Ensaios e Ciência
ISSN 1415-6938 e ISSN 2178-695X

**DOI:** 10.17921/1415-6938.2025v29n3p608-617

# Standard Deviation of Trees' Leaf Characteristics in Tropical Humid Urban Forest with Different Light Intensities

# Desvio Padrão das Características Foliares de Árvores em Floresta Tropical Úmida Urbana com Diferentes Intensidades de Luz

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**Receveid on:** February 20, 2025
**Accepted on:** July 07, 2025

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## Abstract

It is known that there is still a gap regarding the relationship among basal area, light and the variation in functional characteristics. Admitting that light availability is a good predictor of trait variation, we hypothesize that in environments where there is a greater amount of light, there will be greater variation in the mean and standard deviation of the four traits. If this is true, a greater standard deviation in leaf dry matter content, specific leaf area, leaf area and chlorophyll content in these environments are expected. To test the hypothesis, data were collected on 10 functional characteristics (leaves, trunk and root) in 41 species, distributed in four environments: one with a larger basal area ($A_1$>AB), two with an intermediate basal area ($A_2$ABI and $A_3$ABI) and one with smaller basal area ($A_4$<AB). The hypothesis of this work was not corroborated, since all four characteristics evaluated (AF, TMSF, AFE and Cc_mass) showed less variability in A4<AB, contrary to what would be expected. The fact that the area with the most light (A4<AB) demonstrated this smaller variation in standard deviation revealed that the plants in this environment were greatly influenced by the disturbances, which caused their variability to be reduced.

**Keywords:** Anthropogenic Factors. Restoration. Environmental Filter.

## Resumo

Sabe-se que, ainda existe uma lacuna sobre a relação entre área basal, luz e a variação das características funcionais. Admitindo que a disponibilidade de luz é um bom preditor da variação das características, hipotetizamos que em ambientes onde há maior quantidade de luz, haverá maior variação na média e no desvio padrão das quatro características. Caso isto seja verdade, espera-se maior desvio padrão no conteúdo de matéria seca foliar, área foliar específica, área foliar e conteúdo de clorofila nesses ambientes. Para testar a hipótese, foram coletados dados de 10 características funcionais (foliares, tronco e raiz) em 41 espécies, distribuídas em quatro ambientes: um com maior área basal ($A_1$>AB), dois com área basal intermediária ($A_2$ABI e $A_3$ABI) e um com menor área basal ($A_4$<AB). A hipótese deste trabalho não foi corroborada, uma vez que das quatro caracteristicas avaliadas todas (AF, TMSF, AFE e Cc_mass) apresentaram menor variabilidade na $A4_{<AB}$, ao contrário do que seria esperado. O fato da área com mais luz ($A4_{<AB}$) ter demonstrado essa menor

variação do desvio padrão, revelou que as plantas desse ambiente foram bastantes influenciadas pelas perturbações, o que fez com que sua variabilidade fosse reduzida.

**Palavras-chave:** Fatores Antrópicos. Restauração. Filtro Ambiental.

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## 1 Introduction

It is well established that plant functional trait values may respond differently to the availability of a given resource (i.e., water, light, etc.) (Pérez-Harguindeguy *et al.*, 2013). These responses manifest in distinct survival patterns, resulting from the species potential for acquiring and using the resource in question (Menge; Chazdon, 2016). Understanding the functional trait values of species within a community helps elucidate how plants respond to changes in the availability of a given resource.

In forest ecosystems, where light is the primary limiting resource, it is known that in the early stages of forest succession there is greater light availability and lower basal area values (Boukili; Chazdon, 2017). In such habitats, high values of leaf area, specific leaf area, and chlorophyll content are commonly observed (Pérez-Harguindeguy *et al.*, 2013), along with low stem and root wood density and high water content in stem and root tissues, which reflect strategies associated with resource acquisition (Boukili; Chazdon, 2017). As succession progresses, the canopy closes, reducing light availability in the lower forest strata and favoring the survival of species with strategies more aligned with light conservation (Cornelissen; Van Hoof; De Jong, 2006).

