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Successional and mature stands in an upper Andean rain forest transect of Venezuela: do leaf characteristics of woody species differ?

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Abstract: Changes in morphological and anatomical leaf characteristics of woody plant species along an altitudinal gradient as well as between a late-successional and mature upper montane rain forest were examined. For leaf size, the Raunkiaer–Webb classification system was applied. The mature-forest transect comprised eight plots of 0.1 ha between 2300 and 3300 m asl, the successional-forest transect, four plots between 2400 and 2750 m asl. The latter comprised structurally heterogeneous vegetation patches. For each plot the proportions of leaf size classes and of the different categories of leaf shape, margin, and apex were calculated. Leaf size and the proportion of drip-tips decreased with increasing elevation. Serrate leaf margins were more prominent at higher elevations. Stomatal density, leaf thickness and related anatomical characteristics did not show significant trends. Differences between the mature and successional forest plots were generally slight. The advanced age of the successional forest probably led to a convergent development of leaf characteristics.

Resumen: Se examinaron los cambios morfológicos y anatómicos foliares de diferentes especies de plantas leñosas tanto a lo largo de una gradiente altitudinal así como también comparando un bosque húmedo altimontano sucesional tardío con un bosque maduro. Para la clasificación del tamaño foliar se aplicó el sistema de Raunkiaer–Webb. El bosque maduro comprendió ocho parcelas de 0,1 ha distribuidas entre los 2300 y 3300 m snm, mientras que el bosque sucesional incluyó cuatro parcelas entre los 2400 y 2750 m snm. El último se compuso de manchas de vegetación estructuralmente heterogéneas. Para cada parcela se calcularon las proporciones de las clases de tamaño foliar y de las diferentes categorías de forma, margen y ápice foliar. El tamaño foliar y la proporción de hojas con ápice gotero decaen con el incremento altitudinal. En altitudes superiores se presenta una mayor abundancia de hojas con margen aserrado. En cuanto se refiere a la densidad de estomas, el grosor foliar y características anatómicas relacionadas, no existen tendencias significativas. Debido a la falta de diferencias obvias entre el bosque maduro y bosque sucesional, se puede suponer que la edad avanzada del bosque sucesional probablemente condujo a un desarrollo convergente de las características foliares.

Key Words: Andes, disturbance, drip-tip, leaf anatomy, leaf morphology, leaf size classification, succession, upper montane rain forest, vegetation zonation

INTRODUCTION

Leaf characteristics of woody plants are a useful tool for describing and defining vegetation types in tropical forests, but a lot of basic work is still required (Rundel & Gibson 1996). Leaf morphology and anatomy are known to correlate with climate (Dolph & Dilcher 1980, Dudley 1978, Geeske *et al.* 1994, Givnish 1987, Gutschik 1999, Press 1999, Richter 1991, Smith *et al.* 1998) and disturbance (Cuatrecasas 1934, Leal & Kappelle 1994, Ohsawa 1993, Roth 1984).

Some of the most intriguing trends for altitudinal and successional gradients may be outlined here. Leaf size increases with increasing precipitation, humidity and soil fertility, but tends to decrease with increasing irradiance and elevation. Mid-elevational forests are dominated by meso- and notophylls, while in treeline forests the proportion of microphylls increases (Grubb & Stevens 1985, Howard 1969, Ohsawa 1995, Roth 1990, Roth & Mérida de Bifano 1971, Sugden 1985, Tanner & Kapos 1982, Young 1998). Leaf thickness often behaves conversely: the higher the elevation, the thicker the leaves (Grubb 1974, Roth 1990, Sugden 1985). Compound leaves are most frequent in arid to semi-arid regions, in lowland rain

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forests and in gap-phase forest successions (Aiba & Kitayama 1999, Givnish 1978*a*, 1979, 1984; Greller & Balasubramaniam 1988, Rollet 1990, Stowe & Brown 1981). Certain leaf margin types seem to correlate with the environment too (Bailey & Sinnott 1916, Brown 1919, Dudley 1978, Givnish 1978*b*, Wilf 1997).

Since most studies are principally dedicated to primary forests, knowledge of leaf characteristics along successional gradients in tropical forest ecosystems is scarce. Therefore – apart from the altitudinal changes – the principal aim of this study was to analyse in what ways morphological and anatomical leaf diversity changes in a heterogeneous successional montane rain forest in comparison with a mature forest.

