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Ecological Correspondence Between Morphological Variation and Germplasm Movement Zones of *Cedrela odorata* L. in Southeastern Mexico

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Abstract

This study analyzed seven foliar traits of *Cedrela odorata* L. (Meliaceae) in 87 individuals across three germplasm movement zones in Tabasco, Mexico (VIII: humid; XIV: intermediate; XXI: dry) to assess differentiation and climatic relationships. Leaf length, area, petiolule length, leaflet number, rachis length, width, and stomatal density were measured. Univariate tests, canonical correlation analysis, redundancy analysis, and a relative phenotypic plasticity index were applied. Significant morphological differentiation was found: zone XIV exhibited the largest leaves and longest rachises, zone VIII the highest stomatal density, and zone XXI smaller, more subdivided leaves. The first canonical axis ($r = 0.846$, $p < 0.001$) associated long and wide leaves with warm, humid conditions, while the second ($r = 0.810$, $p < 0.001$) linked stomatal density and width to temperature minimum. Climate explained 55.7% of morphological variation, primarily through water and temperature gradients. High plasticity in leaf area, rachis length, and stomatal density suggests adaptive flexibility, yet consistent inter-zonal differences indicate local adaptation. These results demonstrate a strong correspondence with Tabasco's germplasm movement zones and providing morphological evidence to support reforestation and germplasm management strategies under variable climatic conditions.

Keywords: forest conservation; germplasm management; leaf traits; seed zones

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1. Introduction

Plants reflect their ability to respond to environmental changes through morphological variation [1,2]. Morphological traits represent phenotypic expression derived from ecological and physiological processes [3,4]. Leaf anatomy determines how plants regulate their energy balance, gas exchange, and water loss [5,6]. The most sensitive traits of plasticity that respond to environmental gradients such as temperature, humidity, and solar radiation area leaf length, stomatal density, and lamina segmentation [7–9]. In tropical regions, broadleaf species exhibit patterns where stomatal density increases while in

dry environments it decreases. Likewise, leaves tend to be larger and thinner in warmer and more humid regions, suggesting a link between environmental conditions and plant physiological performance [10].

Changes in precipitation patterns, droughts, and heat waves resulting from climate change put key forest species of high economic value at risk [11,12]. Therefore, the success of reforestation should not be limited to good-quality seed lots or well-manage collection sources, but rather a long-term planned strategy that considers the use of germplasm adapted to current and future conditions [13,14].

In México, the National Forestry Commission (CONAFOR) has promoted the creation of germplasm movement zones, which group together climatically homogeneous regions where local adaptation is assumed to exist [15]. This scheme seeks to reduce the risks of introducing poorly adapted material. However, the biological correspondence of germplasm movement zones has not always been corroborated by morphological or genetic studies.

It has been documented for Mexico that the measurement of morphological traits in conifers can support and suggest decisions about seed transfer and assisted migration. The work of Sáenz-Romero et al. [16] proposes three altitudinal zones of 200 m for *Pinus oocarpa* Shiede ex Schltdl. in addition to upward transfers of 150 m as an adaptive measure. Provenance trials established for *Pinus pseudostrobus* Lindl. by Soto-Correa et al. [17] revealed differences between populations, with height and biomass being greater in high populations than in low ones, proposing four altitudinal zones at 150 m intervals. Similarly, Castellanos-Acuña et al. [18] delimited three altitudinal zones (2800–3050, 3050–3300 and 3300–3550 m) for the safe movement of germplasm. Studies that integrate morphological evidence with environmental variables provide information that facilitates decision-making to improve survival rates in reforestation.

Despite the significant number of studies on conifers in seed zones, information on tropical broadleaf species is scarce or non-existent. Such is the case of *Cedrela odorata* L. (Meliaceae), commonly known as red cedar, one of the most prized species for its wood in tropical regions, valued for its quality, workability, and resistance in carpentry and cabinetmaking [19,20]. High demand has led to a decline in its natural populations due to overexploitation and habitat loss [21,22]. Widely used in reforestation programs as a pioneer species, it establishes itself easily in clearings [23–25]. Despite high demand, reforestation and planting with this species has declined considerably. Among the most significant limitations is its high susceptibility to the meliaceous borer pest (*Hypsiphylla grandella* Zeller), which affects the profitability of commercial plantations [26,27].

The distribution of *C. odorata* ranges from the gulf to the pacific coast of Mexico, reaching as far north as Argentina [23]. The species' extensive distribution and different environmental gradients can be seen in its morphological and adaptive differentiation [28]. Currently information on how leaf traits relate to environmental conditions and vary between different regions is in its infancy and has begun to be generated for some specific traits and areas of the tropical region [1].

Government institutions such as CONAFOR have promoted the regulation of germplasm management using the criterion of movement zones [15]. However, the correspondence between these zones and the morphological or genetic differentiation between populations is poorly documented and even less so in tropical broadleaf species.

The state of Tabasco provides favorable climatic conditions for determining whether contrasting climatic gradients in a small territory can influence the leaf morphology of a species such as *C. odorata*. In the last two decades, southeastern Mexico has been subject to intensive reforestation programs, leading to an increase in the demand for germplasm [25]. In this regard, Nuñez-Piedra et al. [29] propose germplasm movement zones in the southeastern Mexico, highlighting important differences between the zones resulting from their

work and those stipulated by CONAFOR [15]. Considering above, determining whether the zones correspond to morphological or genetic differences is key to increasing survival rates in reforestation actions in the short and long-term.

