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Leaf Morphology of 89 Tree Species from a Lowland Tropical Rain Forest (Atlantic Forest) in South Brazil

Maria Regina Torres Boeger*, Luiz Carlos Alves and Raquel Rejane Bonatto Negrelle
Universidade Federal do Paraná; Setor de Ciências Biológicas; Departamento de Botânica; Laboratório de Ecologia; rboeger@ufpr.br; C. P. 19031; 81.531.990; Curitiba - PR - Brazil

ABSTRACT

We examined the leaf morphology and anatomy of 89 tree species growing in an area of coastal Atlantic Forest in South Brazil. The majority of the species (> 75%) had small (notophyll and microphyll) elliptical simple leaves with entire margins. These leaves presented a typical anatomical structure consisting of a single epidermal cell layer, single palisade parenchyma cell layer, and spongy parenchyma with 5 to 8 cell layers. The sclerenchyma was limited to the vascular bundles. The majority of the tree species (91%) had leaves with mesomorphic characteristics. Few species depicted leaves with xeromorphic features as would be expected in such oligotrophic sandy soil. These mesomorphic features appeared to be associated to high efficiency mechanisms for nutrient cycling that compensated for the low nutrient content of the mineral soil.

Key words: Leaf morphology; leaf anatomy; lowland tropical forest; Atlantic Forest

INTRODUCTION

Morpho-anatomical characteristics of the plants are greatly influenced by environmental factors associated with climate, light, amount of rainfall, soil, relief, and altitude (Givnish, 1984). These factors vary in space and time and can be limiting to the establishment and growth of the vegetation. Leaves are directly subjected to these environmental variations and are, thus, important probes for autecological or synecological studies because they evolve specific strategies to certain environmental characteristics (Pyykko, 1979).

The morphology of leaves has been used to describe and compare tropical rain forests (Sobrado and Medina, 1980; Bongers and Popma, 1990; Medina et al., 1990). One of the first authors to use this methodology, Richard (1952), noted that plants of different families in a tropical forest depicted similar morphology while species of the same genera in temperate forests presented distinctive morphological characteristics. Further studies (Grubb et al., 1963; Gentry, 1969) provided support for Richard's hypothesis, showing that 50% of the species in the lowland tropical forests of Ecuador, Brazil, and Australia presented mesophyllous leaves while 95% of the plants in montane forests in Costa Rica had microphyllous leaves.

Leaf morphology is also related to environmental gradients (Geeske et al., 1994) and foliar nutrient content (Sobrado and Medina, 1980; Peace and Macdonald, 1981; Körner et al., 1986; Medina et al., 1990). Some tropical plant formations (e.g. campinarana and heath forests) are categorized as sclerophylls based partially on the

*Author for correspondence

morphology of the leaves of their plant species (Sobrado and Medina, 1980; Turner et al., 1995). Most of these studies, however, have been developed in the tropical forests of the Amazon, Central America, New Zealand, and Hawaii. In the Atlantic Forest, the great majority of the studies are descriptive for a single or for a related group of species (Coutinho, 1962; Souza, 1971; Rôças et al., 1997). The Atlantic Forest extends from 30º N to 30º S along the coast of Brazil and originally occupied about 1.227.600 Km^2. Today, this forest has been reduced to only 7.5 % of its original extent (Myers et al., 2000). It has a high plant diversity (20,000 plant species), among which, 8,000 plant species are endemic (Myers et al., 2000). In the State of Santa Catarina (South Brazil) alone, more than 191 species of trees have been reported (Siqueira, 2001). This study presents the results of a morphological study of 89 tree species from a remnant of the Atlantic Forest located in State of Santa Catarina, Brazil. The morphological patterns reported herein are discussed in relation to environmental conditions and compared to those of other tropical forests.

MATERIAL AND METHODS

Plant material was collected in the Volta Velha Reserve, a privately owned reserve in South Brazil (26º04'S, 48º38'W Gr) and considered part of the Atlantic Forest Biosphere Reserve, located in the Municipality of Itapoá, State of Santa Catarina. The reserve occupies approximately 1.200 hectares and is located in the coastal plain, 5 km from the Atlantic Ocean and 9 m above sea level (Fig. 1). The area shows no obvious recent evidence of human disturbance. The forest is classified as a lowland rain forest, with a dense vegetation of 15 to 20 m. tall and is composed by lianas, epiphytes, and palms, besides the tree species (Veloso et al., 1991). The mean annual temperature in the area is 20.3 ºC. The hottest month, February, has a mean maximum temperature of 27.2 ºC; the coldest month, July, has a mean minimum temperature of 16.5 ºC. The mean annual precipitation is 2170 mm. Although there is no distinct dry season, maximum precipitation occurs from January to March.

