

Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador

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Abstract: We tested the hypothesis that tree species diversity and stem density in tropical forests are both positively related to leaf area index and negatively to percent diffuse transmittance of photosynthetically active radiation. Eighty old-growth stands were selected in the Sumaco Biosphere Reserve, Ecuador, at 500, 1000, 1500 and 2000 m elevation. Leaf area index decreased significantly with elevation by about 1.1 per 1000 m altitude, from a mean of about 6.6 at 500 m to 5.2 at 2000 m a.s.l., while diffuse transmittance increased significantly with elevation. Diffuse transmittance at the forest floor averaged 2.1 % at 500 m and 4.0 % at 2000 m (relative to incident radiation). There were significant positive relationships between both tree species diversity and stem density on the one hand and leaf area index on the other, whereas both were negatively related to diffuse transmittance. The observed decrease in leaf area index with elevation appears to be a consequence of an altitudinal decrease in stem density and in tree species diversity, combined with a soil fertility effect.

Resumen: Probamos la hipótesis de que la diversidad de especies arbóreas y la densidad de tallos en los bosques tropicales están relacionadas positivamente con el índice de área foliar y negativamente con el porcentaje de transmitancia difusa de la radiación fotosintéticamente activa. Se seleccionaron 80 rodales de bosque maduro en la Reserva de la Biosfera de Sumaco, Ecuador, a 500, 1000, 1500 y 2000 m de altitud. El índice de área foliar disminuyó significativamente en alrededor de 1.1 por cada 1000 m de altitud, desde una media de alrededor de 6.6 a 500 m hasta una de 5.2 a 2000 m s.n.m., mientras que la transmitancia difusa aumentó significativamente con la altitud. La transmitancia difusa en el piso del bosque fue en promedio 2.1 % a 500 m y 4.0 % a 2000 m (en relación con la radiación incidente). Hubo relaciones positivas significativas tanto entre la diversidad de especies arbóreas y la densidad de tallos, por un lado, y el índice de área foliar por el otro, a la vez que ambas variables estuvieron relacionadas negativamente con la transmitancia difusa. La disminución altitudinal observada en el índice de área foliar parece deberse a una reducción en la densidad de tallos y en la diversidad de especies de árboles, en combinación con un efecto de la fertilidad del suelo.

Resumo: Testámos a hipótese de que a diversidade de espécies arbóreas e a densidade do tronco em florestas tropicais estão positivamente relacionados com o índice de área foliar e negativamente com a percentagem da transmitância difusa da radiação fotossinteticamente ativa. Oitenta parcelas florestais velhas e não intervencionadas foram selecionados na Reserva da Biosfera Sumaco, no Equador, a 500, 1000, 1500 e 2000 m de altitude. O índice de área foliar diminuiu significativamente com a elevação em cerca de 1,1 por 1000 m de altitude, de uma média de cerca de 6,6 a 500 m para 5,2 a 2000 m de altitude, enquanto que transmitância difusa aumentou significativamente com a elevação. A transmitância difusa no solo da floresta era em média de 2,1 % a 500 m e 4,0 % a 2000 m (em relação à radiação incidente). Verificaram-se, por um lado, relações positivas significativas entre a diversidade de espécies de árvores e a

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densidade do tronco e, por outro com o índice de área foliar, enquanto ambas estavam negativamente relacionadas com a transmitância difusa. A diminuição observada no índice de área foliar com a elevação parece ser uma consequência de uma diminuição na densidade do tronco e na diversidade de espécies arbóreas com a altitude, combinadas com o efeito da fertilidade do solo.

Key words: Altitude effects, diffuse transmittance of PAR, leaf area index, photon flux density, stem density, Sumaco Biosphere Reserve, tree species diversity.

Introduction

Of all environmental factors affecting plants, light is probably the most heterogeneous, both spatially and temporally. Light heterogeneity in space is particularly important in tropical forests, where unfavourable temperatures are less significant for plant life and light is considered to be the single most limiting resource for plant growth (Pearcy 2007). Tree seedlings and saplings, herbaceous plants and understorey trees, have been shown to be closely keyed to variation in below-canopy light availability (Denslow 1987; Strauss-Debenedetti & Bazzaz 1991). Canopy closure and the size and abundance of gaps are, therefore, important factors controlling tree regeneration, forest dynamics and forest diversity (e.g. Brokaw 1987; Denslow 1980; Hartshorn 1978; Hubbell 1979; Whitmore 1984). In the absence of canopy gaps, canopy species composition can significantly influence variation in light transmittance within and among stands (Canham *et al.* 1994; Kabakoff & Chazdon 1996; Messier & Bellefleur 1988).

How much light is penetrating through the canopy to the forest floor depends largely on the amount of canopy foliage, most often characterized as leaf area index (LAI, the one-sided cumulative leaf area of a stand per unit ground area). Because it is a dimensionless quantity, LAI can be measured, analysed and modelled across a range of spatial scales, from individual tree crowns to stands, whole regions (Clark *et al.* 2008) or continents (Asner *et al.* 1998). The leaf area is the exchange surface between the photosynthetically active component of the vegetation and the atmosphere (Cohen *et al.* 2003; Fournier *et al.* 2003; Turner *et al.* 1999), which controls not only the radiation regime within the canopy, but also the thermal and hydric conditions (Fournier *et al.* 2003). The net primary production of forests, in most cases, is closely correlated with LAI (e.g.

Asner *et al.* 2003; Battaglia *et al.* 1998; Beadle 1997; Sullivan *et al.* 1996), while canopy transmissivity typically shows a negative relationship with canopy leaf area (Zhou *et al.* 2002). Moreover, LAI is strongly related to forest transpiration because canopy conductance for water vapour is proportional to LAI (Whitehead & Jarvis 1981).