STUDY SITE

The study site is located between 2300 and 3300 m asl, in the Valley of San Javier, 10 km NE of Mérida city (8°43′N, 71°05′W), Venezuela. The mean annual precipitation varies widely with elevation, decreasing from 1965 mm at about 2300 m asl to 1200 mm at 2920 m asl. The mean temperature is 14.9 °C at 2300 m (CIDIAT, unpublished data). Between 1950 and 1955 a fire destroyed a vast area of the forest between 2600 and 2900(–3000) m. Since then, vegetation was left untouched for regeneration, giving rise to a mosaic of patches of low forest, scrub and impenetrable bamboo thickets. Three vegetation units were distinguished within the successional forest according to structure and composition: (1) a forest persistently disturbed by various disturbance agents (cattle grazing, logging, fire?) along roadsides with single emergent old-growth trees on the opposite slope (2400 m), (2) a forest-like vegetation with a closed canopy on the less-inclined lower parts of the slope (2600–2650 m) and (3) a low scrub with an open canopy on the upper slope (2700 m). As previously pointed out (Schneider 2001, Schneider *et al*., in press), the study area belongs largely to the *Podocarpus oleifolius* D. Don ex Lamb. forests of the upper montane rain-forest zone.

Tree species composition of parts of the successional forest is similar to that of the mature forest of comparable altitude with abundant species like *Axinaea grandifolia* (Naudin) Triana, *Brunellia integrifolia* Szyszyl. ssp. *integrifolia*, *Hedyosmum crenatum* Occhioni, *Ocotea calophylla* Mez, and *Ruagea glabra* Triana & Planch. In the more open parts of the successional forest, typical canopy species are scarce and the total aspect is dominated by several Ericaceae species including *Gaultheria buxifolia* Willd. var. *buxifolia*, *Distergima alaternoides* (Kunth) Nied., *Bejaria aestuans* L., *Cavendishia bracteata* (Ruiz & Pav. ex J. St.-Hill.) Hoerold (in order of decreasing abundance). Other abundant and conspicuous species are *Clethra fagifolia* var. *bicolor* (Kunth) Sleumer, *Clusia trochiformis* Vesque, and *Freziera serrata* Weitzman. The third type of successional forest showed a slightly different floristic composition with prominent trees of *Inga oerstediana* Benth. and *Ficus* cf. *cervantesiana* Standl. & L. O. Williams.

METHODS

Sampling methods

Permanent rectangular plots of 0.1 ha were established along a mature- and successional-forest transect. The mature-forest transect comprised eight plots at elevations of about 2300, 2550, 2650, 2750, 2950, 3000, 3080 and 3300 m, the successional forest four plots at 2400, 2600, 2650 and 2700 m. The plot at 2400 m was a smaller forest patch of 0.05 ha, but was included due to the distinct floristic composition and vegetation structure. The plots were placed away from the forest margins in order to avoid edge effects. Both forest transects were about 400 m from each other. The plots below 2600 m had to be placed at some distance from the perpendicular line due to topography. All plants with a diameter at breast height (dbh) of ≥ 2.5 cm were tagged and inventoried. For structural characteristics and diversity of the plots see Table 1. Leaf samples were collected from a total of 126 woody plant species of the above mentioned dbh size, except *Cyathea* tree ferns. The samples were obtained by tree climbing and with telescopic pruning shears. For the study of morphological leaf characteristics, 10 sun-exposed mature leaves per species were collected and dried. For anatomical studies, leaves were stored in ethanol (70%). Reference specimens of the investigated species are kept at the herbaria MERC and FR.

Assessment of leaf characteristics

The morphological characteristics recorded were leaf type, shape, margin, apex and the possession of drip-tips. The character states observed in the study area (Table 2) were determined and classified according to the terminology of Hickey (1979). For the analysis of the leaf size, the classification of Raunkiaer (1916), modified by Webb (1959), was applied (Table 3). The leaf area was measured with an area-meter (LI-COR LI-3100). The leaflets of compound leaves were considered equivalent to simple leaves since they are functionally similar units (Bongers & Popma 1990, Parkhurst & Loucks 1972). The anatomical characters investigated were leaf thickness, thickness of palisade and spongy parenchyma, palisade/non-palisade thickness ratio, presence of an adaxial hypodermis and stomatal density. Leaf sections were made at about two-thirds the way from the leaf base. Thickness of tissue layers was measured from the sections near the midrib using a light microscope with an ocular micrometer. Means of each leaf characteristic were calculated

Table 1. Diversity and structural characteristics of the mature and successional forest plots (0.1 ha) for woody plants (dbh ≥ 2.5 cm) including tree ferns. Height of single emergent trees in parentheses; *sample area 0.05 ha.

