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MORPHOLOGICAL VARIATION OF *Cyrtophyllum fragrans (Roxb.)* AMONG FOUR HABITAT TYPES IN JAMBI PROVINCE: A MULTIVARIATE APPROACH

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Abstract

Cyrtophyllum fragrans (Roxb.) Don is a high-value hardwood tree whose population in Jambi Province is threatened by habitat fragmentation and land conversion, yet morphological data based on local populations remain unavailable. This study examined quantitative and qualitative morphological variation of *C. fragrans* from four locations in Jambi Province representing different ecological conditions, and identified phenotypic clustering patterns using a multivariate approach. Observations were conducted on 39 individual trees; quantitative characters included tree height (TH), diameter at breast height (DBH), leaf length (LL), leaf width (LW), and petiole length (PL), while qualitative characters included lamina shape, apex, base, and margin. Data were analyzed using Principal Component Analysis (PCA) and Hierarchical Clustering on Principal Components (HCPC) with Ward's method and Euclidean distance. All five quantitative characters (TH, DBH, LL, LW, and PL) differed significantly among locations: leaf dimension characters (LL, LW, PL) responded most strongly to light intensity gradients, while tree size characters (TH, DBH) reflected cumulative growth history and habitat fragmentation effects. PCA identified two independent phenotypic gradients explaining 80.4% of total variance: PC1 (45.7%) captured the leaf dimension gradient as a plastic response to light intensity, and PC2 (34.7%) captured the tree size gradient recording long-term growth accumulation. HCPC produced four clusters with cross-site composition: K1 (small leaves, full sun), K2 (suppressed axial growth), K3 (very large DBH, cumulative growth), and K4 (large leaves, shaded). Qualitative leaf characters (simple opposite leaves, elliptic lamina, acuminate to caudate apex, cuneate base, entire margin, and pinnate venation) were consistent with the species description of *C. fragrans* across all four accessions and showed no meaningful variation among locations, confirming their stability as species-level taxonomic markers. Site ecological conditions, not geographic origin, were the primary determinant of morphological phenotype in *C. fragrans*, with implications for individual-based selection of mother trees in breeding programs rather than location-based selection.

Keywords: *morphological variation, phenotypic plasticity, principal component analysis, hierarchical clustering, tembesu*

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INTRODUCTION

Cyrtophyllum fragrans (Roxb.) (synonym: *Fagraea fragrans* Roxb.) is a high-value hardwood tree distributed across Sumatra, Kalimantan, Sulawesi, West Java, and Maluku (Mindawati et al, 2014). Tembesu timber is widely used in heavy construction such as bridge pillars, building foundations, and flooring due to its hardness, natural durability, and resistance to open environmental conditions (Asmaliyah et al., 2012). Beyond its timber value, tembesu leaves contain bioactive compounds including terpenes, phenols, and flavonoids with strong antioxidant activity, with potential for development as phytopharmaceutical raw materials (Wahyudi et al., 2022). In Jambi Province, tembesu is a flagship timber species with high economic and cultural value for local communities, yet its

population is now threatened by the continuous expansion of oil palm plantations (Junaidah et al., 2014; Nursanti et al., 2017). Oil palm area in Jambi reached 559,697 ha in 2015 and continues to grow, intensifying pressure on tembesu in the field while cultivation efforts remain very limited (Nursanti *et al.*, 2017). This habitat fragmentation creates matrix barriers that progressively isolate previously connected tembesu populations into discrete units, which ecologically is expected to drive phenotypic divergence among populations due to restricted gene flow, while simultaneously increasing the risk of genetic diversity narrowing within populations due to genetic drift. These conditions create an urgent need for phenotypic assessment across populations as the foundation for conservation strategies and genetic resource management of tembesu. Artificial propagation efforts, including micropropagation, are increasingly critical given the difficulty of natural regeneration of *C. fragrans* in the field (Fatonah et al. 2025).

Morphological variation among populations reflects the combined expression of genetic factors and phenotypic plasticity in response to site condition heterogeneity. Understanding this variation pattern is important in two contexts: first, to identify individuals or populations with superior phenotypes as seed sources or mother trees in breeding programs; second, to understand the adaptive capacity of the species in facing varying environmental pressures, which is relevant for both ex situ and in situ conservation planning. Morphological characters in woody plants are broadly classified into quantitative characters, which are measurable and continuously variable such as tree height, stem diameter, and leaf dimensions, and qualitative characters, which are descriptive and categorical such as leaf shape, venation pattern, and surface texture (Maya-García et al., 2020; Seid et al., 2022). Both character types reflect the combined influence of genetic factors and environmental conditions, making them informative tools for population-level studies. Bramasto and Sudrajat (2018) demonstrated that all morpho-physiological characters of leaves, fruits, and seeds of *C. fragrans* differed significantly among populations from five locations in South Sumatra and West Java, with environmental variance coefficients exceeding genetic variance coefficients for most leaf characters, indicating a predominant environmental contribution to phenotypic expression. However, a similar study for tembesu populations in Jambi Province has never been conducted.

This study aimed to examine quantitative and qualitative morphological variation of *C. fragrans* from four locations in Jambi Province representing different ecological conditions, and to identify phenotypic clustering patterns among individuals and locations using a multivariate approach. The results are expected to provide baseline morphological data to support genetic conservation, serve as initial information on genetic diversity, and support cultivation and breeding programs of *C. fragrans* in Jambi Province.

