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ORIGINAL PAPER

Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica

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Abstract Epiphytic biomass, canopy humus and associated canopy water storage capacity are known to vary greatly between old-growth tropical montane cloud forests but for regenerating forests such data are virtually absent. The present study was conducted in an old-growth cloud forest and in a 30-year-old secondary forest (SF) on wind-exposed slopes in the Cordillera de Tilarán (Monteverde area) in northern Costa Rica. Epiphytic vegetation in both forests was dominated by bryophytes. Epiphyte mat weight (epiphyte biomass and canopy humus) at the stand level was 1,035 kg ha^{-1} in the SF and 16,215 kg ha^{-1} in the old-growth forest (OGF). The water contents of epiphytic bryophytes in the OGF were determined gravimetrically in situ and showed maximum values of 418% ± 74 (SD)% of dry weight and minimum values of 36% ± 10 (SD)%. Maximum stand water storage of non-vascular epiphytes and canopy humus at Monteverde was estimated at 0.36 mm for the SF and 4.95 mm for the OGF. Epiphytic bryophytes exhibited more dynamic wetting and drying cycles compared to canopy humus. Maximum water loss through evaporation was 251% of dry weight (bryophytes) and 117% of dry weight (canopy humus) within 3 days of sunny weather without precipitation. Despite the high potential water storage capacity of epiphytic bryophytes and canopy humus the actually available storage is likely to be much smaller depending on antecedent rainfall and evaporative conditions.

Keywords Bryophytes · Canopy · Rain forest · Rainfall interception · Succession · Water storage capacity

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Introduction

The epiphyte communities of tropical montane forests constitute a conspicuous feature of the canopy, particularly in cloud forests (Nadkarni 1984). Epiphytic abundance is believed to reflect the prevailing micro-climatic conditions (Frahm and Gradstein 1991) and is expected to influence the interception of rainfall and cloud water (e.g., Pócs 1980; Veneklaas and Van Ek 1990; Ataroff and Rada 2000). One major influence on canopy water fluxes is through the enhancement of overall canopy water storage capacity by poikilohydric epiphytes such as bryophytes. Information on epiphyte biomass and composition as well as the associated water dynamics is a prerequisite for better understanding cloud and rain water interception in montane forests, for example through process modelling (Hölscher et al. 2004; Bruijnzeel 2005).

Published estimates of epiphytic biomass and canopy humus at the stand level for old-growth forests (OGFs) in mainly neotropical montane regions range from 370 kg ha^{-1} in cyclone-ridden stunted ridgetop montane rain forest in Jamaica (Tanner 1980, 1985) to 44,000 kg ha^{-1} in a perhumid upper montane rain forest in Colombia (Hofstede et al. 1993).

As a result of past and ongoing deforestation, land-use types other than OGFs already cover increasingly large areas in the montane tropics (Giambelluca 2002; Bubb and Das in press). After abandonment of agricultural activities, secondary forests (SFs) may establish and influence biodiversity, forest hydrological functioning and biogeochemical cycling (e.g., Kappelle et al. 1995; Helmer 2000; Hölscher et al. 2005). However, data on epiphytic biomass and canopy humus in secondary tropical montane forests are extremely scarce (e.g., Nadkarni et al. 2004).

Data on epiphyte biomass and canopy humus and estimates of the associated maximum water storage alone may not be enough for an improved understanding of canopy water fluxes in montane forests. Also the dynamics of actual water storage are important. For an old-growth upper montane forest in the Cordillera de Talamanca in Costa Rica a modelling study suggested that the non-vascular epiphytes of the dominant oak trees contributed 6% to the total rainfall interception, which was less than expected on the basis of their considerable potential water storage capacity. The main reason for this finding was that during rainy periods with frequent storms only part of the total storage was effectively available as the mosses were persistently close to saturation under such conditions (Hölscher et al. 2004).

The present study was conducted in an old-growth montane cloud forest and in a nearby 30-year-old SF situated on the wet and windward Atlantic slopes of the Cordillera de Tilarán (Monteverde area) in northern Costa Rica. The objectives were to: (i) describe the composition and distribution of the epiphytic vegetation and canopy humus in the two stands, (ii) estimate their biomass at the stand level and (iii) analyse in situ water storage dynamics of epiphytic bryophytes and canopy humus.

