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High litterfall in old-growth and secondary upper montane forest of Costa Rica

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Abstract Tropical upper montane forests usually comprise trees of small stature with a relatively low aboveground productivity. In contrast to this rule, in the Cordillera de Talamanca (Costa Rica), tall trees (>35 m in height and more than 60 cm in diameter) are characteristic for the upper montane old-growth oak forests which are growing at an altitude of almost 3,000 m close to the alpine timberline. For these exceptional forests, productivity data are not yet available. In this study, we analyzed litterfall and its components (tree leaves, litter of epiphytic vascular and non-vascular plants, mistletoes, twigs and other canopy debris) in three forest stands belonging to different successional stages and related seasonal changes in litterfall to micrometeorological variables. The studied stands were early-successional forest (10–15-year-old), mid-successional forest (40-year-old), and old-growth forest. The stands are dominated by *Quercus copeyensis* and are located at 2,900-m altitude. Total litterfall was highest in the mid-successional forest (1,720 g m^{-2} y^{-1}), and reached 1,288 g m^{-2} y^{-1} in the old-growth forest and 934 g m^{-2} y^{-1} in the early-successional forest. Litter mass was dominated by leaves in all stages (56–84% of total litterfall). In the old-growth forest, however, twigs and small canopy debris particles (33%), epiphytes (6%), and mistletoes (5%) also contributed substantially to litter mass. Leaf litterfall showed a clear seasonal pattern with a negative correlation to monthly precipitation and highest values in the dry season (January–April). However, the strongest correlation existed with minimum air temperature (negative), probably because temperatures already dropped at the end of the rainy season, when precipitation had not yet declined and leaf shedding already increased. In contrast, litterfall of epiphyte mass, and twigs and other debris was mostly dependent on occasional strong winds. We conclude that the upper montane oak forests of the Cordillera de Talamanca are exceptional with respect to the large tree size and the relatively high productivity as indicated by litterfall. Litter mass was especially high in the mid-successional and old-growth forests, where the observed annual totals are among the highest recorded for tropical forests so far.

Keywords Epiphytes · Forest succession · Litter production · Quercus · Seasonality

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Introduction

Tropical montane forests typically are built by trees of low canopy height and stem diameter, and a relatively

low aboveground productivity (Whitmore 1998; Lamprecht 1986). In the Cordillera de Talamanca of Costa Rica, however, a montane oak forest type exists in which tall trees with more than 35 m in height and more than 60 cm in diameter prevail (Kappelle et al. 1996). Oaks of this size predominately occur on the west facing slopes and in areas over 2,400 m high, and are not found in other regions of the country. In addition to a presumed high aboveground biomass, these forests also have a high fine root biomass (Hertel et al. 2003). Although data are not available, one may assume that productivity is also relatively high in this high-elevation forest type.

Litterfall may provide an indication of aboveground forest productivity because it is one of its main components. In addition, litterfall is a major pathway in forest nutrient cycles, and gives information on tree phenology (Proctor 1983). Data on aboveground litter production in tropical forests are available for a considerable number of lowland sites and also for various montane stands. However, it is not yet clear how litter mass changes with elevation. Litterfall was found to be relatively low in some montane forests (Bruijnzeel and Proctor 1995; Heaney and Proctor 1989; Moser et al. 2007), whereas other studies suggest that there is no systematic change in litterfall with elevation (Clark et al. 2001; Kitayama and Aiba 2002). Most studies on litterfall in tropical forests refer to old-growth forests. The few available data for young successional forests indicate that litterfall in early- to mid-successional stages may be higher than in mature forests (Ewel 1976; Kellman 1970; Ong et al. 1981).

Litterfall in tropical montane forests may significantly depend on the abundance of epiphytes. This aspect has so far only rarely been addressed, and if so, only in old-growth forests (e.g. Nadkarni and Matelson 1992). Seasonality in epiphytic litterfall may follow other temporal patterns than tree leaf fall because it seems to be controlled by different micrometeorological parameters. Many studies on tree leaf litterfall found a clear seasonal pattern with high rates in the dry season (e.g. Proctor et al. 1989; Tanner 1980). However, maximum litterfall may also occur during the rainy season (Proctor et al. 1983), or no seasonal changes may exist at all (Medina and Klinge 1983; Steinhardt 1979; Veneklaas 1991).

This study was conducted in the upper montane forest belt of the Cordillera de Talamanca, where the old-growth forests are composed of tall tropical oak species. Similarly, the secondary forests are dominated by *Quercus* species as well (Kappelle et al. 1996). The old-growth forests are characterized by the abundance of non-vascular epiphytes (Köhler et al. 2008). Study objectives were (1) to quantify litterfall and its components (tree leaves, epiphytic vascular and non-vascular plants, mistletoes, twigs and other canopy debris) in three successional stages, and (2) to analyze the seasonality of litterfall of the various components and its control by micrometeorological factors.