Altitude (m asl)	Species number	Individual number	Max. tree height (m)	Max. dbh (cm)	Basal area (m^2 ha^{-1})
Mature forest transect					
2300	38	345	38	70.0	55.2
2550	32	546	25	75.1	50.7
2650	19	358	22	82.8	56.9
2750	41	289	25	66.8	39.7
2950	17	199	22	68.4	57.4
3000	19	186	20	62.4	42.8
3080	27	267	20	55.7	53.2
3300	24	417	9 (18)	66.8	38.4
Successional forest transect					
2400*	20	161	11(15)	105.4	42.4
2600	37	396	17	33.4	19.0
2650	44	292	22	50.0	29.6
2700	33	507	30	16.6	14.6

Table 2. Leaf morphology and the definition of character states based on Hickey (1979).

Leaf form	
oblong:	leaf margin running more or less parallel over some part at the midpoint
elliptic:	broadest in about the middle
ovate:	broadest in the basal part
obovate:	broadest in the apical part
linear:	leaf narrow, at least 10 times longer than wide
Leaf margin	
entire:	margin smooth
crenate:	projections with rounded margin
dentate:	dentations perpendicular to the marginal line
serrate:	dentations with an oblique angle
lobed:	incisions at least a quarter of the distance of the margin to midvein
Leaf apex	
acute:	straight to convex margins forming an angle of less than 90°
acuminate:	margins apically conspicuously concave (long or short)
obtuse:	straight to convex margins forming an angle of more than 90°

Table 3. Leaf size classes according to Raunkiaer (1916), modified by Webb (1959).

Leaf size class	Size range (mm^2)
Leptophyll	< 25
Nanophyll	25–225
Microphyll	225–2025
Notophyll	2025–4500
Mesophyll	4500–18 225
Macrophyll	18 225–16 4025
Megaphyll	> 16 4025

for all leaf samples per species. For the assessment of stomatal density, nail-varnish impressions of the abaxial surface from one leaf per species were mounted on slides. Stomata were counted within three fields of 1 mm^2 using a light microscope with a digital camera (Leica DC300) and the image-analysis software Leica IM-1000, version 1.20. In several species, smaller areas were chosen and values had to be extrapolated. For *Cordia cylindrostachya* (Ruiz & Pav.) Roem. & Schult., *Libanothamnus lucidus* (Aristeg.) Cuatrec., *Saurauia excelsa* Willd., *Styrax* sp., *Vallea stipularis* L.f. and bamboo stomata counts were not available since the preparation technique failed due to interfering structures on the leaf surface.

The relative abundance (proportion) of the character states was calculated with reference to the number of species as well as to the number of individuals per category and plot. Box-and-whisker plots were plotted with the statistical package SPSS 10.0 for Windows.

RESULTS

Morphological characteristics

The predominant leaf size classes in both forest types of the study site were micro-, noto- and mesophylls with increasing proportions of smaller leaves towards higher elevations (Table 4). Based on abundance, meso- and notophylls showed even higher proportions in the successional forest. The presence of compound leaves was more obvious at lower altitudes (Table 5). At elevations above 3000 m, there was a single species with pinnate leaves (*Weinmannia fagaroides* Kunth). Its dominance was shown when weighting by abundance. The proportion of leaves with drip-tips decreased with increasing elevation in the mature and the successional forest (Table 5). The proportion of species with acute leaf apices increased with increasing altitude as did those with obtuse apices, while the proportion of acuminate apices dropped (Table 5). The same altitudinal affinity was discerned in the successional forest. The proportion of species with an entire margin decreased with increasing elevation, whereas the proportion of serrate leaves increased (Table 6). For other forms, no trend could be recognized, except that crenate leaves dropped out above 2800 m. The predominant leaf shape category was the elliptic type which showed the highest

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Table 4. Proportion (%) of leaf size classes along the mature- and successional-forest transect based on species (spp.) and individual numbers (ind.).