Study sites

The study was carried out between February and July 2003 in two small headwater catchments in the San Gerardo area within the Caño Negro drainage basin on the Atlantic slopes of the Costa Rican Cordillera de Tilarán located ca. 10 km NE of the town of Santa Elena (10°21′33″N, 84°48′5″W). The old-growth windward lower montane cloud forest (OGF) was located at an elevation of 1,490 m asl. on a steep (32°) slope of westerly aspect. The approximately 30-year-old strip of SF was located at 1,620 m asl. on a slope of 15° having a north-westerly aspect. Both stands were exposed to high rainfall and cloud incidence and separated from each other by approximately 1 km. In the OGF the height of the upper tree layer was 22–25 m with an irregular canopy surface where epiphyte-laden emergent trees were sticking out of the main canopy by several meters. Common tree species of the upper canopy in windward cloud forest included: *Ficus crassiuscula* Warb. ex Standl., *Elaeagia auriculata* Hemsley, *Weinmannia wercklei* Standl. and several species of Myrtaceae e.g., (Lawton and Dryer 1980). In the lower tree layer of the OGF tree ferns and palms were abundant. In the SF stand the height of the upper tree layer was 9–12 m with individual out sticking remnant trees and old stumps from the former OGF. Tree ferns and palms were nearly absent, but Melastomataceae (*Miconia* spec.) were abundant. Long-term rainfall data for the higher parts of the Atlantic slope of the Cordillera de Tilarán are not available, but conventionally measured vertical rain input at the OGF site for the year period between 1 July 2003 and 30 June 2004 was about 6,000 mm (n = 303 rain days). At the windier SF site 4,385 mm of rain were recorded during the same period

(n = 298 rain days). A somewhat drier period prevails between February and April, with monthly rainfall totals generally being less than 150 mm (and typically 13–16 rain days per month) as opposed to 500 mm or more during the remainder of the year (and 27–31 rain days per month). Due to the prevailing high wind speeds there is a major horizontal precipitation component in the form of wind-driven rain and fog. Measured horizontal precipitation totals (defined as having an angle of 85–90° from the vertical) during the July 2003–June 2004 period amounted to 2,740 mm at the OGF site vs. 5,085 mm at the SF site (Bruijnzeel et al. 2006). Similarly, at a leeward lower montane cloud forest site on the other side of the nearby Continental Divide near Monteverde where contributions by wind-driven rain and low cloud are likely to be much lower than at the present study site, Clark et al. (1998) reported vertical and horizontal precipitation totals for a 1-year period of 3,191 mm and 886 mm, respectively. As such, conventional rainfall measurements in the San Gerardo/Monteverde area more or less seriously underestimate the total precipitation input and thus the conditions experienced by the epiphytes will be correspondingly wetter. The average annual temperature at the OGF site in 2003 was 17.0°C (16.6°C at the SF site) with a monthly range between 15.4°C and 17.7°C. Relative humidity was generally above 90% and foggy conditions prevailed for 50% (at night) to 60% (during the day) of the time (K.F.A. Frumau, unpublished data). An overview of stand characteristics is given in Table 1.

Table 1 Characteristics of an old-growth windward montane cloud forest and a secondary montane cloud forest at San Gerardo, Monteverde, Costa Rica. Stem density and basal area are given for trees ≥5cm diameter at breast height only

	Old-growth forest (OGF)	Secondary forest (SF)
Elevation (m asl.)	1,490	1,620
Approx. annual rainfall (mm)	6,000	4,385
Average temperature (°C)	17.0	16.6
Exposition	W	NW
Average inclination (°)	32	15
Plot size (m^2)	1,000	330
Age (yr)	–	30
Average canopy height (m)	22–25	9–12
Number of stems (n ha^{-1})	1,890	2,152
Basal area (m^2 ha^{-1}]	69.6	35.9

Materials and methods

Stand structure

Diameters at breast height (dbh at 1.30 m) were measured on all trees with dbh ≥ 5 cm within a horizontally projected area of 1,000 m^2 (OGF) and 330 m^2 (SF). For trees with buttresses the circumference was measured at the nearest possible height above 1.30 m. Before the measurements were taken, the respective areas of the stems were cleared of epiphytes and climbers. Additional information on stand structure (number of tree ferns, palms as well as number of trees with strongly deformed crowns) was recorded.