Despite its important role in controlling canopy carbon gain and transpirational water loss, not much is known about spatial variation in LAI of tropical forests on a regional or landscape scale. It is assumed that forest LAI is influenced by elevation (or temperature), water availability, soil fertility and topography, but comprehensive studies in forest stand along environmental gradients have mostly focused on temperate biomes (e.g. Bolstad *et al.* 2000; Leuschner *et al.* 2006; Meier & Leuschner 2008). Only recently, a few studies have analysed changes in the LAI of tropical forests along gradients in altitude and soil chemistry (Clark *et al.* 2008; Kitayama & Aiba 2002; Moser *et al.* 2007; Takyu *et al.* 2003).

The possible influence of biotic factors such as tree species diversity, stem density and basal area on LAI and the below-canopy radiation regime has not been investigated in detail in tropical forests.

We conducted a landscape-scale study on the spatial variation of LAI and below-canopy light intensity in 80 stands of old-growth tropical moist forests on the eastern slopes of the Andes in Ecuador. The area represents an altitudinal transect of undisturbed forest from lowlands to montane elevations, providing a suitable setting for analysing the effects of altitude and stand structure on LAI and canopy transmissivity. We tested the hypotheses that (i) LAI decreases, and below-canopy light intensity increases, with elevation, (ii) the forest floor of tropical lowland forests is exposed, on average, to lower photon flux densities than tropical montane forests, and also temperate forests, (iii) both tree species diversity

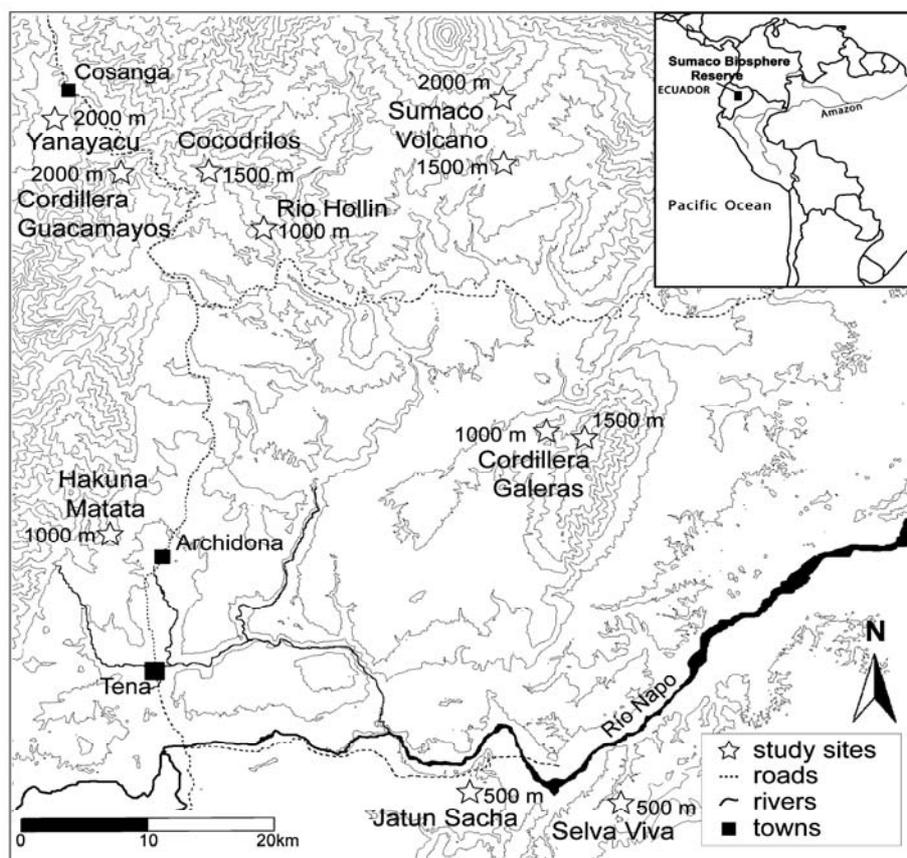


Fig. 1. Map of the eleven study sites with their altitudinal level (m a.s.l.) in the area of the Sumaco Biosphere Reserve in Eastern Ecuador.

and stem density are positively related to LAI, but negatively to below-canopy light intensity, and (iv) soil fertility (especially the availability of N and P) has a positive effect on LAI. This study is part of a more comprehensive investigation on plant diversity patterns and soil fertility in a set of 80 forest plots in the Sumaco Biosphere Reserve of NE Ecuador (Homeier *et al.* 2010b; Unger *et al.* 2010).

Methods

Study area

The study was conducted in the Sumaco Biosphere Reserve (SBR) and its close proximity in the province of Napo, NE-Ecuador. The reserve was established in the year 2000; it is situated on the eastern slopes of the Andes and the adjacent foothills, and includes the Sumaco volcano. The area represents the last existing altitudinal transect of undisturbed vegetation from lowlands (400 m a.s.l.) to páramo (3700 m) in the eastern equatorial Andes, and harbours probably more than

6000 species of higher plants (Neill & Palacios 1997).

The study sites were selected at four elevational levels (500, 1000, 1500, and 2000 m) to establish a sequence covering 1500 m altitudinal distance (Fig. 1, Table 1). Exact data on the annual precipitation of the study sites are lacking, but rainfall in the whole area is thought to exceed 2500 mm year⁻¹. The Sumaco volcano and the Cordillera Guacamayos probably receive more than 4000 mm year⁻¹, and throughout the area monthly precipitation rarely drops below 100 mm (Neill & Jørgensen 1999). The mean annual temperature decreases from approximately 22.9 °C at an altitude of 415 m (Jatun Sacha biological station) to 14.3 °C at 2015 m (Sumaco volcano) (Unger *et al.* 2010).

The geology is variable in the area. Parent rocks from the Cretaceous, mainly limestone, dominate most of the region; however, at Volcano Sumaco (basalt) and at Hakuna Matata (granite), volcanic and intrusive rocks, respectively, are present. Slates are found at Cordillera Guacamayos

Table 1. The 11 study sites on the four elevation levels; number of plots per site; and means of stand structural characteristics (mean \pm 1 SE).

