NOTE

Leaf trait variation in three species through canopy strata in a semi-evergreen Neotropical forest

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Abstract: Morphological and structural changes among and within leaves of *Aphananthe monoica* (Hemsley) Leroy, *Pleuranthodendron lindenii* (Turczaninov) Sleumer, and *Psychotria costivenia* Grisebach were documented through canopy strata (<10, 10–20, and >20 m high) and related to some environmental variables in a semi-evergreen Neotropical forest. The principal components analysis revealed that two components explained 93% of total variation. The first component (76.4%) denoted leaf structure, whereas the second (16.6%) denoted leaf shape. Anatomical differences in transverse leaf sections among different canopy strata were observed in *Aphananthe monoica* and *Pleuranthodendron lindenii*. Variance analyses showed significant differences among strata for leaf characters and light, relative humidity, vapour pressure deficit, and temperature. Canonical correlation analysis revealed that the first pair of canonical variates of leaf characters and environmental variables were closely related. The first environmental variate represented the changes in microclimate along forest canopy strata. Leaf structure observed in *Aphananthe monoica* and *Pleuranthodendron lindenii* suggested that they are intermediate shade-tolerant species, and *Psychotria costivenia* is a shade-tolerant understorey species. *Aphananthe monoica* and *Pleuranthodendron lindenii*, which during their life span occupy different positions in the vertical strata, showed the highest leaf variation.

Key words: tropical trees, *Aphananthe monoica*, *Pleuranthodendron lindenii*, *Psychotria costivenia*, leaf variation, Veracruz.

Résumé : Les auteurs ont étudié les changements morphologiques et structuraux entre et dans les feuilles chez l'*Aphananthe monoica* (Hemsley) Leroy, le *Pleuranthodendron lindenii* (Turczaninov) Sleumer et le *Psychotria costivenia* Grisebach, au sein des strates de la canopée (<10, 10–20 et >20 m en hauteur), et ils les ont reliés à des variables environnementales, dans une forêt néotropicale semi-sempervirente. L'analyse en composantes principales révèle que deux composantes expliquent 93 % de la variation totale. La première composante (76,4 %) implique la structure foliaire, et la deuxième (16,6 %) implique la forme de la feuille. Chez l'*Aphananthe monoica* et le *Pleuranthodendron lindenii,* les auteurs ont observé des différences anatomiques dans les sections transverses des feuilles, selon les différentes strates de la canopée. Les analyses de variance montrent des différences significatives parmi les strates, quant aux caractères foliaires, pour la lumière, l'humidité relative, le déficit de pression de vapeur et la température. Les analyses par corrélation canonique montrent que la première paire des variables canoniques des caractères foliaires et les variables environnementales, sont étroitement reliées. La première variable environnementale représente les changements de microclimat le long des strates de la canopée forestière. La structure foliaire observée chez l'*Aphananthe monoica* et le *Pleuranthodendron lindenii* suggère qu'il s'agit d'espèces tolérantes intermédiaires pour l'ombre, et que le *Psychotria costivenia* est une espèce de sous-étage tolérant l'ombre. L'*Aphananthe monoica* et le *Pleuranthodendron lindenii,* qui occupent au cours de leur vie différentes positions dans les strates verticales, montrent la plus forte variation foliaire.

Mots clés : arbres tropicaux, *Aphananthe monoica, Pleuranthodendron lindenii, Psychotria costivenia,* variation foliaire, Veracruz.

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Introduction

The vertical structure of tropical forests is determined by several more or less distinct and typical canopy layers. The abundant plant life in these various strata is influenced by vertical gradients of many important environmental factors such as light intensity, temperature, and air humidity (Lüttge 1997). The effect of these factors on leaf physiology, anatomy, and morphology in tropical forest tree species has been analysed by several authors (Roth 1984; Oberbauer and Strain 1986; Popma et al. 1988; Rijkers et al. 2000). It has been found that along with the vertical structure of the forest, the percentage of deciduous species and of compound leaf species increases towards the canopy (Givnish 1987). In addition, specific leaf weight, leaf thickness, upper epidermis thickness, number of palisade layers, length of palisade cells, stomatal density, respiration rates, maximum photosynthesis, and nitrogen content tend to increase, whereas chlorophyll content, leaf size, and the angle of blade inclination tend to decrease. These changes in an upward direction through the forest canopy can be adaptations to microclimate mainly increasing light availability, vapour pressure deficit, solar radiation, temperature, and decreasing relative humidity as a result of forest vertical structure (Popma et al. 1988; Kira and Yoda 1989).

