliage; and (2) intensive organic, including chicken manure with 287 kg N ha^{-1}, 205 kg P ha^{-1}, 326 kg K ha^{-1}, and Bordeaux mixture applied to foliage. All shade tree and amendment treatment combinations were then repeated in three distinct blocks within the CATIE farm.

2.2. Plot configurations

A total of 30 circular study plots were established under a representative canopy of the shade tree treatments, where each treatment was repeated twice in each of the three blocks (for a total of 6 plots per shade tree treatment). In single-stratum canopy plots, the center of each plot was one representative shade tree of that species (herein referred to as the central tree). The boundaries of

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these plots were dictated by the size of the selected central tree (dotted boxes in Figure 1a), thus

confining the plot to the area directly beneath this shade tree's canopy and leading to a range of

plot sizes (3 m to 22 m in diameter). In double-strata canopy plots, the center of each plot was

one representative *E. poeppigiana* tree (the shortest tree; herein referred to as the central tree),

whose canopy was situated beneath the canopy of the taller shade tree present. The boundaries of

these plots were dictated by the size of the selected central *E. poeppigiana*, thus confining the

plot to the area directly beneath the overlapping of both shade tree canopies (dotted boxes in

Figure 1b), and again leading to a range of plot sizes (8 m to 22 m in diameter).

In each study plot, we collected measurements to characterize the microclimate within each

plot, the representative shade tree(s), and the incidence of CLR present on the coffee plants

confined within each plot (Figure 1). Each of these measurements are described below.

2.3. Microclimate measurements

The microclimate variables selected for this study reflect the dominant small-scale microclimate

conditions that are important to the lifecycle of *H. vastatrix* (see Avelino et al., 2004; Boudrot et

al., 2016), namely air temperature, relative humidity, leaf wetness duration, and throughfall

kinetic energy (TKE; i.e. the energy of raindrops after passing through a shade tree canopy). A

HOBO® datalogger (Onset Computer Corporation, Bourne, MA) and microclimate sensors were

installed next to the selected central tree between the main stem and canopy's outer edge

between the coffee plant rows. These microclimate stations were installed in five plots (each of

the shade tree treatments) in the same block simultaneously for seven consecutive days, rotating

between each of the amendment regimes and blocks, for a total of nine weeks between early May

and late July 2017 (n = 63 days per treatment). Microclimate measurements were recorded every

five minutes.

Each microclimate station included one HOBO® air temperature and relative humidity

sensor (S-THB-M008) and one HOBO® leaf wetness sensor (S-LWA-M003). All air

temperature and relative humidity sensors were installed on a stable vertical post and positioned

above the average coffee plant height at about 2 m. Daily air temperature and relative humidity

values were calculated based on data collected from midnight CST (or time of microclimate

station installation) until 11:55 pm CST (or time of microclimate station removal). Start and stop

times were kept consistent across all sampling plots.

Leaf wetness sensors were positioned at mid-coffee plant height (about 1 m), between the

coffee plant row directed either north or south, laying horizontally and tilted at a 45° angle facing

east. Leaf wetness duration was calculated as the amount of time (hours) that the leaf wetness

sensor was wet between 6:00 am CST and 7:00 pm CST. All wetting and drying processes were

captured within this timeframe. Leaf wetness sensors were consistently wet outside of these

times due to rainfall events and overnight dew. Leaf wetness sensors were calibrated in the field

prior to data collection to determine the transition point between wet and dry.

Total TKE of rain events was measured using Tübingen splash cups (Scholten, Geißler, Goc,

Kühn, & Wiegand, 2011) with sand calibrated to 150-250 μm (Avelino et al., 2020), where total

sand lost after each individual rain event was converted to the total TKE (J/m^2) of the rain event

using Equation 1 (Scholten et al., 2011). During measurement days, daily rainfall ranged from

about 1 to 63 mm, with rainfall intensities ranging from about 2 to 8 mm/hr. To account for the

variability of TKE as distance from the tree stem increases (Nanko, Onda, Ito, & Moriwaki,

2011), three splash cups were installed within each study plot: close to the central tree stem, mid-

way between the central tree stem and canopy edge, and near the central tree's canopy edge.

Each cup was positioned on a stable vertical post at height of about 2 m (above the average

coffee plant height). Measurements were collected in each of the shade tree treatments in the

same block simultaneously, rotating between each of the amendment regimes and blocks, for a

total of two or four events, for a total of 18 days of TKE measurements per treatment. All

measurements were collected simultaneously across the shade tree treatments on each sampling

day.

$$KE\ (J/m^2) = Loss\ (g) \times 0.1455\ \times \left(\frac{10\ 000\ (cm^2)}{\pi \times r^2\ (cm^2)}\right)$$

Equation 1. *KE* is the kinetic energy of the raindrops in joules per square meter; *Loss* is the loss

of sand in grams; *r* is the radius of the removable splash cup in centimeters; 0.1455 is the

standardized linear regression coefficient between the kinetic energy and the sand loss (Scholten

et al., 2011).