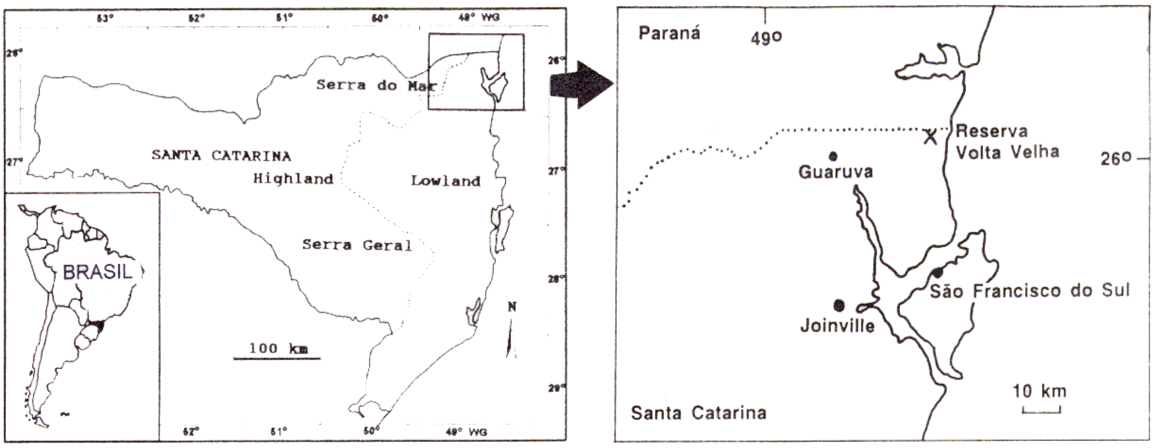

Figure 01 - Location of the study site (Volta Velha Reserve, Santa Catarina State, Brazil).

The soil has been classified as spodsol, non-hydromorphic, with a moderate sand texture, and low concentrations of exchangeable cations (Negrelle, 1995). A previous survey in a 1 ha area found 113 tree species of 34 families. The species studied herein (n=89) were selected based on the number of individuals present in the area (at least 3) and on their high Value of Importance Index (see Negrelle, 1995).

Leaves from branches directly exposed to sunlight (sun leaves) were collected from three individuals of each species. All trees were more than 10 m tall and 10 cm in diameter at breast height. Leaf area was measured with a leaf-area meter (LiCor, Nebraska, USA) and represented the average values for 20 sun leaves. Classes of leaf size were defined according to Raunkiaer's classification, as modified by Webb (1959). Dried and pressed plant material was also used in the analysis of leaf morphology.

The morphological terminology used was that proposed by Leaf Architecture Working Group (1999). The presence of trichomes and stomata on leaf epidermis was determined using epidermal casts made with colorless nail polish. Sections of 1 cm^2 from the central area of each leaf were fixed in 50 FAA (formaldehyde, ethanol 50º, acetic acid – 18:1:1 v/v), dehydrated with ethanol, embedded in glycol methacrylate resin (Reichert-Jung, Germany), and sectioned at 7 µm. Sections were stained with toluidine blue (Sass, 1951). All measurements were determined using a light microscope with ocular micrometer. Leaves used in scanning electron microscopy were fixed in 50 FAA, dehydrated through ethanol series to absolute ethanol, and critical-point dried with CO_2. Dried specimens were mounted on stubs and coated with gold. Abaxial surfaces were observed with a Philips SEM 505 scanning microscope.

Table 1 - Leaf morphological features of trees analysed from Volta Velha Reserve (SC, Brazil) (n=89).

Features	Type: prevalence of species (%)			
Lamina	Simple: 88.5	Compound: 11.5		
Leaf symmetry	Symmetrical: 95.0	Asymmetrical: 5.0		
Leaf shape	Elliptic: 76.7	Obovate: 20	Oblong: 3.3	
Leaf base	Acute: 59.7	Cuneate: 25.7	Obtuse: 12.5	Others: 2
Leaf margin	Entire: 88.8	Serrate: 7.7	Erose: 2.4	Others: 2
Leaf apex	Acuminate: 49.8	Acute: 30.4	Obtuse: 8.2	Others: 11.6
Petiole	Normal: 99	Absent: 1.0		
Leaf texture	Coriaceous: 51.7	Chartaceous: 48.3		
Trichomes	Present: 40.7	Absent: 59.3		
Secretory structures	Present: 41.8	Absent: 58.2		
Phyllotaxy	Alternate: 59.1	Decussate: 21.5	Opposite: 15.1	Others: 4.3
Bundle-sheath extensions	Present: 26.7	Absent: 73.3		
Sclerenchyma type	Fibers:72.7	Sclereides: 3.9	Absent: 23.4	
Nº of cell layers in palisade mesophyll	1: 51.5	2: 29.7	≥ 3: 19.8	
Nº of cell layers in spongy mesophyll	1 to 4: 15.8	5 to 8: 61.2	≥ 9: 23	
Leaf size	Notophyllous: 44.1	Microphyllous: 35.5	Mesophyllous: 14	Others: 6.4

RESULTS AND DISCUSSION

The summary of the morphological analysis of the 89 tree species is presented in Table 1. Main leaf characteristics for all studied species are presented in Table 2. There was no predominance of any state of the following characters: texture, and presence of trichome and secretory structures. Morphologically, the leaves in the area studied (Table 1; Fig. 2) were predominantly simple, symmetrical, elliptic with acuminate apex, entire margin, normal petiole and alternate. These results were very similar to those reported for other tropical forests (Pyykko, 1979; Roth, 1984; Kapelle and Leal, 1996). Elliptical leaves with acuminate or acute apex and entire margins appeared associated with the high pluviosity of the area (Negrelle, 1995).

It has been suggested that this leaf morphology enhances drainage of rainwater, which probably retards the growth of epilhylls and reduces the loss of soluble nutrients by leaching (Whitmore, 1998). The coriaceus texture of leaves observed on more than 50% of plant species apparently were a defense against herbivory because leaf replacement was an energetically expensive process (Coley and Barone, 1996). Also, the development of this texture has been interpreted as a response to the conditions of water stress and high light intensity as that observed in canopies (Roth, 1984).

In the studied area, leaves were predominantly microphyllous and notophyllous (>75% of the species), and smaller than those reported for other lowland tropical forests (Table 3). However, the mesophyll class was overestimated for some tropical forests, because the notophyllous class was also included on the mesophyll class (Webb, 1959; Bongers and Popma, 1990).