MATERIAL AND METHODS

a. Study Site and Research Period

The study was conducted from July to October 2025 at four sites in Jambi Province, selected based on their representativeness of different ecological conditions and habitat status of tembesu populations. L1 (Bupati Bungo Official Residence area, Bungo Regency) represents an open urban environment without canopy competition. L2 (Lapangan Merdeka, Tebo Regency) is an urban public space representing a transitional ecosystem from secondary forest. L3 (Kasang Lopak Alai Village, Kumpeh Ulu) is a tembesu plantation forest with a dense canopy and homogeneous stand. L4 (Jambi Tulo Village, Maro Sebo) is a former tembesu plantation that has been converted to oil palm, with remaining tembesu trees growing in isolation. Environmental characteristics of each site recorded during field data collection are presented in Table 1.

Table 1. Environmental characteristics of the four sampling sites recorded during field data collection.

Site	Air Temperature (°C)	Relative Humidity (%)	Light Intensity (lux)
L1	36	45	1,380
L2	37	48	1,387
L3	29	74	774
L4	30	44	780

Note: All values represent single-point measurements recorded during a single field visit and should be interpreted as qualitative site characterizations rather than long-term averages. L1 = Bupati Bungo Official Residence; L2 = Lapangan Merdeka, Tebo; L3 = Kasang Lopak Alai, Kumpeh Ulu; L4 = Jambi Tulo, Maro Sebo.

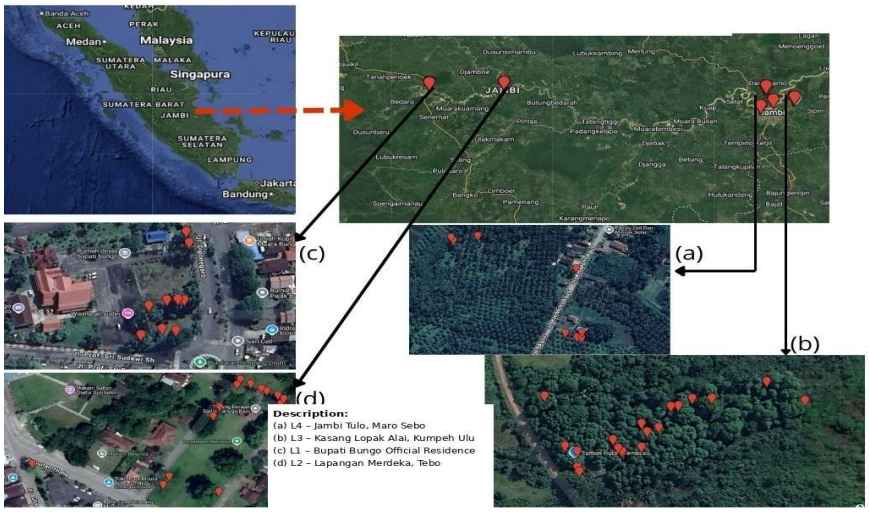

Figure 1. Research location map of *Cyrtophyllum fragrans* sampling sites in Jambi Province, Indonesia

b. Sampling and Character Measurement

A total of 39 *C. fragrans* sample trees were purposively selected based on healthy condition, free from obvious physical damage, and morphologically identified to species level (L1 = 8, L2 = 8, L3 = 15, L4 = 8). Air temperature, relative humidity, and light intensity were each measured on a single occasion at each site using a thermohygrometer and lux meter as descriptive microclimate characterization. Tree height (TH) was measured using a hypsometer and diameter at breast height (DBH) was measured at 1.3 m height using a diameter tape. Leaf samples were taken from one branch per tree at the mid-crown facing east to ensure uniform light exposure. Selected leaves were fully expanded mature leaves, at positions 2 to 4 from the branch tip, totaling 10 leaves per tree. Leaf length (LL) and maximum leaf width (LW) were measured using a digital caliper. Petiole length (PL) was measured from the petiole base to the junction with the lamina. Qualitative leaf characters (shape, apex type, base, margin, and venation) were determined following Ellis et al. (2009), except apex terminology which followed Wong and Manickam, (2012) dan Wong et al., (2025)

c. Data Analysis

Descriptive statistics for all five quantitative characters were calculated per site, including mean, standard deviation, minimum, maximum, and coefficient of variation. Normality was tested using the Shapiro-Wilk test and variance homogeneity using Levene's test. The comparative test among sites was selected based on the results of both tests: One-Way ANOVA (normality and homogeneity met), Welch's ANOVA (homogeneity not met), or Kruskal-Wallis (normality not met). Post-hoc tests used were Tukey HSD, Games-Howell, and Dunn-Bonferroni, respectively. Relationships among characters were analyzed using Spearman correlation. PCA was performed on standardized data (z-score) to identify the multivariate variation structure. HCPC was performed using Ward's criterion with Euclidean distance to identify meaningful phenotypic clusters; the optimal number of clusters was determined based on dendrogram structure and the height values of branch separations. All analyses were performed using R software version 4.x.

RESULTS AND DISCUSSION

a. Quantitative Morphological Variation among Site

Statistical analysis of five quantitative characters: tree height (TH), diameter at breast height (DBH), leaf length (LL), leaf width (LW), and petiole length (PL), revealed significant differences among the four study sites (Table 2). The variation pattern was not randomly distributed, but consistent with differences in ecological conditions among locations, reflecting the phenotypic plasticity of *C.*

fragrans in response to environmental heterogeneity. This plasticity is commonly observed in tropical tree species inhabiting different ecological gradients (Souza *et al.*, 2018; Peña *et al.*, 2025).

Table 2. Quantitative morphological characters of *Cyrtophyllum fragrans* (mean ± standard deviation) among sites in Jambi Province.