In Mexico, particularly in the north-central region of the coastal plain of the Gulf of Mexico, the semi-evergreen tropical forest is floristically and ecologically well defined (Gómez-Pompa 1973; Rzedowski 1963). There are numerous species that constitute the canopy and it is not easy to define the dominant species (Rzedowski 1978; Pennington and Sarukhán 1998). In central Veracruz, Godínez-Ibarra and López-Mata (2002) have characterized a forest in terms of woody species composition, structure, and tree species diversity. Based on relative values of density, basal area, and frequency, *Pleuranthodendron lindenii* (Turczaninov) Sleumer (Tiliaceae), *Psychotria costivenia* Grisebach (Rubiaceae), and *Aphananthe monoica* (Hemsley) Leroy (Ulmaceae) were among the most important species and they currently occupy different canopy strata.

These three species are simple leaf trees and are widespread in tropical forests of Mexico from 0 to 1500 m elevation in riparian or evergreen to semi-evergreen forests (Pennington and Sarukhán 1998). *Aphananthe monoica* is an evergreen canopy tree of 25–40 m height and all life history stages (i.e., mature trees, young trees, saplings, and seedlings) are well represented within a canopy gradient of the forest (Gómez-Pompa 1973; Godínez-Ibarra and López-Mata 2002). *Pleuranthodendron lindenii* is reported as an evergreen tree of up to 15–18 m height, also represented within a canopy gradient (Pennington and Sarukhán 1998; Godínez-Ibarra and López-Mata 2002). *Psychotria costivenia* is a shade-tolerant evergreen small tree of 5–6 m height and 4.5 cm diameter, with continuous reproduction along the year, and occupying only the forest understorey (Hamilton 1989; Godínez-Ibarra and López-Mata 2002).

Leaf morphology of these three species has been described for taxonomic studies (Nee 1984, 1999; Hamilton 1989; Lorence and Ibarra-Manríquez 1990; Pérez-Calix and Carranza 1999). Popma et al. (1992) included *Pleuranthodendron lindenii* in a study of leaf characteristics of tree species in a tropical evergreen rainforest of southeastern Mexico. In this paper, we describe morphological and structural changes among and within leaves of *Aphananthe monoica*, *Pleuranthodendron lindenii*, and *Psychotria costivenia* in a canopy gradient of a semi-evergreen Neotropical forest from central Veracruz, Mexico, and their relationship with some environmental variables.

Materials and methods

The study was conducted in a 1-ha permanent plot within 925 ha of protected forest in central Veracruz, Mexico (19°49′37″–19°51′50″N, 96°32′37″–96°37′39″W and 420 m elevation). The mean annual temperature over 2 years of continued recording since 2000 is 22.4°C. Rainfall data were obtained from Misantla, the nearest meteorological station, 15 km from the study site at the same elevation. Total annual rainfall averages 2217.2 mm with a rainy season of 4 months (June–September). Fifteen percent of total rainfall is present during winter and there is a relatively short dry season (March–April) with monthly rainfall of 82–84 mm. Soils are silty clay loams, rich in organic matter and calcium.

Based on the three canopy strata reported by Godínez-Ibarra and López-Mata (2002) in the plot, three thermohygrometer data loggers (HOBO H8 Pro; Onset Computer Corp., Pocasset, Mass.) were positioned on tree branches 5, 15, and 25 m high beginning in April 2000 to obtain air temperature and humidity data. Based on mean temperature and relative humidity data, the mean monthly (June–August 2000) vapour pressure deficit was estimated. Light availability on trees was estimated using hemispherical canopy photographs taken over individual tree crowns with a 180° diagonal angle of view fisheye lens (Canon Inc., Tokyo, Japan). From these photographs, total, direct, and diffuse photosynthetic photon flux density (PPFD) were calculated for June–August with the Hemiphot software of Ter Steege (1994).