Based on the measuring period for each microclimate variable, we calculated the daily

maximum, minimum and range of air temperature and relative humidity. Leaf wetness duration

was calculated as the total amount of time that the leaf wetness sensor was wet. Since individual

TKE measurements represent a single day's rainfall events, we used the three splash cups in each

plot to determine the daily maximum, minimum and range of TKE in the individual plot.

Therefore, these values reflect a spatial maximum or minimum of TKE beneath a single shade

tree, rather than a temporal measure.

2.4. Shade tree canopy characterization

In every plot, the following canopy characteristics were measured: total canopy height (m), canopy base height (CBH; m), canopy diameter (m) and canopy openness (%). In plots with one shade tree, the central shade tree was used for all measurements. In double-strata canopy plots, total canopy height was recorded as the tallest crown height, CBH was recorded as the shortest tree's CBH, and canopy diameter was recorded as the largest crown diameter. Canopy openness was captured using hemispherical photography and analyzed using Gap Light Analyzer (Simon Fraser University, 1999). Hemispherical photographs were collected at a height above the average coffee plant height (about 2 m) at three positions under the central shade tree: close to the tree stem, in the middle of the canopy, at the edge of the canopy. The average canopy openness value of the three photographs, determined from the zenith angles $0°$ to $45°$ (Park & Cameron, 2008), were used in subsequent analyses.

To characterize the typical leaf functional traits of the shade trees in this study, a subset of six representative trees per species were selected. Following protocols outlined by Pérez-Harguindeguy et al. (2013) and Pisek, Ryu, & Alikas (2011), five replicate leaf samples were collected from the lower canopy of each tree (n = 30 leaves per shade tree species), which were used to determine leaf area (cm^2), specific leaf area (SLA; mg/mm^2), leaf dry matter content (LDMC; mg/g) and leaf angle. The large leaflets of *T. amazonia* and *E. poeppigiana* were analyzed as separate leaves. In plots with double-strata canopies, final leaf trait values were calculated using the relative abundance-weighted mean of the shade tree species present in the plot, similar to Geißler et al. (2013), calculated based on the percent canopy area occupied by each shade tree canopy within the given plot.

2.5. Quantification of coffee leaf rust

Six coffee plants of similar age, based on allometric data (Audebert, 2011), were selected in each plot, located within the boundaries of the study plot (see Figure 1). CLR incidence was measured during the last round of microclimate measurements in July 2017, where coffee plants were assessed on the same day in each of the treatments. CLR incidence was estimated as the average percentage of leaves with CLR chlorotic spots, both with and without emerging mature uredospores, from three branches of varying height (Avelino, Romero-Gurdián, Cruz-Cuellar, & Declerck, 2012). This disease metric was included in this study because of the greater effect of shade on the percentage of leaves infected with CLR (incidence) compared to the percentage of leaf area with CLR (severity) (López-Bravo et al., 2012).

2.6. Statistical analysis

All statistical analyses were performed in RStudio version 1.1.456 (R Foundation for Statistical Computing, Vienna, Austria). We calculated the mean, standard error, and coefficient of variation (CV) for all shade tree canopy characteristics (n = 6 trees per treatment), leaf traits (n = 30 leaves per treatment), and coffee plant CLR incidence (n = 36 plants per treatment). We used a one-way analysis of variance (ANOVA) to compare both shade tree traits and CLR incidence between the shade tree canopy treatments and amendment regimes.

   All daily microclimate measurements were used to calculate the mean and standard error daily maximum, minimum and range or duration for each of the shade tree treatments, where n = 63 days of measurement per treatment for air temperature, relative humidity and leaf wetness duration, and n = 18 days of measurement per treatment for TKE. Because we had multiple temporal measurements for the same treatments, we used a repeated measures ANOVA with a

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Tukey's test with Bonferroni correction using the 'multcomp' R package (Hothorn, Bretz, & Westfall, 2008) to compare the microclimate conditions between the different treatments. We compared TKE variables across all measurement days and separated based on the 5 mm rainfall threshold found by Avelino et al. (2020). Rainfall intensity was included as a multiplicative covariable for all analyses with TKE variables. 'Block' was included as a random variable for all microclimate variables. Only daily minimum relative humidity was log-transformed to achieve normality before analysis.

We used backwards stepwise linear modelling with data from the whole dataset to determine the canopy characteristics and leaf traits that best explain microclimate variability and CLR incidence (Equation 2). We also used this modelling technique to investigate the relationship between plot-average microclimate conditions and CLR incidence. Rainfall intensity was included as a multiplicative covariable with TKE variables in all models. The plot-average values of the shade tree traits, microclimate conditions and CLR incidence were used in these analyses. All shade tree trait variables were log-transformed to achieve normality, except for canopy height. Of the microclimate variables, only minimum relative humidity and both TKE variables were log-transformed to achieve normality. CLR incidence also had a log-normal distribution. Models were compared using Akaike's information criteria (AIC), where the lowest score represents the most parsimonious model. We used multiple regressions to test the significance of predictor variables in the AIC-selected models.

$$\rho_1 = \beta_0 + \beta_1 H + \beta_2 CBH + \beta_3 D + \beta_4 O + \beta_5 LA + \beta_6 SLA + \beta_7 LDMC + \beta_8 Angle$$

Equation 2. ρ_1 represents the microclimate condition or log-mean CLR incidence, β_0 represents an overall model intercept and β_1 through β_8 represent the parameter estimate of the shade tree

traits (canopy height (H), log-canopy base height (CBH), log-canopy diameter (D), log-canopy openness (O), log-mean leaf area (LA), log-mean specific leaf area (SLA), log-mean leaf dry matter content (LDMC), log-mean leaf angle (Angle).