Site	TH (m)	DBH (cm)	LL (cm)	LW (cm)	PL (cm)
L1	31.41 ± 6.50 (20.69%)	40.99 ± 10.17 (24.80%)	8.63 ± 1.00 (11.54%)	3.49 ± 0.47 (13.35%)	0.645 ± 0.138 (21.34%)
L2	28.86 ± 9.00 (31.19%)	83.48 ± 44.52 (53.33%)	9.49 ± 0.74 (7.75%)	4.26 ± 0.39 (9.21%)	1.136 ± 0.170 (15.00%)
L3	22.33 ± 7.79 (34.90%)	46.42 ± 21.22 (45.71%)	10.61 ± 0.98 (9.28%)	4.24 ± 0.51 (12.03%)	1.091 ± 0.194 (17.74%)
L4	11.73 ± 3.44 (29.36%)	24.05 ± 2.73 (11.33%)	10.00 ± 1.19 (11.87%)	3.86 ± 0.60 (15.43%)	0.756 ± 0.205 (27.11%)
Test statistic	F = 12.08*	F = 14.91**	F = 7.42**	F = 4.80*	H = 22.01**

Note: Values in parentheses indicate coefficient of variation (CV, %). TH = tree height; DBH = diameter at breast height; LL = leaf length; LW = leaf width; PL = petiole length. ** = significant at 99% confidence level; * = significant at 95% confidence level. L1 = Bupati Bungo Official Residence; L2 = Lapangan Merdeka, Tebo; L3 = Kasang Lopak Alai, Kumpeh Ulu; L4 = Jambi Tulo, Maro Sebo

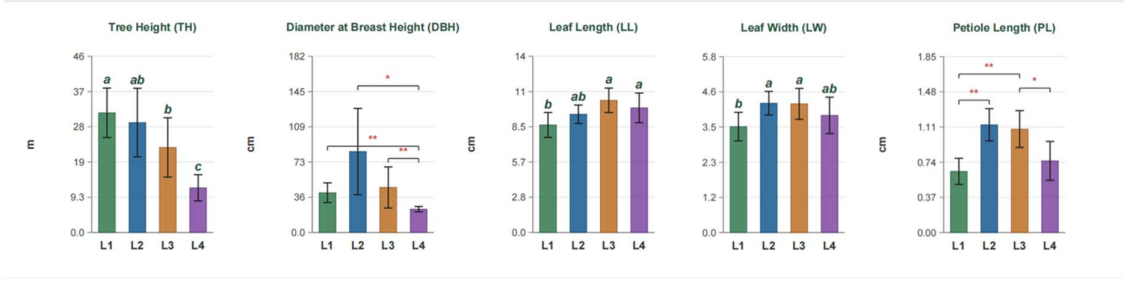

Figure 2. Quantitative morphological characters of *Cyrtophyllum fragrans* (Roxb.) Wall. ex G. Don across four sites in Jambi Province, Indonesia. Note: Bars represent mean values; error bars indicate ±1 standard deviation. Different letters above bars indicate significant differences among sites based on Tukey HSD post-hoc test (TH, LL, LW). Brackets with asterisks indicate significant pairwise differences from Games-Howell post-hoc test (DBH) and Dunn-Bonferroni post-hoc test (PL). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

1. **Tree Height (TH)**

TH differed significantly among locations (Table 2; Figure 2). L1 recorded the highest mean TH (31.41 m), followed by L2 (28.86 m), L3 (22.33 m), and L4 (11.73 m). L1 differed significantly from L3 and L4, but not from L2. L4 differed significantly from all other locations. L2 fell into subset "ab" because its mean difference from L1 was only 2.55 m and its internal variation was high (CV = 31.19%), so its difference from L3 also did not reach the significance threshold. Ecologically, L1 and L2 can still be categorized as open urban trees with the highest light exposure.

Trees at L1 and L2 grew in structurally open urban environments without canopy competition. Light intensity recorded during the field visit at L1 and L2 (1,380 and 1,387 lux, respectively) was higher than at L3 (774 lux), consistent with the absence of overhead canopy cover at both urban sites. Although these values represent single-point measurements rather than long-term averages, the structural openness of both sites supports the inference of consistently higher light availability compared to L3 and L4, consistent with the highest TH recorded at both locations. Cho et al. (2024)

confirmed that trees in open urban environments with unrestricted light access exhibit significant variation in functional responses linked to overall tree growth dynamics.

TH at L3 (mean 22.33 m) was lower than L1, consistent with dense canopy shading (774 lux). However, internal variation at L3 was very high (CV = 34.90%; range 11.5–39 m). Individual P13-L3 with TH 39 m had the highest value at L3, indicating that differences in canopy position among individuals within the stand (gap vs. sub-canopy) contributed substantially to this variation. Canopy position data per individual were not collected in this study, so the contribution of this factor cannot be quantified further. Nascimento et al. (2024) showed that between-crown light gradients have a greater influence on tree morphology than within-crown gradients, supporting the interpretation that canopy position heterogeneity among individuals at L3 is a significant source of TH variation.

L4 recorded the lowest TH (mean 11.73 m; CV = 29.36%). Trees at L4 are remnant individuals in former tembesu land converted to oil palm plantation, growing in isolation with large inter-tree distances. Van Gelder et al. (2006) and Nunes et al. (2023) found that trees in forest edge fragments undergo architectural changes that suppress axial growth due to increased wind turbulence and changes in lateral resource availability. Anderson et al. (2022) in a study of forest edge stands bordering oil palm plantations in Borneo, reported reductions in tree diameter of up to 21% in areas near the edge compared to forest interior, a pattern consistent with conditions at L4.