It is also important to note that plants respond to environmental variation through phenotypic adjustments (ecological responses) or evolutionary adaptations (evolutionary responses) (Schlichting; Wund, 2013). Intra-population variability often reflects adjustments in trait expression from a single genotype in response to environmental changes within the individual's lifespan (Valladares *et al.*, 2014). In contrast, adaptations arise from differential selective pressures over evolutionary time, leading to heritable differences among species through the evolution process (Ramirez-Valiente *et al.*, 2015). Among plant organs, leaves are particularly responsive to light variation, especially during early succession, when light availability is higher (Laurans *et al.*, 2012).

Assuming that light availability is a strong predictor of trait variation, we hypothesize that environments with higher light levels will exhibit greater variation in both the mean and standard deviation of four functional traits. If this hypothesis holds true, we expect to observe higher standard deviations in leaf dry matter content, specific leaf area, leaf area, and chlorophyll content in such environments.

## 2 Material and Methods

### 2.1 Local

The study was conducted in a fragment of Floresta Ombrófila Densa de Terras Baixas (IBGE, 2012), located in Dois Irmãos State Park (Parque Estadual de Dois Irmãos – PEDI), in the northwest region of Recife, Pernambuco, Brazil, between coordinates 7°57'21" and 8°00'54"S; 34°55'53" and 34°58'38"W. The area is dominated by the Barreiras geological formation and podzolic soils, with subordinate latosols, generally sandy-clayey, ranging from deep to very deep (Pernambuco, 2014). Soil acidity ranges from moderate to high, which is expected in regions with high precipitation. The local climate is classified as As' (humid tropical or coastal tropical), with average monthly temperatures above 23 °C, annual rainfall of 2,460 mm, and a rainy season during autumn and winter (Coutinho *et al.*, 1998).

### 2.2 Plot setup, inclusion criteria, and floristic list

A module of the Biodiversity Research Program (PPBio), Atlantic Forest Network, is installed in the area of Dois Irmãos State Park (PEDI), employing the RAPELD method - "which is essentially a combination of Rapid Assessments (RAP) and Long-Term Ecological Research (PELD, in Portuguese)" (Magnusson *et al.*, 2005). This method involves the establishment of two straight trails (plots), each 5,000 meters long and spaced 1,000 meters apart. Along each trail, one-hectare plots were installed according to a standardized protocol.

From the two trails established by PPBio Atlantic Forest researchers, one was selected for the present study. Four plots (each 250 × 40 m) spaced 1,000 meters apart were analyzed, totaling four sampling areas. For each plot, a 250-meter corridor was established following the terrain contour lines, according to the protocol described by Freitas, Costa and Morais (2011).

Within each hectare, twenty 10 × 20 m subplots were randomly selected without overlap. In these subplots, botanical samples and plant functional traits were collected from all the individuals with stem diameter at breast height (DBH) ≥ 5 cm, provided that at least five individuals of the species were present across the four study areas (Table 1). When a species occurred in more than one area, functional traits were sampled in each area where it was present.