3. RESULTS

3.1. Shade tree canopy characteristics and leaf traits vary among shade tree treatments

Shade tree canopy characteristics and leaf traits did not differ significantly between the different amendment regimes included in this study; rather they differed significantly between the shade tree canopies ($p \leq 0.001$; Table 2). *Erythrina poeppigiana* canopies often had the highest or lowest values of canopy and leaf traits compared to the other single-stratum canopies. More specifically, the mean leaf area of *E. poeppigiana* was 2.4- and 8.3-times greater than *C. eurycyclum* and *T. amazonia*, respectively. These large differences were also observed in SLA (about two times greater), total canopy height (about three times lower) and canopy diameter (from 2.5 to four times lower) when compared to the other single-stratum canopies. *Terminalia amazonia* had the smallest leaves and *C. eurycyclum* the highest LDMC and the tallest total canopy height. Within each shade tree canopy treatment, leaf traits had greater coefficients of variation (CV), ranging from 11.20 to 69.96%, compared to those of canopy characteristics, which ranged from 10.96 to 49.37%.

3.2. Microclimate conditions vary among shade tree treatments

Daily maximum air temperature was significantly greater under *E. poeppigiana* ($p = 0.001$) compared to all other canopies except for *T. amazonia* (Table 3). Double-strata canopy

treatments had among the lowest daily air temperature ranges, being significantly lower than *E. poeppigiana* (p = 0.001). Daily maximum relative humidity was lowest under *C. eurycyclum* (p = 0.004), while daily minimum relative humidity was lowest under *E. poeppigiana*. Leaf wetness duration was significantly lowest under *T. amazonia* and *C. eurycyclum* (p < 0.001). TKE did not differ significantly between treatments, regardless of rainfall amount.

3.3. Microclimate conditions relate to shade tree traits

Based on the most parsimonious AIC-selected models, mean daily maximum air temperature significantly increased with decreasing canopy height (R^2 = 0.457, p < 0.001; Table 4). Similarly, mean daily minimum relative humidity significantly increased with increasing canopy height and leaf area, and decreasing CBH (R^2 = 0.452, p = 0.002). Mean leaf wetness duration increased with increasing leaf area and decreasing leaf angle (R^2 = 0.374, p = 0.002). Models for mean maximum and minimum TKE were marginally significant (p = 0.069 and p = 0.077, respectively), both increasing with increasing canopy openness. The variation in mean daily minimum air temperature and maximum relative humidity were not significantly explained shade tree canopy and leaf traits included in this study.

3.4 CLR incidence varies with shade tree traits

Mean CLR incidence did not significantly differ between the different amendment regimes or blocks yet differed significantly between the shade tree treatments. CLR incidence was lowest under *E. poeppigiana* and highest under *C. eurycyclum* (p < 0.001), ranging from 76.54% to 91.38% (Figure 2).

Backwards stepwise linear modelling using all canopy characteristics and leaf traits determined that CLR incidence increased with increasing total canopy height and shade tree leaf angle ($R^2 = 0.293$, $p = 0.004$; Table 4). Given that we observed significantly large differences in the canopy and leaf traits of *E. poeppigiana* compared to the other single-stratum treatments (see Table 2), observations from this treatment were removed and the analysis repeated to eliminate the distortion of our results. Upon their removal, the model results changed, where higher CLR incidence related to higher canopy openness and shade tree leaf area ($R^2 = 0.211$, $p = 0.036$; Figure 3). This change did not occur when the other single-stratum treatments were removed from the analysis. There were no significant random effects in these models. Backwards stepwise linear modelling did not reveal a robust significant relationship between CLR incidence and plot-average microclimate conditions.

4. DISCUSSION

4.1. Complex shade canopies differentially modify microclimate conditions

Previous studies have highlighted the ability of shade trees to modify microclimate conditions. For example, when moving from an unshaded monoculture into an agroforestry system, maximum air temperature decreases (Pezzopane, Marsetti, Ferrari, & Pezzopane, 2011; Pezzopane, Souza, Rolim, & Gallo, 2011), minimum air temperature increases (Siles et al., 2010), relative humidity increases (DaMatta, Ronchi, Maestri, & Barros, 2007; Ehrenbergerová, Šenfeldr, & Habrová, 2017; López-Bravo et al., 2012), leaf wetness frequency increases (López-Bravo et al., 2012), and TKE increases (Avelino et al., 2020; Liu, Liu, & Zhu, 2018). It may be these marked changes from unshaded to shaded positions that substantiates canopy openness as

the main driver of differences in microclimate conditions. However, in our present study, we did not find that canopy openness was a strong predictor of microclimate variability among shade tree treatments, except for TKE variables. Expanding beyond the dichotomous analysis of shaded versus unshaded positions, we complicate the relationship between shade trees and microclimate modifications and demonstrate that these modifications significantly differ among shade tree canopies, depending on specific characteristics of the shade canopy itself.