The TH variation at L2 (CV = 31.19%) reflects the age heterogeneity of trees within that location. The very wide DBH range at L2 (29–155 cm) indicates that individuals originated from different age ranges: some likely represent remnants of pre-fragmentation stands, others result from planting at different periods. This planting history heterogeneity should be acknowledged as a limitation in analyzing L2 as a single homogeneous ecological unit.

2. **Diameter at Breast Height (DBH)**

DBH showed the highest inter-location heterogeneity among all tested variables, as DBH variance among groups was not homogeneous (Levene: F = 5.94; p = 0.002), so Games-Howell was used as post-hoc. L1 did not differ significantly from L2 (p = 0.114) and L3 (p = 0.840), but differed significantly from L4 (p = 0.008). L2 differed significantly from L4 (p = 0.028). L3 differed significantly from L4 (p = 0.006).

DBH at L2 was very high (mean 83.4 cm; CV = 53.33%; range 29–155 cm), but this value does not reflect currently optimal site conditions. Two extreme outlier individuals (P1-L2: 155 cm; P5-L2: 135 cm) drove the location mean upward disproportionately. The large DBH of these two individuals is presumed to represent growth accumulation before the area was converted to a city park, not a product of current ecological conditions. Very large diameter trees in urban landscapes are generally remnants of pre-fragmentation stands that survived land conversion, and their presence does not guarantee equivalent active growth conditions at the same location (Roux *et al.*, 2014).

L4 recorded the lowest DBH (mean 24.05 cm) with high uniformity (CV = 11.33%), indicating uniform ecological pressure on all individuals. L4's position as an isolated stand in an oil palm monoculture landscape is consistent with the pattern of DBH decline in fragmented forest edge areas, where edge effects significantly suppress tree size compared to forest interior (Hending *et al.*, 2023). Lateral microclimate changes at forest edges bordering oil palm plantations, including temperature increases, vapor pressure deficit, and reduced soil moisture are presumed to be the underlying mechanism of diameter growth suppression (Ordway et al., 2020).

3. **Leaf Length (LL) and Leaf Width (LW)**

LL differed significantly among locations (Table 2). L3 produced the highest LL (10.61 cm; group a), followed by L4 (10.00 cm; group a), L2 (9.49 cm; group ab), and L1 (8.63 cm; group b). L1 differed significantly from L3 and L4, but not from L2. LW followed a similar pattern (One-Way ANOVA; F = 4.80; p = 0.007): L2 (4.26 cm; group a) and L3 (4.24 cm; group a) differed significantly from L1 (3.49 cm; group b), while L4 (3.86 cm) fell into group ab.

This pattern is consistent with leaf morphology responses to the light intensity gradient. L1 with the highest light exposure (1,380 lux) produced the smallest leaves, consistent with sun leaf formation, smaller leaves as a strategy to reduce excessive transpiration and photorespiration damage at high light intensity. Poorter et al. (2019), in a meta-analysis of 500 experiments and 760 species, confirmed that individual leaf size correlates negatively with daily light intensity in the moderate to high light range,

with sun-grown leaves consistently smaller than shade-grown. Rozendaal et al., (2006) found significant light effects on LL and LW in 38 tropical tree species: shaded leaves were longer (mean 18.37 cm) and wider (9.79 cm) than leaves in full light (17.51 cm and 9.38 cm). It should be noted that light plasticity for LL and LW is low (PI LL: 4.7%; PI LW: 4.2%) compared to physiological traits such as SLA (PI: 23.2%), indicating that leaf dimensions are responsive but not the primary driver of light acclimation in tropical tree species. The leaf dimension differences observed among locations in this study, although statistically significant, should be interpreted in the context of inherently moderate plasticity of these characters.

Conversely, L3 **(**774 lux; RH 74%) produced wider leaves, consistent with a shade acclimation response to maximize light interception under a dense canopy. Nascimento et al. (2024) confirmed in *Eugenia hiemalis* that between-crown light gradients more strongly determine leaf morphology responses than within-crown gradients, supporting the interpretation that inter-location light intensity differences are the primary driver of the observed LL and LW differences. In addition to the shading factor, L3 was reported by local residents as a location prone to inundation during high rainfall, although this condition was not quantitatively documented. Bramasto and Sudrajat (2018) reported that *C. fragrans* leaf morphological characters differed significantly among populations with greater environmental component contributions than genetic components, and population clustering reflected site condition similarity including dry land to swamp gradients, although that study did not isolate the specific contribution of inundation to lamina dimensions. Accordingly, the larger leaf dimensions at L3 are likely the result of two ecological pressures acting in the same direction: canopy shading driving lamina expansion to maximize light interception, and periodically moist site conditions that do not limit leaf cell expansion. As L3 inundation data were not quantified, the relative contribution of both factors cannot be analytically separated and represents a limitation of this study.

L4 produced LL and LW comparable to L3 despite much lower relative humidity (44% vs. 74%) and strong axial growth suppression in its trees. These two responses are not contradictory: TH suppression is a long-term structural response to edge effects and isolation, while leaf dimensions represent a plastic response to the light intensity currently received by the crown. At similar light intensities between L3 and L4 (774 vs. 780 lux), the comparable leaf dimensions indicate that in this low-to-moderate light range, light more dominantly determines lamina dimensions than humidity. However, this interpretation is limited to descriptive association because microclimate data in this study were instantaneous and cannot be used as analytical covariates.