The correlation between environmental gradients and leaf traits has been widely documented, studies such as those by Leigh et al. [30] and Everingham et al. [31] mention how leaf segmentation influences heat dissipation and thermal regulation, while Kullberg et al. [32] highlighting how density adjust to humidity and the temperature conditions. These studies may prompt analysis in other species such as *C. odorata* under the conditions of the state de Tabasco and determine whether there is differentiation based on functional traits between environmental gradients such as the seed zones of Nuñez-Piedra et al. [29].

The objective of this study is to assess the correspondence of the germplasm movement zones previously delimited by Núñez-Piedra et al. [29] through the morphological evaluation of functional leaf traits and their relationship with bioclimatic variables of great importance in physiological performance [33]. The traits evaluated were leaf area (LA), rachis length (RL), leaf width (LW), number of leaflets (NOL), leaf length (LL), petiolule length (PL), and stomatal density (STD). Additionally, to estimate the species' response to the climatic gradient, the relative phenotypic plasticity of the characters was quantified. Our hypothesis proposes the *C. odorata* populations in each germplasm movement zone exhibit adaptive morphological differences based on local climatic gradients, which would allow us to evaluate the consistency of the previously proposed boundaries based on the species' adaptative response.

2. Materials and Methods

The study area is located in the municipalities of Cárdenas, Cunduacán, Tacotalpa, Jalapa, Macuspana, Tenosique y Balancán in the state of Tabasco, Mexico. Sampling was carried out at 12 sites in seven municipalities. The sampled sites represent three germplasm movement zones delimited under the criterion of bioclimatic variables [29], associated with the genetic differentiation of forest species populations (Figure 1). Three samples of compound leaves were collected from each 87 individuals in natural stands, forest remnants and pastures.

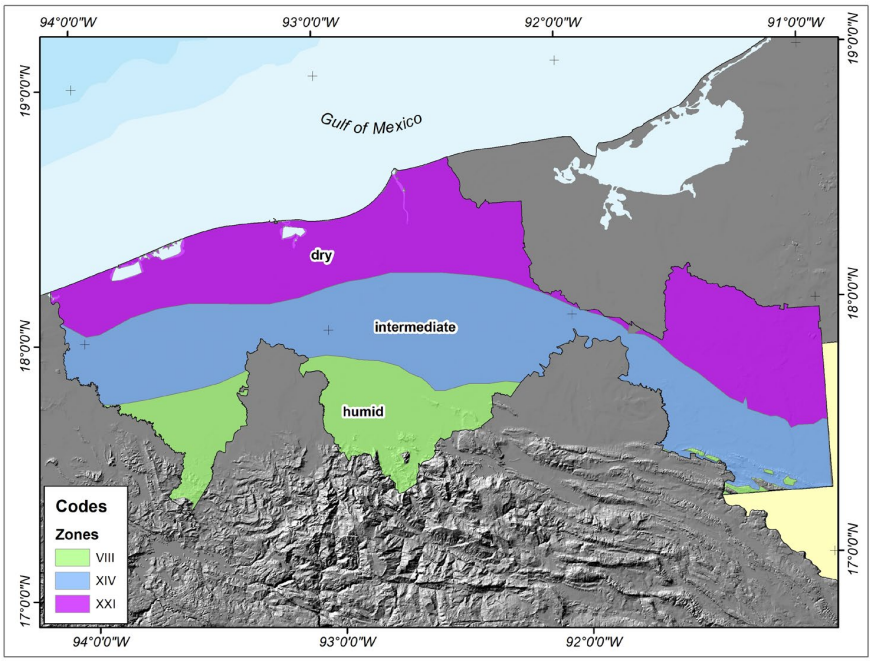


Figure 1. Germplasm movement zones for the state of Tabasco, delimited by bioclimatic variables. Each color refers to a distinct germplasm movement zone according to the legend embedded in the figure.

The sampling units were formed in areas where natural populations of healthy adult trees were recorded, with the prior consent of the owners and/or possessors individuals were chosen at random, maintaining a minimum distance of 30 m between them to reduce spatial autocorrelation and possible kinship between individuals.

One branch was taken from the middle of the canopy of each tree (sun exposure), from which three physiologically mature compound leaves with no visible damage were separated. The samples were stored in airtight bags and transported in isolated containers to the laboratory for processing within 12 h.

Digital images of leaves were captured using a high-resolution 50 MP CMOS (Xiaomi Redmi 13C, manufactured by Xiaomi Corporation, Beijing, China) in a perpendicular position (90°) to a diffused light table to eliminate shadows and ensure uniform illumination. The Images were taken at a height of 35 cm above a matte black background, using manual settings (ISO 100, f/1.8, 1/200 s, no flash) and 30 cm millimetric ruler included in each image for calibration. The files were saved in maximum resolution JPEG format. Processing in JImage version 1.54g [34] was standardized for all measurements, and calibration was performed using the reference ruler in each image.

Stomatal density was calculated based on the methodology suggested by Meister and Bolhar-Nordenkampf [35] and Gitz and Baker [36], by applying clear nail polish to create an impression of epidermal tissue on the central surface of the leaf on the abaxial side. After 10 min, the replica was removed and slide and coverslip. The edges were sealed with adhesive tape to prevent displacement and bubbles.

