

## Phenotypic plasticity of coffee trees in an altitudinal gradient of the Frailesca region of Chiapas

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### Abstract

The cultivation of coffee in agroecosystems atypical for this species affects its growth due to the effect of climate, mainly temperature and solar radiation. In 2021, variations in the microclimate, functional traits, and phenotypic plasticity of the coffee tree were studied in two altitudinal gradients of the Frailesca region, Chiapas. Plant height, stem diameter, length of orthotropic internodes, branches per plant, length of plagiotropic branches, total nodes per plant, leaves per plant, specific leaf mass, and specific leaf area were recorded in two shaded coffee plantations located at 600 and 1 000 masl. Diurnal variations in photosynthetically active radiation, air temperature, and relative humidity were recorded. Photosynthetically active radiation, air temperature, and leaves per plant were greater at 1 000 masl due to the greater amount of shade existing in the coffee plantation located at 600 masl. The photosynthetically active and incident radiation at both altitudes was below the points of light compensation and saturation reported for this crop, while air temperature, leaves per plant, and RH were outside the recommended range for the coffee tree. Stem diameter, branches per plant, length of plagiotropic branches, specific leaf mass, and specific leaf area were higher in coffee trees grown at 1 000 masl. It is concluded that the Costa Rica 95 variety showed phenotypic plasticity in response to the altitudinal gradient reflected in increases in the relative distance plasticity index of stem diameter and specific leaf mass.

### Keywords:

*Coffea arabica* L., functional traits, microclimate.

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## Introduction

Coffee is the second most traded commodity in the world after oil (DaMatta *et al.*, 2007), is grown in 52 countries, which are mostly low-income, and 70% of its production comes from the species *Coffea arabica* L. (Bote *et al.*, 2018). Brazil is the world's largest producer, followed by Vietnam and Colombia (DaMatta *et al.*, 2007), while Mexico ranks tenth, where the state of Chiapas is the largest producer at the national level despite the effects caused in that state by the incidence of the coffee rust disease (Gordillo *et al.*, 2020).

The coffee tree, despite being a species native to the tropical forests of Ethiopia, where it grows and develops well under the strata of gallery forests (Carvajal, 1984), quickly spread in a latitude range that varies between 21° north and 25° south, showing its vast capacity to adapt to various environments. As a result, the main commercial plantations in the world are located in agroforestry systems, although in countries such as Brazil, there are coffee plantations in full sun at altitudes above 1 000 masl (Latifah *et al.*, 2018; Malhi *et al.*, 2021); hence the coffee tree is considered as a facultative shade species with acclimatization patterns to full sun (Fahl *et al.*, 1994).

Nevertheless, in recent decades, climate change has worsened, leading to an increase in temperature and modifications of rainfall patterns (Gómez-Tosca *et al.*, 2021). With the increase in temperature on a global scale, changes in plant growth patterns are expected, depending on their ability to adapt (Nicotra *et al.*, 2010), hence the need for specific studies in crops that, like coffee, represent the fundamental economic base of many low-income families.

The ability of a genotype to generate different phenotypes on a temporal or spatial scale and modify functional traits in plants is called phenotypic plasticity (Valladares *et al.*, 2007), and it is essential for their adaptation in response to abiotic factors. Consequently, the modulations of plant growth as a function of external factors are mainly expressed in morphological, physiological, or biochemical changes (Rahn *et al.*, 2018), where light and water are important factors that, in stressful situations, significantly influence plant growth (Cavatte *et al.*, 2012) and that its variations are generally sensitive to altitude.

In this regard, Zelada and Reynel (2019) have shown that morphologically, the most noticeable changes in plants subjected to pressures from external factors have been observed in the number of leaves, stem diameter, and specific leaf area. While in coffee crops, there have been various studies related to the physiological response to limitations of external resources, namely solar radiation (Rodríguez-Larramendi *et al.*, 2001; Rodríguez-Larramendi *et al.*, 2016; Bernado *et al.*, 2021), temperature (Ovalle-Rivera *et al.*, 2015) and soil moisture (Mofatto *et al.*, 2016). (Cavatte *et al.*, 2012) infer that coffee should have sufficient plasticity in environments that contrast in light, as they exhibit adaptive characteristics with high attributes to tolerate greater sun exposure (Fahl *et al.*, 1994); which increases histological thickness and decreases leaf area (Rodríguez-Larramendi *et al.*, 2016).