4.1.1. Air temperature

We demonstrate that among different shade tree canopies, daily maximum air temperature significantly decreased with taller canopies ($R^2 = 0.457$, $p < 0.001$; Table 4), with smaller canopy diameter and larger leaves as marginally significant parameters in the model. Our results are likely influenced by the scale of our analysis, limited to the area directly beneath a single- or double-strata shade tree canopy. Other studies that considered larger areas found that leaf area index (LAI) was a determining factor across landscapes (Hardwick et al., 2015). Since we were more interested in the smaller plot-level, our results are more comparable to studies on the effect of individual trees in urban landscapes. A study by Helletsgruber et al. (2020) demonstrates that total canopy height and canopy area are more important tree variables in determining air temperature cooling beneath a shade tree compared to LAI measurements in urban European environments. However, in the urban forestry literature, canopy height is often associated with surface temperature cooling rather than air temperature, due to the influence of the area and duration of tree shading directly on surfaces (Rahman et al., 2020).

4.1.2. Leaf wetness duration

The duration of leaf wetness is a complex variable, as it encompasses the dynamic and contrasting cycles of wetting and evaporation, further complicated by the presence of shade trees and their specific traits. Leaf surface wetting in the understory partially depends on the amount of rainfall incident on the understory leaves, impacted by both rainfall amount and canopy traits (Park & Cameron, 2008). Wetting can also result from fog, dewfall or distillation from wet soils (Monteith & Unsworth, 1990). Leaf surface water evaporation depends on the evaporative potential in the subcanopy, decreasing as shade cover increases due to reduced irradiance (Lin, 2010) and as shade strata increase due to reduced wind action (Cleugh, 1998).

While leaf wetness duration is markedly longer under canopies versus open canopy positions (López-Bravo et al., 2012), comparisons among different shade tree canopies reveal the complexity of this variable. We found the longest leaf wetness durations in plots with *E. poeppigiana* in both the single- and double-strata canopy treatments (Table 3); yet these canopies differed greatly (e.g. canopy openness ranged from 7.46% ± 0.85 to 17.34% ± 2.74; Table 2). Based on multiple regression analysis, leaf wetness duration is not significantly related to canopy openness; rather, it significantly increases under canopies with larger leaves with lower leaf angles (more horizontal in orientation) ($R^2 = 0.374$, $p = 0.002$; Table 4). While larger, horizontal shade tree leaves have been associated with increased rainfall interception and redistribution, leading to reduced overall throughfall amounts (Aston, 1979) and, therefore reduced overall leaf wetting potential, the amount of throughfall also depends on the number and positioning of shade tree branches (Nanko et al., 2011), which were not included in our study. Our results highlight the complexity of this microclimate variable, warranting deeper investigation into the specific

shade tree traits that directly and indirectly influence leaf wetness duration via multiple

pathways.

4.1.3. Throughfall kinetic energy

Throughfall kinetic energy (TKE) of rain is consistently higher under shade trees compared to

unshaded positions (Avelino et al., 2020; Nanko, Hotta, & Suzuki, 2004). Recent research has

found that this difference may depend on the quantity of rainfall, where more than 5 mm of

rainfall resulted in significant differences between shaded and unshaded positions (Avelino et al.,

2020). Yet, when comparing among shade tree canopies, we did not find significant differences

or distinct patterns in TKE, regardless of rainfall amount (Table 3). This finding is unlike Goebes

et al. (2015) who found that TKE was species-specific, particularly at low rainfall intensities.

This may be due to the large range in the TKE measurements in this study (with treatment means

ranging from 28.03 J/m^2 ± 12.04 to 70.36 J/m^2 ± 20.16). This range was greater under the

double-strata canopies, confirming the reduced predictability of TKE under multiple shade trees

(Geißler et al., 2013; Liu et al., 2018).

4.2. Shade tree canopy characteristics and leaf traits are predictors of disease incidence

Previous research has outlined the fine temporal and spatial scale at which microclimate

conditions influence the different lifecycle stages of the *H. vastatrix* fungus and resulting

progression of CLR (Merle et al., 2020). We found that these established relationships between

microclimate and CLR do not hold when using plot-level means. Rather, shade tree traits were

strong and robust predictors of CLR incidence. Considering all shade tree treatments included in

this study, taller canopies with higher shade tree leaf angles (more vertical in orientation) had

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higher levels of CLR incidence in their coffee understory (Table 4). However, we found that the

single-stratum *E. poeppigiana* treatment, with the shortest total canopy height (almost 3-fold

difference from the next shortest canopy) and lowest CLR incidence values (76.54% ± 2.54;

Figure 2), was skewing this relationship.