Elevation level (m)	Study site	Conservation status	Elevation range (m)	No. of plots	Per plot of 400 m ²			Rarefied tree species (Δ)
					Stem density	Stand basal area (m ²)	No. of tree species	
500	Jatun Sacha	Private reserve	400 - 450	12	55.5 \pm 2.4	1.5 \pm 0.1	40.5 \pm 2.6	22.8 \pm 0.5
	Selva Viva	Private reserve	445 - 520	8	66.4 \pm 3.5	1.8 \pm 0.2	49.4 \pm 3.2	24.2 \pm 0.5
1000	Hakuna Matata	Private reserve	960 - 1080	6	72.3 \pm 5.0	1.8 \pm 0.1	43.3 \pm 4.3	22.2 \pm 0.9
	Cordillera. Galeras	National park	1050 - 1130	9	50.9 \pm 2.9	2.0 \pm 0.2	35.2 \pm 2.9	21.5 \pm 1.0
1500	Rio Hollín	Private reserve	1165 - 1200	5	75.8 \pm 4.2	2.0 \pm 0.3	28.6 \pm 1.8	15.3 \pm 0.9
	Cordillera Galeras	National park	1450 - 1600	7	76.4 \pm 6.6	1.7 \pm 0.1	40.1 \pm 2.5	20.2 \pm 0.8
	Cocodrillos	National park	1490 - 1570	5	47.6 \pm 3.7	2.2 \pm 0.1	28.1 \pm 1.2	20.2 \pm 0.7
	Sumaco	National park	1580 - 1630	8	41.8 \pm 2.1	2.2 \pm 0.2	26.4 \pm 0.9	19.8 \pm 0.4
2000	Sumaco	National park	1920 - 2015	6 (7)*	38.3 \pm 3.7	2.0 \pm 0.2	22.3 \pm 2.5	16.9 \pm 1.3
	Cordillera Guacamayos	Ecological reserve	1940 - 2000	7 (8)*	57.7 \pm 6.2	1.4 \pm 0.1	29.4 \pm 3.0	19.2 \pm 1.3

* one plot per study site was excluded from the final analysis.

Table 2. Soil chemical properties at the elevations studied (mean \pm SE).

Parameters	Elevation level			
	500 m	1000 m	1500 m	2000 m
Org. layer depth (cm)	1.58 \pm 0.21 ^a	2.39 \pm 0.31 ^a	6.34 \pm 0.47 ^b	5.34 \pm 0.32 ^b
Organic layer horizons				
pH _{KCl}	4.66 \pm 0.56 ^a	5.28 \pm 0.65 ^a	3.86 \pm 0.46 ^b	4.69 \pm 0.57 ^a
C/N (mol mol ⁻¹)	14.68 \pm 0.39 ^a	15.67 \pm 0.31 ^a	14.95 \pm 0.44 ^a	14.66 \pm 0.27 ^a
P _a (μ mol g ⁻¹)	0.59 \pm 0.12 ^a	1.91 \pm 0.44 ^a	2.88 \pm 0.49 ^a	7.29 \pm 1.49 ^b
Upper mineral soil horizon (0-10 cm)				
pH _{KCl}	4.08 \pm 0.42 ^a	4.47 \pm 0.54 ^b	4.44 \pm 0.46 ^{bc}	4.51 \pm 0.47 ^c
C/N (mol mol ⁻¹)	10.24 \pm 0.19 ^a	11.92 \pm 0.23 ^b	13.11 \pm 0.33 ^c	11.85 \pm 0.19 ^b
P _a (μ mol g ⁻¹)	0.10 \pm 0.04 ^a	0.36 \pm 0.08 ^a	0.43 \pm 0.15 ^a	1.20 \pm 0.31 ^b

Note: Superscripts are used to indicate significant differences among the means. Means with the same superscript do not differ significantly.

More details on the soils of the study plots are given by Unger *et al.* 2010.

(Sauer 1971). Though soils are very heterogeneous in the study area, geric Ferralsols are dominant at the study sites at 500 m and 1000 m and Cambisols are preponderant in the sites at 1500 m and 2000 m. Further studies of the soils and soil chemistry at the study sites (Unger *et al.* 2010) indicate that organic matter, total nitrogen and carbon, plant-available phosphorus and extractable calcium content increase with altitude, while N mineralization and nitrification do not show an elevational trend (see also Table 2).

Following the most recent vegetation classification for Ecuador (Palacios *et al.* 1999), the forests studied at 500 m can be classified as evergreen lowland forests, the stands at 1000 m as evergreen premontane forests, and the stands at upper elevations (1500 and 2000 m) as evergreen lower montane forests.

Plot establishment and tree inventory

Overall, we established 80 permanent plots (20 m x 20 m size) at the four different altitudinal levels (20 plots at each level). The study plots are situated at 11 sites, as shown in Table 1. They were selected to represent the forest structure and composition at the elevation in question - avoiding canopy gaps and early successional stages - with the aim of comparing old-growth stands and avoiding the variability associated with temporal forest dynamics (successional stages). Only areas without any kind of visible human or natural

disturbance within the mature forest stands were selected.

At each site plots were located to cover different topographic and ecological conditions. The plot size is small enough to keep environmental factors and forest structure homogeneous within the plots. The plots are independent sampling units each containing 16 - 45 stems exceeding 10 cm in diameter at breast height (dbh). The mean distances between the plots at a site (calculated from the location on the map) were between 0.1 km (Hakuna Matata) and 1.8 km (Galeras). In each plot, all stems of living trees with a dbh (diameter at breast height) \geq 5 cm were counted. The diameters of all trees with a dbh \geq 10 cm were measured and their basal areas were calculated (trees with a dbh < 10 cm were not included in basal area calculations). Voucher specimens of all unknown species were collected, duplicates being deposited at the herbaria QCA and QCNE, Ecuador, and GOET, Germany. Tree diversity (Δ) was calculated according to the individual-based rarefaction method (Gotelli & Colwell 2001) as the number of species (dbh \geq 5 cm) expected in a sample of 28 trees in a 400 m² plot (28 being the smallest number of trees found in any one of the 80 plots).