Altitude	Leptophyll		Nanophyll		Microphyll		Notophyll		Mesophyll		Macrophyll	
(m asl)	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.
Mature-forest transect												
2300	0	0	0	0	21.6	22.8	24.3	9.4	46.0	55.0	8.1	12.8
2550	0	0	0	0	28.1	21.2	37.5	61.6	28.1	15.8	6.3	1.5
2650	0	0	0	0	27.8	38.8	38.9	20.7	33.3	40.5	0	0
2750	0	0	2.5	0.4	32.5	33.8	27.5	22.1	30.0	38.8	7.5	5.0
2950	0	0	6.3	3.8	37.5	45.2	31.3	46.2	12.5	2.7	12.5	2.2
3000	0	0	16.7	15.5	50.0	56.0	33.3	28.5	0	0	0	0
3080	0	0	18.5	25.2	37.0	50.0	33.3	23.0	3.7	0.7	7.4	1.1
3300	4.2	0.9	20.8	19.9	58.3	42.6	8.3	0.5	0	0	8.3	36.1
Successional-forest transect												
2400	0	0	0	0	25.0	15.2	35.0	23.2	35.0	54.3	5.0	7.3
2600	0	0	0	0	36.1	19.7	33.3	57.2	25.0	22.0	5.5	1.1
2650	0	0	2.3	0.7	29.5	19.6	34.1	37.8	29.5	40.4	4.5	1.5
2700	0	0	6.1	0.6	45.5	47.6	27.3	47.0	18.2	4.1	3.0	0.8

Table 5. Proportion (%) of leaf apex categories and compound leaves along the mature- and successional-forest transect based on species (spp.) and individual (ind.) numbers per category.

Altitude	Obtuse		Acute		Acuminate		Drip-tip		Compound	
(m asl)	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.
Mature-forest transect										
2300	8.1	3.4	27.0	12.5	64.9	84.1	24.3	22.8	13.5	10.8
2550	9.4	4.1	25.0	9.3	65.6	86.6	28.1	71.8	12.5	2.6
2650	5.6	2.6	33.3	17.2	61.1	80.2	27.8	45.7	22.2	12.3
2750	7.5	9.2	32.5	24.2	60.0	66.7	17.5	22.9	15.0	10.9
2950	18.8	23.7	50.0	54.3	31.3	22.0	18.8	21.0	12.5	6.5
3000	22.2	28.0	66.7	66.8	11.1	5.2	11.1	5.2	5.6	11.3
3080	25.9	31.5	55.6	61.5	18.5	7.0	11.1	1.9	3.7	17.4
3300	20.8	12.9	70.8	83.1	8.3	4.0	0	0	4.2	3.7
Successional-forest transect										
2400	5.0	7.3	30.0	21.9	65.0	70.9	35.0	49.7	10.0	14.6
2600	5.6	10.5	27.8	34.7	66.7	54.9	30.6	36.2	11.1	12.3
2650	6.8	2.6	34.1	37.5	59.1	60.0	27.3	29.1	15.9	21.9
2700	15.2	7.2	39.4	75.4	45.5	17.4	18.2	9.7	15.2	1.4

Table 6. Proportion (%) of leaf margin categories along the mature- and successional-forest transect based on species (spp.) and individual (ind.) numbers per category.

Altitude	Entire		Serrate		Crenate		Dentate		Lobed	
(m asl)	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.
Mature-forest transect										
2300	70.3	72.5	18.9	10.6	8.1	4.7	2.7	12.2	0	0
2550	68.8	87.0	15.6	8.7	9.4	1.9	3.1	2.0	3.1	0.4
2650	66.7	79.6	22.2	19.8	5.6	0.3	5.6	0.3	0	0
2750	67.5	82.1	17.5	10.8	7.5	2.9	5.0	3.3	2.5	0.8
2950	68.8	68.3	25.0	31.2	0	0	0	0	6.3	0.5
3000	55.6	71.5	44.4	28.5	0	0	0	0	0	0
3080	48.1	53.7	44.4	45.2	0	0	7.4	1.1	0	0
3300	50.0	71.0	45.8	28.1	0	0	4.2	0.9	0	0
Successional-forest transect										
2400	70.0	78.2	15.0	16.6	5.0	0.7	10.0	4.6	0	0
2600	75.0	57.0	16.7	40.4	2.8	0.3	2.8	2.1	2.8	0.3
2650	63.6	55.6	29.5	37.1	2.3	1.1	2.3	5.1	2.3	1.1
2700	51.5	31.7	36.4	64.4	6.1	2.9	3.0	0.2	3.0	0.8

Table 7. Proportion (%) of leaf shape categories along the mature- and successional-forest transect based on species (spp.) and individual (ind.) numbers per category.