This research aimed to study the changes in morphological functional traits and the phenotypic plasticity of coffee trees in an altitudinal gradient of the Frailesca region of Chiapas, Mexico.

## Materials and methods

### Localization

The study was conducted in two localities located in the Frailesca region, Chiapas, which is made up of six municipalities: Ángel Albino Corzo, La Concordia, Montecristo de Guerrero, Villa Corzo, El Parral, and Villaflores. It is bordered to the north by Regions I Metropolitan and IV De Los Llanos, to the east by Region XI Sierra Mariscal, to the south by Region IX Istmo Costa, and to the west by Region II Valles Zoque. Its territory occupies 7 987.19 km<sup>2</sup>, representing 10.7% of the state's territory and the second largest region in the state. Climatically, it is located in the warm

and semi-warm groups, with a predominance of the warm sub-humid with summer rains, followed by the semi-warm humid climate with abundant summer rains.

### Sampling sites

Two coffee plantations located in the municipality of Villa Corzo were selected from coffee trees at two altitudes. The first was located 3.0 km from the municipal seat at 600 masl, at coordinates 15° 54' and 31" north latitude and 93° 15' and 37" west longitude in a loamy soil of moderately acidic pH, medium texture, free of carbonates and salts. With a very high percentage of organic matter, deficient in potassium and very low sulfur contents. Regarding the availability of micronutrients, poor values in zinc and moderately low values in manganese were recorded in the soil. Low copper contents and very low boron contents. The coffee plantation was shaded predominantly by trees of *Mangifera indica* L., *Gliricidia sepium* L., *Cedrela odorata* L. and *Inga edulis* L.

The second site was located in the locality of Nueva Reforma Agraria at 1 000 masl at coordinates 15° 09' and 31" north latitude and 93° 16' and 64" west longitude, in a soil with a moderately acidic pH, medium texture, free of carbonates and salts, with a very high percentage of organic matter, deficient in potassium, and very low sulfur contents. Regarding micronutrient availability, the soil is poor in zinc, moderately low in manganese, low in copper, and very poor in boron. Shade trees of *Conostegia xalapensis* B., *Platymiscium yucatanum* S., and *Ficus carica* L. predominated. Five plots of 20 x 20 m were randomly selected at each site, and two plants with similar phenotypic characteristics (height and number of branches) were randomly selected from each plot. Each plant was considered as an experimental unit, for a total of ten repetitions at each sampling site.

### Plant material

The research was carried out in coffee plantations (*Coffea arabica* L. var. Costa Rica 95), four years old planted at a density of 5 000 plants ha<sup>-1</sup>, in agroforestry systems typical of the Frailesca region, Chiapas.

### Microclimate

In each locality, photosynthetically active radiation (PAR,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was recorded with an Apogee Instruments® Quantum Flux sensor placed in the center of the plots above the coffee canopy. Diurnal air temperature (°C) and relative air humidity (RH, %) were recorded with a Watch Dog 1000 series micro weather station (Spectrum® Technologies, Inc.). All measurements were taken over three days of each month from 7:00 to 17:00, every 30 min, from February to November 2022.

### Functional traits

Plant height (PH) was measured from the base of the stem to the cauline apex with a tape measure (cm plant<sup>-1</sup>). The stem diameter (SD) was taken 30 cm from the base of the stem with a Lenfuch Caliper digital vernier. Orthotropic internode length (IL) measurements were taken with the same equipment. Plagiotropic branch length (PBL) was measured with a tape measure. Leaves per plant (LP), branches per plant (BP) and total nodes (NP) were counted. The specific leaf mass (SLM) and the specific leaf area (SLA) were determined with ten discs of leaves from the middle part of each of the five selected plants, which were placed in a Dakton® gravity convection drying oven, at 80 °C until constant weight. The dry weight was then divided by the area of each disc to obtain the specific leaf mass (g cm<sup>-2</sup>) and vice versa for the specific leaf area (cm<sup>2</sup> g<sup>-1</sup>).



## Quantification of phenotypic plasticity

The quantification of phenotypic plasticity was calculated using the relative distance plasticity index (RDPI) (Valladares *et al.*, 2006).