Measurements of leaf area index and photosynthetically active radiation

The leaf area index (LAI) of the stands was

measured with the LAI-2000 (LI-COR Inc., Lincoln, NE, USA) plant canopy analyser, one of the instruments most commonly used for the purpose. Even though direct destructive measurements of LAI are widely believed to be more accurate than indirect optical measurements, the LAI-2000 system has proven to provide LAI values closest to those obtained with leaf harvest methods in tropical forests (Asner *et al.* 2003; Moser *et al.* 2007).

The leaf area measurements with the LAI-2000 system were conducted in the remote mode, i.e. by simultaneous readings below the canopy at 2 m height above the forest floor and in nearby open areas (“above-canopy” reading) using two instruments.

All measurements were conducted during periods of overcast sky between November 2006 and April 2007. On each plot, 40 individual measurements were made, distributed equally over the plot. Each 20 m x 20 m plot was divided into four quadrants of 10 m x 10 m and ten measurements were made in each quadrant. The measuring points were located at least 2 m from the subplot boundaries and more than 2 m apart. The measurements in the open were conducted in larger gaps at a distance of not more than 3 km from the plots. To avoid reductions in the sky sector seen by the LAI-2000 fish-eye lens in the open sites, such as may be caused by high mountains or trees at the horizon, the data from the three inner rings (0 - 43° from zenith) were used, as recommended by Dufrêne & Bréda (1995), and also data for the inner ring (0 - 7° from zenith) only, to evaluate the LAI unaffected by the partial influence of canopy gaps in the vicinity of the plots. By masking rings selectively, we could compare relative light availability (based on gap fraction) at specific zenith angles and thus evaluate the size of canopy gaps (Nicotra *et al.* 1999). Assuming that leaf area index varies only little over time in these equatorial forests (see Rich *et al.* 1993), we ignored seasonality and conducted all measurements of LAI and radiation transmissivity only once in each plot.

Absolute values of incident and diffuse transmitted (DT) photosynthetically active radiation were obtained with two LI-190 sensors (LI-COR Inc., Lincoln, NE, USA), mounted on the two LAI-2000 instruments. Thus, at each of the 40 measuring points in each of the 80 plots, the LAI-2000 measurements, and those of photosynthetic photon flux density (PPFD) on the forest floor were taken simultaneously. Intensity of diffuse trans-

mittance (DT) was expressed in percent of the simultaneously recorded PPFD in larger gaps and averaged over the 40 measuring points in each plot to give a mean value for percent diffuse transmittance of photosynthetically active radiation (PAR). In addition, absolute values of below canopy PPFD (units: $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) were used in the analysis.

Measuring LAI and PPFD at a height of 2 m ignores the vegetation closer to the ground, which can constitute at least one foliage layer. Tropical forests vary substantially in the contribution of this low understorey layer to the total forest LAI (Montgomery 2004), but seedlings and young trees (< 2 m height) are almost negligible in contributing to the biomass or structure of old-growth tropical forests.

Data analysis

Linear regression analyses were applied to identify significant relationships between elevation as an independent variable and LAI, DT, density of stems ($\text{dbh} \geq 5 \text{ cm}$), tree diversity (Δ), and stand basal area. All regressions were calculated using Xact software (version 8.0; SciLab, Hamburg, Germany). Multiple regressions were calculated (stepwise backward variable elimination, including only variables with $P < 0.05$ in the final models) with the software R 2.8.1 (R Development Core Team 2008) to investigate the relationship of LAI and DT to various soil parameters, tree basal area, stem density and tree diversity. The canopy of one plot in the Cordillera Guacamayos at 2000 m was heavily disturbed by falling trees shortly after we established this plot. Therefore, we excluded it from all analyses. Since there were several large trees on one plot in the Sumaco area (2000 m), the calculated basal area on this plot was extraordinarily high and probably misleading; therefore, it was also excluded and all analyses were conducted with $N = 78$ plots.

Results

Stem density and tree species richness

The number of tree stems ($\text{dbh} \geq 5 \text{ cm}$) per plot ranged from 28 to 110 in the sample of 78 plots considered in the analysis (Table 1). The mean number of stems per plot was 59.9 ± 10.1 (mean \pm SD) at 500 m, 63.6 ± 15.1 at 1000 m, 55.4 ± 19.5 at 1500 m and 46.2 ± 15.3 at 2000 m a.s.l. being highest at intermediate elevation (1000 m) and lowest at 2000 m. Stem density decreased signi-

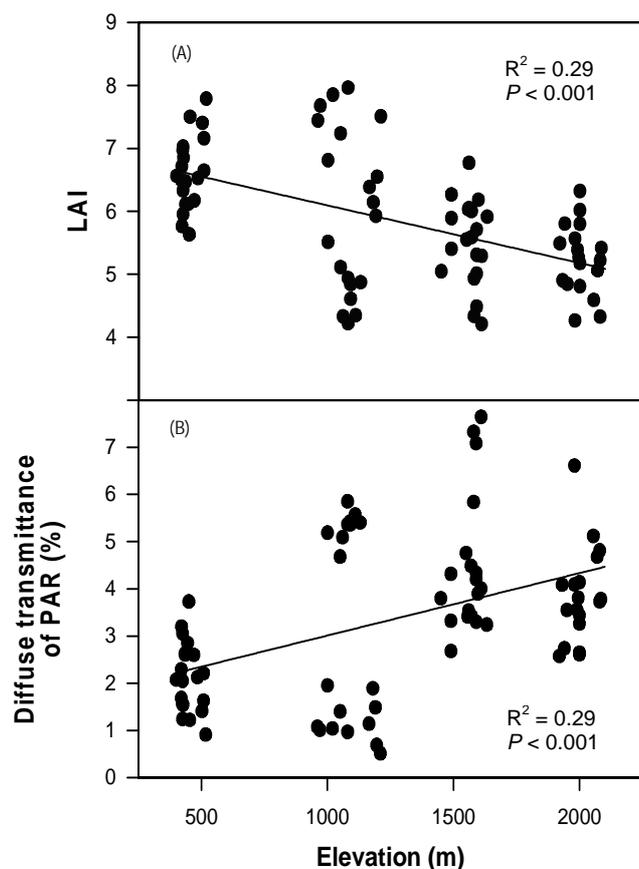


Fig. 2. Altitudinal change of LAI (A) and of percent diffuse transmittance of PAR (DT) (B) in the 78-plot sample (depicted are plot-level means).