Altitude (m asl)	Eliptic		Ovate		Obovate		Oblong		Linear	
	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.	spp.	ind.
Mature-forest transect										
2300	56.8	73.8	18.9	20.9	10.8	3.4	13.5	1.9	0	0
2550	65.6	79.4	15.6	5.4	9.4	13.0	9.4	2.2	0	0
2650	77.8	52.6	5.6	0.3	11.1	37.6	5.6	9.5	0	0
2750	70.0	76.7	7.5	4.2	10.0	11.3	12.5	7.9	0	0
2950	56.3	56.5	12.5	2.2	18.8	21.5	12.5	19.9	0	0
3000	72.2	48.7	11.1	2.1	5.6	11.4	11.1	37.8	0	0
3080	66.7	65.6	18.5	7.8	0	0	14.8	26.7	0	0
3300	83.3	96.5	12.5	2.6	0	0	0	0	4.2	0.9
Successional-forest transect										
2400	65.0	45.7	30.0	47.0	5.0	7.3	0	0	0	0
2600	75.0	74.0	11.1	4.2	8.3	14.2	5.6	7.6	0	0
2650	65.9	74.9	20.5	10.2	9.1	5.8	4.5	9.1	0	0
2700	69.7	53.4	15.2	40.0	6.1	5.2	9.1	1.4	0	0

value in the uppermost plot (Table 7). No consistent altitudinal trends were detected in the mature and successional forest, either for elliptic or for other leaf shapes.

Anatomical characteristics

The results of anatomy did not show any significant trends, either along the altitudinal or across the successional gradient (Figure 1). The means of the thickness of the lamina, adaxial epidermis, palisade and spongy parenchyma were only slightly greater in the upper half of the mature forest transect. The proportion of species with a hypodermis was greater at higher altitudes in the successional forest only (Figure 2).

DISCUSSION

Leaf size patterns

The observed trend of decreasing leaf size with increasing altitude is congruent with previous studies (Aiba & Kitayama 1999, Brown 1919, Cleef *et al*. 1984, Greller & Balasubramaniam 1988, Grubb 1977, Grubb *et al*. 1963, Sugden 1985, Young 1998) and is generally thought to be caused by decreasing (bio-)temperature and precipitation, higher irradiance or strong winds (Buot & Okitsu 1999, Dolph & Dilcher 1980, Givnish 1987, Greller & Balasubramaniam 1988, Sugden 1985, Whitmore 1984). Certainly, the last did not play a role at our site because winds are rarely strong. Among the most important factors in the study site are temperature and precipitation – which decrease continuously towards the upper zones of the area – as well as irradiance which increases conspicuously above the permanent cloud layer at about 3000 m. The successional forest covers a comparatively short elevational range indicating that structural characteristics of the stands may play a more important role than altitudinal differences, particularly among the upper plots. The ecotone between stands with a closed (plots between 2400 and 2650 m) and an open canopy (2700 m) probably has a greater impact on adaptive features of leaves due to stronger diurnal fluctuations and broader amplitudes of temperature, evapotranspiration and relative humidity in the upper plot. This is also reflected by the greater number of species which usually grow above 3000 m, especially in the treeline forest, and which are well-adapted to harsher conditions.

Other morphological characteristics

Species with compound leaves are generally more numerous in lowland sites (Aiba & Kitayama 1999, Givnish 1987, Greller & Balasubramaniam 1988, Rollet 1990). The values for San Javier largely correspond to those generally reported from upper montane rain forests (Kappelle & Leal 1996, Kelly *et al*. 1994, Madsen & Øllgaard 1994, Meave *et al*. 1992, Rollet 1990). There was little variation between mature and successional forests, similar to observations from a Costa Rican upper montane *Quercus*-forest (Kappelle & Leal 1996).