In tropical forests, the leaf size was inversely related to the latitude and altitude, and directly related to the annual pluviosity values (Webb, 1959; Dolph and Dilcher, 1980). As precipitation decreased, the average leaf area in a flora also decreased (Webb, 1959; Dolph and Dilcher, 1980). The leaf size was also influenced by others features such as humidity and temperature. Large leaves were more often in warm and moist tropical forests (Werger and Ellenbroek, 1978).

In this study, the predominance of microphyllous and notophyllous leaves appeared to be influenced by the temperature, which was lower at Santa Catarina state when compared to higher temperature of the equatorial regions (Negrelle, 1995).

Crystals occurred in 50% of the species studied (Table 3). Calcium oxalate crystals are a product of plant metabolism and have been associated with the removal of excess calcium from the system (Volk et al., 2002). The high prevalence of crystals in leaves was also interpreted as a defense against herbivory, by making the leaves less palatable (McKey et al., 1978). According to Aerts and Chapin (2000), leaves with high prevalence of crystals occur mainly in species growing in soils of low fertility where species must avoid loss of leaf tissues and nutrients by the action of herbivores. Only 12% of the wood species growing in fertile soils (e.g. Los Tuxtlas, Mexico) have crystals in the leaves (Bongers and Popma, 1990).

Table 2 - Main leaf characteristics of studied species from Volta Velha Reserve. Adaxial surface thickness (AdST), abaxial surface thickness (AbST), palisade parenchyma thickness (PPT), spongy parenchyma thickness (SPT), and total thickness (TT).

Species	Family	leaf area (cm^2)	leaf size	lamina	apex	ad. surface	mesophyll type	AdST (µm)	AbST (µm)	PPT (µm)	SPT (µm)	TT (µm)
Aiouea saligna	Lauraceae	25,74	notophyll	elliptic	acuminate	uniseriate	asymmetrical	22,99	10,45	96,14	73,15	214,25
Alchornea triplinervia	Euphorbiaceae	46,3	mesophyll	elliptic	acuminate	uniseriate	asymmetrical	14,63	12,54	75,24	52,25	154,66
Amaioua guianensis	Rubiaceae	42,19	notophyll	elliptic	acuminate	uniseriate	asymmetrical	20,9	10,45	48,07	96,14	175,56
Andira anthelminthica	Fabaceae	15,81	microphyll	oblong	acute	uniseriate	homogeneous	22,99	12,54	71,06	48,07	154,66
Aniba firmula	Lauraceae	36,95	notophyll	elliptic	acuminate	uniseriate	asymmetrical	20,9	20,9	125,4	144,21	342,8
Annona cacans	Annonaceae	51,6	mesophyll	elliptic	acuminate	uniseriate	asymmetrical	25,08	12,54	68,97	85,69	192,28
Aparisthmium cordatum	Euphorbiaceae	143,14	mesophyll	elliptic	acuminate	uniseriate	asymmetrical	8,36	10,45	20,9	41,8	87,78
Byrsonima ligustrifolia	Malpighiaceae	4,2	microphyll	elliptic	acuminate	uniseriate	asymmetrical	31,35	20,9	73,15	152,57	277,97
Blepharocalyx salicifolius	Myrtaceae	11,97	microphyll	elliptic	acute	uniseriate	symmetrical	14,63	12,54	79,42	77,33	183,92
Cabralea canjerana	Meliaceae	20,1	notophyll	elliptic	acuminate	uniseriate	asymmetrical	16,72	12,54	35,53	87,78	152,57
Calophyllum brasiliense	Clusiaceae	30,9	notophyll	elliptic	obtuse	uniseriate	asymmetrical	22,99	16,72	41,8	146,3	231,39
Calyptranthes concinna	Myrtaceae	5,6	microphyll	elliptic	acute	uniseriate	asymmetrical	25,08	16,72	129,58	265,67	437,07
Calyptranthes lucida	Myrtaceae	36,27	notophyll	elliptic	acuminate	uniseriate	asymmetrical	12,54	10,45	43,89	231,39	317,09
Campomanesia guaviroba	Myrtaceae	25,5	notophyll	elliptic	acuminate	uniseriate	asymmetrical	18,81	8,36	66,88	83,6	179,97
Clethra scabra	Clethraceae	31,8	notophyll	obovate	obtuse	multiseriate	asymmetrical	14,4	48,8	100,7	119,6	287,8
Clusia criuva	Clusiaceae	25,84	notophyll	obovate	acute	multiseriate	asymmetrical	135,8	29,6	109,9	300	543,2
Coccoloba warmingii	Polygonaceae	230,91	macrophyll	elliptic	obtuse	uniseriate	asymmetrical	35,53	14,63	77,33	52,25	163,02
Conomorpha peruviana	Myrsinaceae	14,14	microphyll	elliptic	acuminate	uniseriate	asymmetrical	25,08	14,63	48,07	121,22	214,25
Copaifera trapezifolia	Caesalpinaceae	22,06	notophyll	elliptic	obtuse	uniseriate	asymmetrical	16,72	16,72	29,26	43,89	106,59
Cupania oblongifolia	Sapindaceae	92,99	mesophyll	obovate	obtuse	uniseriate	asymmetrical	25,08	10,45	20,9	85,69	142,12