Methods

Study sites

The study was conducted in the Los Santos Forest Reserve located on the Pacific slope of the Cordillera de Talamanca in Costa Rica (9°35′40″ N, 83°44′ 30″ W). The sites were situated in the upper montane forest belt of the Los Santos Forest Reserve at an elevation of ca. 2,900 m a.s.l. Three study plots were selected: a 10–15-year-old early-successional forest (ESF), a 40-year-old mid-successional forest (MSF), and an old-growth forest (OGF). The ESF and MSF stands were separated from each other by 200 m. The OGF stand was about 2 km distant from the others. The selected plots were similar in slope (25–31°); the ESF and MSF plots were exposed southward, whereas the OGF showed a NE aspect. Annual average temperature at a station 15 km east of the study sites (Villa Mills, 3,000 m a.s.l.) is 10.9°C. Annual average rainfall is 2,812 mm; a dryer season occurs between December and April with average monthly precipitation of about 30 mm (January–March) and 100 mm (December and April) (Instituto Meteorológico Nacional 1988). Additional inputs via horizontal precipitation at these relatively sheltered sites are considered to be small (Köhler 2002). The soils of the study region are classified as Humic Andosols (FAO system) or Hapludands (USDA system) (Van Uffelen 1991; Kennis and De Vries 1993).

The OGF had previously been described as "primary forest" or "mature forest" (Kappelle et al. 1995, 1996). Stem density (trees ≥3 cm DBH, diameter at breast height) was 5,730, 4,800, and 3,460 n ha^{-1} in ESF, MSF, and OGF, respectively. Average tree basal area

was 5 m^2 ha^{-1} in various ESF stands, 18 m^2 ha^{-1} in the MSF stands and 57 m^2 ha^{-1} in the OGF stands (Kappelle et al. 1996). The height of the upper tree layer in the three stands of our study was about 5–9 m in the ESF, 11–15 m in the MSF, and 30–35 m in the OGF where single trees of even larger height occurred. There was only one tree layer in the secondary forests while there were two to three in the OGF. The stands were dominated by *Quercus copeyensis* (C.H. Müll.). In the old-growth forest, a second oak species (*Q. costaricensis* Liebm.) was also abundant. The ESF site was more species rich and contained more than 15 tree and shrub species on a 40 m × 40 m plot. Beside *Quercus copeyensis* and *Q. costaricensis*, species from the genera *Oreopanax*, *Viburnum*, *Myrsine*, *Weinmannia*, *Cleyera*, *Styrax*, *Cornus*, and others were present. The overall diversity of epiphytic bryophytes and macrolichens was high with a similar number of species occurring in the three forest stands (168 species in total; Holz 2006). At the stand level, the total epiphyte biomass increased with stand age from 160 kg dry - weight ha^{-1} in ESF to 520 kg ha^{-1} in MSF and 3,400 kg ha^{-1} in OGF (Köhler et al. 2008). In all stands, epiphytic vegetation was dominated by non-vascular plants (bryophytes and lichens) which accounted for 99% (ESF), 89% (MSF), and 70% (OGF) of the total epiphyte biomass (including canopy humus).

Measurements of micrometeorological parameters and precipitation

Micrometeorological parameters were automatically recorded at an open field adjacent to the successional forest sites. Air temperature and relative humidity (MP 100 A, Rotronic, Ettlingen, Germany; instruments well shielded) and wind speed (anemometer type 4.3519.00, Thies, Göttingen, Germany) were measured at 1.5 m above the ground. Data were sampled in 10-s intervals with a CR10X datalogger (Campbell, Shepshed, UK) and averaged every 10 min. Incident rainfall was recorded weekly on two clearings; the size of each clearing was several thousand square meters. One clearing was located in direct proximity of the early- and mid-successional forest stands adjacent to the micrometeorological station, the other was close to the old-growth forest. Five rainfall samplers at a height of 70 cm (aperture: 213.8 cm^2) were used on each clearing.

Litter sampling

Litterfall was collected at 4-week intervals during a full year (April 1999–April 2000) with ten, systematically distributed litter traps (2500-cm^2 aperture) in each stand. The litter traps were made of plastic gauze bags (2-mm mesh width) which were attached to wooden frames of 50 cm by 50 cm. They were placed horizontally at a height of about 0.5 m at regular intervals along three transects that run parallel to the contour lines within the 50-m long and 20-m wide study plot. On the upslope side of each trap a net was spread on the soil to avoid litter inputs from the steep slope above. To investigate seasonal dynamics of litter production, the traps were emptied precisely in intervals of 4 weeks (28 days) during the 12-month period. This schedule resulted in 13 sampling periods that do not correspond exactly to the months. Precipitation and other micrometeorological data were related to these sampling periods and therefore might differ slightly from data published before on the "real" month basis. The collected litter was transferred to the laboratory and separated into the following fractions: leaves, epiphytic vascular plants, epiphytic non-vascular plants (mosses, liverworts, and lichens), mistletoes, twigs and debris (which consists of twigs <2 cm in diameter, flowers, fruits, and unrecognizable organic matter particles from the canopy).