Aphananthe monoica, *Pleuranthodendron lindenii*, and *Psychotria costivenia* leaf phenology was monitored during a year. New leaves began unfolding in June, reaching their full size in August. Twelve trees were selected for leaf sampling, two trees per species in each forest stratum (<10, 10–20, and >20 m). Sixty leaves were collected with a tree-pruning pole, or by climbing tall trees, from the fourth-order branches at the top of each tree crown with a northern exposure in August 2000. Ten of these leaves were immediately fixed in formalin – ethanol – glacial acetic acid (Ruzin 1999) until sectioning. The remaining were numbered, pressed with a standard plant press, and dried at room temperature.

Fixed leaves were washed with tap water and stored in 70% alcohol. For surface views, middle blade sections were put into a solution of 5% NaOH at a temperature of 60°C for 6–12 h. They were washed with tap water and bleached with commercial Clorox (50%). Cleared leaf sections were stained with toluidine blue (0.1%) and mounted in a mixture of water and glycerine (1:1) (Roth 1984). A leaf was supported between two pieces of carrot and transverse sections 60 μm thick were obtained with a rotary microtome, stained with safranin-fast green (Ruzin 1999), and mounted with synthetic resin.

Two weeks later, pressed leaves were dried in an oven at 60°C for 48 h. Dried leaves were weighed with an analytical balance and their leaf area measured with a leaf area meter (LI-3100; LI-COR Inc., Lincoln, Nebr.). Length and width and base and tip width of the leaf blade were measured to the nearest millimetre. Specific leaf area (SLA) (square centimetres per gram), shape index (length/width), and tip to base ratio (width/width) were calculated. Stomata were present only on the abaxial surface of the leaves of the three species, and trichomes occurred only on the abaxial surface of *Aphananthe monoica* and *Pleuranthodendron lindenii*, and their densities were calculated in five fields of 1 mm^2. Counts were carried out in the cleared leaves with an image analyser (Image-Pro Plus v. 3.1; Media Cybernetics, Silver Spring, Md.). Transverse sections were used to evaluate anatomical differences in parenchyma, organic deposits, mineral inclusions, and sclerenchyma associated with the sheath of the vascular bundle.

Statistical analyses

A principal components analysis (PCA) was applied to identify which leaf traits represent gradients of maximum variation within a data set (McGarigal et al. 2000). A PCA is concerned with explaining the variance structure through a few linear combinations of the original variables (Johnson and Wichern 1982). A scatterplot of PCA illustrates the relationship among sampling entities, since those in close proximity in ordination space are similar with respect to gradients defined by the PCA (McGarigal et al. 2000). Significant differences among means of those traits identified by PCA among forest strata within species were evaluated with variance analyses (ANOVA) using model II of aleatory effects for nested sampling (Snedecor and Cochran 1970). Significant differences among forest strata for environmental data were also analysed with ANOVA. Differences among means were compared and segregated with a Tukey test ($p <$ 0.05). A canonical correlation analysis (CCA) was used to identify the association between dominant leaf traits extracted by the PCA and environmental variables. The CCA is a technique for analysing two or more sets of variables, which organizes sampling entities (leaf traits) along pairs of continuous ecological gradients (McGarigal et al. 2000). A scatterplot of CCA illustrates the relationship among sampling entities, since those in close proximity occupy the same relative position in the joint space defined by the two sets of variables. A high canonical correlation will appear as a strong linear distribution of sample points (McGarigal et al. 2000). Epidermal cell modifications such as the occurrence of trichomes were not included in the analyses because they are inherent in each species and are not comparable. All statistical analyses were performed with SAS software (SAS Institute Inc., Cary, N.C.).

Results

Leaf characteristics

PCA revealed that two principal components explained 93% of the total sampled variance (Fig. 1). The first component (eigenvalue of 3.06) accounted for 76.4% of the total variation and denoted leaf structure (stomatal density and SLA), whereas the second component (eigenvalue of 0.66)