## Statistical analysis

According to the characteristics of the experiment and for the statistical analyses, a linear mathematical model of fixed effects was considered. Microclimate data were analyzed by descriptive statistics; using average, maximum and minimum values, and standard deviation, supported by frequency histograms and to demonstrate the hypothesis of the effect of altitude (localities) on diurnal variations of the microclimate, Student's t-tests were performed, with a statistical significance level of ( $p \leq 0.05$ ). To compare the variations in functional traits between the two altitudes, Student's t-tests ( $p \leq 0.05$ ) were performed after comparing the assumptions (homogeneity of variance and normality of the data). The Statistica V. 8.0 (StatSoft, 2007) software was used for all analyses.

## Results and discussion

### Microclimate

Photosynthetically active radiation (PAR) records were significantly higher in the coffee plantation located at 1 000 masl ( $p \leq 0.05$ ), except in November (Table 1). The annual average of the PAR at 1 000 masl was  $252.23 \mu\text{mol m}^{-2} \text{s}^{-1}$ , statistically higher than at 600 masl, in a range of 58.86 to  $556.52 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Table 1), which is attributed to a lower density of shade trees at this site. This result confirms the regulating effect exerted by shade trees by attenuating the intensity of solar radiation that reaches the canopy of shaded coffee trees (Lisnawati *et al.*, 2017) and demonstrates that the decrease in available radiation, due to shade, modifies the microclimatic conditions for the associated crop (Andrade and Zapata, 2020).

**Table 1. Monthly and annual variation of microclimate variables in coffee plantations grown at 600 and 1 000 masl in the Frailesca region.**

Months	Variables	600 (masl)	Standard deviation	Minimum	Maximum	1000 (masl)	Standard deviation	Minimum	Maximum	Student's t	p
February	RH (%)	50.08	0.4	49.55	50.41	57.86	0.92	56.61	58.87	-17.35	0
	T (°C)	27.44	0.17	27.28	27.67	28.39	0.18	28.2	28.69	-8.47	0
	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	155.41	48.15	100.05	220.19	410.05	101.58	270.24	556.52	-5.07	0
May	RH (%)	70.89	0.37	70.42	71.2	70.5	0.19	70.28	70.7	2.1	0.05
	T (°C)	27.06	0.2	26.79	27.24	30.51	0.08	30.42	30.61	-36.06	0
	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	100.64	28.33	78.48	147.9	241.61	134.02	64	437.86	-2.3	0.05
August	RH (%)	71.64	1.88	68.44	73.18	75.24	0.19	74.93	75.42	-4.27	0
	T (°C)	24.12	0.1	24.02	24.26	25.7	0.27	25.41	26.07	-12.33	0
	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	61.66	69.61	25.43	185.86	181.70	112.50	58.86	342.43	-2.03	0.08
November	RH (%)	67.51	0.42	66.84	67.84	69.74	0.49	69.08	70.35	-7.72	0
	T (°C)	23.15	0.09	23.02	23.27	23.15	0.09	23.02	23.27	0	1

Months	Variables	600 (masl)	Standard deviation	Minimum	Maximum	1000 (masl)	Standard deviation	Minimum	Maximum	Student's t	p
	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	24.94	5.4	16.76	30.86	175.56	111.11	93.86	359.14	-3.03	0.02
Average	RH (%)	65.03	0.42	49.55	73.18	68.34	0.49	56.61	75.42	-1.32	0.19
	T (°C)	25.45	0.09	23.02	27.67	26.94	0.09	23.02	30.61	-1.95	0.06
	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	85.66	5.4	16.76	220.19	252.23	111.11	58.86	556.52	-4.73	

PAR= photosynthetically active radiation; T= temperature; RH= relative humidity.