All litter samples were dried (70°C, 48 h) and weighed. To determine the percentage of oak leaves, leaves of *Quercus copeyensis* and *Q. costaricensis* were separated from leaves of other tree species from November 1999 to April 2000 in all leaf samples.

Statistical analyses

A Wilcoxon U-test, $P < 0.05$ (epiphytic vascular plants) and a Scheffé-test, $P < 0.05$ (other litter fractions) were used to determine whether significant differences existed between litter values measured in the three stands. Regressions between monthly litterfall values and microclimatological variables were calculated with the computer program Xact (Sci-Lab, Germany). Additionally, multiple linear regression models were applied using SAS software (SAS Institute Inc., Cary, NC, US; version 8.2).

Results

Micrometeorological parameters and precipitation

Rainfall during the study period did not differ much from the long-term average (2,812 mm y^{-1}) (Instituto Meteorológico Nacional 1988). It was 3,049 mm y^{-1} on the successional forest clearing and 3,002 mm y^{-1} on the clearing close to the OGF. Highest monthly precipitation was recorded at both stations in April 1999 with 431 mm (successional forest clearing) and 503 mm on the OGF clearing (Fig. 1a). During the dry season, the lowest precipitation within a 28-d period was 20 mm on the successional forest clearing and 25 mm on the OGF clearing.

Seasonality in temperature was low with the warmest period (May) exceeding the coldest month (January) in mean temperature by only 1.8 K. Absolute minimum temperature showed similar values of about 6°C during the rainy season; it was up to 4 K lower during the dry season (Fig. 1b). At ground level, frost was not uncommon during the dry season. Absolute maximum temperature differed only by 2.5 K during the year (20.6–23.1°C). The absolute maximum of vapor pressure deficit (VPD) was between 12 and 16 hPa during the rainy season and up to 23 hPa during the dry season. During most of the year, the maximum wind speed (10-min averages) ranged between 2 and 4 m s^{-1} but reached higher values (>5 m s^{-1}) in November (Fig. 1c). Single strong gusts, which were not recorded due to the automatic calculation of mean values, must have reached much higher velocities, especially in the tree canopies.

Annual litterfall

Total annual litterfall was 934 g m^{-2} y^{-1} in the ESF, 1,720 g m^{-2} y^{-1} in the MSF, and 1,288 g m^{-2} y^{-1} in the OGF (Table 1). In all three stands leaves were the dominating litter fraction and accounted for 84%, 73%, and 56% of total litter mass in the ESF, MSF, and OGF stands, respectively. While the percentage of leaf litter in total litter mass was decreasing with stand age, the proportion of all other litter fractions increased in this direction.

Litterfall of epiphytes increased with stand age and showed significantly higher values in OGF when compared to the secondary forests. In the OGF stand, litterfall of vascular epiphytes exceeded the corresponding values of ESF and MSF by factors of 29 and 11, respectively. Litterfall of non-vascular epiphytes was 10- and 4-fold higher in OGF than in ESF and MSF. The contribution of epiphytes to total litterfall was low with 0.5% in the ESF and 0.7% in the MSF stands, but accounted for 6.1% in the OGF. Especially vascular epiphytes showed a high spatial and temporal heterogeneity of litterfall as expressed by high standard errors. In the OGF, litter of a mistletoe