4. **Petiole Length (PL)**

PL differed significantly among locations, with Dunn-Bonferroni post-hoc producing significant differences in pairs L1–L2 ($p = 0.007$), L1–L3 ($p < 0.001$), and L3–L4 ($p = 0.010$). Pairs L1–L4 ($p = 1.000$), L2–L3 ($p = 1.000$), and L2–L4 ($p = 0.058$) were not significantly different. L3 recorded the highest value (mean 1.091 cm) and differed significantly from L1 (0.645 cm) and L4 (0.756 cm). L1 and L4 were not significantly different from each other.

This pattern is consistent with the function of the petiole in optimizing lamina position for light interception. Under canopy shade as at L3, a longer petiole allows the lamina to extend further from the branch axis, reducing self-shading and improving efficiency of limited light interception. Yamada et al. (2000) demonstrated in *Macaranga gigantea*, a tropical pioneer tree with continuous leaf growth, that progressive petiole elongation is an active strategy to reduce the degree of self-shading in the crown. Although *M. gigantea* is a pioneer with fast growth strategy different from *C. fragrans* as a lowland forest climax tree, the mechanism of petiole elongation in response to shading is cross-strategy and has been confirmed in species with different growth strategies (Sudhakaran, 2020; Li *et al.*, 2021). Li et al. (2021), in an analysis of petiole-lamina relationships in 325 woody tree species, confirmed that petiole elongation increases in dense-canopy forests as a light competition strategy, and affirmed that PL variation is simultaneously influenced by lamina area, lamina mass, and climate gradients.

Souza et al. (2018) found that in *Copaifera langsdorffii* populations in drier regions, specific petiole length (SPL, petiole length per unit dry mass) was lower, with aridity index as the main predictor ($R^2 = 0.59$ for sun position metamers; $R^2 = 0.49$ for shade), because lighter and denser petioles increase water supply to the lamina by reducing hydraulic flow resistance. This pattern is partially parallel with L1 and L4, which have low RH (45% and 44%) and shorter PL compared to L3. However, the findings of Souza et al. (2018) are stronger for the petiole mass dimension (specific petiole length, SPL) than

absolute petiole length, so this parallel is indicative and cannot be directly confirmed from this study's data.

The periodically inundation-prone site conditions at L3 reported by local residents are also relevant: under periodic waterlogging, limited root aeration can alter growth hormone balance and in some tropical tree species drives elongation of vegetative organs including petioles as an adaptive response. As L3 inundation data are not quantitatively available, this mechanism can only be proposed as a hypothesis requiring further testing

b. Principal Component Analysis (PCA)

Two principal components from PCA explained 80.4% of total variation (PC1 = 45.7%; PC2 = 34.7%; Table 3; Figure 3). PC1 was primarily loaded by leaf dimension variables (LW: 0.932; LL: 0.820; PL: 0.787), reflecting a morphological gradient from sun morphology to shade morphology. This pattern is consistent with findings by Jiang et al., (2021) that lamina and petiole traits correlate strongly within one functional group at both intraspecific and interspecific scales, due to biophysical constraints linking water transport function and mechanical support in the lamina. Tan et al. (2022) confirmed that low far-red light (R:Fr) under canopy shade simultaneously drives petiole elongation and leaf area increase through the phytochrome pathway, explaining the coordination among LW, LL, and PL on positive PC1. The coordination among these three variables reflects biophysical constraints that force plants to integrate petiole dimensions and lamina area as a unified light interception strategy.

PC2 was loaded by TH (0.915) and DBH (0.867), reflecting the tree size axis independently from leaf morphology. Cano et al. (2019) found that the relationship between tropical tree height and diameter is best described by the generalized Michaelis-Menten (gMM) saturation function, not a power function, because the power function overestimates large-diameter trees. The implication in this study is that the extreme position of P1-L2 and P5-L2 on PC2 reflects long-term biomass accumulation, as stem diameter records cumulative growth history that does not reverse even when site conditions change.

Table 3. Eigenvalues, percentage of variance explained, and morphological character loadings on two principal components (PCA) of *Cyrtophyllum fragrans* in Jambi Province.

Character	PC1	PC2
Tree height (TH)	−0.104	**0.915**
Diameter at breast height (DBH)	0.340	**0.867**
Leaf length (LL)	**0.820**	−0.320
Leaf width (LW)	**0.932**	−0.092
Petiole length (PL)	**0.787**	0.189
Eigenvalue	2.285	1.736
Variance (%)	45.7	34.7

All L1 individuals were concentrated in the negative PC1 quadrant with low to moderate PC2 scores, reflecting the small-leaf profile characteristic of full-light exposure in medium-sized trees. Most L3 individuals (12 of 15) were concentrated in positive PC1 with low to moderate PC2, consistent with dominance of large shade-grown leaf characters. This pattern is consistent with univariate character discussion: L3 canopy shade drives leaf dimension increases, and periodically inundation-prone site conditions potentially reinforce this response through a different but non-contradictory mechanism. L4 individuals were distributed on both sides of PC1 (5 individuals negative PC1, 3 individuals positive PC1), but all L4 individuals were in the negative PC2 zone, distinguishing them from L1 despite sharing negative PC1 positions. This intra-site PC1 heterogeneity at L4 is consistent with the separation of L4 individuals into two different clusters (K2 and K4) in the HCPC analysis.