Fig. 1. Principal components analysis biplot showing individual trees grouping in relation to leaf traits in each stratum. Circles, *Aphananthe monoica*; squares, *Pleuranthodendron lindenii*; triangles, *Psychotria costivenia*. Forest strata: solid, <10 m; gray, 10–20 m; open, >20 m.
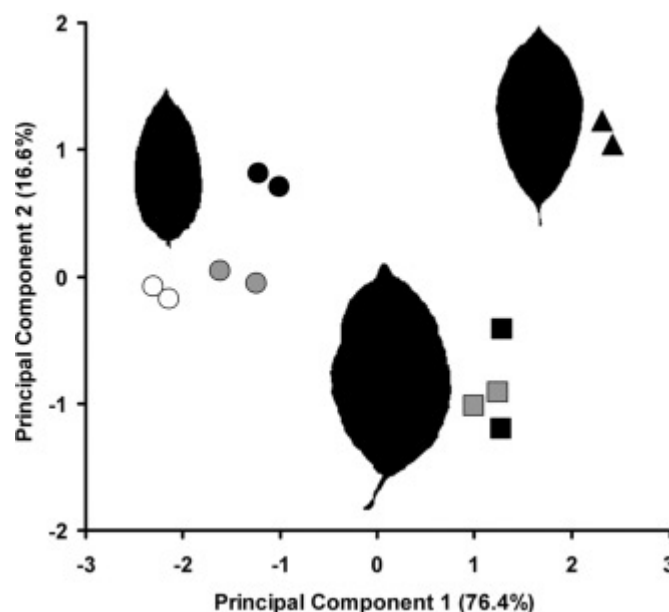
Table 1. Leaf traits of the three species used in principal components analysis and the contribution of the first two components.

	Principal component	
	1	2
Eigenvalue	3.06	0.66
Total variance (%)	76.4	16.6
Characteristic loading		
Specific leaf area (cm^2·g^{-1})	0.521*	0.179
Shape index	−0.394	0.884*
Leaf tip to base ratio	0.501	0.426
Stomatal density (mm^{-2})	−0.568*	−0.074

  Note: An asterisk indicates the strongest partial contribution of leaf traits to the components.

described 16.6% of the remaining variation and denoted leaf shape (Table 1).

The ANOVA detected significant differences among forest strata for leaf area ($F = 27.16$, df = 2, $p < 0.0001$, $n = 600$), SLA ($F = 24.62$, df = 2, $p < 0.0001$, $n = 600$), stomatal density ($F = 467.88$, df = 2, $p < 0.0001$, $n = 600$), and shape index ($F = 12.78$, df = 2, $p < 0.0001$, $n = 600$). Tukey multiple comparison analyses confirmed the existence of statistically significant differences among strata (Table 2).

Leaf anatomy showed that in *Aphananthe monoica*, leaf trichomes were present; they were simple and of two distinct types, glandular and nonglandular. Nonglandular trichomes were short and ornamented with calcified warts, providing a strigose surface appearance to the blade, whereas simple trichomes were restricted to the midrib and secondary veins in *Pleuranthodendron lindenii*. A thick smooth cuticle covered both surfaces, usually more prominent on the adaxial surface

Table 2. Tukey multiple comparsion test for leaf traits mean values (±SE) identified by principal components analysis and the leaf area (cm^2) of the three species within each forest stratum.

Characteristic	<10 m	10–20 m	>20 m
Aphananthe monoica			
Leaf area	18.1±0.7*	23.6±0.9*	11.4±0.4*
Specific leaf area	176.4±5.2*	152.1±2.1*	105.5±2.2*
Stomatal density	1001.9±65.5	1118.9±38.6	1330.2±50.6*
Shape index	2.9±0.1*	2.6±0.1	2.6±0.1
Pleuranthodendron lindenii			
Leaf area	31.0±1.4	29.5±1.5	
Specific leaf area	219.5±7.5*	188.3±5.6	
Stomatal density	451.0±15.7	495.2±18.3	
Shape index	1.5±0.1	1.4±0.1	
Psychotria costivenia			
Leaf area	26.7±1.2		
Specific leaf area	213.4±5.5		
Stomatal density	102.8±3.6		
Shape index	2.2±0.1		

Note: An asterisk indicates a significant difference ($p < 0.05$) among strata.