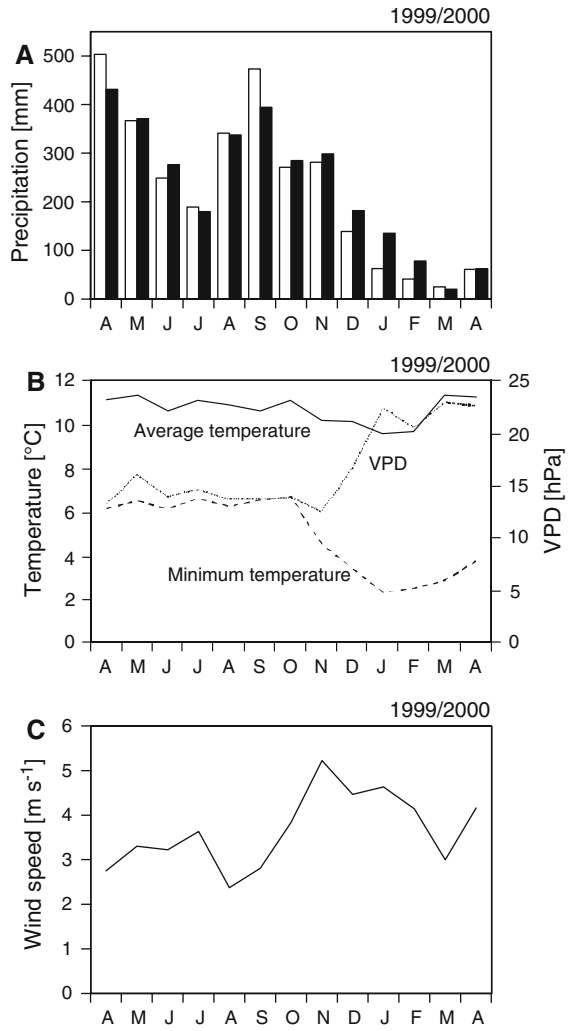

Fig. 1 (**a**) Monthly rainfall on a clearing close to the early- and mid-successional forests (black bars) and on a clearing close to the old-growth forest (white bars). (**b**) Average temperature, absolute minimum temperature and absolute VPD maximum on a clearing close to the successional forests. (**c**) Maximum wind speed. Indicated in **a**– **c** are sampling periods of 28 days that do not exactly correspond to the months

Table 1 Annual litterfall of leaves, twigs (diameter <2 cm), and other debris (including mistletoes), epiphytic non-vascular plants, epiphytic vascular plants, and total litterfall in the studied early-successional forest (ESF), mid-successional forest (MSF), and old-growth forest (OGF) (means ± SE)

	Annual litterfall [g m^{-2} y^{-1}]		
	ESF	MSF	OGF
Tree leaves	787 ± 66 a	1,259 ± 77 b	720 ± 40 a
Twigs and debris	142 ± 22 a	449 ± 50 b	489 ± 32 b
Epiphytic non-vascular plants	3 ± 1 a	8 ± 2 a	35 ± 2 b
Epiphytic vascular plants	2 ± 1 a	4 ± 1 a	44 ± 8 b
Total litterfall	934 ± 78 a	1,720 ± 118 b	1,288 ± 61 a

Significantly different means between the forest types are indicated by different letters. Epiphytic vascular plants: Wilcoxon U-test, $P < 0.05$; other litter fractions: Scheffé-test, $P < 0.05$

(*Phoradendron* spp.) accounted for about 5% of total litterfall, while it was virtually absent (<1 g m^{-2} y^{-1}) in the two successional forests.

Seasonality of litterfall

Leaf litter showed a distinct seasonality with highest monthly values at the beginning of the dry season and much lower quantities in the rainy season (Fig. 2). In all stands, highest values of leaf litter were measured in January when the amount of leaf litter exceeded the minimum values of August by factors of 4, 6, and 12 in ESF, MSF, and OGF, respectively.

In January, when leaf litterfall peaked, percentage of oak leaves was very high in the MSF and OGF stands (97 and 95% of total leaf litter; Table 2). In month with lower leaf litterfall (e.g. April 2000) oak leaves contributed with a lower percentage to the