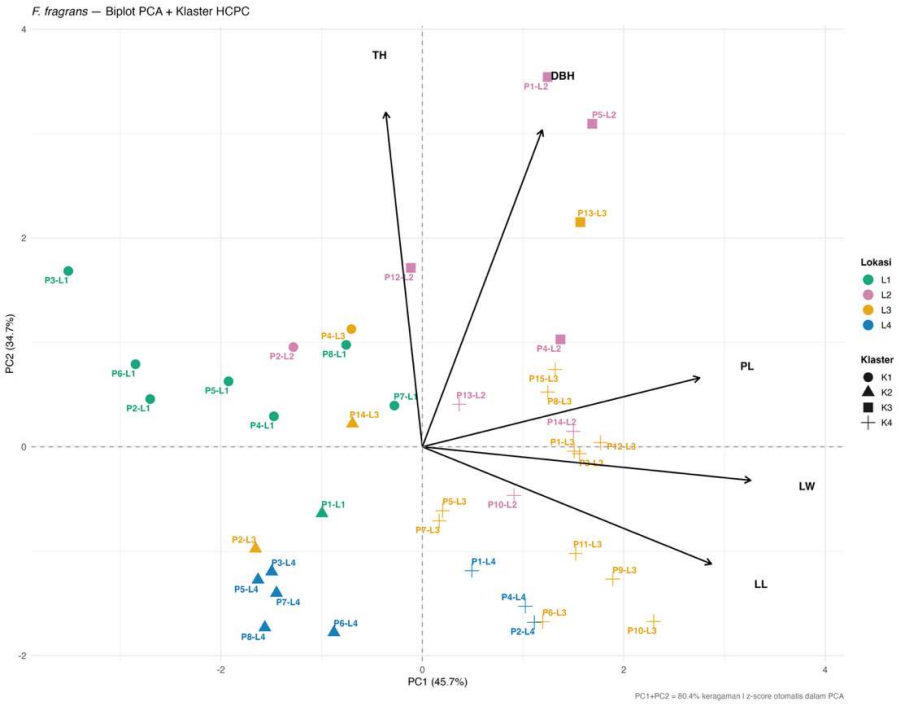

Figure 3. Principal Component Analysis (PCA) biplot of quantitative morphological characters of *Cyrtophyllum fragrans* individuals (n = 39) from four locations in Jambi Province (L1–L4). TH = tree height; DBH = diameter at breast height; LL = leaf length; LW = leaf width; PL = petiole length

c. HCPC Clustering and Cluster Phenotypic Profiles

HCPC based on PCA scores using Ward's criterion and Euclidean distance produced four meaningful clusters (K1-K4). The separation at high dendrogram height values indicates strong phenotypic differentiation among clusters. Seid et al. (2022) applied a similar analytical approach to three tree species in Ethiopia and confirmed that local site conditions are the primary driver of cluster formation, rather than administrative geographic boundaries.

Table 4. Mean ± standard deviation of quantitative morphological characters per cluster derived from Hierarchical Clustering on Principal Components (HCPC) of *Cyrtophyllum fragrans* individuals from four locations in Jambi Province

Cluster	*n*	TH (m) Mean ± SD	DBH (cm) Mean ± SD	LL (cm) Mean ± SD	LW (cm) Mean ± SD	PL (cm) Mean ± SD
K1	9	33.71 ± 4.01	43.99 ± 10.69	8.65 ± 0.97	3.51 ± 0.45	0.674 ± 0.175
K2	8	13.31 ± 4.97	26.52 ± 7.83	9.25 ± 0.76	3.47 ± 0.28	0.768 ± 0.263
K3	5	34.72 ± 7.29	111.60 ± 31.54	9.81 ± 0.75	4.25 ± 0.25	1.206 ± 0.189
K4	17	19.26 ± 5.24	42.26 ± 19.51	10.77 ± 0.86	4.47 ± 0.30	1.084 ± 0.141

Note: TH = tree height; DBH = diameter at breast height; LL = leaf length; LW = leaf width; PL = petiole length. Values are presented as mean ± standard deviation. Clusters were derived using Ward's method with Euclidean distance on PCA scores (PC1–PC5).

K1 (*n* = 9; 7 L1 individuals, 1 L2, 1 L3) is characterized by high mean TH (33.71 ± 4.01 m), moderate DBH (43.99 ± 10.69 cm), and the smallest leaf dimensions among all clusters (LL = 8.65 ± 0.97 cm; LW = 3.51 ± 0.45 cm; PL = 0.674 ± 0.175 cm) (Table 4). This small leaf dimension profile is consistent with sun leaf formation in response to full light exposure at L1. Khan et al. (2020) in a study of leaf morphological plasticity of *Heritiera fomes* in adult trees at various canopy positions in the Sundarbans mangrove forest found that leaves at upper canopy positions with high light had

significantly smaller leaf length and width ($p < 0.01$) compared to lower canopy leaves, a pattern parallel to the K1 profile. The clustering of P2-L2 (TH = 36.1 m; LL = 8.32 cm; LW = 3.47 cm) into K1 is consistent with this cluster profile because its leaf dimensions are below the L2 mean and comparable to the K1 mean. P4-L3 (TH = 35 m; DBH = 62 cm; LL = 9.41 cm) joined K1 based on similar PCA score positions on the tree size dimension, not because of equally small leaf dimensions.

K2 (n = 8; 5 L4 individuals, 2 L3, 1 L1) is characterized by the lowest mean TH among all clusters (13.31 ± 4.97 m) and small DBH (26.52 ± 7.83 cm), with moderate leaf dimensions (LL = 9.25 ± 0.76 cm; LW = 3.47 ± 0.28 cm; PL = 0.768 ± 0.263 cm) (Table 4). The TH SD of K2 is the highest among all clusters (±4.97 m), with an actual TH range of 7.5–20.0 m; two non-L4 individuals in K2 (P1-L1: TH = 19 m; P14-L3: TH = 20 m) approached the mean TH of K4. K2 does not display a clear shade morphology profile in leaf dimensions, reflecting the condition of isolated trees at L4 that receive adequate light but experience axial growth suppression due to edge effects and isolation. Maracahipes-Santos et al. (2023), in a study of tree trait variability in fragmented Amazon riparian forests, found that intraspecific variability in leaf and tree height traits is the primary mechanism enabling generalist species to survive at fragmented forest edges, a pattern relevant to explaining the phenotypic heterogeneity of K2. L4 was divided between K2 (n = 5; mean LL = 9.37 cm) and K4 (n = 3; mean LL = 11.06 cm), indicating intra-site phenotypic heterogeneity that cannot be fully explained from the field condition data in this study.

