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DOI

[10.2307/2389197](https://doi.org/10.2307/2389197)

Publication date

1996

Published in

Biotropica

[Link to publication](#)

Citation for published version (APA):

Kappelle, M., & Leal, M. E. (1996). Changes in leaf characteristics along a successional gradient in upper montane Quercus forest, Costa Rica. *Biotropica*, 28(2), 331-344. <https://doi.org/10.2307/2389197>

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Biotropica, Vol. 28, No. 3. (Sep., 1996), pp. 331-344.

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Changes in Leaf Morphology and Foliar Nutrient Status Along a Successional Gradient in a Costa Rican Upper Montane *Quercus* Forest¹

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ABSTRACT

Morphology and mineral levels of leaves of 19 secondary and 22 primary tree species were studied in *Quercus*-dominated upper montane 10-year-old Early Secondary Forest (ESF), 30-year-old Late Secondary Forest (LSF) and undisturbed Primary Forest (PF) in the Costa Rican Cordillera de Talamanca. In general, the predominant leaf is simple, elliptic, entire, and pinnately veined. Notophyllous and microphyllous-sized leaves dominate all spectra. During secondary succession the mean leaf area of secondary species tends to reduce 30 to 65 percent, while the average leaf area of primary species doubles. Primary species exhibit a greater mean leaf dry weight per unit area than secondary species. As succession proceeds, the mean leaf water content drops among secondary species and rises among primary species. During forest recovery levels of foliar nitrogen, phosphorus, and potassium decline significantly. In leaves of species in ESF nitrogen, phosphorus, and potassium are significantly correlated. Values for leaf characteristics recorded in Costa Rican montane ESF, LSF, and PF fall mainly within the ranges known from other tropical montane forests.

RESUMEN

Se estudiaron la morfología y los niveles de nutrientes de hojas de especies de árboles secundarios (19) y primarios (22) en un robledal secundario temprano (ESF) de 10 años, un robledal secundario tardío de 30 años (LSF), y en un robledal primario no alterado (PF) en la Cordillera de Talamanca, Costa Rica. En general, la hoja que predomina es simple, elíptica, entera y pinatinervada. Hojas notófilas y micrófilas dominan el espectro. Durante la sucesión secundaria el tamaño promedio de las hojas de especies secundarias tiende a reducirse hasta un 30 o 60 por ciento, mientras que el tamaño promedio de las hojas de especies primarias se duplica. Especies primarias exhiben un peso foliar seco por unidad de área más grande que especies secundarias. En cuanto que la sucesión avanza el contenido de agua foliar específico de especies secundarias obviamente baja, mientras que al mismo tiempo este valor sube para las especies primarias. Durante la recuperación del bosque los niveles foliares de nitrógeno, fósforo y potasio bajan significativamente. En hojas de especies en ESF, nitrógeno, fósforo y potasio son correladas significativamente. Los valores de características foliares registrados para ESF, LSF y PF montano en Costa Rica caen principalmente dentro de los alcances conocidos de otros bosques tropicales montanos.

Key words: Costa Rica; foliar nutrient status; leaf morphology; leaf size; montane cloud forest; *Quercus*; recovery; secondary succession.

LEAF CHARACTERISTICS in tropical forests are known to vary along environmental gradients. Changes in leaf morphology and nutrient concentration along latitudinal and altitudinal gradients as well as along moisture and soil gradients have been studied in detail (Webb 1968, Gentry 1969, Leigh 1975, Grubb 1977, Werger & Ellenbroek 1978, Dolph & Dilcher 1980, Givnish 1984, Medina 1984, Sugden 1985, Bongers & Popma 1990, Geeske *et al.* 1994). For instance, it has been well-documented that leaves of tropical rain forests get smaller

with increase of altitude, *i.e.*, decrease of temperature (*e.g.*, Grubb *et al.* 1963, Leigh 1975). Much less is known about changes in leaf traits along successional gradients (Roth 1984, Gómez 1986). Popma *et al.* (1992) showed that obligate gap species in a Mexican tropical lowland forest had larger and less-elongated leaves than both gap-dependent and gap-independent species. According to these authors, the differences in leaf characteristics between species of different groups, classified on the basis of their dependence on gaps for regeneration, are probably related to the way the species exploit their characteristic environments.

The question whether similar trends are to be found in leaves along a successional gradient in the

¹ Received 13 May 1994, revision accepted 31 March 1995.

montane tropics still remains to be answered. More specifically, hardly anything is known about the way in which leaf morphological characteristics and foliar nutrient levels change as secondary succession proceeds and secondary species are being replaced by primary species. Recently, Leal and Kappelle (1994) revealed that in a Costa Rican upper montane secondary forest foliar tissues in secondary tree species are on the average thicker than in primary tree species, due to the high proportion of spongy parenchyma for water storage.

The purpose of the present study is to attempt to contribute our understanding of changes in foliar morphology and nutrient status in tropical montane forests and specifically of oak dominated upper montane forests in the Costa Rican Cordillera de Talamanca.

STUDY SITE

The study was carried out near Jaboncillo de Dota (2950 m asl) in the 62,000 ha Los Santos Forest Reserve, which is located on the Pacific slope of the Costa Rican Cordillera de Talamanca (9°35'40"N, 83°44'30"W). This mountain range is formed of intrusive and Tertiary volcanic rocks, alternated with marine sediments (Weyl 1980). The study area has a Cf climate according to the Köppen Climate System with a dry season lasting from December to April (Kappelle 1993). At the nearby town of Villa Mills (3000 m asl) the average annual temperature is 10.9°C and the average rainfall 2812 mm (IMN 1988, Kappelle 1993). The topography of the area is abrupt (slope angles: 20° to 35°). Soils (Andosols; [Histic] Hapludand) are of volcanic origin, rich in organic matter, well-drained and rather acid with pH ranging from 3.7 to 5.0 (Kappelle *et al.* 1989, J. G. van Uffelen, pers. comm.).

The area has been deforested continuously since the early fifties (Kappelle & Juárez 1994, 1995). The secondary forests have been used for dairy cattle grazing for about five years following clearing and burning of mature upper montane *Chusquea-Quercus* forest of tall stature (Kappelle 1993). A description of the structure, floristic composition and diversity of the successional and mature forests treated in this study is given elsewhere (Kappelle 1993; Kappelle *et al.* 1989, 1994, 1995).