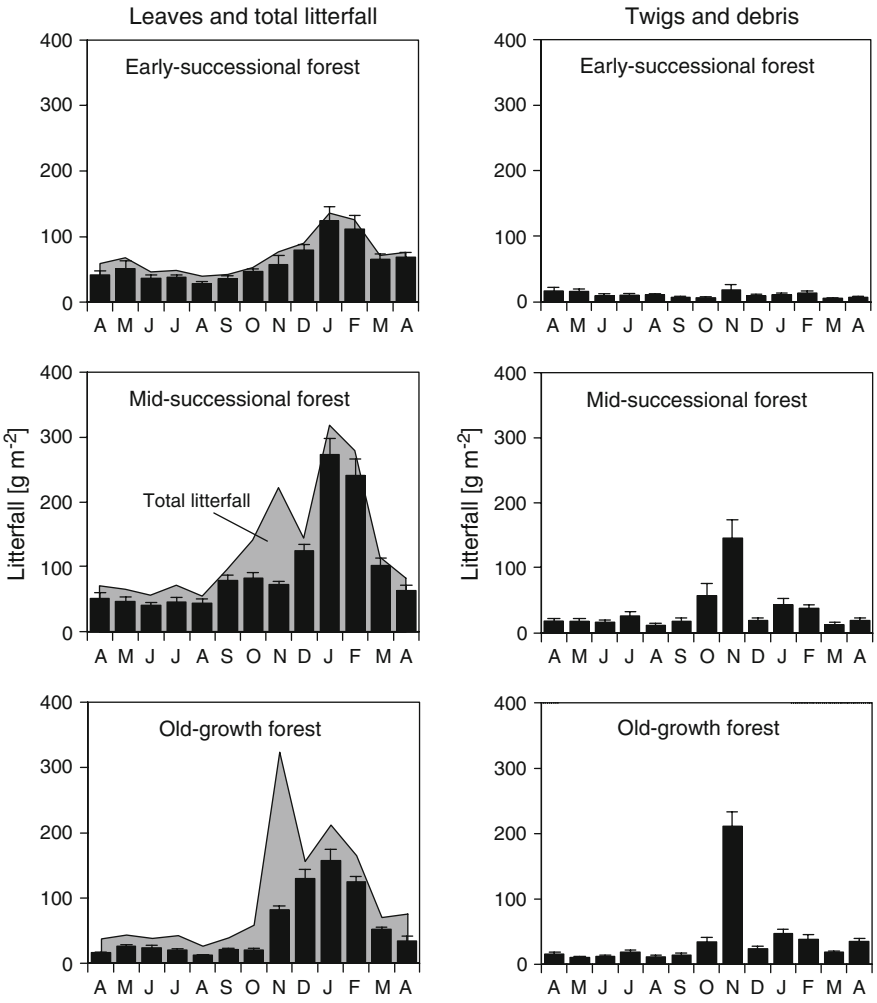

Fig. 2 Mean monthly litterfall of leaves (bars) and total litterfall (shaded area) and of twigs and debris (including mistletoes) in the early-successional forest (ESF), mid-successional forest (MSF), and old-growth forest (OGF). The sampling periods (28 d) do not exactly correspond to the months

Table 2 Percentage of oak leaves (mainly *Quercus copeyensis*) in the leaf litter mass in the early-successional forest (ESF), mid-successional forest (MSF), and old-growth forest (OGF) from November 1999 to April 2000 (means ± SE)

	Oak leaves [% of total leaf litter]		
	ESF	MSF	OGF
November	49 ± 10	–	83 ± 4
December	59 ± 6	91 ± 8	94 ± 1
January	62 ± 8	97 ± 2	95 ± 1
February	40 ± 6	95 ± 4	96 ± 1
March	19 ± 8	88 ± 7	86 ± 3
April	31 ± 9	78 ± 8	56 ± 4

total amount of leaf litter (78% in MSF and 56% in OGF). In the ESF stand, where oak species were also abundant but less dominant, *Quercus* leaves contributed by 62% to the total amount of leaf litter in January. In March, when total litterfall was low in this stand, the percentage of oak leaves was also relatively low (19%).

Because of the dominance of leaf litter, total litterfall in most sampling periods showed a similar pattern as leaves except for November (Fig. 2). Due to the high amount of twigs and debris in the MSF and OGF stations (Fig. 2), total litterfall exceeded the amount of leaf litter by a factor of 3 (MSF) and 4 (OGF) during this period. In the ESF, litterfall of twigs and debris was also highest in this period but contributed less to total litterfall due to the strong dominance of leaves in this stand (84%). Litterfall of twigs and debris showed no clear seasonality but peaked during occasional periods of high wind speed (e.g. November; Fig. 1).