Stomata counts were performed on the preparations using a Zeiss Primo Star microscope equipped with a 40×/0.65 objective lens. Micrographs were captured using the integrated Axiocam ERc 5s camera and Zen Software (Carl Zeiss, Jena, Germany) to document the replicates. The images were stored digitally in TIFF format. For quantification, three compound leaves per tree were sampled.

Stomata were counted within a total micrograph field of 280 × 200 µm, which was specifically calibrated using the built-in scaling tools of the software. To ensure systematic and precise counting, this field was subdivided into four quadrants of 0.014 mm^2 each (140 × 100 µm). Three independent measurements were made per tree and resulting averages per individual were utilized for statistical analysis. To minimize inter-observer variability and ensure data consistency, the entire procedure was conducted by a single person.

Statistical analyses were performed in R 4.3.2 running in RStudio [37], using the packages tidyverse 2.0.0 [38], car 3.12 [39], FSA 0.9.5 [40], vegan 2.64 [41], CCA 1.2.2 [42], and CCP 1.1.3 [43]. Before comparisons between seed zones were made, the normality (Shapiro-Wilk test) and homogeneity (Levene's test) of variances were assessed. Variables that met both assumptions were subjected to one-way ANOVA with Tukey's contrast, while those that did not were analyzed using the Kruskal-Wallis test followed by Dunn's comparisons with Bonferroni correction. A significance level of 0.05 was established for all statistical tests [44].

A canonical correlation analysis was applied to identify multivariate covariation patterns between leaf traits and environmental conditions, revealing the interdependence between the physiology of organisms and their environment. We started with the complete set of 18 climate indices generated with ClimateNA v7.01 for the period 1991–2020, at a spatial resolution of 1 km [33] and eliminated predictors with a variance inflation factor greater than ten [45,46] or absolute bivariate correlations greater than 0.7 [47]. The resulting subset of ten climatic variables was refined by progressive forward selection with restricted permutations (999 iterations), the canonical model was adjusted, and the overall and individual axis significances were tested with the same permutations [48].

Using the same refined climate matrix, a redundancy analysis was designed to quantify the proportion of morphological variance explained by climate. Collinearity was verified again, and significance was assessed using 999 permutations [41].

The correspondence between the morphological groups obtained by hierarchical clustering and the germplasm movement zones was evaluated: first, we assigned each *C. odorata* sample to one of three clusters based on the Euclidean distance of seven leaf traits and Ward's method [49]. Secondly, the sampling coordinates were converted into a spatial point object and superimposed on the seed zone polygons to extract the corresponding zone of each point using a spatial union. This was used to construct a "Cluster × Zone" contingency table and to calculate Cramér's contingency coefficient (Cramér's V), obtained from Pearson's χ^2 statistic and scaled for larger tables. At the same time, both classification vectors (cluster and zone) were transformed into numerical factors, and the Adjusted Rand Index (ARI) was estimated to quantify the random-corrected agreement between the two partitions. Both metrics offer complementary perspectives: Cramér's V measures the intensity of the overall association in the contingency table, while the ARI penalizes the degree of agreement expected by chance between partitions of equal size [50].

To quantify the plasticity of the leaf traits, the Relative distances plasticity index (RDPI) was used [51–53], defined as (Equation (1)):

$$\text{RDPI} = \frac{1}{n} \sum \frac{\left| x_{ij} - x_{i'j'} \right|}{\left(x_{ij} + x_{i'j'} \right)} \quad (1)$$

where x_{ij} and $x_{i'j'}$ are the values of a trait measured in two different individuals (or zones) and n is the total number of pairs compared. This index ranges from 0 (no plasticity) to 1 (maximum plasticity).

We calculated the relative distances plasticity index (RDPI) for each leaf trait using the average values per tree in the three seed zones (VIII, XIV, and XXI), comparing all pairs of zones to obtain the overall relative plasticity. Likewise, for each zone, the average RPPI of the pairs that included that zone was considered, thus producing the relative phenotypic plasticity per zone.

3. Results

The results of the one-way ANOVA showed significant overall differences among individuals from trees sampled in the germplasm zones for the traits analyzed (Table 1). The effect of zone was significant (F (df = 2, 258) = 5.23, p = 0.00522) on leaf length (LL): in pairwise comparisons, plants in zone XXI had significantly shorter leaf lengths than plants in zone XIV (difference = −1.30 mm, 95% CI: −2.25 to −0.35, p = 0.00452), while no differences were detected between plants in zones XIV and VIII (p = 0.184), or between plants in zones XXI and VIII (p = 0.429).

Table 1. Summary of the six canonical functions (CF) of the CCA: correlation, variance explained, and main morphological and climatic contributors.

CC	r	r^2 (%)	Eigenvalue	Main Morphological Traits (Coeff.)	Main Climatic Traits (Coeff.)
1	0.846	71.63	2.524	LW (−1.237), LL (−0.161)	MAT (114.773), MCMT (−88.102)
2	0.81	65.6	1.908	LW (0.599), EST (0.251)	MAT (116.916), MCMT (−97.655)
3	0.66	43.57	0.772	LL (−0.485), FOL (−0.381)	MAT (−39.970), TD (9.469)
4	0.484	23.45	0.306	LL (−1.078), LW (1.042)	MAT (12.793), MCMT (−11.584)
5	0.363	13.19	0.152	LL (1.272), NOL (0.225)	MWMT (−14.856), MAT (10.704)
6	0.256	6.53	0.07	LW (2.978), NOL (0.287)	MAT (99.676), MCMT (−67.877)

A significant zone effect was also found (F (df = 2, 258) =12.45, $p < 0.0001$) on rachis length (RL). Plants in zone XIV had a significantly longer rachis than plants in zone VIII (difference = 7.57 mm, 95% CI: 1.89 to 13.25, $p = 0.00577$), and plants in zone XXI had a significantly shorter rachis than plants in zone XIV (difference = −11.24 mm, 95% CI: −16.83 to −5.64, $p < 0.001$). There were no significant differences between plants from zones XXI and VIII ($p = 0.38$) (Appendix A Table A1).