Cont. Table 2

Cont. Table 2

Drymys brasiliensis	Winteraceae	18,42	microphyll	obovate	emarginate	uniseriate	asymmetrical	31,35	37,62	135,85	150,48	342,8
Endlicheria paniculata	Lauraceae	29,94	notophyll	elíptica	acuminate	uniseriate	asymmetrical	31,35	29,26	104,5	222,82	402,79
Erythroxylum vaciniifolium	Erythroxylaceae	3,89	microphyll	elíptica	retuse	uniseriate	asymmetrical	33,44	12,54	37,62	129,58	213,18
Esembeckia grandiflora	Rutaceae	32,5	notophyll	elliptic	acute	uniseriate	asymmetrical	25,08	18,81	56,43	205,68	308,52
Eugenia cerasiflora	Myrtaceae	40	notophyll	elliptic	acuminate	uniseriate	asymmetrical	12,54	12,54	43,89	175,56	248,53
Eugenia obovata	Myrtaceae	17,67	microphyll	elliptic	acuminate	uniseriate	asymmetrical	20,9	10,45	83,6	79,42	282,81
Eugenia subavenia	Myrtaceae	6,3	microphyll	elliptic	acute	multiseriate	asymmetrical	48,07	20,9	117,04	274,24	454,21
Eugenia tristis	Myrtaceae	14,07	microphyll	elliptic	acuminate	uniseriate	homogeneous	10,45	10,45	0	300,96	325,66
Eugenia umbelliflora	Myrtaceae	35,34	notophyll	elliptic	acuminate	uniseriate	asymmetrical	12,54	10,45	37,62	222,82	282,81
Faramea marginata	Rubiaceae	25,6	notophyll	elliptic	acuminate	uniseriate	asymmetrical	14,63	6,27	39,71	96,14	156,75
Garcinia gardneriana	Clusiaceae	27,82	notophyll	elliptic	acuminate	uniseriate	asymmetrical	16,72	12,54	35,53	171,38	236,17
Gomidesia affinis	Myrtaceae	17,46	microphyll	elliptic	acute	uniseriate	asymmetrical	14,63	10,45	60,61	102,41	188,1
Gomidesia schaueriana	Myrtaceae	25,15	notophyll	elliptic	acute	multiseriate	asymmetrical	62,7	10,45	89,87	325,66	505,63
Guarea macrophylla	Meliaceae	29,65	notophyll	obovate	acuminate	uniseriate	asymmetrical	25,08	16,72	64,79	158,84	265,67
Guatteria australis	Annonaceae	15,5	microphyll	elliptic	acuminate	uniseriate	asymmetrical	27,17	20,9	52,25	64,79	165,11
Heisteria silvianii	Olacaceae	32,65	notophyll	elliptic	acute	uniseriate	asymmetrical	22,99	14,63	41,8	169,29	274,24
Hieronyma alchorneoides	Euphorbiaceae	105,8	mesophyll	elliptic	obtuse	uniseriate	asymmetrical	32,8	20	82,9	132,6	284,5
Ilex dumosa	Aquifoliaceae	8,1	microphyll	elliptic	obtuse	uniseriate	asymmetrical	22,99	18,81	137,94	119,13	299,95
Ilex interregima	Aquifoliaceae	62,6	mesophyll	oblong	emarginate	uniseriate	asymmetrical	37,62	25,08	299,95	257,1	634,18
Ilex pseudobuxus	Aquifoliaceae	5,3	microphyll	obovate	emarginate	uniseriate	asymmetrical	20,9	10,45	125,4	68,97	267,52
Ilex theezans	Aquifoliaceae	40,2	notophyll	obovate	emarginate	uniseriate	asymmetrical	54,34	25,08	239,96	317,09	608,47
Manilkara subsericea	Sapotaceae	32,3	notophyll	obovate	acute	multiseriate	asymmetrical	58,52	10,45	125,4	127,49	317,09
Maprounea guianensis	Euphorbiaceae	6	microphyll	elliptic	acute	uniseriate	asymmetrical	22,99	22,99	52,25	77,33	173,47
Marlierea eugeniopsoides	Myrtaceae	26,76	notophyll	elliptic	acuminate	uniseriate	asymmetrical	12,54	12,54	94,05	194,37	308,52
Marlierea reitzii	Myrtaceae	30,2	notophyll	elliptic	acuminate	uniseriate	asymmetrical	16,72	10,45	41,8	183,92	265,67
Matayba guianensis	Sapindaceae	42,5	notophyll	elliptic	acute	multiseriate	asymmetrical	35,53	25,08	60,61	81,51	202,73
Maytenus robusta	Celastraceae	7,6	microphyll	elliptic	acuminate	uniseriate	asymmetrical	27,17	18,81	112,86	114,95	274,24
Miconia cabuçu	Melastomataceae	227,04	macrophyll	elliptic	acuminate	uniseriate	asymmetrical	22,99	10,45	33,44	106,59	173,47
Miconia cubatanensis	Melastomataceae	13,82	microphyll	elliptic	acute	uniseriate	asymmetrical	12,54	8,36	31,35	52,25	104,5
Miconia hymenonervia	Melastomataceae	19	microphyll	elíptica	acuminate	multiseriate	asymmetrical	14,63	8,36	112,86	445,64	582,76
Miconia sellowiana	Melastomataceae	20,64	notophyll	elíptica	acute	uniseriate	asymmetrical	12,54	8,36	29,26	100,32	146,3
Mollinedia uleana	Monimiaceae	38,36	notophyll	elliptic	acuminate	uniseriate	asymmetrical	73,15	20,9	58,52	146,3	299,95
Mouriri chamissoniana	Melastomataceae	40,29	notophyll	elliptic	acuminate	uniseriate	asymmetrical	33,44	12,54	83,6	171,4	282,81
Myrceugenia campestris	Myrtaceae	4,01	microphyll	obovate	acute	uniseriate	asymmetrical	25,08	10,45	104,5	202,73	342,8
Myrceugenia reitzii	Myrtaceae	56,1	mesophyll	elliptic	acute	uniseriate	asymmetrical	14,63	8,36	112,86	445,64	582,76
Myrcia acuminatissima	Myrtaceae	14,97	microphyll	elliptic	acuminate	uniseriate	symmetrical	12,54	6,27	35,53	85,69	140,03
Myrcia fallax	Myrtaceae	14,14	microphyll	elliptic	acuminate	uniseriate	symmetrical	18,81	12,54	66,88	104,5	219,45
Nectandra grandiflora	Lauraceae	20,85	notophyll	obovate	acuminate	uniseriate	asymmetrical	27,17	14,63	100,32	135,85	277,97
Nectandra megapotamica	Lauraceae	18,66	microphyll	elliptic	acuminate	uniseriate	asymmetrical	25,08	10,45	89,87	108,68	231,39
Nectandra oppositifolia	Lauraceae	72,75	mesophyll	elliptic	acute	uniseriate	asymmetrical	13,6	23,2	103,4	64,7	210,2
Ocotea aciphylla	Lauraceae	28,69	notophyll	elliptic	acute	uniseriate	asymmetrical	25,08	14,63	62,7	110,77	213,18
Ocotea dispersa	Lauraceae	29,51	notophyll	elliptic	acuminate	uniseriate	asymmetrical	20,9	16,72	5,225	125,4	231,39