Epiphyte sampling

Distribution and composition of epiphytes

A total of 265 epiphyte mat samples were collected from nine trees in the OGF and from six trees in the SF plot (Table 2). Sampled trees belonged to seven species in the OGF vs. six species in the SF. In the OGF three trees in each

Table 2 Epiphyte sampling in an old-growth and a secondary montane cloud forest at San Gerardo, Monteverde: Sampling positions, numbers of samples per category and average tree surface areas of samples

Sampling position	Number of samples	Average Sample area (cm^2)
Old-growth forest		
Inner branches	45	636
Middle branches	35	327
Outer branches	45	178
Stems	62	708
Secondary forest		
Inner branches	30	429
Outer branches	30	470
Stems	18	898

of three dbh-classes (5–20 cm, 20–60 cm, and >60 cm) were selected to represent different tree size classes. Since all trees in the SF ranged between dbh 5 and 25 cm no different tree size classes were established there. Selection of sample trees was based on crown accessibility for climbing as well as on visual assessment of their representativity in terms of epiphyte biomass. Trees were climbed using single-rope techniques (Perry 1978), or by ladder in the case of smaller trees in the SF. For trees in the SF, trunks, and inner- and outer branches were distinguished. In the OGF the sampled trees were stratified into main sections (trunk, inner branches, middle branches and outer branches) in accordance with the specifications of Johansson (1974). Epiphyte mat dry weight-to-substrate surface area ratios were obtained by collecting five samples from each branch section per tree. Samples were collected from areas encircling the branches. Samples from inner and middle branches were taken in situ but samples from the outer branches were collected after cutting off the outer branch sections (as these were inaccessible through climbing) and lowering them to the ground by rope. The latter procedure was not possible for branches of the tallest dominant trees in the OGF stand where the cut-off sections were allowed to just fall onto the ground. The forest floor underneath the sample trees was cleaned previously from epiphytic material. Loss of epiphytes from fallen branches was negligible.

The trunks were sampled by stripping off epiphyte mats within bands encircling the trunk at different heights. For trees of the bigger dbh-classes rectangular areas of 20×30 cm (expositions N, S, W, E) were sampled at different heights on the trunk. All samples were taken to the Santa Elena field laboratory and subsequently separated into the following fractions: (1) bryophytes, (2) lichens, (3) ferns, (4) bromeliads, (5) remaining vascular plants and (6) canopy humus. The category canopy humus refers to both partly and highly decomposed organic matter. The fractionated samples were oven-dried at 70°C for 48 h to obtain dry weight with a precision of 0.1 g (Sartorius BL 3100). In view of the abundance of tree ferns in the OGF plot having a dense epiphyte cover on their stems while the leaf rosettes were generally free of epiphytes, the stems of three tree ferns were sampled by collecting epiphyte mats at three different heights on the trunk.

Total epiphyte mat weight

One branch from each individual sample tree was sawn off and lowered to the forest floor for the estimation of total epiphyte mat weight. These were the same branches as used for the distribution and composition sampling of epiphytes (see previous section). Total remaining epiphyte mat cover of the three different branch sections was removed and weighed in the field. A sub-sample taken from each section was oven-dried to obtain a conversion factor to dry weight. Total epiphyte mat weight of the crown per tree was then estimated by multiplying weight of epiphyte biomass and canopy humus of the single branches times the total number of branches within the crown. Epiphyte mat weight of the trunks was obtained by multiplying the epiphyte mat dry weight-to-substrate surface area ratio times stem surface area per tree. To calculate the latter, the stem was divided into segments of varying length that were assumed to be cylindrical in shape. For each section, length and mid-segment diameter were measured and section surface areas were summed. Stems were often also covered with climbers that (in contrast to the epiphytes) rooted in the soil of the forest floor. However, it was not always possible to determine whether plants had a connection to the ground or were true epiphytes. Only clearly recognizable epiphytes were sampled, and therefore the epiphyte biomass obtained for the trunks must be regarded as conservative. However, very few climbers occurred in the tree crowns and differentiating between epiphytes and climbing plants was much easier there.

The average epiphytic mat weight values for single trees were extrapolated to estimate epiphyte mat weight at the stand level. Single-tree values were multiplied times the number of stems within the corresponding dbh-class. For tree ferns, and trees with a strong crown deformation, only the average epiphyte mat weight on the trunks was taken into account, neglecting crown epiphyte mat weight. Palms were usually free of epiphytes and canopy humus and therefore assumed not to contribute epiphyte mat weight to the overall total.