At the population level, petiolule length (PL) ranged between 0.42 and 1.33 cm, leaf length (LL) between 5.04 and 13.20 cm, leaf area (LA) between 151.92 and 1031.20 cm^2, and the number of leaflets (NOL) between 11 and 26, with an overall average of 18.43 ± 3.77 leaflets; rachis length (RL) showed a 15% population coefficient of variation while stomatal density (STD) presented 22% (Appendix A Table A2).

The seed zones show contrasting patterns in the functional leaf traits of *C. odorata*. Zone XIV is prominent for presenting the largest leaf area, with values exceeding 1000 cm^2 and a mean value that is significantly higher than those of zones VIII and XXI ($p < 0.001$). In addition, plants in this zone also had the highest number of leaflets, with an average of close to 20 units. In contrast, plants from Zone XXI had the lowest values for leaf area and number of leaflets, suggesting a more compact leaf structure. Plants from Zone VIII, meanwhile, showed intermediate values, although they were notable for having the longest petiolule on average as well as the highest number of stomata (Figure 2).

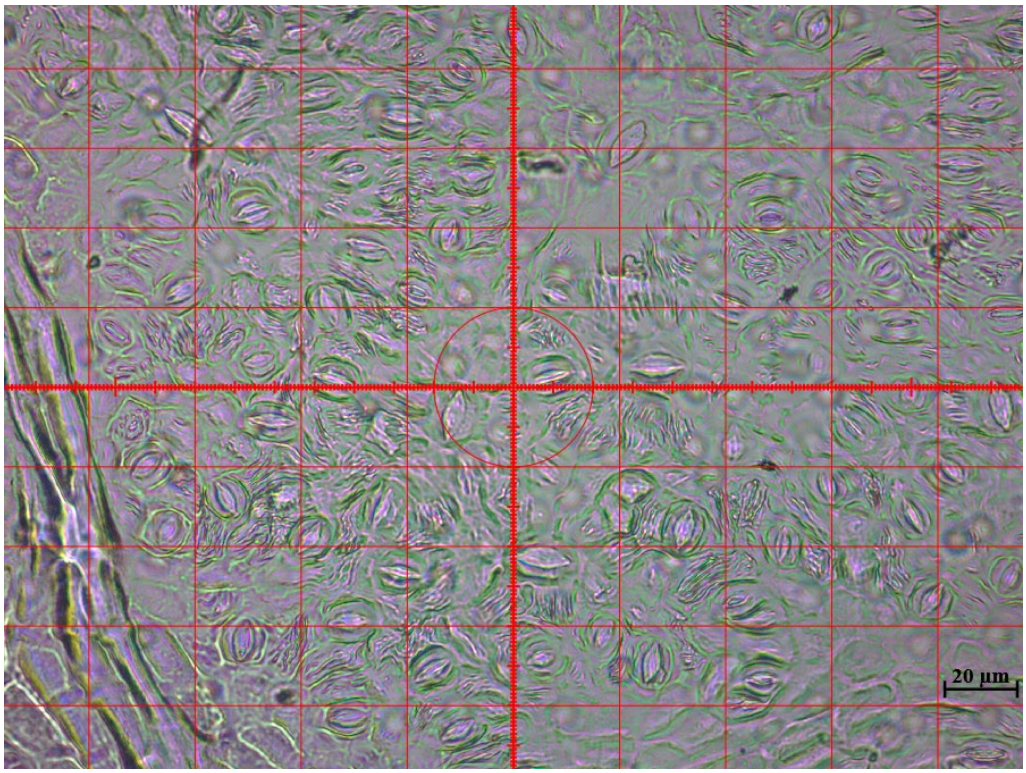


Figure 2. Counting field divided into rectangles (red lines) of 0.014 mm^2 (100 × 140 µm), the red circle indicates the center of the micrograph; locality of Macuspana.

3.1. Results of Canonical Correlation Analysis (CCA)

The canonical correlation analysis identified six components (CC), of which the first two were highly significant and explained most of the covariation between morphological traits and climatic variables in *C. odorata*.

The first canonical component (CC1) showed a high correlation (r = 0.846; $p < 0.001$ explaining 71.6% of the joint variance. On this axis, leaf width (LW) and leaf length (LL) stood out as the main associated traits in terms of morphology. In terms of climate, the

most influential variables were mean annual temperature (MAT), mean coldest month temperature (MCMT), and extreme temperature (EXT).

The second component (CC2) was also significant (r = 0.810; $p < 0.001$), explaining 65.6% of the variance. In this case, the covariation was mainly structured by leaf width (LW) and stomatal density (STD), while MAT and MCMT again dominated the climatic aspect. This axis seems to reflect a compromise between leaf traits and physiological strategies in response to minimum temperature gradients.