**Table 1 -** List of species analyzed across the four study areas

| Family | Species | A1$_{>AB}$ | A2$_{ABI}$ | A3$_{ABI}$ | A4$_{<AB}$ |
|---|---|---|---|---|---|
| **Anacardiaceae** | *Anacardium occidentale L.* |  | X |  |  |
|  | *Tapirira guianensis* Aubl. | X | X | X | X |
|  | *Thyrsodium spruceanum* Benth. | X | X | X |  |
| **Apocynaceae** | *Himatanthus phagedaenicus* (Mart.) Woodson |  | X |  |  |
| **Araliaceae** | *Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin | X | X |  |  |
| **Boraginaceae** | *Cordia superba* Cham. |  | X |  |  |
| **Burseraceae** | *Protium giganteum* Engl. | X |  |  |  |
|  | *Protium heptaphyllum* (Aubl.) Marchand | X |  |  |  |
| **Clusiaceae** | *Clusia nemorosa* G.Mey. |  | X |  |  |
| **Elaeocarpaceae** | *Sloanea guianensis* (Aubl.) Benth. | X |  |  |  |
| **Euphorbiaceae** | *Pera ferrugínea* (Schott) Müll. Arg. |  | X | X | X |
|  | *Pogonophora schomburgkiana* Miers ex Benth. | X | X | X | X |
| **Fabaceae** | *Albizia pedicellaris* (DC.) L. Rico | X |  | X |  |
|  | *Bowdichia virgilioides* Kunth | X | X |  |  |
|  | *Chamaecrista ensiformis* (Vell.) |  |  | X | X |
|  | *Dialium guianense* (Aubl.) Sandwith | X |  |  |  |
|  | *Inga capitata* Desv. |  | X |  |  |
|  | *Inga thibaudiana* DC. | X | X | X |  |
|  | *Parkia pendula* (Willd.) Benth. ex Walp. | X |  |  |  |
|  | *Plathymenia reticulata* Benth. |  | X | X | X |
|  | *Pterocarpus violaceus* DC. | X | X |  |  |
|  | *Tachigali densiflora* (Benth.) L.G.Silva & H.C.Lima | X |  |  |  |
| **Lauraceae** | *Ocotea glomerata* (Nees) Mez | X |  | X |  |
| **Lecythidaceae** | *Eschweilera ovata* (Cambess.) Mart. ex Miers | X | X | X |  |
|  | *Lecythis pisonis* Cambess. |  | X | X |  |
| **Malvaceae** | *Apeiba albiflora* Ducke |  |  | X |  |
|  | *Luehea ochrophylla* Mart. |  | X | X |  |
| **Malpighiaceae** | *Byrsonima sericea DC.* |  | X | X | X |
| **Melastomataceae** | *Miconia prasina* (Sw.) DC. | X | X |  |  |
| **Moraceae** | *Brosimum guianense* (Aubl.) Huber | X | X |  |  |
|  | *Helicostylis tomentosa* (Poepp. & Endl.) Rusby | X |  |  |  |
| **Myrtaceae** | *Campomanesia dichotoma* (O. Berg) | X | X |  | X |
|  | *Myrcia splendens* (Sw.) DC. |  | X |  |  |
|  | *Myrcia sylvatica* (G.Mey.) DC. | X | X | X | X |
| **Nyctaginaceae** | *Guapira laxa* (Netto) Furlan |  | X | X |  |
| **Ochnaceae** | *Ouratea castaneifolia* (DC.) Engl. |  |  | X |  |
| **Polygonaceae** | *Coccoloba mollis* Casar. | X | X | X |  |
| **Rubiaceae** | *Alseis pickelii* Pilger & Schmale |  | X |  |  |
| **Sapotaceae** | *Pouteria bangii* (Rusby) T.D. Penn. | X |  |  |  |
| **Urticaceae** | *Cecropia pachystachya* Trécul |  | X | X |  |
| **Sapindaceae** | *Talisia macrophylla* (Mart.) Radlk. | X |  |  |  |

A1>AB (area with the highest basal area), A2ABI (intermediate basal area), A3ABI (intermediate basal area), and A4<AB (area with the lowest basal area).
**Source**: research data.

The floristic list was organized following the APG IV classification system (2016). All the specimens were deposited in the Vasconcelos Sobrinho Herbarium (VSH) at Universidade Federal Rural de Pernambuco (UFRPE).

## 2.3 Foliar characteristics

Leaf trait measurements followed the protocol proposed by Pérez-Harguindeguy *et al*. (2013), which provides a step-by-step guide for assessing various plant functional traits and includes methods considered by researchers to be the most reliable and feasible for application.

Four leaf traits were measured (see Table 2). As previously noted, traits were collected only from species with five or more individuals across the four sampling areas (250 × 40 m plots). For each species, five individuals were sampled. From each individual, ten mature, sun-exposed leaves were collected from the mid-canopy, without visible signs of pathogen or herbivore damage. After collection, the samples were wrapped in moist paper, placed in sealed plastic bags, and stored in coolers with ice. In the laboratory, the leaves (excluding petioles) were rehydrated in deionized water, kept in the dark for at least six hours.