METHODS

Mature leaves of 41 abundant tree species were sampled in three 0.1 ha plots, representing 10-year-

old Early Secondary Forest (ESF), 30-year-old Late Secondary Forest (LSF) and undisturbed (mature) Primary Forest (PF), respectively. Only well-developed leaves without herbivore damage or epiphylls were collected in order to avoid their potential influence on the foliar nutrient status and water content. Special care was taken in the cases of *Myrciantes fragrans* and *Ocotea pittieri*, as these species appear frequently in association with epiphyllic organisms and only young leaves are found free of epiphyllism. The set of sampled tree species (Appendix) accounted for 83.6 percent of the entire tree flora as found in these successional forest phases. The sample consists of a group of secondary (19) and primary (22) tree species classified on the basis of earlier studies (*e.g.*, Kappelle 1993).

Following Bongers & Popma (1990) 20 mature and undamaged leaves were taken from treecrowns at heights between 3 and 6 m in the ESF plot and between 5 and 10 m in the LSF and PF plots. In the case of compound leaves 20 leaflets were collected, since the leaflet is functionally analogous to the simple leaf (Dolph & Dilcher 1980, Bongers & Popma 1990). These leaves or leaflets were used for morphological measurements (10 leaves) and subsequent nutrient level assessments (20 leaves). Tall tree sampling was done using alpine rope climbing techniques (Perry 1978, Ter Steege & Cornelissen 1988).

Leaf form characteristics were assessed for each species following the leaf form classification system proposed by Radford *et al.* (1974) and modified by Heywood (1985). Form characteristics included the division, shape, margin, venation, apex, and base of leaves. Leaf area was measured using a compensation pole planimeter (HOTL, Germany) after drawing the leaf circumference on graphical paper in the field. Nonsaturated fresh weight was measured on a contrabalance (TORBAL, USA). Afterwards leaves were oven-dried (24 hours, 60°C) and weighed again. Thus the following leaf characteristics could be derived: specific leaf weight (leaf dry weight/leaf area [$\text{g} \cdot \text{m}^{-2}$]), and (non-saturated) leaf water content ($[\text{fresh weight} - \text{dry weight}] / \text{leaf area}$ [$\text{g} \cdot \text{m}^{-2}$]). Additionally, the leaf water content/specific leaf weight ratio was calculated as a measure of the amount of water stored by a leaf in association with one g of dry matter (Von Willert *et al.* 1990). Leaf form and leaf size spectra were established for all three successional forest phases. Following the Raunkiaer Leaf Size Class System as modified by Webb (1959) the following leaf size classes were distinguished: nanophyllous (0.25–2.25 cm^2), microphyllous (2.25–20.25 cm^2), notophyl-

FIGURE 1. Leaf form spectra for percentages of species in upper montane Early Secondary Forest (ESF, $N = 27$, open bars), Late Secondary Forest (LSF, $N = 31$, shaded bars) and Primary Forest (PF, $N = 23$, closed bars), Cordillera de Talamanca, Costa Rica. Leaf form characteristics are according to the classification proposed by Radford *et al.* (1974) and modified by Heywood (1985). They include the division, shape, margin, venation, apex, and base of leaves.

lous (20.25–45.0 cm²), mesophyllous (45.0–182.25 cm²), and macrophyllous (182.25–1640.25 cm²).

After grinding the leaf samples, nutrient levels were measured. Samples were digested using concentrated H₂SO₄ and H₂O₂ (30%) following Lindner & Harley (1942). Total nitrogen and phosphorus were determined colorimetrically in a Technicon II autoanalyzer following standard procedures. Total potassium was measured by flame atomic absorption spectrophotometry using a Perkin Elmer 1100 B instrument. For matters of reference, certified standard material (code: IAEA/V-10 Hay Powder) was analyzed, provided by the International Atomic Energy Agency at Vienna.

Student's *t*-statistic tests were used to compare leaf characteristics among successional forest phases (ESF, LSF, and PF) and species groups (secondary vs. primary species). However, in PF there were too few secondary species (*N* = 3) to make any comparison. Associations between pairs of leaf characteristics (interdependence) were established using Pearson product moment correlation coefficients (Sokal & Rohlf 1981, Tanner & Kapos 1982, Bongers & Popma 1990).

RESULTS

LEAF FORM.—Simple leaves were dominating all three successional forest phases (Fig. 1). Only ca 10 percent of the species had compound leaves: the pinnately compound *Weinmannia pinnata* and *Zanthoxylum scheryi* and the palmately compound araliaceous *Schefflera rodriguesiana* and *Oreopanax xalapensis*. The elliptic leaf form was the most common shape found along the successional gradient. Oblanceolate and lanceolate shapes occurred especially among secondary species. Leaflets of some compound species had an oval shape. The primary species *Oreopanax capitatus* and *O. nubigenus* had cordate and orbicular leaf shapes, respectively. Entire leaf margins were most common among primary species in PF, while non-entire leaves, *i.e.*, with crenate/crenulate, dentate/denticulate, serrate/serrulate or lobed margins, prevailed among secondary species in ESF and LSF. Lobed leaves occurred in the pioneering secondary species *Bocconia frutescens* and *Senecio copeyensis*. The majority of the species had pinnately veined leaves, while only *Oreopanax capitatus* and *O. nubigenus* showed palmate leaf venations. No species had parallel-veined leaves. Both primary and secondary species showed great variation in leaf apices and bases in all three forest phases. However, the mucronate, cuspidate, and caudate apex types prevailed—*i.e.*, with some kind

FIGURE 2. Leaf size spectra for percentages of species in upper montane Early Secondary Forest (ESF, *N* = 27), Late Secondary Forest (LSF, *N* = 31) and Primary Forest (PF, *N* = 23), Cordillera de Talamanca, Costa Rica. Leaf size classes are according to the Raunkiaer classification as modified by Webb (1959).

of driptip. Among the leaf base types predominated the attenuate base. Truncate leaf bases were found in ESF among secondary species such as *Saurauia veraguasensis*, *Senecio copeyensis*, and *S. multivenius*. In general, the predominant leaf was simple, elliptic, entire, pinnately veined with a mucronate or cuspidate apex and an attenuate base.