Water content of epiphyte mats

The monitoring of the water content of epiphyte mats focused on bryophytes and canopy humus because: (i) they are known to have high water storage capacity, and (ii) they made up a high percentage of the total epiphyte mat weight of the investigated stands (see results below).

The water contents of bryophytes and canopy humus were monitored in situ in the OGF from March to July 2003. More than 600 samples were collected in total. Sampling was carried out at irregular intervals in order to determine the minimum and maximum water storage values under the prevailing climatic conditions. Mean sampling interval was 4.7 days (range 1–18 days). Samples of entire bryophyte mats (range of fresh weight: 10–86 g) were taken from different branches at a height of 15–20 m above ground level of the inner crown section ('inner branches') of one to four individual trees of the upper canopy layer (six samples per tree). In addition, in each tree two samples of canopy humus (range of fresh weight: 13–100 g) were collected separately on each sampling occasion except on four sampling days.

Sampling was carried out between 9 a.m. and 1 p.m., and the sampling period included both dry and rainy spells. After collection, samples were stored immediately in plastic bags and transported to the field laboratory. Water content was determined gravimetrically by measuring fresh weight and reweighing after oven-drying (70°C for 48 h) and expressed as percentage of dry weight.

To estimate the water storage capacity of non-vascular epiphytes and canopy humus at the stand scale the respective total mass values were multiplied times the maximum amounts of water stored (calculated in turn as the difference between lowest and highest water content of epiphytic bryophytes or canopy humus observed in the field).

Results

Distribution and composition of epiphyte mats

In the OGF, the epiphytic vegetation on large trees (dbh ≥ 60 cm) was dominated by bryophytes (Fig. 1). Bryophytes made up 49% of total epiphytic biomass on the inner branches whilst their portion increased towards the middle (59%) and outer branches (78%). Only very few lichens were found in the samples and their biomass was negligible. Canopy humus showed a reverse distribution pattern, with the highest occurrence (28%) on the inner branches and gradually lower values on the middle and outer branches (Fig. 1). The percentage of vascular epiphytes was 17–23%, with no clear distribution pattern within the respective branch sections (Fig.1).

The epiphytic vegetation on the trunks of the canopy trees was also dominated by bryophytes (73%). Canopy humus on trunks was 5%, whereas contributions by vascular plants were 22%. The absolute biomass of bryophytes per unit branch surface area was 620 ± 329 (SD) g m^{-2} on the inner branches, 849 ± 373 (SD) g m^{-2} on the middle branches and 603 ± 494 (SD) g m^{-2} on the outer branches.

The smaller tree size classes within the OGF had relatively low percentages of vascular epiphytes and canopy humus compared with the bigger trees, especially in the 5–20 cm dbh-class (Fig. 1). Bryophytes were the dominant epiphyte fraction again throughout all tree sections, reaching their highest levels on the outer branches. Epiphyte mats on tree ferns, which were all within the 5–20 cm dbh-class, were only present on the stems and were (again) dominated by bryophytes (82%).

As observed for the smaller sized trees in the OGF, bryophytes also contributed a very high percentage (83–97%) to the total epiphyte mat weight in the SF (Fig. 1). Similarly, the percentages of vascular epiphytes and canopy humus in the SF were low, with maximum values for the inner branches.

Epiphyte mat weight at the stand level

On average, epiphyte mat weight of tree branches in the OGF (dbh-class > 60 cm) was higher on