K3 (n = 5; 4 L2 individuals, 1 L3) is the most distinctive cluster with its primary distinguishing feature being very large DBH (111.60 ± 31.54 cm) and high TH (34.72 ± 7.29 m), while leaf dimensions fell in the moderate range (LL = 9.81 ± 0.75 cm; LW = 4.25 ± 0.25 cm; PL = 1.206 ± 0.189 cm). Lam et al. (2024), in a study of leaf and twig traits in 29 adult tree species in a tropical freshwater swamp forest in Singapore, found that species associated with inundated habitats tend to reach greater maximum heights and have more conservative long-term growth strategies. The four L2 individuals in K3 had DBH of 72–155 cm, consistent with the interpretation of pre-fragmentation legacy growth. Without dendrochronological data or land use history records for L2, this interpretation is inferential and cannot be confirmed from morphological data alone. The inclusion of P13-L3 (DBH = 95 cm; TH = 39 m) with L2 individuals reflects similarity in PCA score positions based on tree size, not ecological similarity between locations.

K4 (n = 17; 11 L3 individuals, 3 L4, 3 L2) is the largest and most cross-site cluster in the dataset, with the largest leaf dimensions among all clusters (LL = 10.77 ± 0.86 cm; LW = 4.47 ± 0.30 cm; PL = 1.084 ± 0.141 cm) and moderate-low TH (19.26 ± 5.24 m) (Table 2). This profile is consistent with a wide-leaf response to low-to-moderate light conditions: Poorter et al. (2019) found in a meta-analysis of more than 500 experiments that individual leaf area consistently decreased with increasing daily light intensity, with a plasticity index of 2.2. Khan et al. (2020) confirmed the same pattern in field conditions of adult trees in wetland ecosystems, where leaves at lower canopy positions had significantly higher leaf area and SLA ($p < 0.01$). The cross-site composition of K4 reflects convergent phenotypic responses to comparable low-to-moderate light intensity between L3 (774 lux) and some of L4 (780 lux). The three L2 individuals in K4 (P10-L2: DBH = 29 cm; P13-L2: DBH = 72 cm; P14-L2: DBH = 74 cm) had smaller DBH than L2 individuals in K3 (DBH 72–155 cm), consistent with the interpretation that these individuals have not accumulated the same amount of legacy growth and their phenotypes more reflect current site conditions.

The four-cluster structure as a whole reflects the two main phenotypic gradients identified by PCA: the tree size gradient separating K3 from K2, and the leaf morphology gradient separating K1 from K4. Neither gradient perfectly overlaps with location geographic boundaries, affirming that *C. fragrans* morphological phenotype is more determined by site ecological conditions than geographic origin. Seid et al., (2022) reached a parallel conclusion that morphological variability in the studied tree species appeared cross-site because site conditions are the primary driver of cluster formation. The separation of some L2 individuals into K4 and some L3 individuals into K2 shows that ecological boundaries among locations do not always align with phenotypic cluster boundaries. This cross-site pattern cannot be fully explained from the morphological and environmental data available, and likely reflects intra-population genetic variation, differences in individual growth history, or a combination of both. Testing these hypotheses requires molecular genetic data and individual growth history data not available in this study.

d. Correlation Analysis

Spearman correlation was used because PL did not meet normality assumptions at L2 (p = 0.009) and L3 (p = 0.008) based on the Shapiro-Wilk test. The correlations formed two functionally distinct blocks: a tree size character block (TH-DBH) and a leaf dimension character block (LL-LW-PL), with weak and largely non-significant relationships between blocks (Table 5).

Table 5. Spearman's correlation coefficients among quantitative morphological charactersof *Cyrtophyllum fragrans* individuals (n = 39) from four locations in Jambi Province.

Variable	TH	DBH	LL	LW	PL
TH	1				
DBH	0.788**	1			
LL	−0.282 ns	−0.037 ns	1		
LW	−0.127 ns	0.207 ns	0.731**	1	
PL	0.067 ns	0.337*	0.405*	0.579**	1

Note: TH = tree height; DBH = diameter at breast height; LL = leaf length; LW = leaf width; PL = petiole length. Values are Spearman's rs. Significance levels: ** p < 0.001; * p < 0.05; ns = not significant.

TH and DBH were very strongly positively correlated (rs = 0.788; p < 0.001), reflecting the allometric relationship between height growth and stem biomass accumulation in mature trees. This coordination of axial and radial growth is consistent with patterns reported across tropical tree species in response to long-term light competition (Cano *et al.*, 2019). However, most of the TH and DBH variation among individuals in this study originated from differences in site conditions among locations, not from intrinsic growth relationships that can be generalized. K3 individuals with very large DBH but disproportionately lower TH indicate that diameter growth can decouple from height growth, possibly due to different growth histories before fragmentation.

LL and LW were strongly positively correlated (r*s = 0.731; p < 0.001)*, reflecting proportional coordination of lamina dimension growth. Bramasto and Sudrajat (2018) reported a strong positive correlation between leaf length and width (r = 0.89) in five *C. fragrans* populations, directly supporting the pattern observed in this study.