ificantly with elevation ($r^2 = 0.09$, $P = 0.004$). In contrast, stand basal area showed no significant elevational trend (mean over the whole transect: $1.8 \pm 0.5 \text{ m}^2$ in a plot of 400 m^2 , Table 1). Calculated per hectare, the mean basal area was $40.8 \pm 12.3 \text{ m}^2 \text{ ha}^{-1}$ at 500 m, $48.6 \pm 12.1 \text{ m}^2 \text{ ha}^{-1}$ at 1000 m, $50.5 \pm 11.4 \text{ m}^2 \text{ ha}^{-1}$ at 1500 m, and $44.0 \pm 13.5 \text{ m}^2 \text{ ha}^{-1}$ at 2000 m.

The total number of tree species recorded in all 80 plots (total area: 3.2 ha) was 646 (J. Homeier *et al.* unpubl.). At lower elevations (500 and 1000 m), the most important tree families in terms of species and stem numbers were Myristicaceae, Moraceae and Euphorbiaceae, whereas Lauraceae and Rubiaceae dominated at higher elevations (1500 and 2000 m). The mean number of tree species per plot showed a significant decrease with elevation from 43.4 ± 9.7 at 500 m to 36.1 ± 9.9 at 1000 m, 30.8 ± 7.3 at 1500 m and 23.8 ± 8.0 at 2000 m (altitudinal trend: $r^2 = 0.41$, $P \leq 0.001$). The rarefied number of tree species (see *P* above) also showed an altitudinal trend: $r^2 = 0.38$, $P \leq 0.01$ (see also Table 1).

Leaf area index (LAI) and diffuse transmittance (DT)

Leaf area index decreased significantly with elevation - by about 1.1 per 1000 m from about 6.6 at 500 m to 5.2 at 2000 m (Fig. 2). The highest LAI plot mean was 8.0 at 1000 m (Hakuna Matata), the lowest 4.2 at 1500 m (Sumaco). The LAI measurements at angles $< 7^\circ$ from zenith showed a similar trend with elevation ($r^2 = 0.37$, $P \leq 0.001$), but the correlation was weaker.

The coefficient of variation for LAI between plot means at a particular elevation level increased with altitude from 11.8 % at 500 m to 19.7 % at 2000 m (Fig. 3). Diffuse Transmittance (DT) generally increased with elevation, showing an opposite trend to that found for LAI (Fig. 2). The lowest mean of DT over the 40 measurements in a plot was recorded at 1000 m elevation (Rio Hollin, mean = 0.5 % of incident radiation), while the highest value was found at 1500 m (Sumaco, mean = 7.6 %). In the 20 plots at a given elevation, the mean of DT varied from 0.9 to 3.9 % at 500 m, but from 2.5 to 6.7 % at 2000 m. The frequency distribution diagrams of the individual DT values (Fig. 3B) reveal a left-skewed distribution at all four elevations, but more flattened curves with greater abundance of higher DT values at 1500 and 2000 m as compared to the lower elevations. Synchronous measurements of DT (quantum sensors) and of LAI (LAI-2000 canopy analyzer) gave a close negative correlation of the two variables ($r^2 = 0.81$, $P \leq 0.001$).

We observed a significant increase of LAI with stem density across the 78-plot sample ($r^2 = 0.26$, $P \leq 0.001$), while DT decreased ($r^2 = 0.19$, $P \leq 0.001$), as shown in Fig. 4. Tree diversity (Δ) was related to both parameters in the same way (LAI: $r^2 = 0.16$, $P \leq 0.001$; DT: $r^2 = 0.04$, $P \leq 0.001$) (Fig. 5), whereas stand basal area showed no significant relationship, either to LAI or to DT.

In addition, we found significant relationships of LAI and DT to the plant-available P of the organic layer - negative for LAI ($r^2 = 0.21$, $P < 0.0010$ and positive for DT ($r^2 = 0.13$, $P < 0.001$) and to the C/N ratio in the mineral soil, negative for the LAI ($r^2 = 0.03$, $P = 0.05$) and positive for the DT ($r^2 = 0.06$, $P = 0.01$) (Fig. 6).

Measurements of PPFD at 2 m above the forest floor showed a significant increase with altitude (Table 3). The lowest mean of a plot was observed at 1000 m altitude ($1.4 \pm 0.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$), the highest at 2000 m ($67.7 \pm 3.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