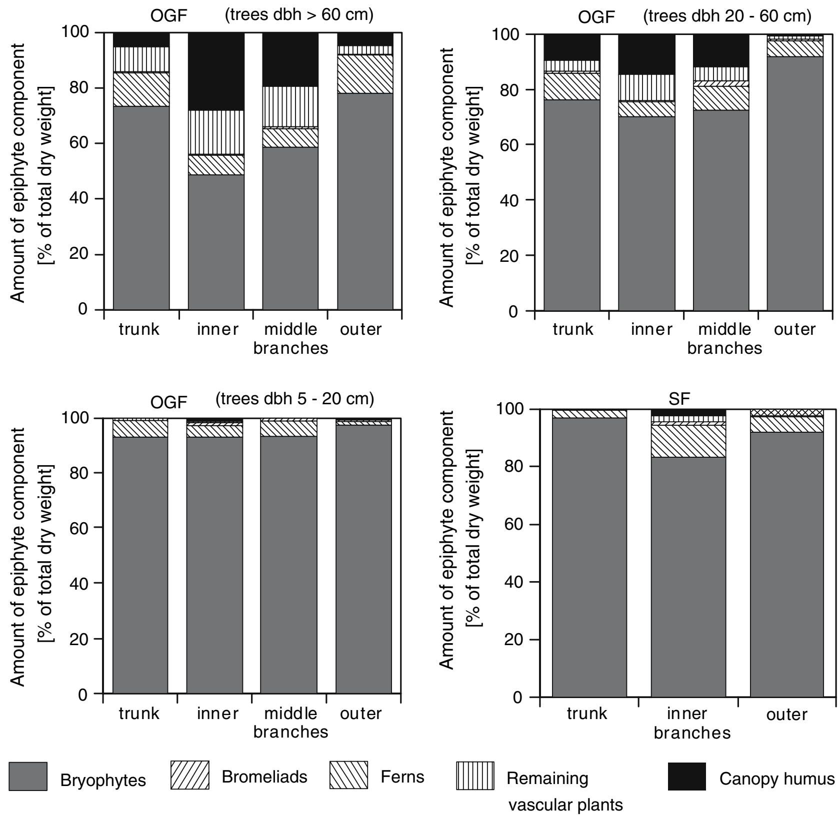

Fig. 1 Distribution and composition of epiphytic biomass and canopy humus in an old-growth (OGF) and a secondary (SF) cloud forest at San Gerardo, Monteverde. In the OGF trees were divided into three different dbh-classes

the inner branches and decreased towards the middle and outer sections (Table 3). Inner branches of smaller trees in the OGF had relatively low epiphyte mat weight compared to other branch sections. Also, the stems of all dbh-classes showed only low weight of epiphytes and canopy humus compared to the crowns (ratio 1:22).

In the OGF the average epiphyte mat weight on large trees (dbh > 60 cm) was estimated at 140.9 ± 103.1 (SD) kg per tree ($n = 3$). Trees with dbh between 20 cm and 60 cm exhibited intermediate values (36.6 ± 18.8 kg per tree) ($n = 3$) whereas the lowest epiphyte mat weight was found for the smallest trees (dbh 5–20 cm), with an average of 1.8 ± 0.5 kg per tree ($n = 3$) (Table 3). In the SF, the epiphyte mat weight on inner and outer branches exhibited similar values on average (Table 3). Epiphyte mat weight on stems was relatively high compared to the crowns (ratio 1:3). Overall epiphyte mat weight per tree was very low at 0.49 ± 0.37 (SD) kg ($n = 6$).

The overall epiphyte mat weight in the OGF amounted to 16,215 kg ha^{-1} (non-vascular epiphytes: 11,505 kg ha^{-1}, vascular epiphytes: 2,615 kg ha^{-1}, canopy humus: 2,095 kg ha^{-1}; Table 4). Trees > 60 cm dbh contributed 44% of total stand epiphyte mat weight. Trees with dbh 20–60 cm had a much lower epiphyte mat weight per tree but were more abundant. Consequently their contribution to overall epiphyte mat weight was high (48%). Although the smallest trees (dbh 5–20 cm) had a high stem density, their very low weight of epiphytes and canopy humus per tree resulted in a low contribution to total epiphytic mat weight (8%). Epiphytic mat weight on tree ferns was only 21.5 kg ha^{-1} (0.1%). Palms, which were equally abundant in the lowest dbh-class in the OFG, were

Table 3 Epiphyte mat weight of different tree dbh-classes in an old-growth and a secondary montane cloud forest at San Gerardo, Monteverde. Biomass values given for different sections of single branches (inner, middle, outer) and stems. Whole-crown values calculated by multiplying epiphyte mat weight of single branches times number of branches on the respective trees. Whole tree = whole crown + stem. Values in kg dry weight