After removing the observations from this shade tree treatment, canopies with greater

openness and larger leaves increased CLR incidence in the coffee understory (Table 4). Other

studies comparing shaded and unshaded positions have found that the presence of shade, and

therefore lower canopy openness, increased CLR incidence due to, for example, increased

dispersal via rain events (Boudrot et al., 2016), reduced spore wash-off from leaf surfaces

(Avelino et al., 2020), and improved microclimate conditions for the pathogen (namely reduced

air temperature ranges and increased leaf wetness frequency) (López-Bravo et al., 2012).

However, our results demonstrate that among shade tree canopies, increased canopy openness

significantly relates to increased CLR incidence, indicating the important role of subtle

differences between shade canopies. Previous research has highlighted how increased light levels

increase coffee leaves' susceptibility to CLR, due to either reduced physiological resistance

(Eskes, 1982), or increased levels of coffee fruit load (López-Bravo et al., 2012), likely leading

to plant re-allocation of phenolic compounds away from leaf defenses (Kushalappa & Eskes,

1989). Our results also demonstrated that larger shade tree leaves increased the incidence of

CLR, which can likely be traced to the role of shade tree leaves in intercepting and redistributing

rainfall. Although not included in this study, rainfall has the potential to wash spores off of

coffee leaves, in turn reducing CLR incidence levels (Avelino et al., 2020). This measure of leaf

washing is different from leaf wetness duration and TKE, as it captures the quantity of rainfall

incident on the coffee leaves. Therefore, as shade tree leaves increase in size, they intercept and

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redistribute more rainfall, reducing the amount of rainfall incident on the understory canopy

(Aston, 1979), in turn reducing the potential wash-off effect and increasing CLR incidence.

Given the interacting nature of shade tree characteristics, future research should explore their

interacting effects on microclimate modifications and CLR incidence.

4.3. Conclusions

This research expands beyond the dichotomous analysis of shaded agroforestry systems versus

unshaded monocultures and investigates the nuanced effect of shade tree trait diversity. We show

significant differences in microclimate conditions and CLR incidence under a range of shade tree

species combinations and multi-strata arrangements, specifically related to shade tree canopy

architectural characteristics and leaf functional traits. Based on our results, shade tree canopies

with smaller leaves and reduced canopy openness may lead to reduced incidence of CLR in this

region during the rainy season. These results can more directly inform coffee farm management

practices, especially for shade tree species selection (i.e. selecting species with specific canopy

and leaf traits) and shade tree canopy management (i.e. pruning practices to shape shade tree

canopies). Additional research is required, including more mechanistic analyses and the

incorporation of different shade tree species and compositions to create a more complete picture

of how shade tree architectural characteristics and leaf functional traits can be used by farmers to

better inform sustainable pathogen-suppressive agroecosystems.

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Table 1. Summary of canopy and leaf characteristics of the three shade tree species included in this study. Average canopy height (H), average canopy diameter (D), and average leaf area (LA) are based on data from this study. Drawings by S Gagliardi.

Species	Family	Canopy	Average H, D (n = 6)	Leaf (habit, arrangement, shape)	Average leaf area (n = 30)
Erythrina poeppigiana (Walp) O.F. Cook (E)	Fabaceae	Low compact*	7.88 m, 4.80 m	Leguminous deciduous, trifoliate, ovate-rhomboidal	157.75 cm^2
Terminalia amazonia (J.F.Gmel.) Exel (T)	Combretaceae	High compact	22.63 m, 11.81 m	Woody evergreen, palmately compound, cuneate shape	18.97 cm^2

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| *Chloroleucon eurycyclum* Barneby & J.W.Grimes (C) | Fabaceae | High spreading | 26.99 m, 19.11 m | Leguminous deciduous, bipinnately compound, linear | | 65.92 cm^2 |

* *E. poeppigiana* is pruned twice annually (at the end of the coffee harvest and at the beginning of the rainy season).

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Table 2. Mean, standard error (*SE*) and coefficient of variation (CV; %) of leaf functional traits (leaf area; specific leaf area (SLA); leaf dry matter content (LDMC); leaf angle) and canopy architectural characteristics (canopy openness; total canopy height; canopy base height (CBH); canopy diameter) for each of the canopy configurations (*E. poeppigiana* (E); *T. amazonia* (T); *C. eurycyclum* (C); *E. poeppigiana + T. amazonia* (ET); *E. poeppigiana + C. eurycyclum* (EC)), where n = 30 for leaf traits and n = 6 for canopy characteristics. Different letters beside mean values denote significant differences (*p* < 0.05) based on a one-way ANOVA.