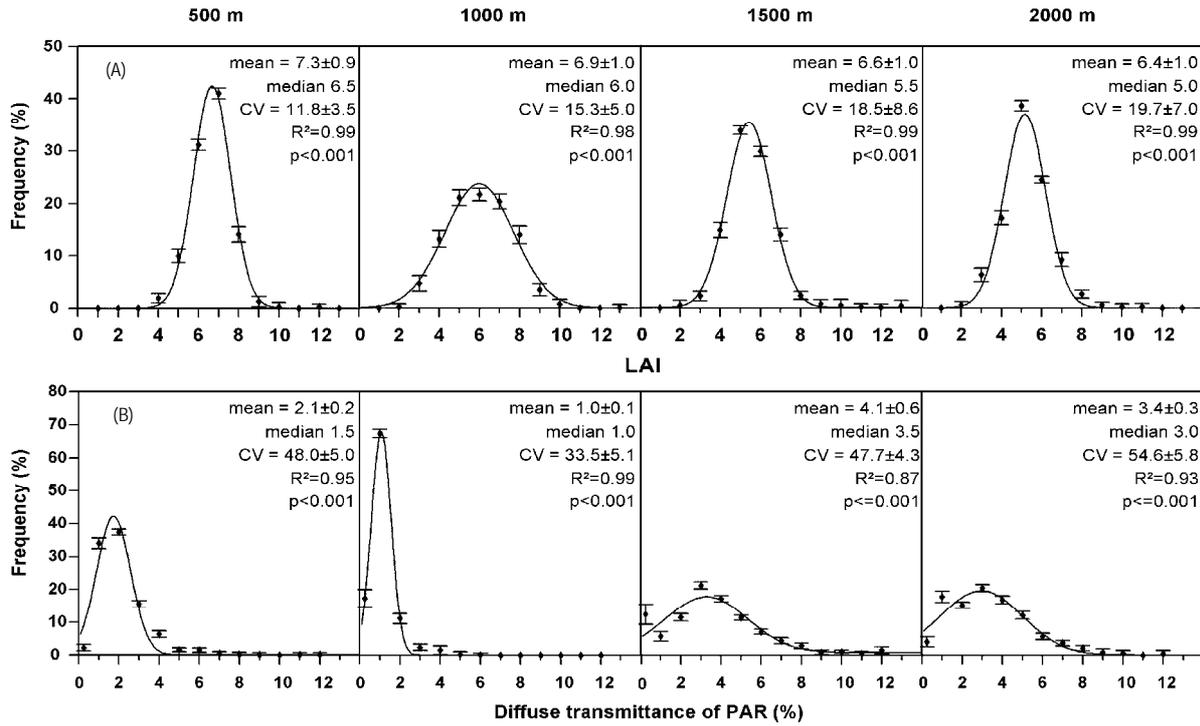


Fig. 3. Frequency distribution diagrams for plot-level means of LAI (A) and diffuse transmittance of PAR (B) in stands at different elevations (each 40 measurements in the each 20 plots per elevation level). The mean and median over the 20 plot-level mean values per elevation and the corresponding CV (coefficient of variation in % of the mean) for the each 20 plots are also given.

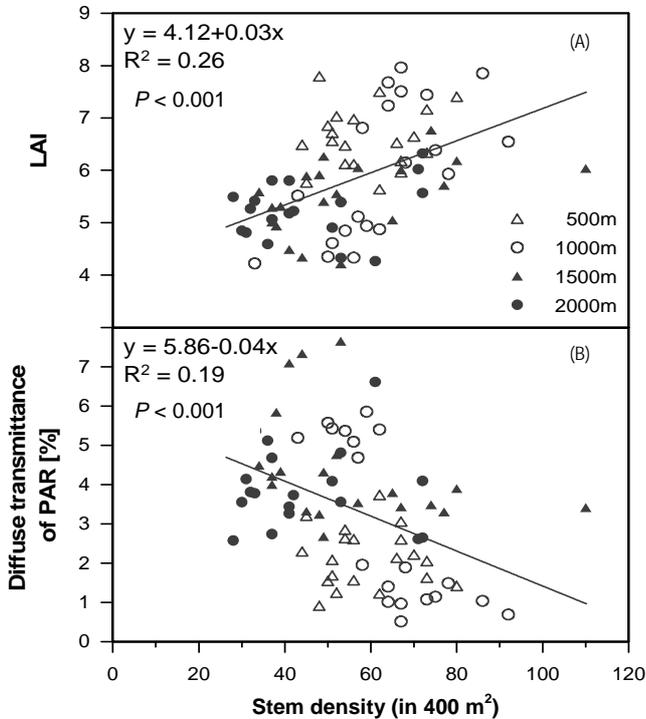


Fig. 4. LAI (A) and percent diffuse transmittance of PAR (B) as a function of stem density per plot in the 78 plots (all stems ≥ 5 cm dbh considered).

The final models of the multiple regression analyses for both LAI and DT yielded the source variables stem density and C/N ratio of the mineral soil as influential parameters; the plant-available P of the organic layer was also found to influence LAI significantly (Table 4).

In addition, the relation of LAI and DT to stand structural properties was analysed separately for the four elevations, thereby excluding the effect of altitude (data not shown). While the significance of the relationships was generally lower in these sub-samples, some differences between the four elevation levels became evident. While stem density was identified as the only structural variable significantly affecting LAI and DT at the medium elevation levels of 1000 m and 1500 m, stand basal area affected them at 500 m. Rarefied tree species density (Δ) was the only structural variable that influenced LAI and DT significantly at an elevation of 2000 m.

Discussion

Our average leaf area indices between 5.2 and 6.6 at lowland to lower montane elevations (500 to 2000 m) are somewhat higher than the global means

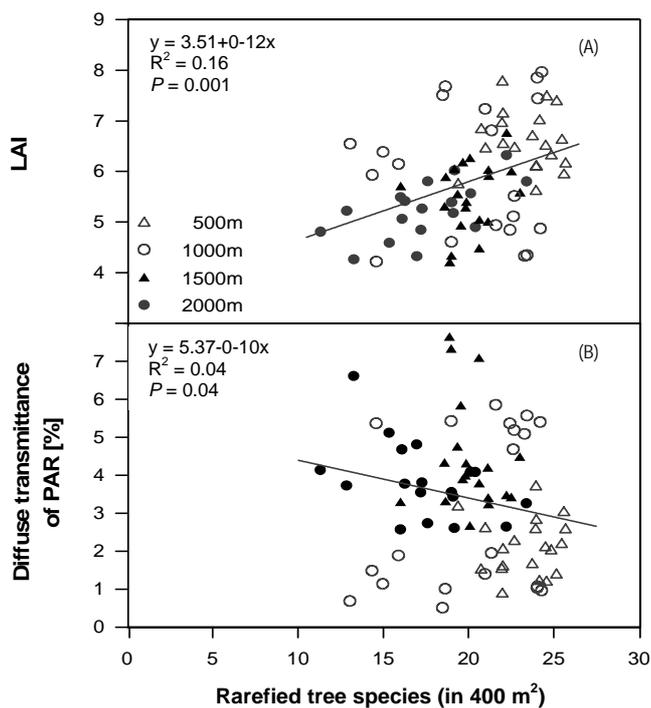


Fig. 5. LAI (A) and percent diffuse transmittance of PAR (B) as a function of tree diversity (rarefied trees per N = 28 trees) in the 78 plots (all stems ≥ 5 cm dbh considered).