	Inner branches	Middle branches	Outer branches	Whole crowns (kg)	Stems	Whole trees	Trees average	Deviation
Old-growth forest								
Trees dbh > 60 cm								
1	3.9	2.8	3.6	72.3	4.9	77.2		
2	2.5	1.2	0.7	79.8	5.9	85.7		
3	5.9	5.2	1.6	253.8	6.1	259.9	140.9	103.1
Trees dbh 20–60 cm								
4	0.3	1.1	0.3	22.3	1.0	23.3		
5	0.8	2.0	1.9	57.1	1.1	58.2		
6	0.3	0.6	0.4	24.5	3.9	28.4	36.6	18.8
Trees dbh 5–20 cm								
7	0.1		0.1	1.9	0.2	2.1		
8	0.1		0.1	0.8	0.4	1.2		
9	0.2		0.3	1.9	0.2	2.1	1.8	0.5
Secondary forest								
Trees dbh 5–25 cm								
1	0.0		0.1	0.3	0.3	0.6		
2	0.1		0.1	0.3	0.1	0.4		
3	0.1		0.0	0.7	0.2	0.9		
4	0.1		0.1	0.8	0.1	0.9		
5	0.0		0.0	0.0	0.1	0.1		
6	0.0		0.0	0.1	0.0	0.1	0.5	0.4

Table 4 Epiphyte mat weight at the stand level in an old-growth and a secondary montane cloud forest at San Gerardo, Monteverde. Ferns and Bromeliads included in total vascular epiphytes

	Epiphytic component (kg ha^{-1})					
	Total	Non-vascular	Vascular	Ferns	Bromeliads	Canopy humus
OGF	16,215	11,505 (71%)	2,615 (16%)	1,228	131 (1%)	2,095 (13%)
SF	1,035	944 (91%)	84 (8%)	64 (6%)	6 (1%)	7 (1%)

usually free of epiphytes and canopy humus. In the SF the total epiphyte mat weight at the stand level was estimated at 1,035 kg ha^{-1} (non-vascular epiphytes: 944 kg ha^{-1}, vascular epiphytes: 84 kg ha^{-1}, canopy humus: 7 kg ha^{-1}; Table 4).

Water content of epiphytes and canopy humus

Water contents of bryophytes in the OGF as measured in situ fluctuated between 36 ± 10 (SD)% of dry weight during dry periods and 418 ± 74% of dry weight after prolonged wetting by rain and fog (Fig. 2a). During rainy months, values were usually around 300% whereas values below 100% were only recorded during (rare) extended precipitationless periods in the dry season (Fig. 2c). The water storage capacity of epiphytic bryophytes, calculated as the difference between the observed minimum and maximum water contents, was 382%, implying that the non-vascular epiphytes (11,505 kg ha^{-1} in the OGF) represented a stand water storage capacity of 43,719 l ha^{-1} or 4.4 mm. By contrast, the corresponding value derived for the SF was estimated at only 0.36 mm.