LEAF SIZE.—The average leaf size (mean $\pm$ SD) of species was 76.6 ± 14.4 cm² in ESF (*N* = 27), 34.2 ± 24.4 cm² in LSF (*N* = 31), and 57.8 ± 91.8 cm² in PF (*N* = 23). These data imply an increasing variability in leaf size along the successional gradient. The average leaf size was greatest in ESF's secondary species (*N* = 17) and smallest in ESF's primary species (*N* = 10); see Table 1. Leaf sizes ranged from nanophyllous to macrophyllous (0.94–642.74 cm²; Appendix). The only nanophyllous-sized leaflet was found in the primary species *Weinmannia pinnata*. Macrophyllous-sized leaves were noted in the secondary canopy species *Bocconia frutescens* and *Senecio copeyensis*, as well as in the primary understory species *Oreopanax capitatus* and *O. nubigenus*. In the spectrum for the entire sample of 41 tree species the notophyll class was the largest, followed by the mesophyll and microphyll classes. The notophyll class was most important in ESF and PF, while the microphyll class predominated in the LSF spectrum (Fig. 2). In general, leaves tended to be larger in ESF than in LSF, since secondary species in ESF tended to have larger leaves than secondary species in LSF. However, no statistically significant differences in leaf size were found between successional forest phases.

TABLE 1. Leaf characteristics of secondary and primary tree species in upper montane Early and Late Secondary and Primary Forest, Cordillera de Talamanca, Costa Rica.

	Secondary species			Primary species		
	Mean	SD ^a	C.V. ^b	Mean	SD ^a	C.V. ^b
Early secondary forest		(N = 17)			(N = 10)	
Leaf Area (cm ²)	107.4	175.6	163.5	24.3	22.7	93.4
SLW ^c (g·m ⁻²)	123.0	65.8	53.4	165.2	43.0	26.0
LWC ^d (g·m ⁻²)	231.6	86.6	37.6	156.7	56.7	36.3
N/weight (mg·g ⁻¹)	18.7	10.1	54.0	12.3	1.7	13.8
P/weight (mg·g ⁻¹)	1.3	0.6	44.8	0.8	0.2	20.8
K/weight (mg·g ⁻¹)	14.2	8.1	57.0	10.6	5.0	47.1
LWC/SLW ratio	2.4	1.2	52.1	1.1	0.4	39.5
Late secondary forest		(N = 14)			(N = 17)	
Leaf Area (cm ²)	38.2	25.4	66.5	30.9	23.9	77.3
SLW ^c (g·m ⁻²)	126.6	47.7	41.9	128.6	62.8	48.8
LWC ^d (g·m ⁻²)	182.4	72.5	39.7	187.1	117.8	63.0
N/weight (mg·g ⁻¹)	12.1	3.4	28.1	10.7	2.8	26.2
P/weight (mg·g ⁻¹)	1.1	0.5	44.0	1.0	0.3	27.3
K/weight (mg·g ⁻¹)	11.3	4.9	43.4	9.5	5.6	58.9
LWC/SLW ratio	1.6	0.7	43.3	1.7	1.4	80.8
Primary forest		(N = 3)			(N = 20)	
Leaf Area (cm ²)	77.3	89.7	116.0	54.9	94.0	171.2
SLW ^c (g·m ⁻²)	136.8	15.2	11.1	152.5	61.0	32.5
LWC ^d (g·m ⁻²)	150.3	77.2	51.4	222.1	153.8	69.2
N/weight (mg·g ⁻¹)	11.4	0.9	7.9	10.7	2.5	23.4
P/weight (mg·g ⁻¹)	0.9	0.3	32.4	0.9	0.5	55.6
K/weight (mg·g ⁻¹)	11.5	3.6	31.3	8.8	4.0	44.7
LWC/SLW ratio	1.1	0.4	26.0	1.4	0.7	52.5

^a Standard deviation.^b Coefficient of variation = 100 × (SD/Mean).^c Specific leaf weight (= Leaf dry weight/leaf area).^d Leaf water content.

In the PF phase secondary species had almost totally disappeared, with exception of three, probably gap-dependent species: *Cornus disciflora* and *Myrsine coriacea* in the notophyll size class and *Oreopanax xalapense* in the mesophyll size class (Appendix). Almost half of the primary species in the PF phase had notophyllous-sized leaves. The fact that both *Quercus* species, which were the most abundant and dominant taxa of mature montane forests at the study site (Kappelle *et al.* 1989), had notophyllous-sized leaves in PF supported this view. Other examples of abundant primary species presenting leaves in the notophyll size class were *Nectandra cufodontisii*, *Ocotea pittieri*, *Prunus annularis*, *Rhamnus oreodendron*, and *Styrax argenteus*.

LEAF WEIGHT AND WATER CONTENT.—The specific leaf weight of secondary and primary species did not show any particular pattern along the successional gradient, although primary species exhibited a greater mean leaf dry weight per unit area than

secondary species. In ESF the leaf water content was significantly higher ($P = 0.021$) in secondary species ($N = 17$) than in primary species ($N = 10$). Generally, the leaf water content of secondary species dropped as succession proceeds, while at the same time the leaf water content of primary species rose. Thus, the measure for the amount of dry leaf material needed for the storage of 1 g of water (the leaf water content/specific leaf weight ratio) declined quickly for secondary species: from 2.4 in ESF to 1.6 in LSF (Table 1). At the same time the ratio for primary species increased slightly from 1.1 in ESF to 1.7 and 1.4 in later successional phases. However, these results must be interpreted with care as the leaf water content is derived from unsaturated fresh leaves and the degree of unsaturation may differ in different species.