Cont. Table 2

Cont. Table 2

Ocotea elegans	Lauraceae	13,25	microphyll	elliptic	acuminate	uniseriate	asymmetrical	16,72	12,54	35,53	140,03	325,66
Ocotea glaziovii	Lauraceae	18,76	microphyll	elliptic	acuminate	uniseriate	asymmetrical	25,08	12,54	83,6	114,95	231,39
Ocotea odorifera	Lauraceae	38,08	notophyll	elliptic	acuminate	uniseriate	asymmetrical	14,63	8,36	83,6	121,22	274,24
Ocotea pulchella	Lauraceae	7,98	microphyll	elliptic	acuminate	multiseriate	asymmetrical	50,16	14,63	68,97	140,03	282,81
Ocotea pulchra	Lauraceae	18,99	microphyll	elliptic	acuminate	uniseriate	asymmetrical	22,99	14,63	75,24	114,95	222,82
Oreopanax capitatum	Araliaceae	51	mesophyll	obovate	acuminate	multiseriate	homogeneous	41,8	14,63	0	0	222,82
Ormosia arborea	Fabaceae	130,3	mesophyll	elliptic	acuminate	uniseriate	asymmetrical	25,08	16,72	45,98	79,42	167,2
Ouratea parviflora	Ochnaceae	14,96	microphyll	elliptic	acute	uniseriate	asymmetrical	18,81	16,72	31,35	73,15	142,12
Pera glabrata	Euphorbiaceae	21	notophyll	elliptic	acute	uniseriate	asymmetrical	27,17	20,9	112,86	167,2	334,23
Pithecellobium langsdorffii	Mimosaceae	7,1	microphyll	elliptic	acute	uniseriate	asymmetrical	16,72	16,72	73,15	71,06	177,65
Pouteria beaurepairei	Sapotaceae	31,11	notophyll	obovate	acute	uniestrat	asymmetrical	25,08	20,9	29,26	112,86	188,1
Pouteria venosa	Sapotaceae	58,91	mesophyll	obovate	acuminate	uniseriate	asymmetrical	14,63	10,45	20,9	87,78	129,58
Protium kleini	Burseraceae	19,98	notophyll	elliptic	acuminate	uniseriate	asymmetrical	15,2	25,6	67,9	116,4	262,8
Prunus sellowii	Rosaceae	15,19	microphyll	elliptic	acute	uniseriate	asymmetrical	25,08	20,9	129,58	135,85	317,09
Psidium catlteyanum	Myrtaceae	23,14	notophyll	obovate	acute	multiseriate	asymmetrical	75,24	16,72	160,93	229,9	488,49
Rapanea ferruginea	Myrsinaceae	9,23	microphyll	elliptic	acute	uniseriate	asymmetrical	20,9	14,63	87,78	117,04	231,39
Rapanea venosa	Myrsinaceae	29,86	notophyll	obovate	obtuse	uniseriate	asymmetrical	41,8	35,53	68,56	222,82	359,94
Rudgea villiiflora	Rubiaceae	33,63	notophyll	elliptic	acuminate	uniseriate	asymmetrical	45,98	33,44	60,61	359,94	497,06
Sloanea guianensis	Elaeocarpaceae	57,5	mesophyll	elliptic	acuminate	uniseriate	asymmetrical	8,36	8,36	25,08	91,96	133,76
Solanum inaequale	Solanaceae	21,85	notophyll	elliptic	acute	úniestrat.	asymmetrical	14,63	14,63	20,9	48,07	98,23
Styrax glabratus	Styracaceae	33,7	notophyll	elliptic	acuminate	uniseriate	asymmetrical	20,9	10,45	35,53	68,97	131,67
Tapirira guianensis	Anacardiaceae	16,87	microphyll	elliptic	acuminate	uniseriate	asymmetrical	27,17	18,81	167,2	114,95	299,95
Ternstroemia brasiliensis	Theaceae	22,6	notophyll	obovate	acute	uniseriate	asymmetrical	23,2	40,8	184,3	333	598,2
Tetrastylidium grandifolium	Olacaceae	64,8	mesophyll	elliptic	acute	uniseriate	asymmetrical	20,9	12,54	37,62	177,65	248,53
Virola oleifera	Myristicaceae	22,3	notophyll	oblong	acute	uniseriate	asymmetrical	27,4	19,2	87,3	100,2	249,1
Weinmannia paulliniifolia	Cunoniaceae	2,8	microphyll	obovate	acute	uniseriate	asymmetrical	29,26	14,63	158,84	121,22	325,66
Xylopia brasiliensis	Annonaceae	6,12	microphyll	elliptic	acute	uniseriate	asymmetrical	18,81	14,63	91,96	64,79	190,19