	Units	E Mean ± SE	E CV	T Mean ± SE	T CV	C Mean ± SE	C CV	ET Mean ± SE	ET CV	EC Mean ± SE	EC CV
Leaf traits											
Leaf area	cm^2	157.8[a] ± 18.4	63.88	19.0[c] ± 1.7	49.16	65.9[b] ± 7.9	65.37	20.6[c] ± 2.0	54.38	35.2[bc] ± 3.7	58.23
SLA	mg/ mm^2	27.7[a] ± 2.8	55.29	11.2[bc] ± 0.3	12.95	12.8[b] ± 0.5	22.29	7.0[c] ± 0.4	32.22	6.7[c] ± 0.3	20.97
LDMC	mg/g	277.1[c] ± 22.7	44.93	377.7[b] ±7.7	11.20	501.0[a] ± 13.6	14.83	181.9[d] ± 4.9	14.87	257.3[c] ± 7.4	13.77
Angle	°	42.1[a] ± 4.9	63.42	41.2[a] ± 4.1	54.24	31.9[ab] ± 4.1	69.96	25.3[bc] ± 2.3	49.62	17.6[c] ± 2.1	65.98
Canopy characteristics											

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Openness	%	17.3[a] ± 2.7	38.65	16.4[ab] ± 1.0	14.44	10.3[bc] ± 1.7	35.30	10.9[abc] ± 1.6	38.10	7.5[c] ± 1.9	28.05
Height	m	7.9[b] ± 0.6	18.26	22.6[a] ± 1.3	14.18	27.0[a] ± 1.2	10.96	23.7[a] ± 1.5	15.39	22.8[a] ± 1.2	12.55
CBH	m	4.8[b] ± 0.4	18.50	8.1[ab] ± 1.6	49.37	9.8[a] ± 0.8	19.38	4.6[b] ± 0.4	18.96	5.3[b] ± 0.4	17.00
Diameter	m	4.8[c] ± 0.6	29.86	11.8[b] ± 1.2	24.38	19.1[a] ± 1.1	13.84	8.7[b] ± 0.6	17.88	10.6[b] ± 0.5	11.54

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Table 3. Mean and standard error of microclimate conditions across all measurement days (daily maximum air temperature (T_{max}), daily minimum air temperature (T_{min}), daily air temperature range (T_{range}), daily maximum relative humidity (RH_{max}), daily minimum relative humidity (RH_{min}), daily relative humidity range (RH_{range}), leaf wetness duration (LW), maximum TKE (TKE_{max}), minimum TKE (TKE_{min}), range of TKE (TKE_{range})) for each of the canopy configurations (*E. poeppigiana* (E); *T. amazonia* (T); *C. eurycyclum* (C); *E. poeppigiana + T. amazonia* (ET); *E. poeppigiana + C. eurycyclum* (EC)), where n = 63 for T, RH and LW, and n = 18 for TKE. A repeated measures ANOVA is presented as *p*-values, where different letters beside mean values denote significant differences between groups based on a Tukey's test with Bonferroni correction.

	Units	E	T	C	ET	EC	*p*-value
T_{max}	°C	29.30[a] ± 0.24	28.75[ab] ± 0.24	28.26[b] ± 0.26	28.13[b] ± 0.25	28.17[b] ± 0.22	0.001
T_{min}	°C	20.09 ± 0.12	20.18 ± 0.13	20.20 ± 0.13	20.29 ± 0.11	20.23 ± 0.12	0.832
T_{range}	°C	9.22[a] ± 0.29	8.57[ab] ± 0.27	8.06[b] ± 0.27	7.84[b] ± 0.29	7.94[b] ± 0.24	0.001
RH_{max}	%	98.64[ab] ± 0.15	98.91[a] ± 0.21	98.18[b] ± 0.20	98.98[a] ± 0.19	99.03[a] ± 0.14	0.004
RH_{min}	%	70.56[b] ± 0.92	71.56[ab] ± 0.91	73.59[ab] ± 0.96	74.90[a] ± 0.93	74.12[a] ± 0.79	0.001
RH_{range}	%	28.08[a] ± 0.90	27.35[ab] ± 0.86	24.59[ab] ± 0.93	24.09[b] ± 0.91	24.90[ab] ± 0.79	0.001
LW	Hrs	8.06[a]	6.03[b]	6.92[b]	8.13[a]	8.64[a]	<0.001

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		± 0.41	± 0.35	± 0.46	± 0.48	± 0.42	
TKE $_{max}$ * Intensity	J/m^2	48.75 ± 12.33	61.00 ± 16.56	46.92 ± 13.63	55.35 ± 16.68	70.36 ± 20.16	0.886
TKE $_{min}$ * Intensity	J/m^2	29.84 ± 9.69	46.12 ± 13.89	33.51 ± 10.58	28.03 ± 12.04	33.58 ± 11.22	0.907
TKE $_{range}$ * Intensity	J/m^2	18.90 ± 4.15	14.88 ± 3.80	13.41 ± 3.48	27.31 ± 5.74	36.78 ± 11.78	0.265

Table 4. Stepwise and multiple regression model analysis evaluating the relationship between different daily microclimate conditions and CLR incidence (CLR $_{inc}$) with canopy characteristics and leaf functional traits. AIC values for both the full model and the most parsimonious model are presented, with ΔAIC values representing the difference between the two. Parameter estimates (and *p*-values in brackets) are shown only for those parameters retained in the AIC-selected model. Parameters highlighted in bold are those that were significant ($p < 0.05$) in a multiple regression analysis. Also shown for each AIC-model is the explained variance.