LEAF NUTRIENT STATUS.—In general, foliar nutrient concentrations (per unit weight) were significantly higher ($P = 0.001$ for nitrogen; $P = 0.008$ for

phosphorus; $P = 0.011$ for potassium) for the whole sample of individuals belonging to secondary species ($N = 34$) than for the whole sample of individuals belonging to primary species ($N = 47$). During succession nitrogen per unit weight declined strongly from 18.7 to 11.4 $\text{mg} \cdot \text{g}^{-1}$ among secondary species and from 12.3 to 10.7 $\text{mg} \cdot \text{g}^{-1}$ among primary species (Table 1). The foliar nitrogen concentration was significantly higher ($P = 0.004$) in ESF ($N = 27$) than in LSF ($N = 31$) or PF ($N = 23$). Considering only secondary species, the nitrogen concentration was significantly higher ($P = 0.027$) in ESF ($N = 17$) than in LSF ($N = 14$). Leaf phosphorus was highest in secondary species in ESF ($N = 17$) and differed significantly ($P = 0.023$) from the phosphorus concentration in leaves of ESF's primary species ($N = 10$). Foliar potassium per unit weight was higher in secondary species than in primary species and continuously decreased with time of recovery: from 14.2 to 11.5 $\text{mg} \cdot \text{g}^{-1}$ in secondary species and from 10.6 to 8.5 $\text{mg} \cdot \text{g}^{-1}$ in primary species. The foliar concentration of potassium was significantly higher ($P = 0.033$) in ESF ($N = 27$) than in PF ($N = 23$).

On the species level, relatively high nutrient concentrations were found in ESF in *Hedyosmum mexicanum* as well as in *Symplocos serrulata*. In this forest phase *Ilex pallida* also had a high foliar concentration of potassium. In LSF the species *Abatia parviflora* and *Quercus costaricensis* displayed nutrient-rich leaves. Considering nitrogen *A. parviflora* showed the highest value among secondary species and *Q. costaricensis* among primary species. Potassium values were highest in *Comarostaphylis arbutoides* and *Schefflera rodriguesiana*. In undisturbed PF nitrogen levels remained below 15 $\text{mg} \cdot \text{g}^{-1}$. Here, the phosphorus concentration of leaves was highest in *Oreopanax capitatus*. In the mature forest potassium concentrations ranged from low levels in *Miconia tonduzii* to relatively high levels in *Oreopanax nubigenus*.

ASSOCIATIONS BETWEEN PAIRS OF LEAF CHARACTERISTICS.—Most significant Pearson product moment correlations ($P < 0.05$) were found in ESF among secondary species (Table 2). In ESF nitrogen, phosphorus and potassium were strongly correlated positively. Specific leaf weight and leaf water content were in no case correlated. In LSF significant negative correlations were found between leaf area and specific leaf weight in both secondary ($N = 14$) and primary ($N = 17$) species, while only in primary species leaf area was also negatively correlated with leaf water content. Leaf area was positively corre-

TABLE 2. Correlations^a between leaf characteristics for secondary and primary tree species in upper montane Early Secondary, Late Secondary and Primary Forest, Cordillera de Talamanca, Costa Rica. Abbreviations as in Table 1.

Characteristic	Early Secondary Forest						Late Secondary Forest						Primary Forest					
	2	3	4	5	6		2	3	4	5	6		2	3	4	5	6	
Secondary species																		
1 Leaf Area	—	—	.45	—	—	(N = 17)	—	—	—	—	—	(N = 14)	—	—	—	—	—	(N = 3)
2 SLW	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
3 LWC	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
4 N/weight	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
5 P/weight	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
6 K/weight	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
Primary species																		
1 Leaf Area	—	—	—	—	—	(N = 10)	—	—	—	—	—	(N = 17)	—	—	—	—	—	(N = 20)
2 SLW	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
3 LWC	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
4 N/weight	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
5 P/weight	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	
6 K/weight	—	—	—	—	—		—	—	—	—	—		—	—	—	—	—	

^a Pearson product moment correlation coefficients; "—" not significant and "values" significant, while $P < 0.05$.

lated with specific leaf weight in primary species found in PF ($N = 20$).

DISCUSSION

TRENDS ALONG THE SUCCESSIONAL GRADIENT.—The present study focused at leaf variation in secondary and primary species recorded along a man-induced successional sere in a tropical montane oak forest ecosystem. It showed the large variation in leaf traits such as foliar forms, sizes and nutrient status, well-spread over different successional forest phases. Leaf shapes, margins, apices, and bases varied greatly among species present in one particular successional stage. Such considerable variation in leaf types seems to be the result of a long evolutionary history (*cf.* Gentry 1969, Parkhurst & Loucks 1972, and more recently Givnish 1987, Bongers & Popma 1990).

According to their habitat conditions taxa were conveniently classified as either secondary (pioneer) or primary (climax) species in order to search for differences in leaf traits between these ecological species groups. Earlier, this was done successfully in a Mexican lowland rain forest (Gómez-Pompa & Vázquez-Yanes 1985), where shade-intolerant, obligate gap genera such as *Cecropia*, *Heliocarpus*, *Myriocarpus*, *Piper*, and *Urera* had much larger leaves than both gap-dependent and gap-independent species (Popma *et al.* 1992). The foliar characteristics found in these secondary taxa seem similar to those observed in this study's montane large-leaved secondary genera *Abatia*, *Bocconia*, *Hedyosmum*, *Oreopanax*, *Saurauia*, *Senecio*, and *Verbesina*. A comparative study dealing with the autecology of certain large-leaved secondary species in both tropical lowlands and montane areas (*e.g.*, *Cecropia* spp. vs. the palmately compound-leaved *Oreopanax xalapensis*) is required to find out whether they have similar, analogous life strategies. Furthermore, several primary species were found with very large leaf sizes too. Most of these species such as *Oreopanax capitatus* and *O. nubigenus* inhabit sites near the forest floor. Their macrophyllous leaf sizes are related to the shaded environment and the relatively stable microclimate prevailing near ground level, where extreme fluctuations in temperature and humidity are less frequent than in the upper part of the wind-exposed canopy.

Leaf size spectra for this study's Talamanca montane oak forests did not differ much from those known from other sites in the same region (Table 3). In general, microphyllous and notophyllous leaf sizes predominate in Costa Rica's oak forests at these altitudes. However, at Dolph and Dilcher's (1980)

nearby site at 2700 m asl (Villa Mills) the mesophyllous size class was most prominent, especially in the subcanopy of the forest. On the other hand, these authors included only nine species in their assessment and noted the dominance of microphyllous species in the canopy layer.