Components CC3 to CC6 showed progressively lower correlations (r = 0.66 to 0.26) and weaker contributions. Although some traits (e.g., LL and NOL in CC3) and climatic variables e.g., summer heat-moisture index (SHM) and temperature difference or continentality (TD) in CC4 showed specific associations, these axes were less biologically relevant and lacked significance in the latter two cases ($p > 0.05$) (Table 1).

In the first canonical component (CC1), the shared variance was 0.716, which means that it explained 71.6% of the covariation between morphology and climate. Redundancy showed that climate explained 55.7% of the morphological variation, while morphology explained only 17.0% of climatic variation, evidencing that environmental conditions have a greater influence on leaf traits than vice versa

The sampled sites are clearly distributed along two morpho-climatic axes. The canonical axis 1 (CC1) reflects how the increase in annual temperature (MAT, MCMT, mean warmest month temperature MWMT, Hargreaves Evaporation reference Eref) is associated with a decrease in precipitation (MAP, SHM), evidencing a "warm-humid" climatic gradient in which thermal conditions dominate the pattern of variation. The second canonical axis (CC2) contrasts relative humidity with the thermal deficit. Along this axis, higher relative humidity corresponds to lower TD values, defining a gradient from humid to thermally deficient conditions.

The leaf trait vectors (LW, LA, LL, and RL) align with CC1, indicating that populations with larger and wider leaves are found in warmer environments. In contrast, number of leaflets (NOL) and stomatal density (STD) are associated with CC2, indicating that these characteristics respond mainly to relative humidity and thermal stress at the site (Figure 3).

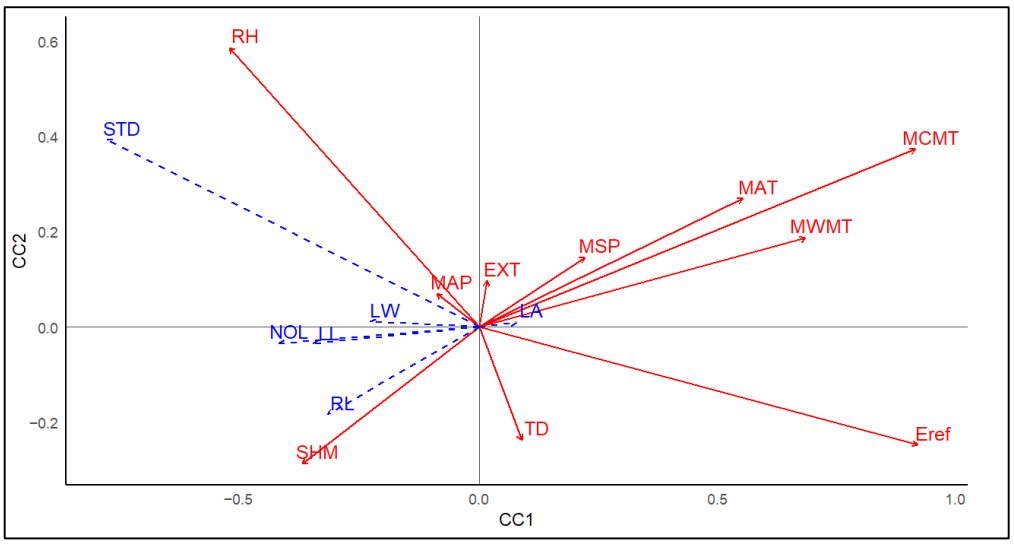


Figure 3. Biplot of the first two canonical components (CC1 vs. CC2) of Cedrela odorata, showing leaf traits (blue arrows) and climatic variables (red arrows). These show the relationship between leaf traits and the warm-humid gradient (CC1) and relative humidity vs. thermal deficit (CC2).

3.2. Structural Loads

Canonical Component 1 (CC1) accounts for 39.2% of the joint covariance, dominated by leaf size traits (LW = 0.91; LA = 0.88; LL = 0.76; RL = 0.69) and, to a lesser extent, by thermal and evaporative variables, Hargreaves Evaporation reference (Eref) = 0.47; MCMT = 0.43; MAT = 0.26).

Canonical component 2 (CC2) accounts for 8.7% of the variance, contrasting stomatal density and foliar amplitude (STD = −0.75; LW = −0.29) with thermal gradients (TD = 0.13; MCMT = −0.19).

Canonical component 3 (CC3) emphasizes the morphology of the compound leaf (FOL = −0.79), with a probable influence from annual precipitation and temperature extremes (MAP, EXT, RH) (Figure 4).