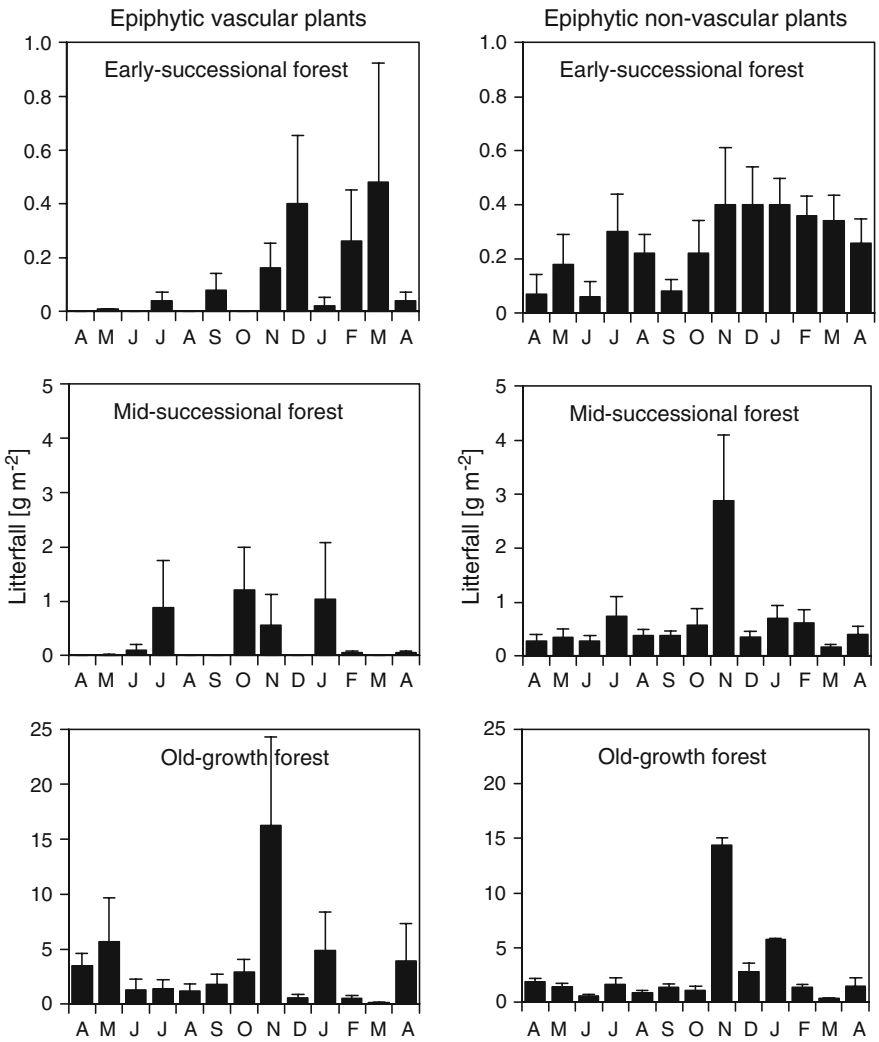

Fig. 3 Mean monthly litterfall of epiphytic vascular plants and of epiphytic non-vascular plants in the early-successional forest (ESF), mid-successional forest (MSF), and old-growth forest (OGF). The sampling periods (28 d) do not exactly correspond to the months

Table 3 Regression of monthly litterfall data on microclimatological variables (monthly means) in the studied early-successional forest (ESF), mid-successional forest (MSF), and old-growth forest (OGF). Maximum wind speed is given for 10-min averages

	Direction of effect	ESF		MSF		OGF	
		$r^2_{adj.}$	P	$r^2_{adj.}$	P	$r^2_{adj.}$	P
Leaf litterfall							
Precipitation	–	0.35	*	0.20	n.s.	0.32	*
Mean temperature	–	0.45	**	0.60	**	0.71	***
Absolute min. temperature	–	0.77	***	0.57	**	0.68	***
Absolute max. temperature		0.05	n.s.	0.04	n.s.	0.08	n.s.
Absolute max. of VPD	+	0.50	**	0.31	*	0.19	n.s.
Max. wind speed	+	0.34	*	0.17	n.s.	0.46	**
Litterfall of epiphytic non-vascular plants							
Max. wind speed	+	0.47	**	*0.93*	***	*0.96*	***
Litterfall of epiphytic vascular plants							
Max. wind speed	+	0.00	n.s.	*0.01*	n.s.	*0.81*	***
Litterfall of twigs and debris							
Max. wind speed	+	*0.12*	n.s.	*0.87*	***	*0.97*	***

Given are adjusted regression coefficients, significance is indicated at $P < 0.001$***, $P < 0.01$**, and $P < 0.05$*; n.s., not significant. Italic values represent exponential regressions; all other regressions are linear. + or – behind the variables indicate the direction of the effect

Similarly, the litterfall of epiphytic vascular and non-vascular plants showed no clear seasonal pattern and in most cases highest litterfall was measured in the sampling period of November (Fig. 3). For example, litterfall in the OGF was 7 times higher (epiphytic vascular plants) in November and more than 8 times higher (epiphytic non-vascular plants) as compared to the average litter production during the rest of the year. Within this 4-week period 37% of the annual litterfall of epiphytic vascular plants and 42% of the annual litterfall of epiphytic non-vascular plants were measured in the OGF. In the two successional forests, litterfall of epiphytes during November was less pronounced with the exception of the litterfall of non-vascular epiphytes in the MSF which accounted for 35% of the annual total of this litter fraction in this month (Fig. 3).

Litterfall and its relation to micrometeorological parameters

In the MSF and the OGF stands, strong correlations existed between litterfall and some of the micrometeorological parameters (Table 3). Negative relationships were found between leaf litterfall and mean temperature and absolute minimum temperature in all stands; this indicates that litter production was higher in the dry season with lower temperatures. Negative correlations were also found between leaf litterfall and precipitation, while leaf litterfall was positively related to maximum VPD and maximum wind speed. No correlation was found between leaf litterfall and absolute maximum temperature. For leaf litter fall in the ESF, minimum temperature was the only significant parameter in a multiple linear regression and explained 79% of the variation observed. In the MSF 87% of the variation in leaf litterfall can be explained by average temperature (63%) and VPD (24%). In the OGF average temperature (73%) and minimum temperature (18%) explained 91% of the variation observed in leaf litterfall.

Litterfall of vascular and non-vascular epiphytes in the OGF was highly influenced by wind speed as indicated by the strong correlation between maximum wind speed and litterfall in this stand (Table 3). In the MSF stand, a strong correlation with wind speed was found for non-vascular epiphytes while no relationship existed between wind and litter in the case of vascular epiphytes. In the ESF, where biomass of epiphytes was low, litterfall of epiphytes was much less influenced by wind (Table 3). There was no correlation between litterfall of epiphytes and temperature, VPD, or precipitation. A close correlation existed between

litterfall of twigs and debris and maximum wind speed in the OGF and MSF stand. The multiple linear regression also confirms the strong impact of the wind on the litterfall of epiphytes. In the MSF 65% of the variation in litterfall of non-vascular epiphytes can be explained by wind (43%) and VPD (22%). In the OGF wind (51%) and rainfall (18%) explained 69% of the variation observed in litterfall of non-vascular epiphytes. In the ESF probably due to the very low biomass of non-vascular epiphytes there was no significant influence of the wind but minimum temperature explained 53% of the observed variation. In the OGF 65% of the variation in litterfall of vascular epiphytes can be explained by wind (43%) and VPD (22%). In the secondary forests (ESF and MSF) where biomass of vascular epiphytes was low there was no impact of the factor wind and minimum temperature was the only significant parameter that explained 45% of the variation in litterfall both, in ESF and MSF.