in the three species, except for *Psychotria costivenia*, which had a rugose cuticle. Epidermal cells were mainly square. Stomata occurred at the same level as the other epidermal cells. The mesophyll comprised a layer of palisade cells, a narrow spongy region, and abundant idioblasts with druses in *Aphananthe monoica*, raphides in *Psychotria costivenia*, and tannins in *Pleuranthodendron lindenii*. Foliar vascular bundles were collateral with a uniseriate bundle sheath composed of sclerenchyma in *Aphananthe monoica* and *Psychotria costivenia*, but *Pleuranthodendron lindenii* had a mulseritate bundle sheath with abundant prismatic crystals. The midrib had several layers of collenchyma under the epidermis and a well-developed vascular bundle with secondary growth. Longer palisade cells were present in leaves of *Aphananthe monoica* at the >20 m stratum, whereas the <10 m stratum had shorter ones (Figs. 2*a* and 2*c*). Periclinal divisions occurred in the palisade cells developing a two-layered region in leaves growing in the 10–20 m stratum (Fig. 2*b*). Also, a two-layered palisade region was present in *Pleuranthodendron lindenii* (Fig. 2*d*). In both species, spongy tissue was denser. Tannins were distributed abundantly throughout the adaxial epidermal and palisade cells in mature leaves distributed at the higher stratum in both species (Figs. 2*a* and 2*d*), but also common in *Psychotria costivenia* (Fig. 2*f*). In *Aphananthe monoica*, tannins were scarce or absent in leaves distributed in the understorey, while no differences in cellular contents were detected in the other two species (Figs. 2*c*, 2*e*, and 2*f*). In the surface view, there were only glandular trichomes on leaves of *Aphananthe monoica* in the <10 m stratum.

Environmental variables

The ANOVA showed highly significant differences among strata for the environmental variables temperature ($F = 56.83$, df = 2, $p < 0.0001$, $n = 36$), vapour pressure deficit ($F = 21.77$, df = 2, $p < 0.0001$, $n = 36$), relative humidity ($F = 20.51$, df = 2, $p < 0.0001$, $n = 36$), total PPFD ($F = 4157.68$, df = 2, $p < 0.0001$, $n = 36$), direct PPFD ($F = 3980.92$, df = 2, $p < 0.0001$, $n = 36$), and diffuse PPFD ($F = 3862.41$, df = 2, $p < 0.0001$, $n = 36$). Tukey multiple comparison analyses showed the existence of statistically significant differences only between some forest strata (Fig. 3).

The CCA revealed that the first pair of canonical variates of leaf traits and environmental variables were closely related ($R_c^2 = 0.93$) (Fig. 4). Leaf structure loaded positively on the first environmental canonical variate, whereas shape index and stomata density loaded negatively (Table 3). The first environmental canonical variate represented the changes in microclimate along forest strata. Temperature, vapour pressure deficit, and PPFD loaded negatively on the first leaf traits canonical variate, whereas relative humidity loaded positively (Table 3).

Discussion

According to Raunkiaer's size classes of leaves (Lüttge 1997), *Psychotria costivenia* and *Pleuranthodendron lindenii* were classified as mesophyll (20–180 cm^2) and *Aphananthe monoica* as microphyll (2–20 cm^2). Moreover, *Aphananthe monoica* showed variation in leaf size among forest strata. An increment in leaf area was present at the 10–20 m stratum, declining towards the >20 m stratum. This variation seems to be a distinctive trait of plants growing in the humid tropical forest (Roth 1990). Leaf variability relates not only to size but also to shape and structure. The PCA showed that the observed leaf values displayed gradual changes related to height. Mean values of SLA showed that *Psychotria costivenia* had the highest value followed by *Pleuranthodendron lindenii*, the species up to the 10–20 m stratum, and finally *Aphananthe monoica*, the species occurring higher than 20 m. The same tendency of SLA distribution has been observed in other tropical forests (Roth 1990).

Pronounced differences in the SLA of the three species were associated with leaf anatomy. Usually, the leaves of plants grown in the sun are thicker than those developed in the shade (Lambers et al. 1998). As a rule, if the leaves are exposed to full sun, the mesophyll becomes more compact, the palisade cells longer or several layered, and the spongy parenchyma reduced (Roth 1984; Lambers et al. 1998). Observations on the leaf anatomy of the species suggested that *Aphananthe monoica* is an intermediate shade-tolerant species with the lowest value of SLA, a thick cuticle, mesophyll with longer palisade cells, denser spongy tissue, and vascular bundles with sclerenchyma. A similar interpretation is suggested for *Pleuranthodendron lindenii*, which had a two-layered palisade and a denser spongy region occluded with tannins. On the other hand, *Psychotria costivenia* is a shade-tolerant species, with short palisade cells and a spongy region with abundant larger spaces. In addition, as observed in *Aphananthe monoica* and *Pleuranthodendron lindenii* in the transition from the understorey to the canopy within each species, leaves became progressively smaller, thicker, and more leathery in texture and had a lower SLA. This has also been reported in other species (Roth 1984; Anten et al. 2000; Rijkers et al. 2000). Low SLA values in both species may be associated with the presence of additional layers of palisade parenchyma, occurrence of