LW and PL were strongly positively correlated (r*s = 0.579; p < 0.001)*, and LL with PL were moderately positively correlated (r*s = 0.405; p = 0.011)*. This pattern reflects functional coordination between lamina dimensions and petiole length: wider leaves require longer petioles to mechanically support the lamina weight and optimally position the lamina toward the light source. Li et al. (2021) confirmed across 325 woody tree species that the PL–LL relationship is positively isometric, reflecting the balance between light interception needs and petiole support needs as a stable mechanism in most species. The LL–LW–PL coordination observed is consistent with the PC1 loading structure in the PCA analysis.

DBH was significantly positively correlated with PL (r*s = 0.337; p = 0.036)*, while correlations of DBH with LL (r*s = −0.037; p = 0.821)* and LW (r*s = 0.207; p = 0.207)* were not significant. The weak but significant DBH–PL correlation in this study more reflects the sample composition structure than a direct physiological mechanism: large-DBH individuals at L2 and L3 simultaneously inhabited locations with long PL, so this correlation is contextual-correlational, not causal.

TH was not significantly correlated with LL (rs = -0.282; p = 0.082), LW (rs = -0.127; p = 0.440), or PL (rs = 0.067; p = 0.687). The absence of correlation between these two-character blocks indicates that tree size and leaf dimensions do not respond along the same axis. TH and DBH more closely reflect long-term growth accumulation influenced by site history and canopy competition, while leaf dimensions are more responsive to current light and humidity conditions through phenotypic plasticity mechanisms. This separation of two functional blocks is consistent with the structure of two principal components in the PCA.

e. Qualitative Leaf Characters

All four accessions observed (Figure 2) showed leaf morphological characters consistent with the description of *C. fragrans* (Roxb.) DC. Leaves are simple, oppositely arranged (*folia opposita*), with yellowish-green petioles that represent a diagnostic character of the genus *Cyrtophyllum* (Wong *et al.*, 2025). Lamina shape in all four accessions is elliptic, with the widest point located in the mid-lamina zone and a L:W ratio ranging from 2.23 to 2.59, consistent with the species description of *C. fragrans* (Ellis *et al.*, 2009; Wong and Manickam, 2012; Wong *et al.*, 2025). L3 had the widest lamina (mean LW 4.24 cm; L:W ratio 2.23), consistent with its position as the dominant member of K4 with the most pronounced *shade morphology*. L1 had the narrowest lamina (mean LW 3.49 cm; L:W ratio 2.47), consistent with the *sun leaf* phenotype of K1. L2 showed a wider lamina than L1 despite similar site conditions. L4 was intermediate (mean LW 3.86 cm; L:W ratio 2.59), consistent with the division of L4 individuals into two different clusters (K2 and K4).

Figure 2. Leaf morphology of *Cyrtophyllum fragrans* from four sampling locations in Jambi Province: (a) L1, (b) L2, (c) L3, (d) L4

Leaf apex in all accessions was classified as *acuminate*. In the taxonomic terminology of Wong et al. (2025) apex variation ranged from *short-cuspidate* (L1, L2) to *caudate* (L3, L4). Leaf bases in all accessions were *straight cuneate*, tapering gradually toward the yellowish petiole. Leaf margins were *entire* in all accessions. Slight undulation on the abaxial-adaxial surface observed in some laminae of L3 and L4 was categorized as *undulate* and is not diagnostically significant, consistent with the observation by Wong and Manickam, (2012 and Wong et al., (2025) that the leaf margin is "plane when fresh, in dried specimens sometimes slightly wavy". Leaf venation was pinnate.

These qualitative characters showed no meaningful variation among accessions. Qualitative leaf characters are more phenotypically stable than quantitative characters and serve as reliable taxonomic diagnostic characters at the species level. (Jarapan *et al.*, 2025) reported a similar pattern in *Rhizophora apiculata*, where quantitative characters such as leaf width, lower quarter width, and base angle showed significant plasticity across environmental gradient zones ($p < 0.0001$), while leaf thickness did not differ significantly among zones. (Bramasto and Sudrajat, 2018) demonstrated that differences among five *C. fragrans* populations occurred across all measured quantitative leaf characters, while qualitative characters were not included as measurement variables in that study, meaning a direct comparison for qualitative characters cannot be made.

CONCLUSION

`C. fragrans at four locations in Jambi Province exhibited significant quantitative morphological variation across all five measured characters (TH, DBH, LL, LW, and PL), driven primarily by differences in site light intensity and habitat fragmentation history. Leaf dimension characters (LL, LW, PL) responded most strongly to light intensity gradients, while tree size characters (TH, DBH) recorded cumulative growth history and fragmentation effects rather than current site conditions. Qualitative leaf characters (elliptic lamina, acuminate to caudate apex, cuneate base, entire margin, and pinnate venation) showed no meaningful variation among locations, confirming their stability as species-level taxonomic markers regardless of site condition differences.

Phenotypic clustering based on PCA scores produced four distinct clusters with cross-site composition, affirming that site ecological conditions, not geographic origin, are the primary determinant of morphological phenotype in this species. K4 confirmed phenotypic convergence between L3 and L4 individuals driven by comparable low-to-moderate light intensity, while K3 was distinguished by very large DBH representing pre-fragmentation legacy growth rather than current ecological conditions.

These findings indicate that selection of mother trees for breeding programs must be based on individual quantitative characters, not location identity. Further research integrating molecular markers, dendrochronological data, and quantitative site hydrology is needed to separate the relative contributions of genetic factors and phenotypic plasticity to the observed variation patterns.

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