Model	AIC-retained parameters (β values in Equation 2)	Coefficient (*p*-value)	Full AIC	Model AIC	Δ AIC	Model R^2 (*p*-value)
T $_{max}$	Intercept	**30.808 (<0.001)**	-22.10	-28.54	6.44	**0.457**
	Height	**-0.137 (<0.001)**				**(<0.001)**
	Diameter	0.741 (0.056)				
	Leaf area	-0.330 (0.052)				
T $_{min}$	Intercept	**18.384 (<0.001)**	-45.47	-51.39	5.92	0.155
	Height	**0.042 (0.011)**				(0.090)
	CBH	**-0.411 (0.045)**				
	Leaf angle	0.272 (0.159)				
	Leaf area	0.193 (0.087)				
RH $_{max}$	Intercept	**98.836 (<0.001)**	23.26	12.35	10.91	
RH $_{min}$	Intercept	**4.170 (<0.001)**	-193.79	-197.92	4.13	**0.452**
	Height	**0.004 (0.004)**				**(0.002)**
	CBH	**-0.036 (0.029)**				
	Leaf angle	0.026 (0.171)				
	Leaf area	**0.033 (0.004)**				

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	SLA	-0.046 (0.060)				
LW	Intercept	**11.785 (<0.001)**	21.56	15.33	6.23	**0.374**
	CBH	-0.809 (0.166)				**(0.002)**
	Leaf angle	**-1.760 (0.005)**				
	Leaf area	**0.779 (0.008)**				
TKE $_{max}$	Intercept	13.213 (0.096)	105.74	97.39	8.35	0.123
* Intensity	Openness	**5.427 (0.031)**				(0.069)
	Leaf area	-4.372 (0.085)				
TKE $_{min}$	Intercept	7.924 (0.309)	105.22	97.29	7.93	0.116
* Intensity	Openness	**5.581 (0.027)**				(0.077)
	Leaf area	-3.404 (0.174)				
CLR $_{inc}$	Intercept	**4.023 (<0.001)**	-134.86	-143.58	8.72	**0.293**
	Height	**0.008 (0.001)**				**(0.004)**
	Angle	0.072 (0.059)				
Shade tree treatment with extreme traits removed						
CLR $_{inc}$	Intercept	**3.975 (<0.001)**	-105.42	-114.15	8.73	**0.211**
	Openness	**0.117 (0.015)**				**(0.036)**
	Leaf area	**0.061 (0.049)**				

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Figure 1. Study plot configurations with (a) single-stratum canopies of *Erythrina poeppigiana* (E), *Terminalia amazonia* (T), and *Chloroleucon eurycyclum* (C); and (b) double-strata canopies of *E. poeppigiana + T. amazonia* (ET) and *E. poeppigiana + C. eurycyclum* (EC). Dotted boxes represent study plot boundaries for all measurements. Drawings by S Gagliardi.

Figure 2. CLR incidence (%) for each of the canopy configurations (*E. poeppigiana* (E); *T. amazonia* (T); *C. eurycyclum* (C); *E. poeppigiana + T. amazonia* (ET); *E. poeppigiana + C. eurycyclum* (EC)), where n = 36. Each box represents first and third quartiles, the central line is the median, the dot is the mean, and the whiskers are the confidence limits (95%). Mean and standard error (SE) values correspond with each boxplot. Different letters beside mean values denote significant differences ($p < 0.001$) based a one-way ANOVA with a Tukey's test.

Figure 3. Schematic of backwards stepwise linear model results predicting coffee leaf rust (CLR) incidence (excluding *E. poeppigiana* treatment), where CLR incidence increases beneath canopies with greater openness and larger leaves (see Table 4). Drawings by S Gagliardi.

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Authors' contributions

SG, JA, and MEI were responsible for conceptualization and methodology; SG was responsible

for the collection of data and formal analysis, with supervision by JA and MEI, and resources

from JA, EMV-F, and MEI. All authors contributed to the writing, review and editing process.

Conflict of interest

The authors declare that they have no known competing financial interests or personal

relationships that could have appeared to influence the work reported in this paper

Data availability statement

The data that support the findings of this study are deposited in the Dryad Digital Repository

https://doi.org/10.5061/dryad.zcrjdfnbw (Gagliardi et al., 2021). Data are also archived in the

TRY functional trait database at try-db.org.

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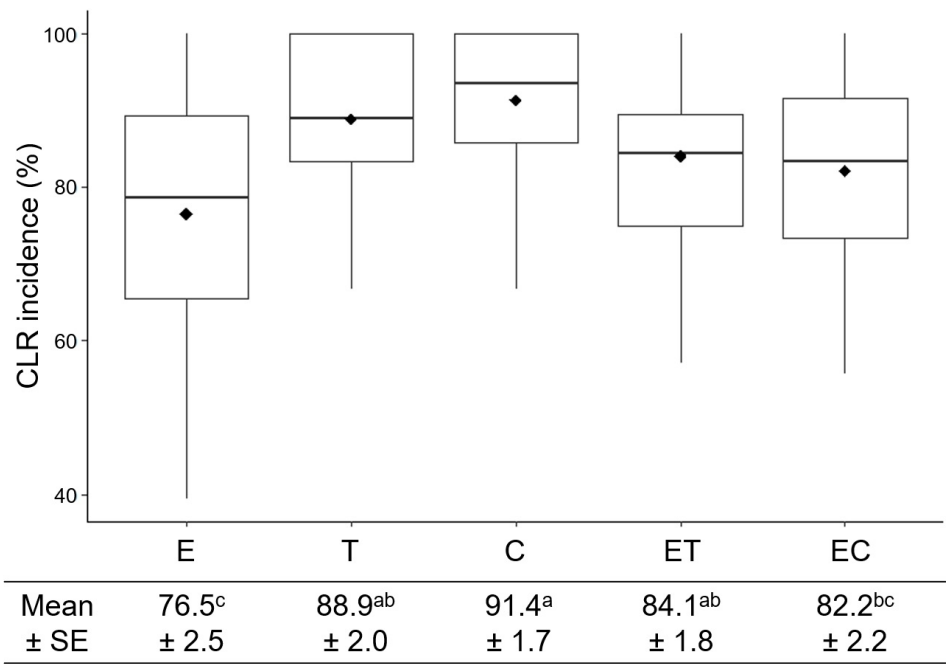
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(a) Plots of single-stratum canopies