A remarkable feature were the very small-sized leaves observed among some species with gnarled or twisted branches. Out of 41 species the compound-leaved *Weinmannia pinnata* had the smallest leaf area (per leaflet) and was the only nanophyllous species. The ericad *Vaccinium consanguineum* with leaf areas ranging from 3.34 to 5.52 cm² can be considered as "near-nanophyllous". *Escallonia myrtilloides* found in LSF had leaf sizes in between the two former species. As we know from different studies these very small-leaved tree species are even more abundant at higher elevations, just below the upper tree line at 3200–3400 m asl (Gómez 1986, Kappelle *et al.* 1991, Islebe & Kappelle 1994). There, they occupy sites in subalpine (dwarf) forests bordering the treeless paramo vegetation (Gómez 1986). They are accompanied by many other woody nanophyllous species restricted to the subalpine environment, *e.g.*, *Hypericum strictum*, *Pentacalia firmipes*, *Pernettya coriacea*, *Vaccinium floribundum*, and *Weinmannia trianae* (Kappelle *et al.* 1991).

It is interesting to note that the lowest specific leaf weight values were found among secondary species in ESF. Here, *Hedyosmum mexicanum*, *Saurauia veraguasensis*, and *Symplocos serrulata* had a specific leaf weight ranging from 43.9 to 49.0 g·m⁻². The most heavy leaves (high specific leaf weight) were recorded for *Comarostaphylis arbutoides* in ESF, *Weinmannia pinnata* in LSF, and *Quercus costaricensis* in PF. Leaf water content was highest (>450 g·m⁻²) in the secondary species *Senecio copeyensis* (ESF), and the primary species *Viburnum costaricanum* (LSF), *Miconia tonduzii* (PF), *Oreopanax capitatus* (PF), and *O. nubigenus* (PF). Again, both secondary species occupying space in ESF's canopy and primary species thriving in PF's understory showed similar extreme values. As has been mentioned before, this finding must be interpreted with care as the measured leaf water content value corresponds to the unsaturated status of the collected fresh leaves, while the degree of unsaturation may differ in different species. The presence of *V. costaricanum* in this group is somewhat unclear, unless we realize its function as a gap-dependent species prevailing in closing natural treefall gaps in mature forest. At such temporarily disturbed sites it occurs in association with other gap-de-

TABLE 3. Leaf-size spectra^a of some tropical montane forests.

Country/source	Altitude (m asl)	Spp. Nr.	Lepto	Nano	Micro	Noto	Meso	Macro	Dom ^b
Costa Rica ^c									
This study (ESF ^d)	2975	27	0.0	3.7	25.9	37.0	25.9	7.4	Noto
This study (LSF ^e)	2975	31	0.0	3.2	38.7	25.8	32.3	0.0	Micro
This study (PF ^f)	2975	23	0.0	4.3	26.1	47.8	13.0	8.7	Noto
Richter 1991 (Chirripó) ^g	2950	—	0.0	15.0	60.0	←25.0→		0.0	Micro
Dolph & Dilcher 1980	2700	9	0.0	11.1	22.2	22.2	33.3	11.1	Meso
Dolph & Dilcher 1980	2300	14	0.0	0.0	50.0	35.7	14.3	0.0	Micro
Colombia									
Cuatrecasas 1934 ^{g,h}	2500	30	3.3	3.3	26.7	←60.0→		6.7	Noto/Meso
Jamaica									
Tanner 1986 (Gap Gully)	1550	15	0.0	2.0	42.0	49.0	6.0	0.0	Noto
Tanner 1986 (Mature, Mull Ridge)	1550	17	2.0	7.0	47.0	40.0	4.0	0.0	Micro
Tanner 1986 (Mature, Mor Ridge)	1550	11	0.0	12.0	50.0	31.0	7.0	0.0	Micro
Tanner 1986 (Mature, Wet Slope)	1550	19	2.0	5.0	51.0	38.0	4.0	0.0	Micro
Puerto Rico									
Howard 1969 (Elfin) ^g	1050	52	1.9	11.5	57.6	←25.0→		3.8	Micro
Venezuela									
Sugden 1985 (Wet Thicket)	900	23	0.0	0.0	82.6	17.4	0.0	0.0	Micro
Sugden 1985 (Cloud)	700	22	0.0	0.0	50.0	40.9	9.1	0.0	Micro
Sugden 1985 (Transition)	500	23	4.3	0.0	47.8	34.8	13.0	0.0	Micro
Ecuador									
Grubb <i>et al.</i> 1963	1710	27	0.0	0.0	13.0	26.0	57.0	4.0	Meso
Sri Lanka									
Greller & Balasubramaniam 1988	2135	13	0.0	0.0	69.0	23.0	8.0	0.0	Micro
New Guinea									
Grubb 1974	3300	61	8.0	11.0	47.0	25.0	8.0	2.0	Micro
Grubb 1974	2500	55	4.0	6.0	20.0	49.0	18.0	4.0	Noto

^a Proportions of Raunkiaer's leaf size classes as modified by Webb (1959): Lepto-, Nano-, Micro-, Noto-, Meso- and Macro-phyllous, in percentages of total numbers of species studied.

^b Dominant leaf size class.

^c All Costa Rican sites: Talamanca *Quercus* forests.

^d Early Secondary Forest.

^e Late Secondary Forest.

^f Primary Forest

^g Noto- and Meso-phyllous size classes combined according to Barkman (1979).

^h Colombian site: Andean *Quercus* forest at La Suiza.

pendents such as *Cornus disciflora*, *Fuchsia arborescens*, and *Oreopanax xalapensis*.