Most species studied (84.9%) had a single-layered adaxial surface of the epidermis and in all of them, the abaxial surface was formed by a single layer (Table 1, Figs 4c, 4d, 4e, 4f). All species possessed hypostomatic leaves (Figs. 3a, 3b), which could be related to the relative humidity (higher at the abaxial surface than at the adaxial surface) and to temperature (higher at the adaxial surface than abaxial surface) of leaves at the canopy of the forest (Lleras, 1977). Also, the presence of stomata in the abaxial surface could represent a way to prevent the obliteration of the pores of stomata by epyphyllous organisms (Coutinho, 1962).

Although the cuticle of the adaxial surface was not separately measured, most of the investigated species (75.3 %) had a thick cuticle and several species had an epicuticular wax layer (Figs. 3a, 3b). Thick cuticle, associated with their chemical composition, helps to repel water, reducing leaching and transpiration (Martin and Juniper, 1970).

Most of the species studied in the Volta Velha Reserve (91%) had mesomorphic leaves, with a single-layered epidermis, well-developed spongy parenchyma, palisade parenchyma composed of 1 to 2 layers, and reduced supporting tissue (Fig. 4c, 4d, 4e, 4f). Only few trees of this area (9%) presented xeromorphic characteristics such as the presence of sclereids, sub-epidermal layers (Fig. 4a, 4b), bundle-sheath extension (Fig. 4b), and 2 or 3 layers of palisade parenchyma (Fig. 4a; 4b). These features increased the total thickness and also influenced the coriaceous texture of these xeromorphic leaves (Table 4).

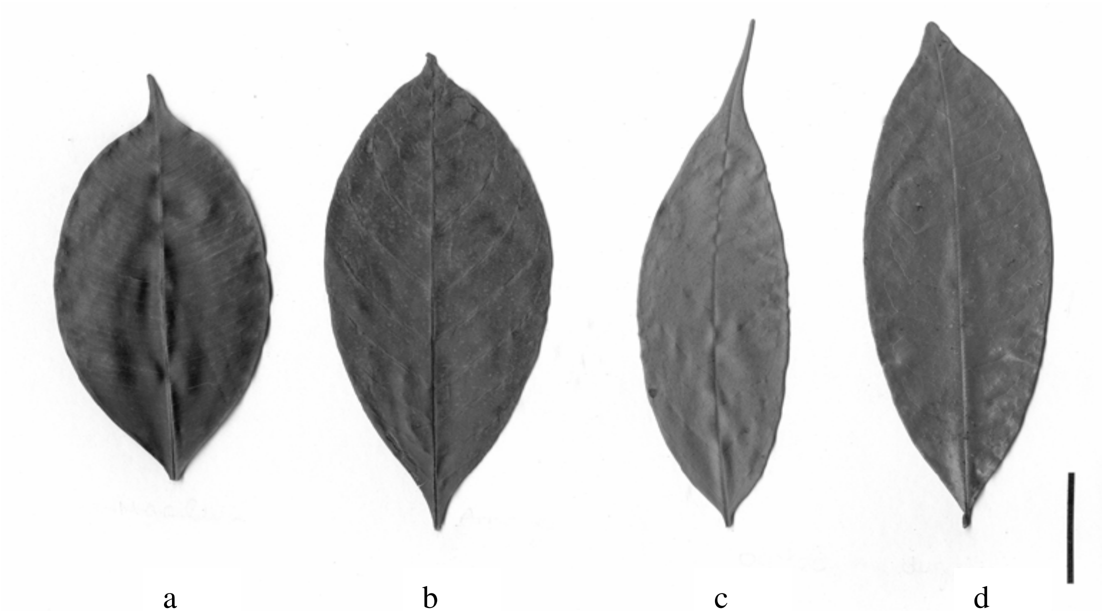

Figure 02 - Leaf shapes of tree species from the study area, in the Volta Velha Reserve: a) *Marlierea eugeniopsoides;* b) *Amaioua guianensis*; c) *Ocotea aciphylla*; d) *Duguetia lanceolata.* Scale = 3 cm.

Table 3 - Leaf morphological features (average values) of trees from Volta Velha Reserve (SC - Brazil) and a comparison with other tropical forests.