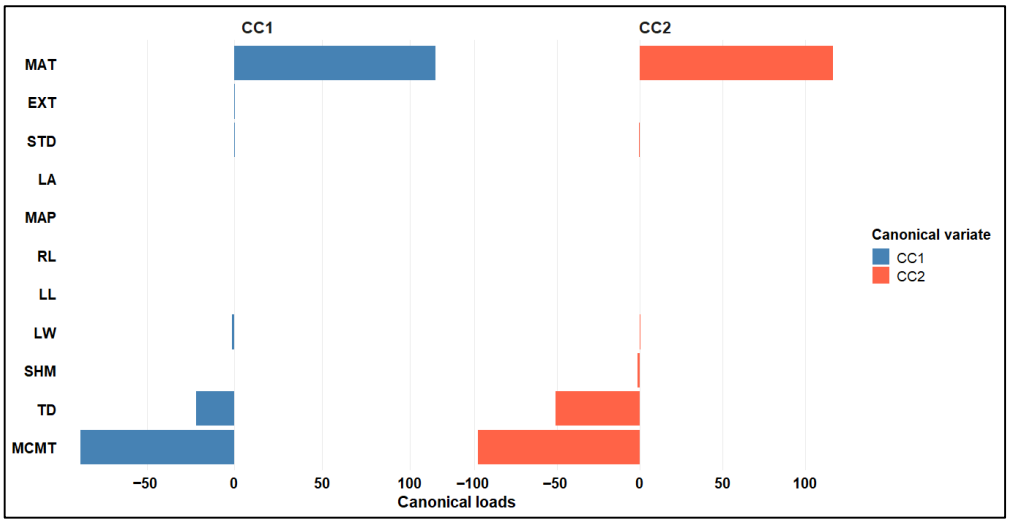


Figure 4. Structural loads of the variables in the first two canonical components (CC1 and CC2).

3.3. Redundancy Analysis

The redundancy analysis (RDA) applied to standardized leaf traits and the ten climatic variables revealed a total inertia of 6.0, of which 3.342 (55.7%) was "constrained" by the model, i.e., explained by the climatic block, while 2.658 (44.3%) was not explained by these variables (Table 2).

Table 2. Inertia and variance explained per axis in the redundancy analysis (RDA) of leaf traits.

Axis	Eigenvalue	% Var Total	% Var Constrained	Cumulative % Constrained
RDA1	2.35	39.17	70.31	70.31
RDA2	0.5235	8.73	15.66	85.97
RDA3	0.3719	6.20	11.13	97.10
RDA4	0.0795	1.33	2.38	99.48
RDA5	0.0148	0.25	0.44	99.92
RDA6	0.0028	0.05	0.08	100.00

The first axis (RDA1) had an eigenvalue of 2.35, representing 39.2% of the total variance of the traits and 70.3% of the variance explained by the climatic variables. The second axis (RDA2) had an eigenvalue of 0.5235, contributing 8.7% of the total variance and 15.7% of the restricted variance. The subsequent axes (RDA3-RDA6) contributed successively smaller percentages (6.2%, 1.3%, 0.3%, and 0.05% of the total variance, respectively), accumulating 100% of the restricted variance after RDA6.

3.4. Seed Zone Comparison Analysis

The three morphological clusters consisted of 40 samples in Cluster 1, 30 in Cluster 2, and 17 in Cluster 3. When compared with the germplasm movement zones (VIII, XIV, and XXI), cluster 1 mainly coincided with zone XIV (34 out of 40 samples, 85%), cluster 2 with zone XXI (19 out of 30, 63%), and cluster 3 with zone VIII (13 out of 17, 76%).

The χ^2 test of the contingency table (four degrees of freedom) was highly significant ($\chi^2 = 75.55$, $p < 0.001$). Cramer's coefficient, V = 0.659, indicates a strong association between the morphological groups and seed zones, while the adjusted Rand index, ARI = 0.499, reflects a moderate agreement between morphological grouping and movement zones, discounting that expected by chance (intrinsic property of the ARI, 0 indicates agreement equivalent to chance and 1 indicates perfect agreement)

4. Discussion

The variation in leaf area (LA) observed for *C. odorata*, across the studied regions demonstrates a clear correspondence to the humidity gradient and environmental stress, where leaf size reaches its maximum under intermediate conditions and decreases in both very humid and very dry environments.

Plants in zone XIV have the highest leaf size values, showing congruence with global studies that have documented similar responses: Peppe et al. [54] found that leaf size does not increase indefinitely with precipitation, but rather reaches an optimum in intermediate humidity ranges and declines in very humid and very dry climates due to factors such as the risk of nighttime chilling in very large leaves [55] and water stress in extremely dry environments.

Rodríguez-Ramírez et al. [56] studied four species of *Magnolia* L. in tropical montane cloud forests at different latitudes in Mexico (from the more humid South to the drier North), comparing leaf traits (length, blade width, venation characteristics) between populations. These authors found a clear geographical gradient in leaf size: in the warmer, wetter southern sites, the leaves were significantly longer and wider, while in the northern sites, with a less humid climate and greater seasonal variation, leaf size gradually decreased with increasing latitude. Specifically, they observed that the largest leaves (with the greatest leaf blade length) corresponded to populations in the humid tropical south, while populations in the north (in drier forests) presented smaller, narrower leaves.

In this study, the leaflets were consistently longer (9.30 cm $\pm$ 1.67) and wider (3.89 cm $\pm$ 0.60) in plants from zone XIV, which has intermediate humidity conditions and warmer temperatures. In zone VIII, characterized by being the most humid and with the least temperature variation, the leaflets were intermediate (8.58 cm $\pm$ 1.44; 3.23 cm $\pm$ 0.50). Finally, in zone XXI, the driest and most seasonally variable, the leaves were shorter (8.00 cm $\pm$ 1.28) and narrower (3.09 cm $\pm$ 0.53). Similarly, rachis length (RL) was greater in the intermediate zone (XIV) at ~55 cm, shorter in the wettest zone (VIII) at ~50 cm, and shortest in the driest zone (XXI) at ~49 cm. The number of leaflets (NOL) showed less marked differences: plants in the intermediate (XIV) and most humid (VIII) zones presented similar average values (19.9 and 18), while plants in the driest zone (XXI) had a slightly lower number of leaflets (15.8) and also presented more variability. In contrast, petiolule length (PL) did not vary significantly between zones, with values ranging around 0.8 cm.