Discussion

Litterfall in tropical montane forests

Litterfall in tropical upper montane forests has often been reported to be lower than in forests of lower elevations (Bruijnzeel and Proctor 1995; Heaney and Proctor 1989; Moser et al. 2007). Along an elevational transect at Volcán Barva (Costa Rica), which is not far from our study sites in the Cordillera de Talamanca, total litterfall at four different sites decreased continuously from 900 g m^{-2} y^{-1} at 100 m a.s.l. to 530 g m^{-2} y^{-1} at 2,600 m a.s.l. (Heaney and Proctor, 1989). In contrast, Kitayama and Aiba (2002) found no reduction in litterfall along an elevational transect from 700 to 3,060 m a.s.l. at Mt. Kinabalu (Malaysia). By comparing litterfall of 28 old-growth tropical forest sites, Clark et al. (2001) concluded that litterfall does not change systematically with elevation. This agrees with the results of a meta-analysis of leaf litter data from various tropical montane forests by Röderstein et al. (2005) who also did not find a significant elevational change in leaf litter mass between 1,000 and 3,060 m a.s.l. This data compilation of 18 montane forest stands revealed a mean leaf litterfall of 474 g m^{-2} y^{-1} for old-growth tropical montane forests (Röderstein et al. 2005). The highest leaf litterfall was measured in a tropical montane forest in Ecuador (862 g m^{-2} y^{-1} at 1,890 m a.s.l.); these data, however, included a small fraction of non-leaf fine litter <5 mm as well (Röderstein et al. 2005). These authors assume that litterfall quantities are still underestimated because a certain degree of decomposition may have taken place within the 6-week sampling intervals. Our leaf litterfall total for the OGF stand (720 g m^{-2} y^{-1} at 2,900 m a.s.l.) thus seems to be the second highest value so far reported for tropical old-growth montane forests. However, there is a lack of studies on litterfall from upper montane forests since most studies were carried out at elevations well below 2,500 m a.s.l.

Data from young successional forests by Ewel (1976), Kellman (1970), and Ong et al. (1981) suggest that after 15 years (or even less) litterfall of leaves and other small particles may be as high as, or even higher than, in tropical mature forests. A comparison of litter production in 9 tropical montane secondary forests by McDonald and Healey (2000) also revealed a high average value of 1,170 g m^{-2} y^{-1} for total litterfall. This average includes the extremely high value measured by Fournier and Comacho de Castro (1973) in a premontane secondary forest stand in Costa Rica (2,700 g m^{-2} y^{-1}). When excluding this study, the mean litterfall rate of secondary forests is 980 g m^{-2} y^{-1}. This is still higher than average litter production measured in montane old-growth forests (790 m^{-2} y^{-1}; 20 studies, McDonald and Healey 2000). The litterfall amount of the ESF stand in our study (934 g m^{-2} y^{-1}) lies within the range of values reported for other secondary forests (700–1,250 g m^{-2} y^{-1}; excluding Fournier and Comacho de Castro (1973)) by McDonald and Healey (2000). The high litterfall measured in our MSF stand (1,720 g m^{-2} y^{-1}) exceeds this range significantly but is lower than the very high value found by Fournier and Comacho de Castro (1973).

Herbivory may significantly reduce litter mass collected in litter traps. Clark et al. (2001) estimated that herbivory results in an underestimation of leaf litter mass in tropical forests by about 12%. We have no exact data on herbivory in our forest stands but based on observations of tagged leaves and leaves inside the litter traps, which showed only little signs of herbivory, we assume that mass loss due to herbivory must be relatively low in the studied stands. One reason for a low herbivory rate might be the relative low specific leaf area of the dominating

oak species *Quercus copeyensis* and *Q. costaricensis* (74.1 and 67.6 cm^2 g^{-1}; Köhler 2002). Moreover, herbivory should be rather low in the cool mountain climate of the Cordillera de Talamanca, when compared to hot lowland environments.