As has been indicated above, the chemical abundance of foliar nitrogen is highest for leaves of secondary species in ESF. This finding is especially interesting in the light of an increased photosynthetic capacity and maximum photosynthetic rate with a higher level of total leaf nitrogen (*cf.* Givnish 1988). This makes us suggest that individuals of secondary species in ESF can take advantage of the high ir-

radiance levels prevailing in the open ESF environment when favored by sufficient leaf nitrogen needed for a fast photosynthesis. In this way they may grow rapidly to canopy height and compete successfully with neighboring species. In this context it is clear that levels of leaf nitrogen are highest in secondary species of ESF. High levels of nitrogen were also found in leaves of the canopy species *Quercus costaricensis* in LSF and *Q. copeyensis* in PF. The known presence of mycorrhiza in the soil (Chaverri & Rojas

1985) may explain the high nitrogen levels in the leaves of these oaks (M. J. A. Werger, pers. comm.), but reliable data on this issue are still lacking. An additional study is needed to determine possible differences in exchangeable soil fractions related to specific foliar nutrient levels.

Thus, secondary forest succession started with an ESF phase made up of a combination of secondary species with mostly non-entire, mesophyll-sized leaves and primary species with intermediate-sized leaves. It finally leads to a mature PF phase dominated by two kinds of primary species: species with mainly entire, notophyll-sized leaves in the canopy and species with thick, non-elliptic, meso- and macrophyll-sized leaves inhabiting the understory. Species occurring in natural treefall gaps in mature PF forest displayed similar leaf characteristics as found in early and late secondary forest.

COMPARISON TO OTHER TROPICAL MONTANE FORESTS.—

The proportions of leaf size classes recorded for this Costa Rican montane study site fall mainly within the ranges known from other tropical montane forests (Table 3). The microphyllous leaf size class is best represented throughout the montane Tropics. Notophyllous-sized leaves occupy a second place and may dominate the spectrum at disturbed sites such as at this study's ESF site. Occasionally notophyllous species become preponderant in some mature montane forests (Grubb 1974, this study).

A possible reason for the large amount of notophyllous taxa in this study's PF is found in the leeward position of the study site at Jaboncillo de Dota. Sugden (1985) showed that in a Venezuelan montane forest leaves become significantly smaller and thicker with increased exposure to wind. In the Costa Rican Cordillera de Talamanca windward sites are mainly found on the Atlantic slope, which is under the influence of trade winds coming in from the Caribbean lowlands. These winds strongly affect the structure and physiognomy of the upper montane forest vegetation (Kappelle 1992) and seem to reduce leaf size (pers. obs.). The present site at Jaboncillo de Dota is located on the southwest oriented, wind-protected Pacific slope of the mountain range. Here, environmental stress on leaves is much less pronounced than on the Atlantic slope, causing a general shift towards greater leaf sizes.

Mesophyllous species become important at tropical latitudes below elevations of 2000 to 2400 m asl (*cf.* Cuatrecasas 1934). This has been illustrated by Grubb *et al.*'s (1963) classical study from a montane forest site at 1710 m asl in Ecuador. Leptophylls range from 0 to 5 (8) percent of the

species in several tropical montane forests, while nanophylls can reach values up to 15 percent, probably as a result of responses to locally harsher circumstances. Moreover, decreasing leaf size with increasing aridity is a trend observed in many tropical regions (*e.g.*, Richards 1952). Finally, macrophylls account for less than *ca* 11 percent of the species in montane forests in different continental and insular parts of the Tropics. Furthermore, this leaf size class becomes prominent at lower elevations, for leaf size in tropical ecosystems is negatively related to altitude (Grubb 1974, Leigh 1975, Dolph & Dilcher 1980, Cleef 1981).

Leaf nutrient concentrations in the Costa Rican forests sampled are similar to those reported from other tropical montane forests (Table 4). Undisturbed PF in the Cordillera de Talamanca has a foliar nitrogen concentration almost equal to that of Colombian upper montane rain forest (Hofstede *et al.* 1993), Jamaican Mor Ridge forest (Tanner 1977) or Puerto Rican Elfin forest (Grubb 1977, Medina *et al.* 1981). Costa Rican ESF has a relatively high leaf nitrogen concentration, which is comparable to the value found by Tanner (1977) in Jamaican Gap forest. Recently, Scatena *et al.* (1993) came across high levels of nitrogen in above-ground biomass of Puerto Rican montane forest, apparently due to a combination of natural and anthropogenic factors. These authors found several fast-growing species (*e.g.*, *Cecropia peltata* and *Dydimopanax morototoni*) with high nitrogen concentrations in their tissue. The levels of leaf phosphorus in Costa Rican montane forests fall within the range for Andean forests in Colombia (Hofstede *et al.* 1993, Veneklaas 1991) and montane Jamaica (Tanner 1977). The similarity with foliar phosphorus levels in Andean Colombia is explained by the presence of phosphorus-rich soils in both highland areas (Andosols), which developed from volcanic ash deposits of geologically recent origin (Van Uffelen, 1991). Similar high levels of leaf phosphorus are also encountered in Neotropical lowland forests on rich, volcanically derived soils (Bongers & Popma 1988, Bigelow 1993). The presence of many active volcanoes just north of the present study area (*e.g.*, Poás, Irazú, and Arenal) supports this suggestion. The potassium levels recorded in this study fit in the range known from other tropical montane forests. Especially the values found in Colombian, Jamaican, and New Guinean forests are similar to those calculated for Costa Rica (*cf.* Grubb 1977, Tanner 1977, Veneklaas 1991 & Hofstede *et al.* 1993). Finally, it is worth noting that Grubb (1977) in primary montane rain forests in the Far

TABLE 4. Leaf nutrient concentrations ($\text{mg}\cdot\text{g}^{-1}$) of some tropical montane forests.