The finding that leaves with drip-tips were frequent within the upper montane forest but absent from the treeline forest coincides with the results from New Guinea (Grubb 1977, Grubb & Stevens 1985). The drier conditions of the treeline forest and the open successional forest seem to give an advantage to plants with smaller leaves without drip-tips, in line with the idea that drip-tips are favoured under humid conditions as they help leaves to dry more rapidly (Rundel & Gibson 1996, Vareschi 1980).

Among leaf margins, the toothed type has several advantages under unfavourable environmental conditions and these may be reasons for their greater representation

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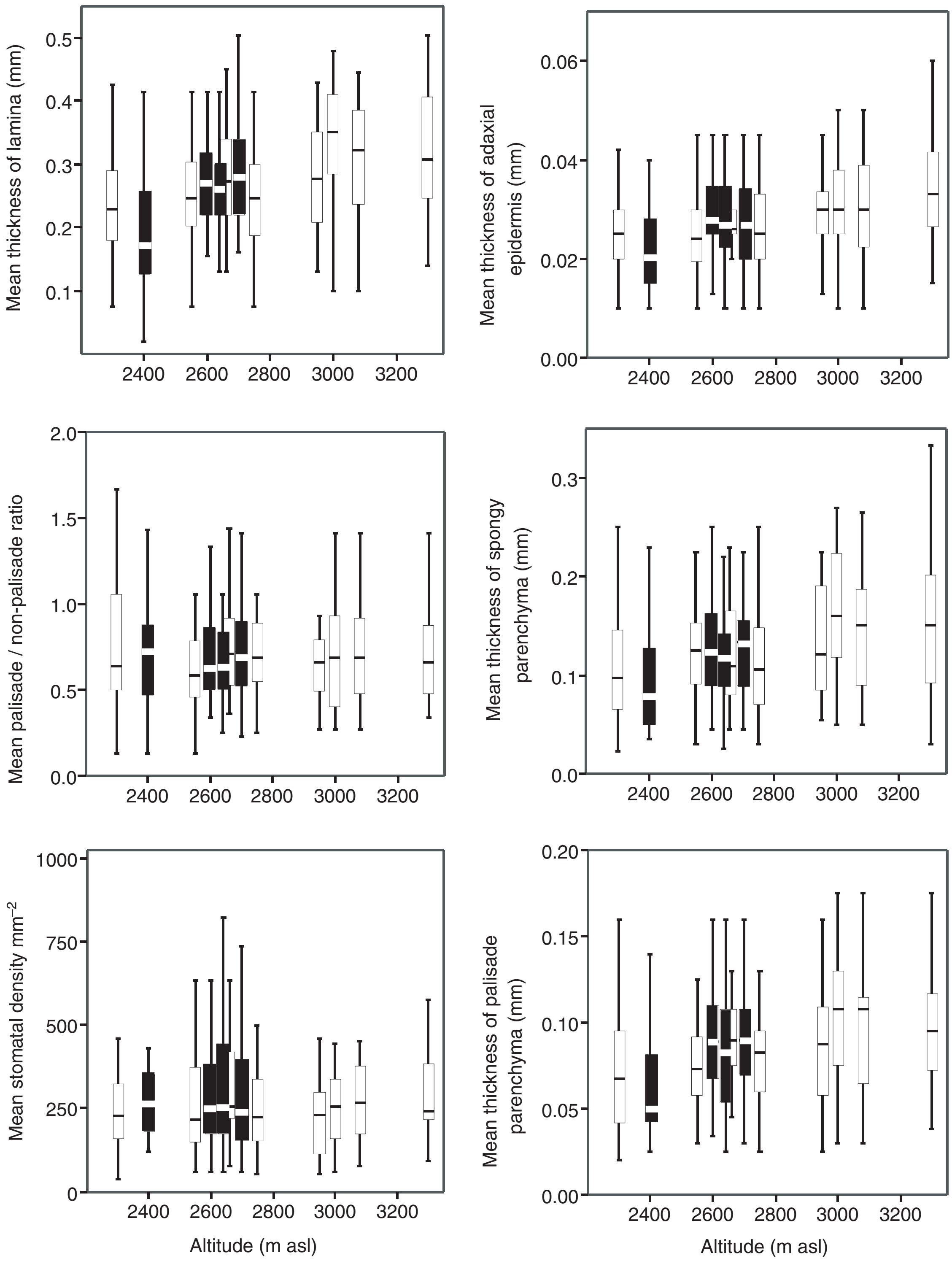