A	B	C	D	E	F	G	H	I	J	L	M	N	O	P
This study	Brazil	Lowland Forest	89	58.1	269.7	78.3	145.1	0.5	10.8	26.4	16.2	44.2	40.7	100
Turner et al. (1995)	Malaysia	Heath Forest	24	14.2	273	96.6	112.6	0.7	28.5	-	-	-	-	100
Medina et al. (1990)	Brazil	Sclerophyllous Forest	15	-	476.4	121.5	-	-	-	9.9	5.6	-	-	-
Bongers and Popma (1990)	México	Lowland Forest	68	79.5	207.6	71.4	91.6	1.4	23	14.4	30.2	12	5	-
Tanner and Kapos (1982)	Jamaica	Upper Montane	50	-	237	69.7	128.1	0.54	28	-	-	76	-	-
Sobrado and Medina (1980)	Brazil	Bana	8	-	457.4	-	-	-	62.5	17.8	10.5	-	50	100
Pyykko (1979)	Venez.	Montane Forest	15	86.6	80-360	-	-	-	14.3	-	-	85.7	57.1	100
Grubb et al. (1975)	Japan	Temperate Rain Forest	60	-	150-250	-	-	-	7	2-6	1-4	27	13	98

A: Author; B: Country; C: Forest type; D: Number of species; E: percentage of notophyllous and mesophyllous species; F: Leaf thickness (µm); G: Palisade parenchyma thickness (µm); H: Spongy parenchyma thickness (µm); I: Ratio of spongy/palisade parenchyma; J: Percentage of species with a hypodermis present; L: Adaxial surface thickness (µm); M: Abaxial surface thickness (µm); N: Percentage of species with crystals; O: Percentage of species with trichomes; P: Percentage of species with stomata only in the lower epidermis.

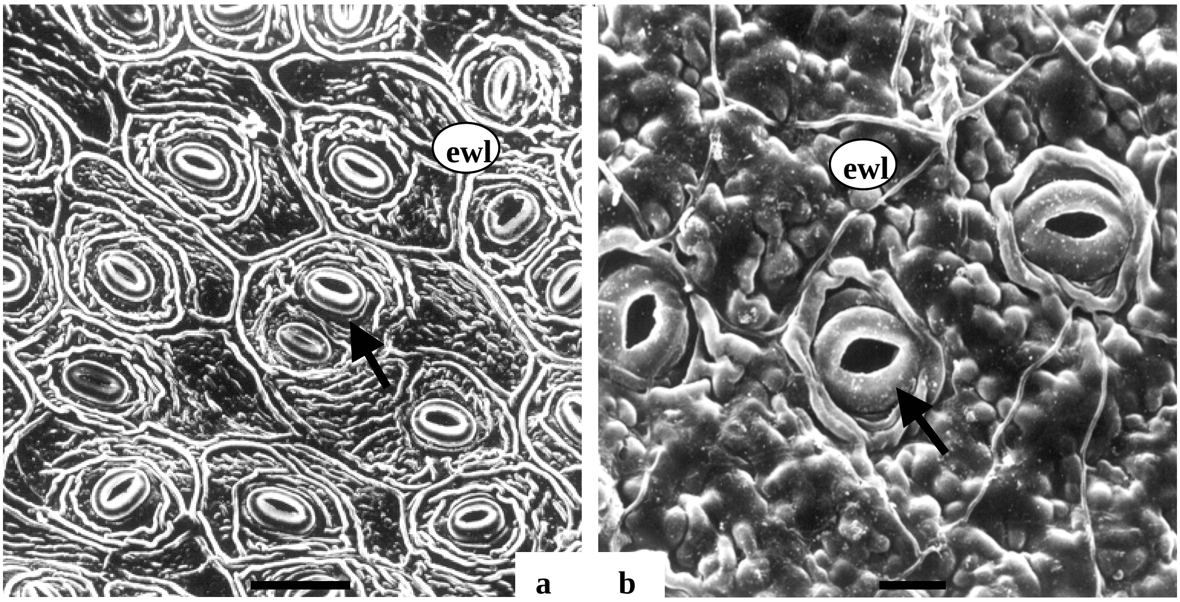

Figure 03 - Stomata (arrow) and epicuticular wax layer (ewl) of the lower epidermis of *Rapanea venosa* (a) and *Clusia criuva* (b). Scale = 50 µm (a); 10 µm (b).

According to Boeger et al. (1997), all species with xeromorphic characteristics are heliophytes occuring at early stages of succession, and have wide geographic distributions (Reitz et al., 1987).

This suggested that the xeromorphic features observed were strategies for survival under adverse environmental conditions, as observed at the early stages of the successional process in sand oligotrophic soils (Boeger et al., 2003).

The morphological parameters of leaves from the most studied species were similar to those of species from other lowland rain forests (Grubb et al., 1975; Pyykko, 1979; Roth, 1984; Bongers and Popma, 1990). This similarity might have resulted from comparable species composition and/or from convergent development as a response to similar environmental conditions (Pyykko, 1979). Most of the studied species (91%) did not have morpho-anatomical characters (thick leaves, small leaf area, hypodermis, several layers of palisade parenchyma and well developed sclerenchyma) as it would be expected for plants growing on sandy soils of low fertility (see Turner, 1994). The mesomorphic features observed here for most of tree species seem to be related to an efficient nutrient cycling. The litter production in the area was 6.9 ton.ha^{-1}.year^{-1} (Boeger et al., 2000) with a slow decomposition rate (data not published). These processes associated with large root biomass and root concentration near surface, in direct contact with the litter (Jordan, 1985) suggested an efficient translocation of foliar nutrients (Vitousek, 1982). These mechanisms expressed by the leaf morphology appear to compensate the low nutrient content of the mineral soil.