Fig. 2. Transverse leaf sections of (*a–c*) *Aphananthe monoica*, (*d* and *e*) *Pleuranthodendron lindenii*, and (*f*) *Psychotria costivenia* by forest stratum: (*a*) >20, (*b*) 10–20, (*c*) <10, (*d*) 10–20, (*e*) <10, and (*f*) <10 m height. Gray represents tannins. Scale bar = 50 μm.
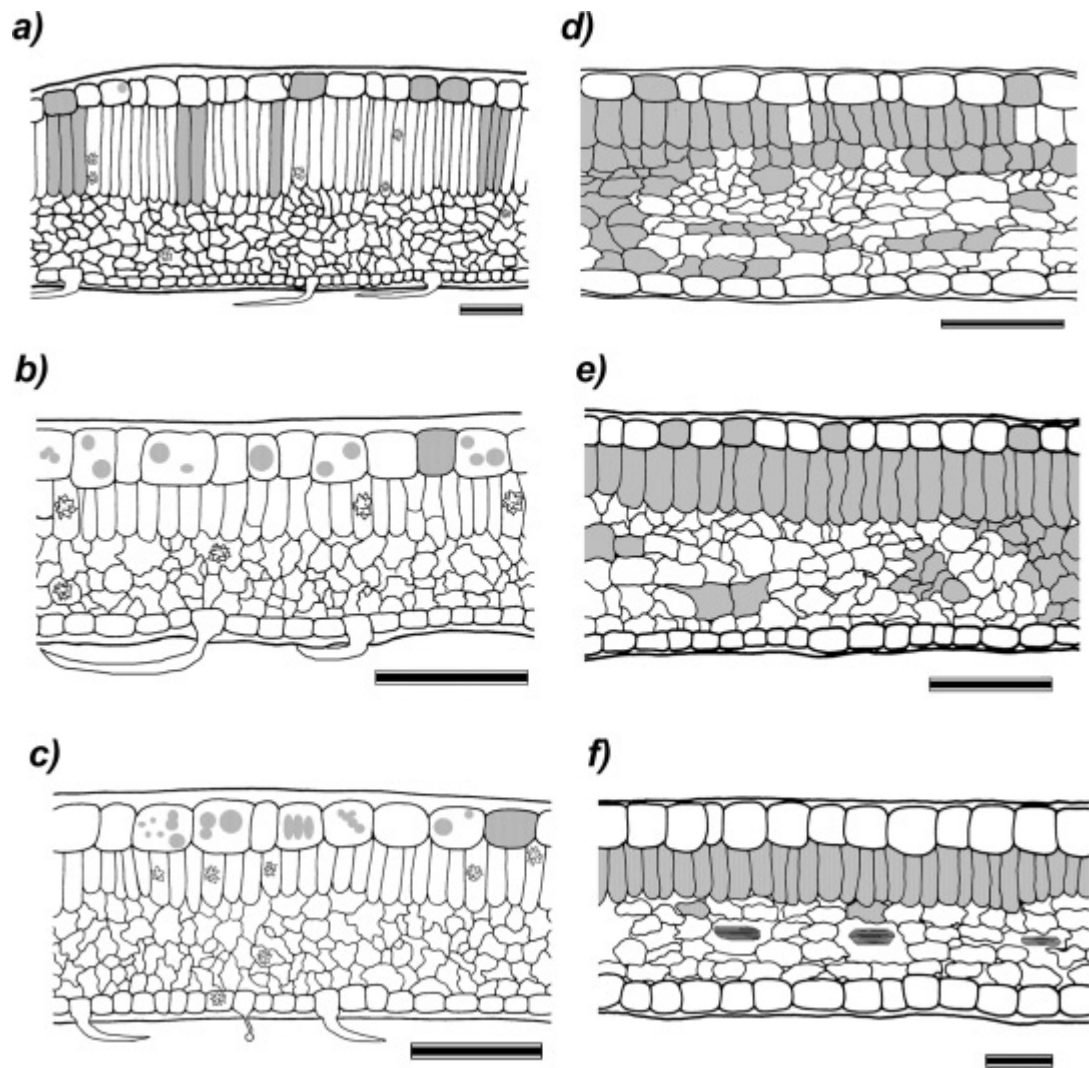
Table 3. Canonical correlation analysis between leaf traits and environmental canonical variates and between environmental variables and leaf canonical variates ($R_c^2 = 0.93$).