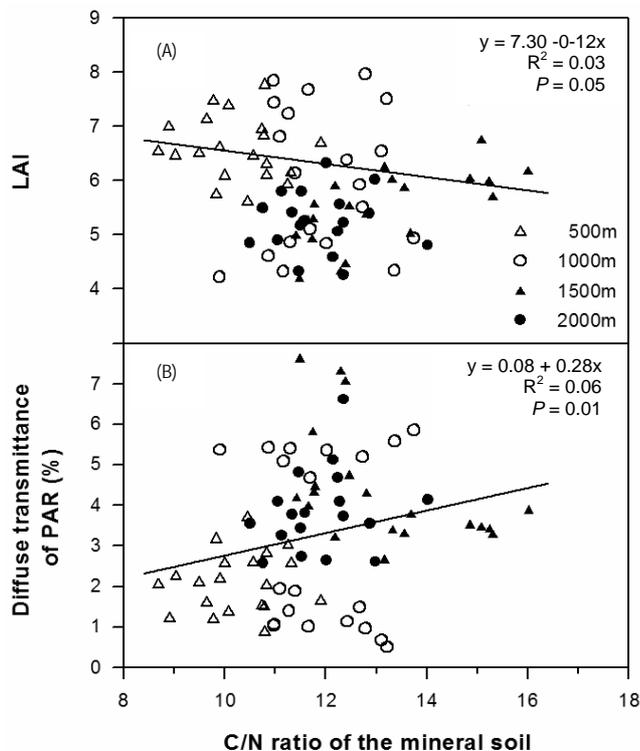


Fig. 6. LAI (A) and percent diffuse transmittance of PAR (B) as a function of the C/N ratio of the upper mineral soil in the 78 plots (all stems ≥ 5 cm dbh considered).

determined by Asner *et al.* (2003) for tropical evergreen forests (4.8 - 4.9). The mean LAI of 6.6 measured in our lowland plots was 10 % higher than the LAI of 6.0 reported by Clark *et al.* (2008) from a lowland rainforest in Costa Rica.

Our values from NE Ecuador are also higher than LAI-2000 measurements in three premontane to lower montane rainforests in South Ecuador (5.1 at 1050 m, 4.6 at 1540 m and 3.9 at 1890 m a.s.l., Moser *et al.* 2007) and in mountain forests in Sabah, Borneo (5.6 at 700 m, Kitayama & Aiba 2002). The comparatively low LAI values in the South Ecuadorian forests may in part result from the trees being less tall, and growing on rather steep slopes and relatively poor soils in that region (Homeier *et al.* 2010a).

We observed an altitudinal decrease of LAI by about 1.1 per 1000 m up the slope of the eastern Andes between 500 and 2000 m a.s.l. Similarly, Moser *et al.* (2007) found a leaf area decrease by 40 - 60 % between 1000 and 3000 m elevation in South Ecuador; they concluded from a pan-tropical data review that the LAI of tropical moist forests on average decreases by 1.0 per 1000 m altitude. According to their data, this reduction is mostly a consequence of the altitudinal decrease in tree height and an associated reduction in the number of canopy layers.

The light environment of forest plants in the understorey of tropical lowland and lower-montane rainforests is strictly energy-limited. How much radiation is available for forest-floor herbs and tree seedlings is dependent on the flux density of incident radiation, canopy PAR transmissivity, and day length, and thus may vary considerably with latitude, altitude, and forest type. Altitude influences the below-canopy radiation regime of tropical forests by changes in incident radiation and in canopy structure up the slope. In tropical mountains with a moist climate, incident radiation generally tends to decrease with altitude to the height of the condensation level where cloudiness is highest, and thereafter increases again towards the mountain peaks (Hastenrath 1991). On the eastern slopes of the equatorial Andes, the highest cloud frequency throughout the year is typically located at about 3000 m elevation (Bendix *et al.* 2008). In the absence of radiation data for the Sumaco transect, we thus assume, for our study region, that average incident radiation probably decreases from 500 to 2000 m due to increasing cloudiness. However, this putative decrease in incident radiation is fully compensated by an elevational increase in diffuse transmittance of PAR

Table 3. Mean (± 1 SE) of photosynthetic photon flux density (PPFD) at 2 m height above the forest floor at four different elevations.

Elevation (m)	PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
500	11.57 \pm 1.46
1000	7.85 \pm 0.58
1500	19.33 \pm 2.22
2000	35.49 \pm 4.48

from about 2 % at 500 m to ca. 4 % at 2000 m, as a result of the decrease in LAI by 1.4 over this altitude range in our transect. In fact, we measured average below-canopy PPFD rates under overcast sky (during the time interval 10 a.m. to 2 p.m.) that increased from 8 - 12 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 500 and 1000 m to $> 35 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 2000 m, despite a general increase in cloudiness with elevation. A tendency from closed to more open canopies with more gaps is also reflected by the within-plot coefficients of variation for LAI, which increase up the slope. The decrease in zenith LAI values with elevation confirms this tendency. Moreover, values for diffuse transmittance of PAR above 5 % are much commoner at 1500 and 2000 m than at 500 and 1000 m. Thus, tree seedlings and saplings, and also forest-floor herbaceous plants, are exposed to deeper shade in lowland forests than higher upslope in the montane forests of the Eastern Andes. This should have consequences for the survivorship of tree seedlings and the abundance of herbaceous plants in the forest communities up the slope. From his studies in lowland forests, Leigh (1999) concluded that, in both the tropics and the temperate zone, mature forests with leaf area indices around 7 are characterized by about 1 % of incident radiation reaching the forest floor. In our study, forests with LAI of about 7 reached a DT somewhat higher than this figure - about 1.4 ± 0.7 %. With average DT in the range of 2.0 to 2.7 %, the forests studied here at an elevation of 500 to 1000 m are comparable with two neotropical lowland forests investigated by Johnson & Atwood (1970, Puerto Rico) and Rich *et al.* (1993, Costa Rica), while two paleotropical lowland forests in Queensland and Malaysia were somewhat darker (about 0.4 % of canopy PAR transmissivity; Björkman & Ludlow 1972; Yoda 1974).