Country/Source	Altitude (m asl)	Spp. Nr.	N	P	K	N/P
Costa Rica						
This study (Early Secondary)	2975	27	16.4	1.1	12.9	14.9
This study (Late Secondary)	2975	31	11.3	1.0	10.3	11.3
This study (Primary)	2975	23	10.8	0.9	9.2	12.0
Colombia						
Hofstede <i>et al.</i> 1993	3700	1	10.2	0.9	5.0	11.3
Veneklaas 1991	3370	5	14.7	0.9	6.1	16.3
Veneklaas 1991	2550	12	17.8	1.3	12.4	13.7
Jamaica						
Tanner 1977 (Gap Gully)	1550	9	17.6	1.0	14.9	17.6
Tanner 1977 (Mature, Mull Ridge)	1550	14	16.1	0.7	12.3	23.0
Tanner 1977 (Mature, Mor Ridge)	1550	13	10.5	0.5	5.5	21.0
Tanner 1977 (Mature, Wet Slope)	1550	9	12.7	0.8	9.7	15.9
Puerto Rico						
Grubb 1977 (Elfin)	1050	15	9.7	0.5	3.9	19.4
Medina <i>et al.</i> 1981 (Elfin)	1035	7	9.9	0.6	5.1	16.5
New Guinea						
Grubb 1977	3300	15	14.2	0.8	10.1	16.9
Grubb & Edwards 1982	2500	15	13.2	0.9	7.7	14.7

East revealed that Ericaceae, Myrtaceae, and Theaceae tend to have low foliar levels of nitrogen and phosphorus in comparison to *e.g.*, Lauraceae. This trend is also seen in this study's PF, where *Cleyera theaeoides* and *Vaccinium consanguineum* have much lower foliar concentrations of nitrogen and phosphorus than the lauraceous *Ocotea pittieri*.

In conclusion, it is clear that the values we recorded for different leaf characteristics in Costa Rican montane *Quercus* forests fall mainly within the ranges known from other tropical montane forest sites. Further research on changes in leaf traits along successional gradients in tropical high altitude forests is strongly recommended, in order to find out whether the results of this study reflect patterns that are common in the equatorial uplands or are no

more than local trends restricted to the Neotropical montane fagaceous forest ecosystem.

ACKNOWLEDGMENTS

We are most grateful to A. M. Cleef and F. Bouman, who took the initiative for the present study. The Universidad Nacional in Costa Rica provided laboratory facilities for drying and weighing leaf material. R. Bregman and A. Philip assisted with the nutrient analysis. F. Bongers, A. M. Cleef, E. V. J. Tanner, E. Veneklaas and M. J. A. Werger kindly commented on earlier versions of the manuscript. M.K. was supported by grant no. W 84-331 of the Netherlands Foundation for the Advancement of Tropical Research (WOTRO/NWO), and M.E.L. received primary financial support from the University of Amsterdam.

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APPENDIX. Means of leaf characteristics of 41 secondary and primary tree species in upper montane Early and Late Secondary and Primary Forest, Cordillera de Talamanca, Costa Rica.

Species	Family ^a	Early Secondary Forest						Late Secondary Forest						Primary Forest					
		LA ^b	SLW ^c	LWC ^d	P ^e	N ^f	K ^g	LA ^b	SLW ^c	LWC ^d	P ^e	N ^f	K ^g	LA ^b	SLW ^c	LWC ^d	P ^e	N ^f	K ^g
Secondary species (19)																			
<i>Abatia parviflora</i> Ruiz																			
López & Pavon	FLC	38.46	130.5	304.2	1.8	27.1	17.2	34.91	134.6	209.1	1.9	21.7	15.2	—	—	—	—	—	—
<i>Bocconia frutescens</i> L.	PAP	642.74	90.8	338.3	1.5	11.5	5.1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Buddleja nitida</i> Benth.	LOG	—	—	—	—	—	—	15.45	132.7	77.0	0.9	10.4	8.6	—	—	—	—	—	—
<i>Comarostaphylis arbutioides</i> Lindley	ERI	12.07	270.1	199.7	0.8	9.4	6.4	11.03	156.8	391.7	1.0	11.8	19.6	—	—	—	—	—	—
<i>Cornus disciflora</i> Mociño & Sessé	COR	35.08	92.6	121.2	0.8	11.2	8.0	23.60	100.4	128.8	0.9	9.0	6.2	27.88	125.5	77.5	1.1	11.5	8.0
<i>Eucallonia myrtilloides</i> L.f.	ESC	—	—	—	—	—	—	2.46	187.0	239.8	0.8	10.1	9.9	—	—	—	—	—	—
<i>Fuchsia arborea</i> Sims.	ONA	26.09	116.5	230.4	1.5	16.3	7.6	43.68	57.7	173.1	1.1	13.7	8.7	—	—	—	—	—	—
<i>Garrya laurifolia</i> Hartweg ex Benth.	GAR	20.85	223.5	188.5	0.8	8.6	10.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hedyosmum mexicanum</i> Cordemoy	CLR	49.63	43.9	172.3	1.2	42.4	26.6	71.27	96.0	175.5	1.1	9.8	16.4	—	—	—	—	—	—
<i>Ilex discolor</i> Standley	AQF	29.56	183.1	218.2	0.5	9.3	8.5	53.66	114.6	160.3	0.6	9.6	12.1	—	—	—	—	—	—
<i>Monnina crepinii</i> Chodat.	PGL	22.77	79.1	178.7	2.2	28.1	11.3	62.54	68.9	154.0	2.3	15.4	17.8	—	—	—	—	—	—
<i>Myrcianthes fragrans</i> McVaugh	MRT	14.20	185.3	199.7	0.9	18.8	6.2	11.33	221.5	125.3	0.6	11.5	3.9	—	—	—	—	—	—
<i>Myrsine coriacea</i> (Sw.) R. Br. ex R. & Sch.	MRS	18.13	183.1	195.3	1.0	16.8	9.2	19.00	162.6	186.3	0.9	12.8	4.1	23.31	130.8	142.0	0.6	12.3	11.5
<i>Oreopanax xalapense</i> (Kunth) Decne. & Pl.	ARL	63.69	91.5	200.3	1.2	16.8	16.6	86.50	154.3	204.0	1.1	13.6	11.7	180.83	154.1	231.3	1.1	10.5	15.1
<i>Saurauia veraguensis</i> Seemann	SRA	68.75	49.0	184.4	1.9	21.3	16.3	—	—	—	—	—	—	—	—	—	—	—	—
<i>Senecio copeyensis</i> Greenm.	AST	473.95	135.4	494.9	1.1	15.8	24.9	—	—	—	—	—	—	—	—	—	—	—	—
<i>Senecio multivittatus</i> Benth.	AST	143.11	68.9	285.0	2.7	10.6	11.6	—	—	—	—	—	—	—	—	—	—	—	—
<i>Symplocos serrulata</i> Kunth	SYM	85.99	43.9	172.3	0.8	39.4	25.3	48.23	122.1	182.7	0.8	12.5	10.4	—	—	—	—	—	—
<i>Verbesina oerstediana</i> Benth.	AST	80.03	104.0	254.5	1.2	15.3	30.5	50.99	63.3	146.5	1.5	8.1	13.7	—	—	—	—	—	—
Primary species (22)																			
<i>Ardisia costaricensis</i> Lundell	MRS	—	—	—	—	—	—	—	—	—	—	—	—	15.39	131.3	232.6	0.6	8.7	6.0
<i>Cleyera theaeoides</i> (Sw.) Choisy	TEA	17.67	186.8	262.0	0.8	13.0	8.9	15.82	177.6	153.0	0.7	12.7	4.5	16.08	114.4	176.0	0.2	8.6	6.2
<i>Drimys granadensis</i> L.f.	WIN	—	—	—	—	—	—	75.06	75.5	160.7	0.7	8.8	5.7	36.96	165.0	288.1	0.6	5.4	4.4
<i>Ilex pallida</i> Standley	AQF	14.16	190.0	175.8	0.8	13.4	21.6	10.82	160.8	147.9	0.9	7.6	15.9	14.43	173.9	95.6	0.4	8.9	6.0
<i>Miconia schneelii</i> Wurd.	MLS	—	—	—	—	—	—	34.36	99.0	137.1	1.1	10.1	3.9	—	—	—	—	—	—
<i>Miconia tonduzii</i> Cogn.	MLS	—	—	—	—	—	—	—	—	—	—	—	—	49.05	255.7	576.3	0.9	10.5	4.6
<i>Nectandra cufodontiisii</i> (Schmidt) Allen	LAU	—	—	—	—	—	—	35.39	141.3	181.1	0.8	10.4	6.6	30.86	158.8	172.7	0.7	10.0	7.6
<i>Ocotea pittieri</i> (Mez) Van der Werff	LAU	—	—	—	—	—	—	26.64	98.8	173.7	1.1	11.8	7.3	27.77	125.0	94.7	1.4	14.7	10.1