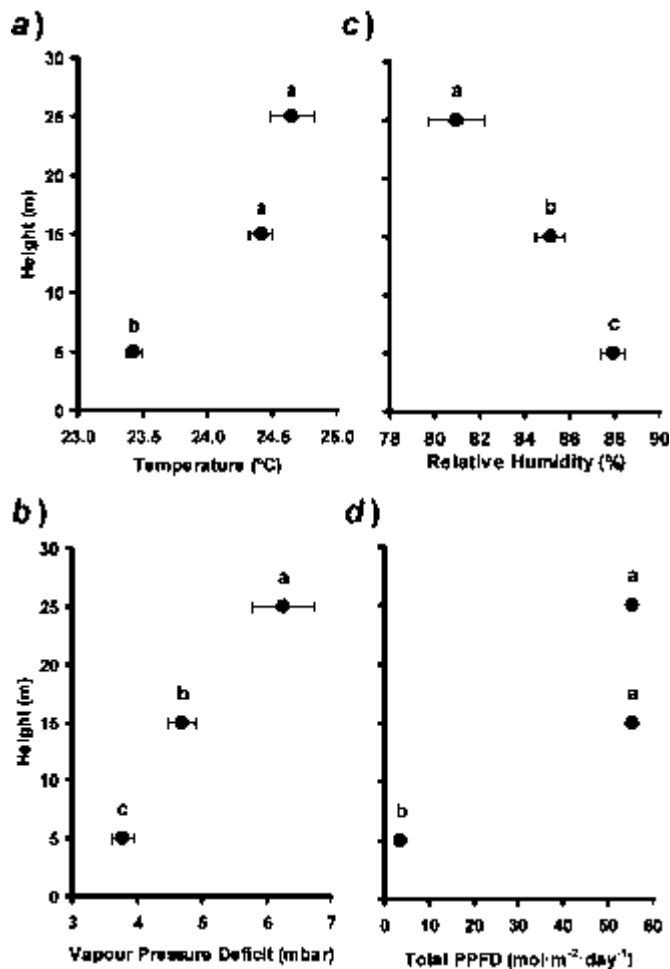
Variables	Canonical variates
Leaf	**Environmental**
Specific leaf area ($cm^2 \cdot g^{-1}$)	0.871
Shape index	–0.102
Stomata density (mm^{-2})	–0.653
Environmental	**Leaf**
Temperature (°C)	–0.875
Relative humidity (%)	0.933
Vapour pressure deficit (mbar)	–0.929
Direct PPFD ($mol \cdot m^{-2} \cdot day^{-1}$)	–0.806
Diffuse PPFD ($mol \cdot m^{-2} \cdot day^{-1}$)	–0.802
Total PPFD ($mol \cdot m^{-2} \cdot day^{-1}$)	–0.805