**Table 2 -** List of leaf traits analyzed in a fragment of urban forest

| Functional Trait | Description | Functional Role |
|---|---|---|
| SLA (Specific Leaf Area) | Leaf area / dry mass (LA / DM) | Photosynthetic rate, leaf lifespan, relative growth rate |
| LDMC (Leaf Dry Matter Content) | (Turgid mass – Dry mass) / Dry mass | Resistance to physical damage (herbivory) |
| LA (Leaf Area) | Blade area | Light capture |
| Cc_mass (Chlorophyll Concentration per Mass) | Chlorophyll content × SLA / 10,000 | Photosynthetic process, involved in the conversion of light energy into chemical energy |

LA – leaf area ($cm^2$); SLA – specific leaf area ($cm^2 \cdot mg^{-1}$); Cc_mass – chlorophyll concentration ($\mu mol \cdot g^{-1}$); LDMC – leaf dry matter content ($mg \cdot g^{-1}$).
**Source**: research data.

Chlorophyll content was measured immediately after collection at four points per leaf using a SPAD chlorophyll meter (Minolta SPAD 502 D, Spectrum Technologies Inc., Plainfield, IL, USA). Chlorophyll content per mass (Cmassa) was determined as chlorophyll content × specific leaf area (SLA) / 10,000, following Poorter (2009). After rehydration, the leaves were weighed on an analytical balance to determine their saturated fresh mass. They were then scanned to measure leaf area using the software “Image-Tool” and subsequently dried in an oven at 60 °C for 72 hours to determine dry mass.

## 2.4 Light data collection

Total radiation (light availability) was measured in each of the 80 randomly selected 10 × 20 m plots (20 per area). Hemispherical photographs were taken at the center of each plot using a Nikon D50 camera with a hemispherical lens (Nikon DX 18–105 mm adapted to a 67–58 mm fisheye lens), mounted on an adjustable tripod positioned one meter above the ground, leveled horizontally, and aligned with magnetic north using a compass. The photographs were taken between August and December 2015, between 8:30 and 11:00 AM, to avoid direct sunlight (Venturoli *et al*., 2012). Image processing was carried out using the software GLA (Gap Light Analyzer), version 2.0 (Frazer ;

Canham; Lertzman, 1999), in order to estimate the total radiation penetrating the canopy (light availability) in each plot.

To verify whether light availability varied among the four study areas (each 4000 m²), a non-parametric Kruskal-Wallis test was performed, since the basal area data did not follow a normal distribution. This test was followed by the Student-Newman-Keuls post hoc comparison. As shown in Table 3, light availability decreased from area A1>AB to A4<AB.

**Table 3 -** Mean light intensity in the four areas of an urban tropical forest fragment

| Area | Light (%) |
|---|---|
| A1> AB | 06.09c |
| A2ABI | 12.94c |
| A3ABI | 31.75b |
| A4< AB | 46.97a |

A1>AB (area with the highest basal area); A2ABI (intermediate basal area); A3ABI (intermediate basal area); and A4<AB (area with the lowest basal area). Means followed by the same letter do not differ according to the Student-Newman-Keuls test ($p < 0.05$).
**Source**: research data.

### 2.5 Data analysis

Four leaf traits were analyzed due to their high variability: specific leaf area, leaf area, chlorophyll content, and leaf dry matter content (Rozendaal *et al.*, 2006; Laurans *et al.*, 2012). We calculated the weighted mean and standard deviation of these traits, as these measures provide information on the central tendency and data variability, respectively.

The mean light intensity, as well as the weighted mean and standard deviation of leaf traits in each area, were subjected to the Shapiro-Wilk test to assess normality. Since the data did not follow a normal distribution, we performed a non-parametric Kruskal-Wallis analysis of variance, followed by the Student-Newman-Keuls post hoc test, to evaluate differences in light variation and in the mean and standard deviation of traits across the four areas. These analyses were conducted using SPSS software (IBM Corp. Released 2011. IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.).