(b) Plots of double-strata canopies

E   T   C   ET   EC

345x138mm (144 x 144 DPI)

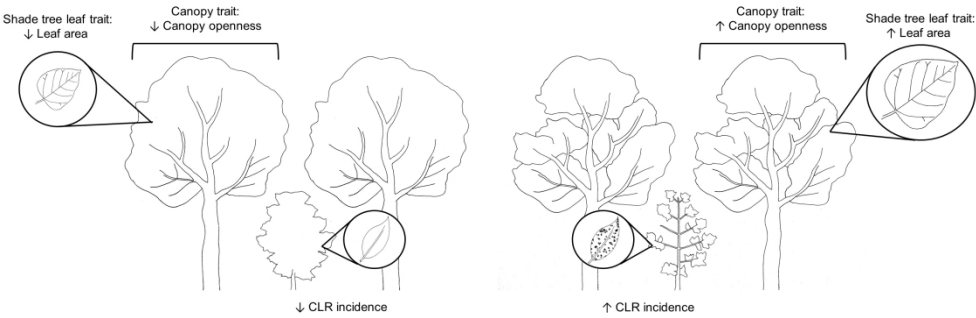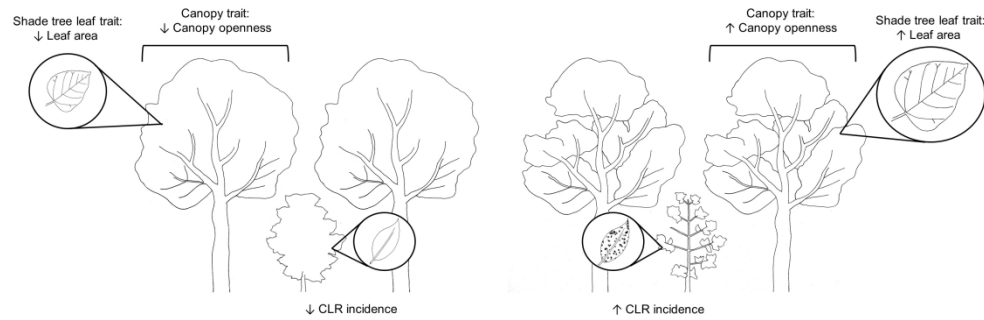|	E	T	C	ET	EC
Mean	76.5^c	88.9^{ab}	91.4^a	84.1^{ab}	82.2^{bc}
± SE	± 2.5	± 2.0	± 1.7	± 1.8	± 2.2
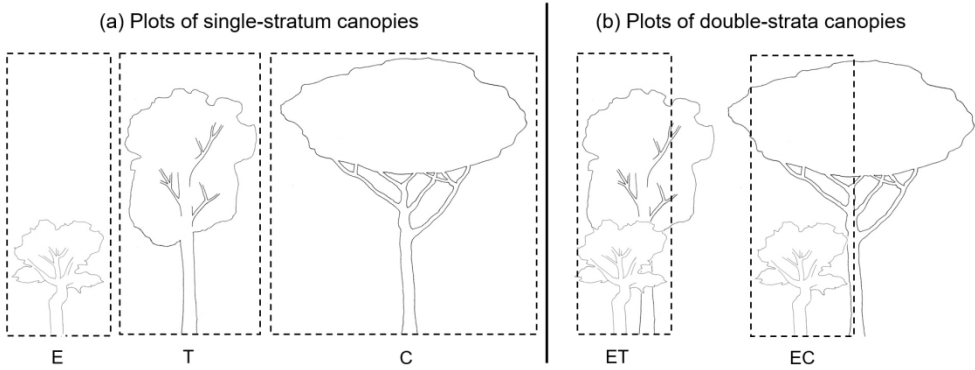
239x172mm (144 x 144 DPI)

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Our results demonstrate the cumulative effects of shade tree canopy architectural characteristics and leaf functional traits in biodiverse agroforests on microclimate modifications and disease incidence in the understory. We found that shade tree trait expression significantly explained most microclimate conditions, and that shade canopies with greater openness and leaf area significantly related to increased disease incidence levels.