Note: PPFD, photosynthetic photon flux density; 1 mbar = 0.1 kPa.

sclerenchyma, and occlusion of epidermal and palisade lumina, as has been reported for other species by Doley (1981) and Lambers et al. (1998). Roth (1984) mentioned that leaves of canopy trees are more exposed to solar radiation and wind, and they develop sclerenchyma either in the mesophyll or in the bundle sheath, increasing their strength. Stomatal density also showed a tendency to increase from the understorey to the canopy, having the same tendency as leaf thickness and the inverse of the tendency in SLA. These results agree with other studies of tropical tree species, interpreting these as adaptations of leaf structure to stronger solar radiation and drought (Gutschick 1999).

Leaf shape is characteristic of each species. According to the categories of leaf shape index proposed by Roth (1990), *Aphananthe monoica* possessed an elongated narrow blade (narrowly ovate), *Psychotria costivenia* an intermediate form (obovate), and *Pleuranthodendron lindenii* a broad leaf (elliptic). PCA detected a trend of highest shape index in the understorey for all three species, which diminished toward the canopy: slightly in *Pleuranthodendron lindenii* and markedly in *Aphananthe monoica*. The more elongated leaf
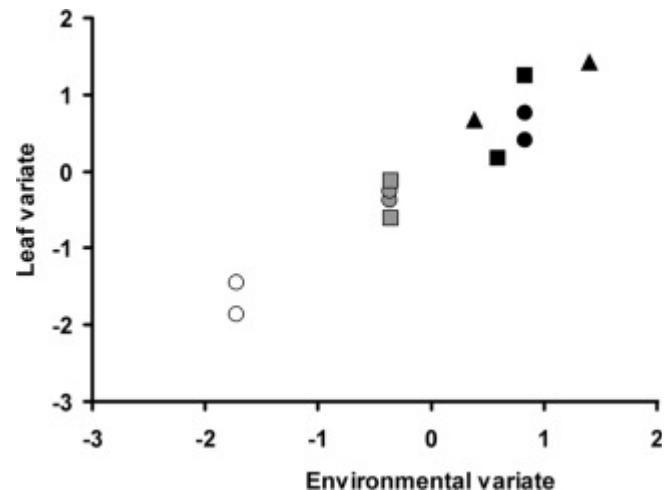
Fig. 3. Environmental mean values (±SE) by stratum: (*a*) temperature, (*b*) vapour pressure deficit, (*c*) relative humidity, and (*d*) total photosynthetic photon flux density. Different letters indicate significant differences (Tukey, $p < 0.05$).

Fig. 4. Scatterplot showing the relationship between the first pair of canonical variates, where leaf and environmental variates denoted a high canonical correlation. Circles, *Aphananthe monoica*; squares, *Pleuranthodendron lindenii*; triangles, *Psychotria costivenia*. Forest strata: solid, <10 m; gray, 10–20 m; open, >20 m.

types growing in the understorey had a drip tip, whereas in the canopy the leaves lacked this feature. Most studies of tropical forest trees indicate that in the understorey, leaves are larger and elongated in form, with a high shape index and a conspicuous drip tip, whereas in the canopy, leaves of the same species are smaller and broad in form, with a low shape index and a shorter tip, different from the drip tip type (Roth 1984). Rollet (1990) also pointed out that drip tips decrease progressively in frequency and length from the sapling stratum to the emergent trees and are more frequent and longer in the understorey. Although the function of the drip tip has been discussed extensively, many authors agree that it ensures a rapid drainage of the blade, preventing the establishment of epiphylls (Doley 1981; Roth 1990).

Canonical correlation between leaf shape and structure and canopy environment detected species leaf adaptation to an environmental gradient through the canopy. Also, the leaf ecophysiological adaptation or leaf structural changes from shade- to sun-leaf within species through the forest strata was revealed. Elevated SLA and lower stomatal density and shape index were associated with a decrease in light intensity, temperature, and water loss by transpiration (vapour

pressure deficit) as well as an increase in humidity. It must be considered that differences in SLA could be explained by the increase in sclerenchyma and reduction of open lumina to supply support to the mesophyll during periods of water loss in the canopy or changing water relationships within a tree caused by increased hydraulic limitations in taller trees (Rijkers et al. 2000).

The results showed that below the 10 m stratum, there was an association among lower temperature, vapour pressure deficit, and PPFD but higher relative humidity with leaf shape index and anatomical structure in each of the three species. In contrast, higher temperature, vapour pressure deficit, and PPFD as well as lower relative humidity were associated with the same leaf traits for *Pleuranthodendron lindenii* and *Aphananthe monoica* at higher forest strata. The transition in leaf structure in the 10–20 m stratum for *Aphananthe monoica* was more similar to leaves growing in the canopy. It corresponded to an increase in stomatal density and a decrease in SLA; however, leaf shape was more similar to that of leaves growing on saplings in the understorey. Most *Psychotria* species are understorey species (Popma et al. 1992), and *Psychotria costivenia* was not an exception. *Aphananthe monoica* and *Pleuranthodendron lindenii*, which during their life span occupy different positions in the vertical strata, showed the highest leaf variation, confirming previous reports for species distributed in other tropical forests.

Acknowledgements

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