The response of the leaf architecture in *C. odorata* throughout the seed zones reflects a balance between exploiting the greater light capture capacity and minimizing risks caused by high temperatures and abundant precipitation. These risks include excessive nocturnal cooling in large leaves, water loss through transpiration in high temperature conditions [57], mechanical damage from torrential rains [58], and high susceptibility to leaf pathogens [59], a pattern corroborated in various tropical broadleaf species.

In contrast to leaf size, stomatal density (STD) shows a different pattern: the most humid zone (VIII) has the highest mean (13.3 stomata $mm^{-2} \pm 4.1$), followed by the driest zone (XXI) (10.4 ± 1.7), and finally the intermediate zone (XIV) with the lowest values (9.0 ± 2.1). This indicates that, while the intermediate zone (XIV) concentrates plants that investment in larger and broader leaves, the most humid zone (VIII) prioritizes plants with greater gas exchange capacity per unit area, and the driest zone (XXI) presents plants with an intermediate value. The combination of these variations suggests that the plants in each zone responds differentially to local environmental factors.

Plants in the most humid zone (VIII), with high water availability or lower water stress, have a strategy of high stomatal density (13.3 stomata $mm^{-2} \pm 4.1$), which can facilitate gas exchange in environments where water loss is not a major constraint, while in the intermediate zone (XIV), stomatal density is lower (9.0 ± 2.1 stomata mm^{-2}), possibly as a control mechanism in less favorable, i.e., drier, humidity conditions (XXI). Stomatal density maintains intermediate values between the two previous zones. This pattern is also reported in the study of Liu et al. [9], who analyzed 4492 species records at 340 sites along climatic gradients (from cold to tropical forests) in China. These authors found that average community stomatal density was strongly associated with water availability. In particular, seasonal precipitation (warmest trimester) explained much of the variation: plant communities at sites with higher precipitation showed higher stomatal densities, while at drier sites, stomatal density tended to be lower. These authors conclude that water availability is a major environmental filter that shapes stomatal density in each community since high stomatal density confers advantages in photosynthesis when water is abundant. In this sense, our results show that zone VIII, the most humid, is where *C. odorata* exhibits the highest stomatal density, coinciding with the pattern of broadleaf species: water availability promotes increases in the number of stomata. However, the pattern is not absolute and is not apparent in all situations. Interaction with other environmental factors (such as sunlight, temperature, atmospheric CO_2, and nutrition) and the evolutionary strategy of each species modulate stomatal density in complex ways [60]. For example, sun-exposed leaves in the canopy (drier and warmer environment) tend to have more stomata than shaded leaves in the more humid understory, even within the same rainforest. Likewise, moderate water stress during leaf development sometimes induces smaller leaves with denser stomata, while severe droughts can reduce stomatal density by inhibiting leaf growth.

4.1. Canonical Correlation Analysis

The high correlation observed (r = 0.846) suggests a strong correspondence between leaf size and shape, particularly leaf width (LW) and leaf length (LL), as well as in the dominant thermal gradients represented by mean annual temperature (MAT), mean coldest month temperature (MCMT), and extreme temperatures (EXT). In this regard, for large-scale ecological analyses of this type, the results are considered reliable in such multivariate models when they meet an enhanced significance criterion of $p < 0.001$ [61]. On the other hand, thresholds considered standard, such as $p < 0.01$ and $p < 0.05$, are regarded as indicators of strong correlations in smaller sample sets. In the present study, the results obtained ($p < 0.001$) suggest a robust biological interdependence between the leaf morphology of *C. odorata* and its environment.

Studies such as Lusk et al. [55] document how leaf size (especially leaf width and length) varies depending on thermal conditions, from average temperature to extremes of heat or cold, and as a function of seasonality. Lusk et al. [55] showed that, on clear nights, the broadest leaves of evergreen species in New Zealand cool significantly more (~3.2 °C) than the smaller leaves (~0.9 °C), and that mean annual temperature and frost-free period can explain leaf size in evergreens, but not in deciduous species.

Wright et al. [6] state in their study of global patterns of variation that, in terms of leaf size, in general, larger leaves are usually found in warm and humid tropical environments, while smaller leaves predominate under thermal stress due to dry heat or intense cold. In our CCA, the first component (CC1) strongly associated wide and long leaves with warm and humid seasons, while smaller leaves were linked to lower temperature gradients and greater seasonality. This finding coincides with the observation by Wright et al. [6] that species with large leaves are predominant in warm and humid climates, where a larger leaf area favors light capture and maintains the thermal exchange limit gap. In contrast, under extreme thermal stress, from either dry heat or intense cold, leaves tend to reduce their size to minimize temperature differences between the leaf and the air and to avoid overheating or excessive cooling.

The morphological patterns analyzed in *C. odorata* closely match the trait syndromes identified by Wang et al. [2] in woody communities in China. In that study, broadleaf species with small to large leaves and acuminate apices (drip-tips) predominate in humid climates with low seasonality. This is consistent with our findings in *C. odorata* individuals from zone XIV, where the canonical axis 1 (CC1) associates wider and longer leaves with higher temperatures and humidity.