Figure 1. Box-and-whisker plots of means of anatomical leaf characteristics for each plot along the altitudinal transects (white bars = mature forest; black bars = successional forest).

at higher elevation and in the open successional forest (2700 m) of the present study as well as in early successional stages of a Costa Rican upper montane forest (Kappelle & Leal 1996). Teeth are often transpiration hot spots boosting sap flow, especially in colder climates (Canny 1990, Wilf 1997). Moreover, they seem to provide a more cost-effective venation pattern, at least when associated with craspedodromous venation (Roth *et al*. 1995).

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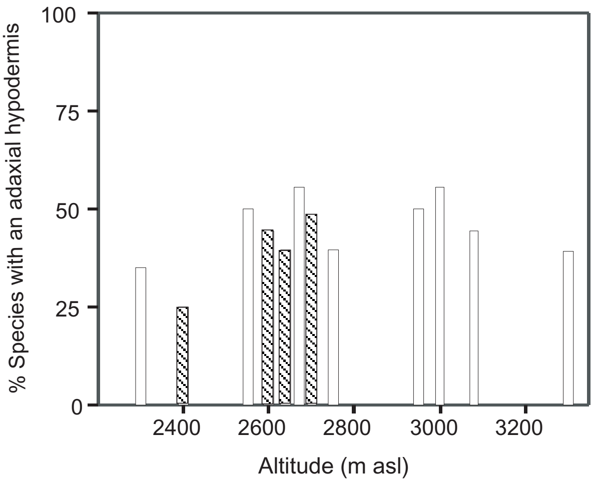

Figure 2. Percentage of species possessing an adaxial hypodermis for plots of the mature (white bars) and successional (hatched bars) forest transect.

Additionally, incised margins may be interpreted as a reduction of leaf surface under unfavourable environmental conditions (Schuepp 1993). A higher proportion of temperate floristic elements at high altitudes as a further explanation was not confirmed by the observed biogeographical affinities of the inventoried genera (unpubl. data). For leaf shape, there is very little information on adaptive relevance and it seems to be controlled primarily by mechanical constraints (Niklas 1999). A comparison with the previously mentioned secondary *Quercus*-forests (Kappelle & Leal 1996) shows the same preponderance of the elliptic shape. Small leaves with elliptic shape, serrate margin, acute apex, without drip-tips were the most frequently observed leaf type of the open vegetation.

Anatomy

In the present study, leaves and their component tissues tended to be only slightly thicker at higher altitude. This trend was expected to be more conspicuous (see Grubb 1974, Sugden 1985). Nevertheless, values were within the range known from other tropical montane rain forests (see Bongers & Popma 1990), though tissue shrinkage due to storage of leaf samples in alcohol may have caused a generally lower thickness. The most reasonable explanation for thicker leaves at higher sites seems to be that they allow the most effective use of photosynthetically active radiation in short spells of good weather (Grubb 1974), thus providing high energy input while water loss is low. An assumed selective advantage of a hypodermis providing a water reservoir for the mesophyll and enabling plants to transpire for longer periods of time at drier sites (Cavelier & Goldstein 1989) was not obvious in the present study since highest proportions were observed in the mature forest at intermediate altitudes, not above the permanent cloud layer.

Mean stomatal densities and the ratio of palisade to non-palisade tissue were almost invariant along the environmental gradients of the study site. Thus, the higher evaporative demands, water stress, and the higher insolation – these factors are generally associated with higher stomatal densities (Napp-Zinn 1984, Roth 1984) – that operate on plants above the permanent cloud layer or in the open successional forest were not reflected in the plot means.

The present study did not provide evidence for significant differences in leaf characteristics between a late-successional and a mature forest. Moreover, the differences within the successional forest transect were slight, in spite of apparent shifts in habitat conditions. The advanced age of the successional forest most likely led to a convergence of these traits. In the future, studies from successional chronosequences are necessary to show the effect of time on patterns of leaf characteristics.

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