To examine whether geographic distances influenced the standard deviation of leaf traits across areas, we applied the Bray-Curtis dissimilarity index to the data matrix, followed by a partial Mantel test (McCune; Mefford, 2011). The correlations significance was tested using 999 permutations (Legendre; Fortin, 1989), with the *nortest*, *vegan*, and *APE* packages in R version 3.3.1 (R Core Team, 2016).

To test the hypothesis that greater light availability is associated with greater variability in leaf trait values, Linear Mixed Models (LMMs) were constructed to assess the influence of light intensity on leaf trait values. Light was used as the independent variable (fixed effect), and the leaf trait values per species, per plot and area, were treated as dependent variables (random effects). The minimal adequate model was obtained by stepwise removal of fixed effects, followed by deviance analysis (Crawley, 2007). All the LMMs were performed using the *lme4* package in R version 3.3.1 (R Core Team, 2016).

## 3 Results and Discussion

The the mean ($\bar{X}$) and standard deviation (SD) analysis of the traits across environments revealed two distinct patterns (Table 5). In general, the areas with lower light availability (see Table 4, A1>AB and A2ABI) did not differ significantly from each other and exhibited higher means and standard deviations, whereas A3ABI and A4<AB showed distinct patterns.

The expectation that the environment with the highest light availability (A4<AB) would exhibit greater variation in both the mean and standard deviation of the four traits (LA, LDMC, SLA, and Cc_mass) was not supported, as all traits showed lower mean and standard deviation values: LA (37.09 ± 1.74), LDMC (1.13 ± 1.60), SLA (165.04 ± 1.59), and Cc_mass (0.75 ± 1.00) (Table 4). Thus, the hypothesis that higher light availability would lead to greater variability in leaf trait values was not confirmed, as area A4<AB (with the highest light availability, see Table 3) exhibited the lowest standard deviations (Table 4).

**Table 4 -** Mean ($\bar{X}$) and standard deviation (SD) of leaf traits in the four areas of an urban tropical forest fragment

| **Areas** | **LA**<br>**($\bar{X}$) ± SD** | **LDMC**<br>**($\bar{X}$) ± SD** | **SLA**<br>**($\bar{X}$) ± SD** | **Cc_Mass**<br>**(X) ± SD** |
|---|---|---|---|---|
| $A1_{>AB}$ | 943.07 ± 5.75 a | 5.98 ± 5.47 a | 1214.84 ± 6.15 a | 6.13 ± 4.00 a |
| $A2_{ABI}$ | 996.87 ± 6.04 a | 4.86 ± 5.80 a | 1293.34 ± 5.08 a | 5.76 ± 2.48 a |
| $A3_{ABI}$ | 404.17 ± 3.50 b | 2.71 ± 3.76 b | 509.14 ± 3.50 b | 2.44 ± 1.44 b |
| $A4_{<AB}$ | 37.09 ± 1.74 c | 1.13 ± 1.60 c | 165.04 ± 1.59 a | 0.75 ± 1.00 c |

LA: leaf area (cm²), LDMC: leaf dry matter content ($mg \cdot g^{-1}$), SLA: specific leaf area ($cm^2 \cdot mg^{-1}$), Cc_mass: chlorophyll content ($\mu mol \cdot g^{-1}$). A1>AB (area with the highest basal area), A2ABI (intermediate basal area), A3ABI (intermediate basal area), and A4<AB (area with the lowest basal area); $\bar{X}$: weighted mean of leaf traits per area; ($\bar{X}$): mean, SD: standard deviation of the community per area. Means followed by the same letter do not differ according to the Student-Newman-Keuls test ($p < 0.05$).
**Source**: research data.

To test the hypothesis that greater light availability would result in higher standard deviation values of leaf traits, Linear Mixed Models (LMMs) were constructed (Table 5). Among the four traits analyzed (LA, LDMC, SLA, and Cc_mass), all were influenced by light intensity. However, the results did not align with the expectations, as the environment with the highest light availability

(A4<AB, see Table 4) exhibited the lowest standard deviation values for those traits (Table 4).