Only few studies have quantified litterfall of epiphytes, which were, as far as we know, all conducted in mature forest. At four different sites of the Jamaican montane rain forest, Tanner (1980) reported 0.4 to 18 g m^{-2} y^{-1} of epiphyte litterfall (mainly bromeliads). In a montane rainforest in Colombia, Veneklaas (1991) documented an epiphytic litterfall of 22 and 23 g m^{-2} y^{-1} in two forest stands at different elevations (2,550 and 3,370 m a.s.l., respectively). Similar litter quantity of epiphytes (23 g m^{-2} y^{-1}) was measured in a cloud forest in Venezuela (Steinhardt 1979). The highest value reported so far (50 g m^{-2} y^{-1}) was found in a cloud forest in Monteverde, Costa Rica, by Nadkarni and Matelson (1992) which consisted by more than 75% of bryophytes. Epiphyte litterfall measured in our OGF stand (79 g m^{-2} y^{-1}) was higher than the value measured in Monteverde, despite a relatively small epiphyte biomass in the Talamanca OGF stand (3.4 Mg ha^{-1} in the Talamanca *vs.* 33.1 Mg ha^{-1} in Monteverde) (Köhler et al. 2008; Nadkarni et al. 2004). However, biomass and annual litterfall of epiphytes in different stands are not necessarily related to each other. Litter mass may also depend on species composition and species longevity, the structure of the host trees, the aerodynamic roughness of the stand, and wind speed. In our study, biomass and litterfall of epiphytes both increased with increasing stand age from ESF to OGF. The percentage of litterfall from epiphytic vascular plants in relation to total epiphytic litterfall increased with stand age (31% ESF, 33% MSF, 56% OGF), thus reflecting the higher biomass of vascular epiphytes in the OGF (Köhler et al. 2008).

Since litterfall is one of the main pathways in the nutrient cycles of forests, it is often measured to quantify nutrient transfer from the plants to the forest floor. In our three forest stands, nutrient concentrations in leaf litter for most elements were in the range of values reported for other old-growth montane forests in the tropics (Heaney and Proctor 1989). Nutrient return with leaf litterfall was very high in comparison to other tropical montane forests, which was mainly due to the high amounts of leaf litter in these stands (Köhler et al. 2006). However, nutrient flux with litterfall of epiphytic non-vascular plants was low. It accounted for only 2–5% of the nutrient flux with leaf litter in the OGF while it was less than 1% in the two successional forests (Köhler et al. 2006). Compared with the nutrient input into the forest floor via net precipitation, the nutrient flux with leaf litterfall was 16–20 times larger for N, 4–10 for Ca, and 2–4 for Mg. Only K flux, which is often underestimated in litterfall due to leaching losses from the litter traps, showed about 2 times larger fluxes via net precipitation than by leaf litter for all three stands (Köhler et al. 2006).

Seasonal dynamics of litterfall

Studies in tropical rainforests have shown that litterfall may be either peak in dry periods (Proctor et al. 1989; Tanner 1980) or alternatively in the wettest season (Proctor et al. 1983). Other studies found subsequent litterfall peaks in the dry and also in the wet season (Röderstein et al. 2005), or identified no marked seasonal changes in litterfall at all (Medina and Klinge 1983; Steinhardt 1979; Veeneklaas 1991). Our results revealed a pronounced seasonal pattern in leaf litterfall with higher values at the beginning of the dry season and a strong dependence of litterfall on micrometeorological parameters. Because maximum litterfall occurred in January, when temperatures were relatively low, a strong negative correlation was found between temperature (mean and absolute minimum) and leaf litterfall. Low temperatures may play a key role as a trigger for the initiation of leaf abscission. Although there was a negative correlation between precipitation and leaf litter production, it is unlikely that decreasing precipitation plays a key role as a trigger for leaf litterfall in these montane oak forests. In the OGF, the increasing leaf litter production started already in November at the end of the rainy season when precipitation was still high (281 mm). During this month, the minimum temperature already had decreased by more than 2 K in comparison to the previous month.

Seasonality in leaf litterfall in the Cordillera de Talamanca was highly determined by tree species of the genus *Quercus* (mainly *Quercus copeyensis*, and to a lesser extent *Q. costaricensis*). The genus *Quercus*, on many sampling occasions accounted for over 90% of the total leaf litter and oak leaves were particularly frequent when total leaf litterfall

was highest. The ESF stand where oaks are less dominant, showed a lower percentage of oak leaves and less pronounced seasonal dynamics in leaf litter production than the MSF and OGF stands.

The litterfall of epiphytes showed no clear seasonal pattern, which is in accordance with other studies that quantified seasonal litterfall of epiphytes (Steinhardt 1979; Tanner 1980; Veneklaas 1991; Nadkarni and Matelson 1992). Litterfall of vascular and non-vascular epiphytes in the OGF was highly influenced by sporadic strong winds as indicated by the tight correlation between maximum wind speed and litterfall in this stand. The lower wind influence in the two successional forests is probably a consequence of the lower epiphytic biomass in these stands and also their smaller aerodynamic roughness.

Conclusions

The old-growth oak forests in the high Cordillera de Talamanca are characterized by tall trees with a large basal area, which differs noticeably from many other tropical montane forests. We found that this forest is also remarkably productive in terms of annual litter mass produced. However, litterfall peaked in a 40-year-old secondary forest, where the observed values are among the highest recorded for tropical forest so far. In old-growth and secondary forests there was also a marked seasonality with high leaf litterfall during the dry season which was mainly attributed to the occurrence of oak trees.

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