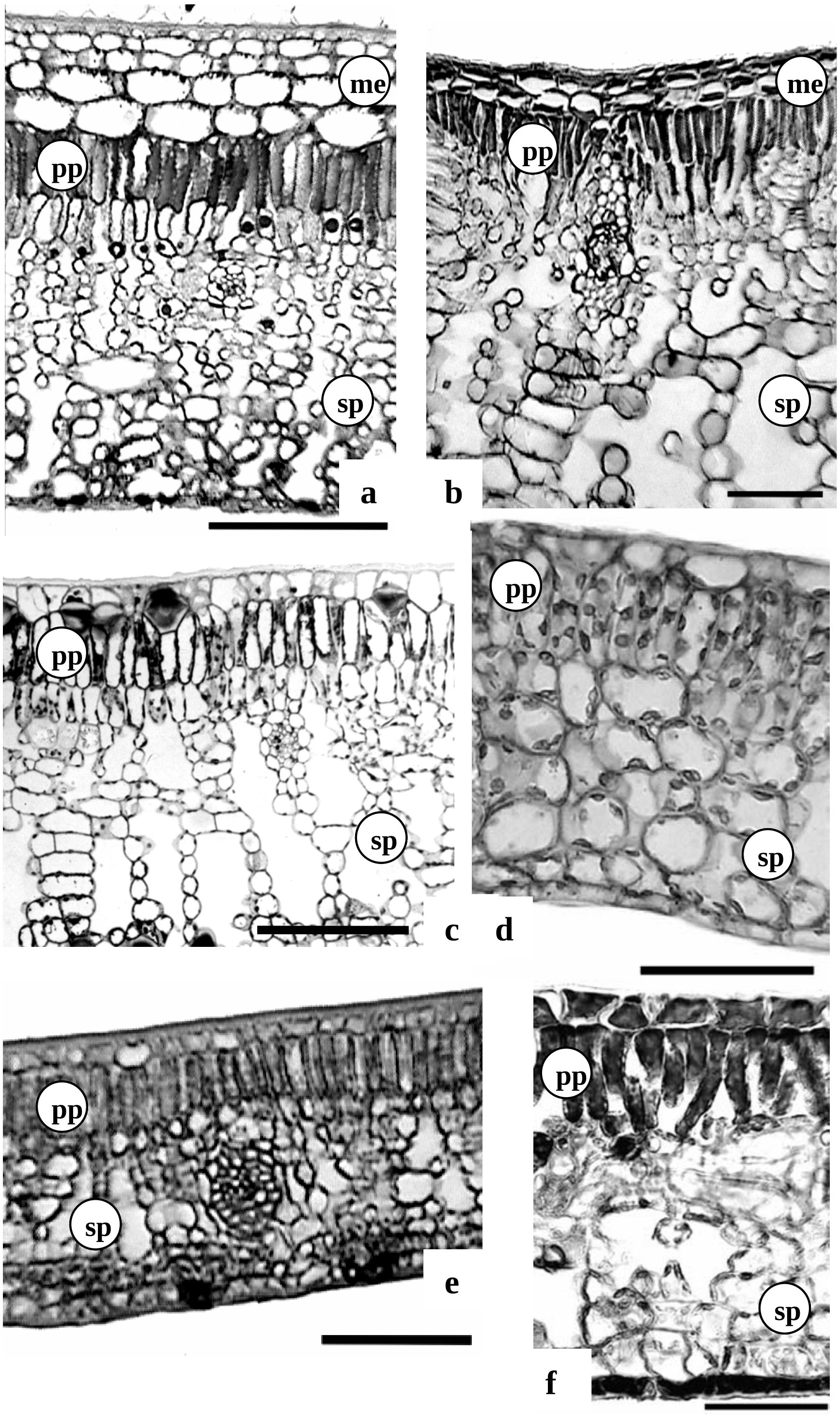

Figure 04 - Transverse sections from the leaf of *Clusia criuva* (a), *Gomidesia schaueriana* (b), *Ilex theezans* (c), *Myrcia acuminatissima* (d), *Pouteria beaurepairei* (e), and *Tapirira guianensis* showing the mesophyll.
(me = multiseriate epidermis; pp = palisade parenchyma; sp = spongy parenchyma).
Scale = 200 µm (a); 100 µm (b, c, e); 50 µm (d, f).

Table 4 - Mean values of leaf histological parameters (µm) for species with xeromorphic (n=8) and mesomorphic characteristics (n=81) and respective standard deviations. * Adaxial surface of the epidermis includes sub-epidermical layer.

	Xeromorphic plants	Mesomorphic plants
Adaxial surface of the epidermis*	57.7 (±36.2)	21.6 (±10.8)
Abaxial surface of the epidermis	23.2 (±9.3)	14.4 (±7.3)
Palisade parenchyma	166.4 (±72.1)	66.4 (±48.5)
Spongy parenchyma	287.8 (±36.7)	121.8 (±86.4)
Total thickness	533.7 (±74.1)	229.0 (±23.9)

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RESUMO

Este estudo examinou a morfologia e anatomia foliar de 89 espécies arbóreas de uma área de Floresta Atlântica Litorânea no Sul do Brasil. A maioria das espécies (>75%) possuem folhas pequenas (notófilas e micrófilas) elípticas e simples com margens inteiras. Essas folhas apresentam uma estrutura anatômica formada por epiderme uniseriada, parênquima paliçádico composto por um único estrato de células e o parênquima esponjoso composto por 5 to 8 estratos celulares. O tecido esclerenquimático é limitado aos feixes vasculares. A maioria das espécies arbóreas (91%) possui folhas com características mesomórficas Poucas espécies (9%) são xerófilas como era esperado em florestas que crescem sob solo arenoso oligotrófico. As características mesomórficas parecem estar associadas a eficientes mecanismos de ciclagem de nutrientes que compensam o baixo conteúdo de nutrientes do solo mineral.

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