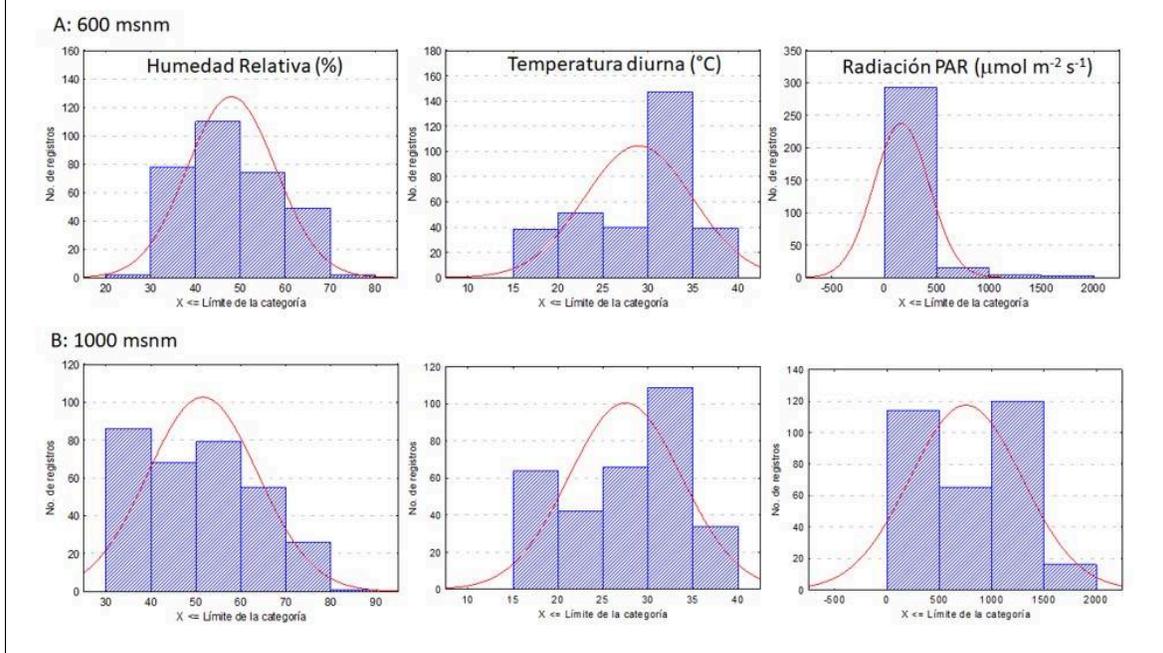
At 600 masl, more than 250 records of PAR ranged from 0 and  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , while at 1 000 masl, 120 records ranged from 1 000 to  $1\ 500 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( Figure 1), lower than the values reported by Andrade and Zapata (2020) at noon in coffee plantations with low shade levels. Under these conditions, photosynthesis is more affected, as it has been shown that in *C. canephora*, the points of compensation and saturation of radiation fluctuate between  $10.7\text{-}27.6$  and  $552\text{-}660 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively (Rodríguez *et al.*, 2012) and although in arabica coffee trees (*C. arabica* L.), higher light saturation values (600-700) are reported (DaMatta *et al.*, 2007), they are still above those recorded in this research.

However, the response of plants to PAR is complex as it depends on the species and the solar radiation itself since the light compensation point is higher in leaves exposed to the sun and in heliophilous plants than in shaded leaf blades and shade-tolerant plants (Matos *et al.*, 2009; Andrade and Zapata, 2020), so it will be necessary to delve into the effect of the relationship between photosynthesis and PAR at both altitudes to reach more solid conclusions about the relationship between solar radiation and coffee tree growth.

The mean diurnal air temperature was higher at 1 000 masl compared to the lowest altitude, associated with higher incident solar radiation, with minimum and maximum values of 23.02 and 30.61 °C. At 600 masl, the mean annual diurnal temperature ranged from 23.02 to 27.67 °C, with an annual mean value of 25.45 (Table 1).



**Figure 1. Histogram of frequencies of the diurnal air temperature, relative humidity, and PAR records in coffee plantations at 600 and 1 000 masl in the Frailesca region.**



It is worth mentioning that the temperature range of 18 to 21 °C indicated as optimal for coffee crops (Carvajal, 1984) includes nocturnal values, while in this research diurnal values are reported, which could lead to erroneous interpretations. Even so, it can be said that the average annual temperature values (February to November) recorded at 600 masl manage to be within the appropriate range and presumably it should not affect stomatal conductance or affect gas exchange; it has been shown that such repercussions should occur when plants grow in an environment where temperature records reach values between 30 and 35 °C (Taiz and Zeiger, 2007; Andrade and Zapata, 2020).

The average annual relative humidity value was slightly higher at 1 000 masl and fluctuated between 49.55 and 73.18% at 600 masl and between 56.61 and 75.42% at 1 000 masl. It has been reported that *Coffea arabica* L. grows and develops well in a range of 70-95% relative humidity (Carvajal, 1984).