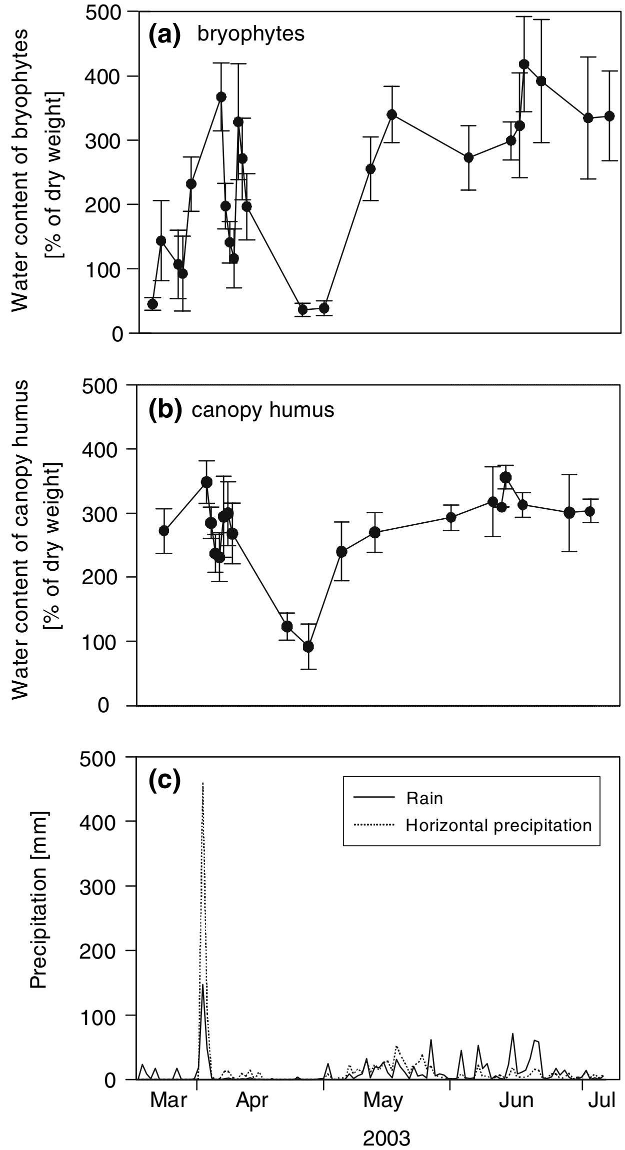

Fig. 2 (**a**) Water content of epiphytic bryophytes measured in situ within the tree crowns of an old-growth cloud forest at San Gerardo, Monteverde. Number of sampled canopy trees: 1–4. Number of bryophyte samples per tree: $n = 6$. (**b**) Water content of canopy humus within the tree crowns of the San Gerardo—Monteverde OGF plot. Number of sampled canopy trees: 1–4. Number of humus samples: $n = 2$ per tree. (**c**) Precipitation (vertical rain and horizontal precipitation) during the period of epiphyte sampling (March–July 2003). Horizontal precipitation refers to fog and wind-driven rain

Water contents of canopy humus in the OGF fluctuated between 92% ± 35 (SD)% of dry weight during dry periods and 356% ± 19 % of dry weight after prolonged wetting by rain or fog (Fig. 2b and c). The maximum amount of water stored in canopy humus per unit dry weight (264%) was much lower than that associated with epiphytic bryophytes (382%; cf. Fig. 2a and b). The corresponding stand water storage capacity of canopy humus was estimated at 0.55 mm in the OGF. Only 7 kg ha^{-1} of canopy humus were found in the SF and therefore the associated water storage capacity was negligible (0.002 mm).

Short-term water dynamics of epiphytic bryophyte vegetation and canopy humus

More detailed information on the water dynamics of epiphytic bryophytes and canopy humus in the OGF is provided by Fig. 3, which shows one week of consecutive daily values of water contents. The first samples were collected on April 3rd 2003, a few hours after more than 48 h of continuous rainfall had delivered 222 mm. Initially, both bryophytes (367 ± 52 (SD)%) and canopy humus (348 ± 34%) showed very high water contents. During the following 3 days of sunny weather without rain or fog, both bryophytes and canopy humus were drying out and water contents decreased by 251% (bryophytes) and 117% (canopy humus). Converted to mm of water at the stand level, this corresponded to a loss of 2.9 mm from the bryophytes vs. 0.24 mm from the canopy humus during this 3-day period. Between April 6th and 7th, rewetting took place, mostly by horizontal precipitation (wind-driven rain and fog; Fig. 3). As a result, the water contents of bryophytes and humus nearly reached the initial values again. During the following two rainless days with some light fog events the bryophytes dried out again, whereas the water content of the canopy humus continued to increase before starting to decline again the following day (Fig. 3). This suggests a delayed response of canopy humus water content to wetting and drying as well as more suppressed dynamics compared to epiphytic bryophytes. Nevertheless, even for bryophytes to reach their lowest water content will take at least 3 days under sunny conditions.

Discussion

Composition of epiphytic vegetation

The composition of epiphyte mats varied with location within the crown and tree size. However, the percentage of bryophytes was generally lower on the inner branches and increased towards the middle and outer branches. Canopy humus showed a reverse distribution with a high percentage on the inner branches and lower values on the middle and outer branches. Similar patterns of epiphytic composition and distribution have been reported for dominant trees in several other old-growth neotropical montane forests (Nadkarni 1984; Ingram and Nadkarni 1993; Wolf 1995; Freiberg and Freiberg 2000). The higher percentage of bryophytes towards the outer crown reflects the fact that cryptogams are typically the first to colonize small (young) branches, gradually giving way to vascular epiphytes which may require dead organic matter, the presence of bryophytes as well as more time to establish (Ingram and Nadkarni 1993; Freiberg and Freiberg 2000). Canopy humus also needs much more time to accumulate and consequently its percentage is higher in the inner crown where branches