**Table 5 -** Linear Mixed Models (LMMs) of functional traits as a function of light intensity in a fragment of urban tropical forest

| | **Light Intensity (%)** | | | | |
|---|---|---|---|---|---|
| | D | Df | P | E | SE |
| **SD_LA ($cm^2$)** | 254.65 | 1 | 0.00** | $-1.84^{e-02}$ | $3.71^{e-02}$ |
| **DP_SLA ($cm^2.mg^{-1}$)** | 250.32 | 1 | $0.00^{**}$ | $-1.22^{e-01}$ | $4.25^{e-02}$ |
| **DP_Cc_mass (micromol.$g^{-1}$)** | 174.24 | 1 | $0,00^{**}$ | $-0.13^{e-01}$ | $0.23^{e-01}$ |
| **DP_LDMC (mg.$g^{-1}$)** | 300.46 | 1 | $0.00^{**}$ | $-2.96^{e-01}$ | $1.24^{e-02}$ |

SD: standard deviation, D: residual deviance after variable removal; Df: degrees of freedom; P: associated p-value; E: estimate; SE: standard error of the mean. SD_LA:le af area; SLA: specific leaf area; Cc_mass: chlorophyll concentration; LDMC: leaf dry matter content. A1>AB (area with the highest basal area), A2ABI (intermediate basal area), A3ABI (intermediate basal area), and A4<AB (area with the lowest basal area). *values indicate statistical significance (** = p < 0.01).

It is worth noting that when we conducted the partial Mantel test to verify whether geographic distance affected the standard deviation of trait values, the results indicated that spatial distance had no effect on trait variation ($r = -0.0577$; $p = 0.001$).

The fact that the lowest standard deviations for leaf traits (LA, LDMC, SLA, and Cc_mass) occurred in the environment with the highest light availability (A4<AB, 46.97%) leads us to hypothesize that although these traits are typically more variable in open areas, such variability may be reduced under environmental stress factors, such as disturbances, degradation, and others (Dorn *et al.*, 2000). It is important to recall that A4<AB is the most disturbed area, which may have contributed to the lower variation in those traits, as previously discussed in section 4.1 (lower SLA and Cc_mass in A4<AB) (see Table 5).

Considering that A4<AB is the youngest or most disturbed area, we expect that early successional species - characterized by rapid growth, lower investment in structural carbon, higher mortality, and faster colonization - are also more susceptible to abrupt changes. Thus, we may infer that these traits also contributed to the lower leaf trait variability observed in A4<AB (Valladares *et al.*, 2014).

The fact that the three areas with lower light availability (A1>AB, A2ABI, and A3ABI) exhibited greater variation in LA, SLA, LDMC, and Cc_mass values runs contrary to our initial expectations. This allows us to hypothesize that such increased variability in shaded environments may be due to species experiencing several ontogenetic shifts under low irradiance throughout their life cycle, which can lead to greater trait variability (Rozendaal *et al.*, 2006).

It is also relevant to mention that although leaf traits generally exhibit greater variability in environments with higher light intensity (Laurans *et al*., 2012), physiological traits tend to be even more variable, as they respond more rapidly and over shorter timescales (Gratani, 2014). This may help explain the lower chlorophyll content observed in the highest-light environment (A4<AB). Therefore, we conclude that the reduced variability in leaf traits in the high-light environment appears to be related to the effects of disturbance, which may limit trait plasticity in such environments.

## 4 Conclusion

The study hypothesis was not supported, as all four evaluated traits exhibited lower variability in area A4<AB. The fact that the area with the highest light availability (A4<AB) showed the lowest standard deviation suggests that plants in this environment are more strongly influenced by disturbance.

The greater variation in traits observed in A1>AB, A2ABI, and A3ABI - areas with lower light availability - indicates that species growing under shaded conditions undergo multiple ontogenetic changes in response to varying light intensities throughout their life cycles.

The LMM analyses revealed that light is not a reliable predictor of leaf trait variability in arboreal species within urban forest fragments.

The evaluated traits, which vary in both morphological and physiological dimensions, once again reinforce that in more disturbed environments, leaf trait variability may be reduced.

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