APPENDIX. Continued.

Species	Family ^a	Early Secondary Forest					Late Secondary Forest					Primary Forest							
		LA ^b	SLW ^c	LWC ^d	P ^e	N ^f	K ^g	LA ^b	SLW ^c	LWC ^d	P ^e	N ^f	K ^g	LA ^b	SLW ^c	LWC ^d	P ^e	N ^f	K ^g
<i>Oreopanax capitatus</i> (Jacq.) Decne. & Pl.	ARL	80.18	117.2	145.8	1.2	12.6	7.0	83.22	95.9	249.5	1.6	10.7	11.6	387.66	16.4	522.8	2.7	14.5	15.3
<i>Oreopanax nubigenus</i> Standley	ARL	—	—	—	—	—	—	—	—	—	—	—	—	250.02	205.0	529.2	0.8	9.0	17.2
<i>Persea vesticula</i> Standley & Seyerm.	LAU	—	—	—	—	—	—	47.36	120.4	165.1	0.8	4.2	12.6	—	—	—	—	—	—
<i>Prunus annularis</i> Koehne	ROS	—	—	—	—	—	—	—	—	—	—	—	—	22.50	133.3	120.9	0.7	7.4	6.5
<i>Quercus copeyensis</i> Corn. Mueller	FAG	26.61	124.4	109.4	0.7	15.3	5.3	14.99	159.4	89.4	0.8	11.5	9.2	24.79	183.5	91.9	0.9	14.4	15.5
<i>Quercus costaricensis</i> Liebm.	FAG	36.26	162.2	139.8	1.0	11.6	15.4	15.57	176.6	122.0	1.5	16.5	6.2	35.16	294.6	289.8	0.9	12.0	4.6
<i>Rhamnus oreodendron</i> L.O. Williams	RHM	—	—	—	—	—	—	47.48	94.8	119.0	1.0	12.1	16.1	34.34	90.3	122.6	0.7	12.7	10.1
<i>Schefflera rodriguesiana</i> Frodin	ARL	—	—	—	—	—	—	55.97	98.8	173.7	1.3	14.0	24.0	59.94	156.8	230.6	1.0	11.2	12.0
<i>Syrax argenteus</i> Presl.	STY	31.37	117.3	156.8	0.7	11.4	10.2	25.08	119.6	88.9	0.9	12.7	4.5	21.60	113.0	137.0	0.8	12.5	5.3
<i>Symplocos austiniimithii</i> Standley	SYM	—	—	—	—	—	—	—	—	—	—	—	—	20.14	131.3	232.6	0.6	9.3	6.7
<i>Vaccinium consanguineum</i> Klotzsch	ERI	3.93	188.3	124.7	0.9	13.9	11.9	5.52	59.8	67.0	0.8	9.7	3.9	3.34	119.8	170.7	0.9	9.1	7.6
<i>Viburnum costaricanum</i> (Oerst.) Hemslley	CPR	22.56	122.8	194.7	0.7	11.4	9.5	18.16	87.6	556.0	1.1	11.3	15.2	24.99	136.1	112.4	1.2	12.1	14.7
<i>Weinmannia pinnata</i> L.	CUN	2.06	203.9	199.0	0.8	9.5	5.0	0.94	329.8	361.7	0.9	9.0	9.6	2.11	227.5	37.9	1.0	10.7	7.2
<i>Zanthoxylum scheryi</i> Lundell	RUT	8.20	239.0	53.7	0.7	10.8	11.4	12.65	90.9	235.6	0.7	8.2	5.5	19.96	119.2	207.4	0.9	11.7	8.3

^a Families are given as mnemonic tree-letter acronyms following Weber (1982).

^b Leaf area (cm²), for N = 10 leaves or leaflets.

^c Specific leaf weight = leaf dry weight/leaf area (g·m⁻²), for N = 20 leaves or leaflets.

^d Leaf water content (g·m⁻²), for N = 20 leaves or leaflets.

^e Phosphorus/weight (mg·g⁻¹), for N = 20 leaves or leaflets.

^f Nitrogen/weight (mg·g⁻¹), for N = 20 leaves or leaflets.

^g Potassium/weight (mg·g⁻¹), for N = 20 leaves or leaflets.