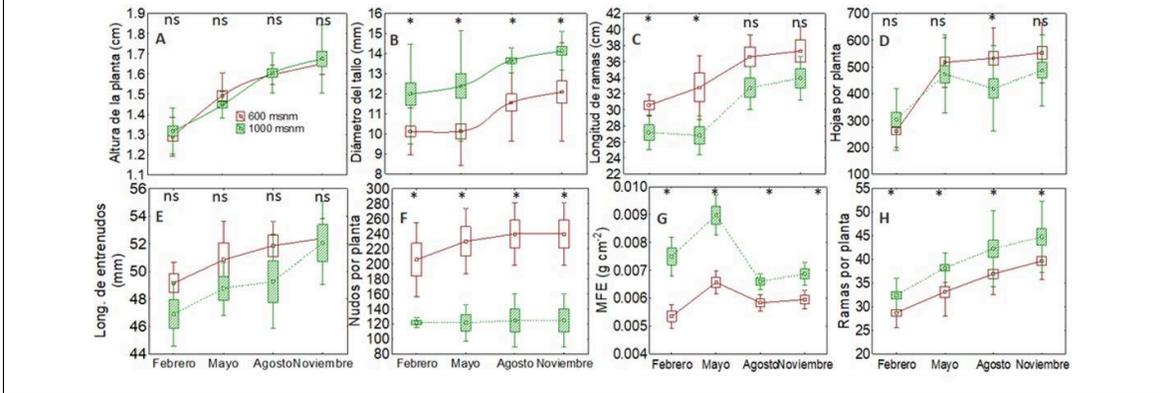
In this sense, special interest should be paid to future findings since the information obtained with this research shows that the microclimate at both sampling sites is drier than that indicated for the genus *Coffea*.

### Functional traits

SD, BP, PBL, NP and SLM were the functional traits that showed the greatest response to variations in altitude. Nonetheless, the growth of the orthotropic axis (PH and IL) did not change significantly with altitude (Figure 2A and E), which shows that this variable is not sensitive to changes produced by altitude and suggests that it is not a good indicator to assess the plasticity of the coffee tree in ecologically contrasting environments. NP were higher at lower altitudes (Figure 2F).



**Figure 2. Changes in the functional traits of the growth of coffee trees grown at different altitudes in the Frailesca region of Chiapas, Mexico. ns= not significant; \*= significant ( $p \leq 0.05$ ). A= Plant height (PH); B= stem diameter (SD); C= plagiotropic branch length (PBL); D= leaves per plant (LP); E= internode length (IL); F= nodes per plant (NP); G= specific leaf mass (SLM); H= branches per plant (BP).**



The number of LP (Figure 2D) only showed significant differences in favor of coffee trees grown at 600 masl in August. SLM (Figure 2G) was higher at higher altitudes in all months, most likely due to the higher incidence of PAR (Table 1). In this sense, it has been shown that leaves exposed to greater solar radiation are thicker in coffee trees exposed to greater solar radiation and tend to form a double layer of palisade parenchyma, which gives it greater internal volume for CO<sub>2</sub> assimilation (Rodríguez-Larramendi *et al.*, 2016).

In general, a higher emission of plagiotropic branches (PB) was observed in coffee trees grown at 1 000 masl (Figure 2H), contrary to what was observed in the growth of the branches (PBL) (Figure 2C), which presented higher values at 600 masl during February and May. SD was consistently higher in coffee trees grown at higher altitudes, with differences greater than 2 cm at all times of sampling (Figure 2B), which is due to the fact that morphologically the most notable changes in the functional traits of the plants in contrasting environments are mostly expressed in the number of leaves, stem diameter and specific leaf area (Zelada and Reynel, 2019).

Canonical correlations between functional traits and microclimate variables at both altitudes showed a significant correlation (Table 2). At 600 masl, RH favored the growth in height of the coffee trees, as well as the emission of leaves, branches, nodes, and the accumulation of biomass per unit of leaf area (SLM), while at 1 000 masl, RH positively influenced the growth in height of the coffee trees, as well as the emission of leaves and plagiotropic branches.