Gas exchange measurements (Björkman *et al.* 1972; Mulkey 1986) revealed that extremely shade - tolerant ground herbs of tropical forests reach

light compensation of photosynthesis already at PPFD rates of 0.5 to 1.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and may survive at flux densities of 2 - 4 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which equals about 0.3 - 0.6 % of incident radiation under overcast sky. In the darkest stand of our study, we measured a mean below-canopy PPFD under overcast sky of 1.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which seems to be close to this physiological limit of shade tolerance. However, the long-term average of forest-floor irradiance may be substantially higher, because our measurements did not include the penetration of direct sunlight through the canopy during irregularly occurring light flecks. Moreover, the large majority of our stands showed higher below-canopy PPFD rates, which in a few cases at higher elevation exceeded 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$. With a range of plot means of DT (averaged over the 40 measurements in a stand) from 0.5 to 7.7 %, the forest stands of our transect are slightly darker on the forest floor than a range of temperate broad-leaved forests in the lowlands of Central Europe at their maximum leaf area development (Ellenberg & Leuschner 2010), where plot-level means reach minima of about 1 % in certain beech (*Fagus sylvatica* L.) stands, but are often higher in oak, birch or pine forests where 8 % is often exceeded (Hagemeyer 2002). We conclude that extremely dense tropical - forest canopies can reduce PAR transmissivity to the forest floor to a greater extent than has been observed in most species-poor temperate forests. This discrepancy is valid, however, only in lowland forests; tropical lower montane and mid-montane forests typically have smaller leaf area indices. Thus, their PAR transmissivities are as high as, or even higher than, those of temperate lowland forests.

Effects of soil fertility, tree diversity and stand structure on LAI and canopy transmissivity

We found a significant increase in LAI with increasing stem density in our sample of 78 plots. A similar stem-density effect on stand leaf area was reported by Leuschner *et al.* (2006) for a sample of 23 closed, mature beech stands in Germany. In the Ecuadorian forests, increasing stem density was also associated with a decrease in percent diffuse transmittance of PAR. Several factors may affect the stem-density in relation to leaf area and transmissivity. First, a higher number of stems increases the surface area of woody axes in the canopy, thereby enlarging the plant surface-area index (PAI) which is the variable recorded by optical measurement; PAI is often

Table 4. Results of multiple regression analyses on the dependence of LAI and DT on various environmental and biotic factors. The following variables were tested: organic layer depth, stem density, stand basal area, tree species diversity, plant-available soil phosphorus concentration, soil C/N-ratio and pH of the organic layer and the upper mineral soil (0-10 cm). Only the significant factors ($P < 0.05$) were included in the final models.

Dependent variable	Model R ² (adjusted)	Source variable	Parameter estimate	R ²	P
LAI	0.35	Stem density	0.026	0.21	< 0.001
		P _a (organic layer)	-0.059	0.12	0.012
		C/N ratio (mineral soil)	-0.182	0.05	0.004
DT	0.27	Stem density	-0.051	0.20	< 0.001
		C/N ratio (mineral soil)	0.394	0.09	< 0.001

taken to be equal to LAI. Second, more stems can support more epiphytes and more lianas, which contribute to radiation interception in the canopy. Clearly, this explanation may not apply to temperate forests which lack vascular epiphytes.

Our data also reveal a significant positive relationship between tree diversity and leaf area index, LAI being on average about 1.3 higher in a stand with 50 species in an area of 400 m² than in a stand with only 20 species. This result might represent evidence in support of a positive diversity - productivity relationship in these tropical forests. Canopy carbon gain is a function of the amount of radiation absorbed by the stand leaf area, absorbed radiation being the difference between incident radiation and transmitted plus reflected radiation. Assuming that canopy reflectivity is less variable across the stands than is absorptivity, a decreasing PAR transmissivity would then be indicative of a higher radiation absorption, and thus higher productivity, of stands with larger leaf area indices. As with stem density, the apparent species diversity relation to LAI may have several reasons: First, the complementary use of canopy space by the foliage of different tree species could increase stand leaf area and canopy absorptivity, and would represent a true diversity effect. On the other hand, a sampling effect (species with large leaf areas are more likely to be included in species - rich than in species - poor stands), might also explain the observed relationship between diversity and leaf area.

The significant effect of tree species diversity (but not of stem density) on LAI disappeared when soil fertility indicators such as the N and P content of the upper mineral soil (0 - 10 cm) or the organic-layer horizons were included in the multiple regression analysis. The importance of nitrogen is

supported by the fact that properties related to forest structure and productivity (such as tree basal area, aboveground biomass, growth in tree basal area and wood productivity) were all positively related to parameters characterising the availability of mineral - soil N Unger *et al.* (2012).

In conclusion, our results indicate that stem density is the principal factor responsible for a higher LAI (or a lowered canopy transmittance) in the forests of the study region. Soil fertility seems to play only a secondary role for stand LAI. In contrast, the effect of tree diversity on LAI and DT remains speculative because of the close correlation of tree diversity with stem density and the multitude of changes along the elevational gradient of other abiotic and biotic factors that also influence LAI and DT.

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