4.2. Redundancy Analysis

The percentages of variance explained by the first two axes of the redundancy analysis (RDA) can be compared with other studies that consider leaf trait data. Zhou et al. [62], in forests in China, reported that the main axis of their RDA explained 41.7% of the covariation between leaf traits and environmental factors (precipitation, temperature, and humidity). These values are similar and close to those reported in the present study (RDA1 39% of the total variance), which suggests that, as in other forest communities, the main axis of the leaf variation in *C. odorata* reflects the gradient of water availability and temperature; i.e., the interaction between precipitation and temperature acts as the key factor shaping leaf size and shape in both contexts.

4.3. Plasticity Index

The phenotypic plasticity results show high morphological variability both overall and within each zone. However, plasticity varies according to the life history of the species or the environmental gradient: studies such as those by Rozendaal et al. [63] and Bongers et al. [64] have suggested that pioneer species or those from zones of high environmental variability often show greater phenotypic plasticity in their leaf traits (in response to light or water availability gradients) than species from more stable environments. Rozendaal et al. [63] reported wide interspecific differences in the RDPI of traits such as leaf area, leaf thickness, and stomatal density, linked to the ecological strategies of the plants: fast-growing pioneers with high plasticity vs. shade species with more rigid traits. Bongers et al. [64] analyzed more than 30 tropical species under different climate scenarios, finding that the mean values of both functional traits and their plasticity contribute to species coexistence along climate gradients by acting on niche differences. In particular, traits such as leaf size and water efficiency showed within-species variations that buffer the effects of climate variability, complementing local genetic adaptations.

5. Conclusions

Populations of *Cedrela odorata* in the most humid, intermediate, and driest germplasm zones of Tabasco (VIII, XIV, and XXI, respectively) show clear differences in leaf traits: trees sampled from zone XIV (intermediate) exhibit larger leaf area and longer rachis values, while the most humid zone (VIII) has the highest stomatal density, and trees in

the driest/coastal zone (XXI) combine smaller leaves with intermediate stomatal density and greater leaflet subdivision. CCA and RDA analyses both indicate that the observed morphological variations are mainly explained by climatic gradients in temperature and water availability, reflecting two contrasting environmental axes: one warm-humid, and the other associated with a relative humidity gradient in response to water deficit or thermal stress.

The high RDPI in traits such as leaf area, rachis length, and stomatal density is associated with the plastic adjustment capacity of the species to environmental differences, although the patterns of geographic differentiation remain consistent. These results support the delimitation of germplasm movement zones since each region harbors traits adapted to its climatic conditions. At the same time, plasticity indicates some scope for transfer between areas with similar climates. It is recommended to complement this with transfer trials and genetic studies to determine the limits of local adaptation and to ensure the resilience of plantations to environmental changes.

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Abbreviations

The following abbreviations are used in this manuscript:

RDPI	Relative Distances Plasticity Index
ANOVA	Analysis of Variance
LA	Leaf area
RL	Rachis length
LW	Leaf width
STD	Stomatal density
NOL	Number of leaflets
LL	Leaf length
TIFF	Tagged Image File Format
MAT	Mean annual temperature
MCMT	Mean coldest month temperature
EXT	Extreme temperature

SHM	Summer heat-moisture index
TD	temperature difference or continentality
RDA	Redundancy analysis
CONAFOR	Comision Nacional Forestal

Appendix A

Table A1. Results of one-way ANOVA and post hoc comparisons (Tukey HSD) for the traits leaf length (LL) and rachis length (RL) in Cedrela odorata.

Trait	df	ANOVA *p*-Value	Comparison	Difference (95% CI)	*p* Adjusted
LL	2, 258	0.00522	XIV–VIII	0.719 (−0.247, 1.680)	0.184
			XXI–VIII	−0.581 (−1.690, 0.530)	0.429
			XXI–XIV	−1.300 (−2.250, −0.349)	0.00452
RL	2, 258	0.0000126	XIV–VIII	7.576 (1.894, 13.258)	0.00577
			XXI–VIII	−3.665 (−10.200, 2.871)	0.378
			XXI–XIV	−11.240 (−16.834, −5.647)	0.0000207

Table A2. Dunn post hoc comparisons (with Bonferroni correction) for non-parametric leaf traits among *Cedrela odorata* seed zones. *: significant at the 10% level ($p < 0.10$); **: significant at the 5% level ($p < 0.05$); ***: significant at the 1% level ($p < 0.01$).

Variable	Comparison	Z	P.unadj	P.adj	Significance
LA	VIII–XIV	−2.84	0.00	0.0135	*
LA	VIII–XXI	2.01	0.04	0.1342	No
LA	XIV–XXI	5.23	0.00	0.0000	***
NOL	VIII–XIV	−1.96	0.05	0.1513	No
NOL	VIII–XXI	1.95	0.05	0.1519	No
NOL	XIV–XXI	4.27	0.00	0.0001	***
PL	VIII–XIV	1.94	0.05	0.1584	No
PL	VIII–XXI	1.51	0.13	0.3924	No
PL	XIV–XXI	−0.20	0.84	1.0000	No
LW	VIII–XIV	−3.15	0.00	0.0049	**
LW	VIII–XXI	0.78	0.43	1.0000	No
LW	XIV–XXI	4.11	0.00	0.0001	***
STD	VIII–XIV	4.49	0.00	0.0000	***
STD	VIII–XXI	1.81	0.07	0.2112	No
STD	XIV–XXI	−2.45	0.01	0.0431	*

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