**Table 2. Canonical correlations between the functional traits of coffee tree growth and microclimate variables at 600 and 1 000 masl.**

Functional traits	600 (msnm)				Canonical R	Chi <sup>2</sup>	p
	HR (%)	T (°C)	PAR (mol m <sup>-2</sup> s <sup>-1</sup> )				
Plant height (PH)	0.82	-0.86	-0.67		0.98	72.39	<0.01
Stem diameter (SD)	0.3	-0.73	-0.57				
Leaves per plant (LP)	0.9	-0.65	-0.59				
Branches per plant (BP)	0.66	-0.87	-0.6				

Functional traits	600 (msnm)			Canonical R	Chi <sup>2</sup>	p
	HR (%)	T (°C)	PAR (mol m <sup>-2</sup> s <sup>-1</sup> )			
Average length of plagiotropic branches (PBL)	0.53	-0.69	-0.72			
Nodes per plant (NP)	0.62	-0.51	-0.2			
Orthotropic internode length (NL)	0.15	-0.25	-0.39			
Specific leaf mass (SLM)	0.60	-0.02	-0.3			
		1 000 (msnm)				
Plant height (PH)	0.73	-0.75	-0.55	0.97	59.05	<0.01
Stem diameter (SD)	-0.25	-0.44	0.09			
Leaves per plant (LP)	0.6	-0.21	-0.45			
Branches per plant (BP)	0.72	-0.63	-0.43			
Average length of plagiotropic branches (PBL)	0.49	-0.76	-0.25			
Nodes per plant (NP)	-0.36	0.08	0.13			
Orthotropic internode length (NL)	0.05	-0.28	0.04			
Specific leaf mass (SLM)	-0.13	0.76	0.17			

Nevertheless, increases in temperature at 600 masl inhibited PH, SD, LP, and branch growth. At 1 000 masl, the negative effect of temperature became evident in the height of the coffee trees and the growth of the branches, while SLM increased proportionally with temperature (Table 2). The negative effect of PAR was observed only at lower altitudes on PH and the growth of plagiotropic branches.

The significant relationship observed between PH ( $p \neq 0.01$ ), the higher emission of leaves and branches in the coffee trees and the RH at both altitudes demonstrates the high correlation between the air humidity prevailing in the Frailesca region and the vegetative growth of the coffee tree, previously exposed by DaMatta *et al.* (2007), although it has been shown that arabica coffee requires a less humid climate, comparable to that of the Ethiopian highlands (Carvajal, 1984), and although it has been documented that coffee trees of the *Canephora* species are more sensitive to more humid environments, everything seems to indicate that the diurnal air humidity conditions prevailing in the Frailesca region are favorable for the better growth of arabica coffee trees, specifically the Costa Rica 95 variety.

The negative effect of diurnal air temperature on the vegetative growth of the coffee tree observed at both altitudes but with greater relevance at 600 masl due to the number of growth variables affected (PH, SD, LP, BP and PBL), compared to coffee trees grown at 1 000 masl (PH, BP, PBL), show that continuous exposure to temperatures outside the optimal range for the coffee tree and above 30 °C (Figure 1) does not only affect the growth of the coffee tree but

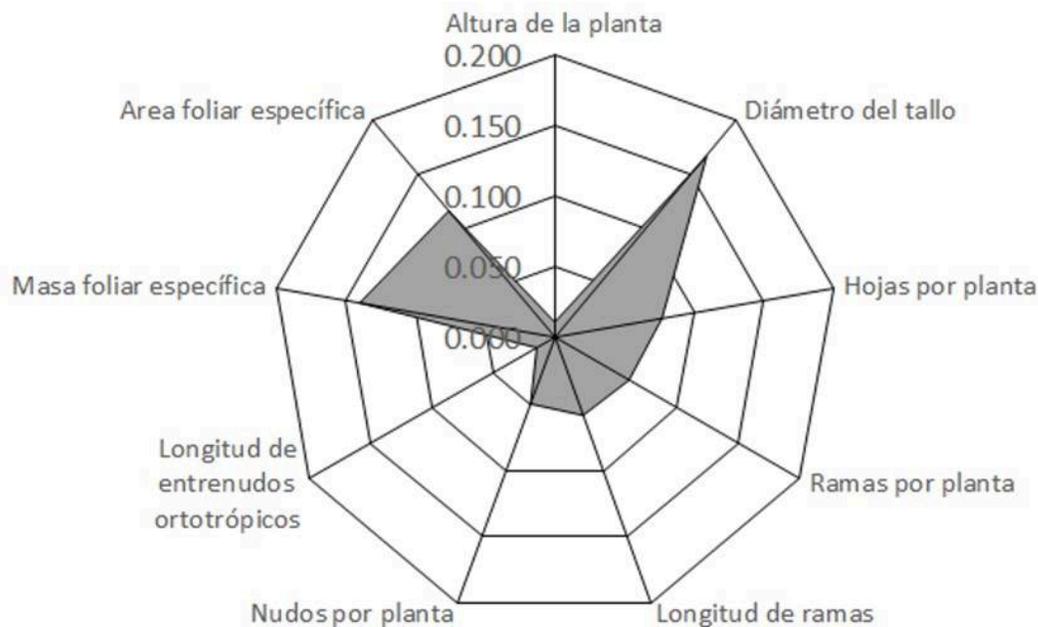
also exposes the plants to yellowing of the leaves (Franco, 1958; Da Matta *et al.*, 2007) and modifications in leaf anatomy and specific leaf mass, especially due to its direct relationship with solar radiation (Rodríguez-Larramendi *et al.*, 2016).

Regarding the negative effect exerted by the intensity of the PAR observed only at 600 masl (Table 2), it is shown that increases in solar radiation affect plant growth (Fahl *et al.*, 1994; Rodríguez-Larramendi *et al.*, 2001) due to reduced growth rates. In this sense (Rodríguez-Larramendi *et al.*, 2001) showed that, in particular, PH and SD were the variables most affected by sunlight levels, but not the number of branches. It is noteworthy that SLM, a variable sensitive to the effect of solar radiation (Rodríguez-Larramendi *et al.*, 2016), was not correlated with the intensity of solar radiation but with diurnal air temperature, as mentioned above.

Calculations of the relative phenotypic distance plasticity index for stem (PH, SD, IL), branches (BP, PBL, and NP) and leaf (LP, SLM, SLA) growth functional traits showed that functional traits related to leaf growth (SLA and SLM) and SD showed the highest phenotypic plasticity (Figure 3). It is followed in that order by traits related to the growth of branches and the emission of leaves by plants.

These results suggest that both SD and leaf unit growth linked to leaf anatomy (SLM and SLA) are more sensitive to altitude and presumably related to higher metabolic activity in these conditions, although it is expected that there is an effect of microclimate covariates that influences the greater growth shown by coffee trees at higher altitudes.

**Figure 3. Relative phenotypic distance plasticity index (RDPI) of functional traits of coffee trees at two altitudes in the Frailesca region of Chiapas, Mexico.**



The higher phenotypic plasticity indices observed for specific leaf mass and area indicate that the variation of leaf area in tropical altitudinal gradients is directly related to the effect of environmental factors, geology, altitude, and latitude, as well as the allometric factors typical of each species (Garnica and Saldarriaga, 2015). It is then confirmed that the coffee tree is a plant that can modify morphological traits, demonstrating its plasticity to the changes produced with altitude. This ability to modulate growth with altitude is reflected more in the morphological

traits linked to plagiotropic branch emission and growth, node emission, stem thickness, and leaf growth.

## Conclusions

Coffee trees grown at 1 000 masl were exposed to higher photosynthetically active radiation (PAR), relative humidity, and diurnal air temperature compared to the site located at 600 masl. At both altitudes, PAR was below the point of light saturation and compensation reported for coffee. Meanwhile, the average monthly and annual temperatures were above the values reported as optimal for this crop.

The functional traits associated with stem diameter, leaf growth (LP, SLM, and SLA), as well as the number of BP and PBL were the most sensitive to differences in altitude, with coffee trees grown at 1 000 masl developing the thickest stems and the highest number of total nodes per plant, while SLM and the number of BP were higher in coffee trees grown at 600 masl. The Costa Rica 95 variety showed phenotypic plasticity in response to the altitudinal gradient reflected in increases in the relative distance plasticity index of SD and SLM.

According to the results and evidence shown in this research, it is recommended that, for the management of coffee plantations in the Frailesca region, the variations caused by altitude in the microclimate are considered. Especially the changes produced in solar radiation and the diurnal air temperature.

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