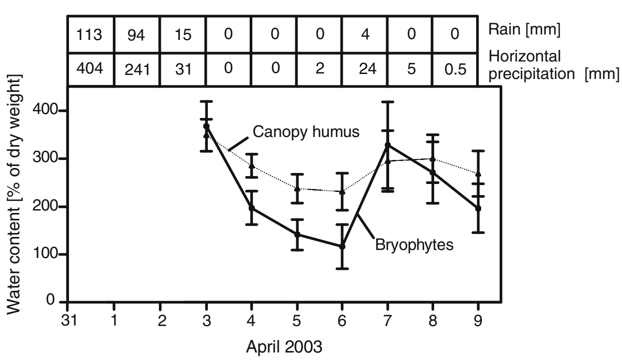

Fig. 3 Short-term variation in water contents of epiphytic bryophytes and canopy humus within the inner crown of three dominant trees in old-growth windward montane cloud forest at San Gerardo, Monteverde. Number of replications per sampling: bryophytes: $n = 6$ per tree, canopy humus: $n = 2$ per tree

are oldest. Despite their relatively high age, the stems of the trees show no or only low values of canopy humus because of the steep inclination of the stem surface which is less favourable for the accumulation of humus. Smaller and presumably younger trees in the OGF at San Gerardo (OGF) showed a high percentage of bryophytes and low percentages of vascular plants and canopy humus.

The SF exhibited a high dominance of bryophytes in all crown sections, which is thought to reflect the low age of the forest. Similar results were reported for a ca. 50-year-old leeward secondary lower montane cloud forest at nearby Monteverde where epiphyte mats in all tree sections and different tree layers were heavily dominated by bryophytes (95%) with only small amounts of dead organic matter (3%) and trace amounts of other components (Nadkarni et al. 2004).

Epiphyte mat weight at the stand level

Estimates of total epiphyte biomass and canopy humus in old-growth tropical montane forests at the stand level as summarized in Table 5 range widely from 370 kg ha^{-1} in a stunted ridgetop upper montane rain forest in Jamaica (Tanner 1980, 1985) to 44,000 kg ha^{-1} in an upper montane forest in Colombia (Hofstede et al. 1993). The epiphyte mat weight estimated for the OGF stand of the present study falls within this range. Also at Monteverde, Nadkarni (1984) estimated the epiphyte mat weight of a wind-exposed elfin cloud forest stand (1600–1800 m asl.) at 4,730 kg ha^{-1}. This forest type, which generally occurs along ridge crests (Lawton and Dryer 1980), is very different in structure and tree height (5–15 m) compared to the OGF site (22–25 m). Despite the reduced stature of the elfin forest, epiphyte mat weight for a single large *Clusia alata* tree sampled by Nadkarni (1984) was effectively equal to the average epiphyte mat weight currently found on much larger trees (dbh > 60 cm) in the OGF (141.9 kg vs. 140.9 kg). However, Nadkarni (1984) only considered trees with dbh > 70 cm for her estimation of epiphyte mat weight at the stand level. As shown in Fig. 1 smaller trees, despite their lower epiphyte mat loading, can make an important contribution to overall epiphytic biomass due to their higher stem density. As a result, our stand-scale estimation is much higher than that derived by Nadkarni (1984). On the other hand, in leeward lower montane cloud forest at Monteverde Nadkarni et al. (2004) estimated the

Table 5 Epiphyte mat weight in old-growth and secondary tropical montane (cloud) forests. For secondary forests age is given instead of forest type. LMRF: Lower Montane Rain Forest, LMCF: Lower Montane Cloud Forest, UMRF: Upper Montane Rain Forest, UMCF: Upper Montane Cloud Forest, ECF: Elfin Cloud Forest

Country	Forest type	Elevation (m asl.)	Exposition	Epiphyte mat weight (kg ha^{-1})	Authors
New Guinea	LMRF	2,500		5,200	Edwards and Grubb 1977
Tanzania	LMRF	1,415		2,130	Pócs 1980
Tanzania	LMCF	2,120		13,650	Pócs 1980
Jamaica (Mull)	LMRF	1,550		370	Tanner 1980, 1985
Jamaica (Mor)	LMCF	1,550		2,100	Tanner 1980, 1985
Colombia	UMCF	3,370		12,000	Veneklaas et al. 1990
Colombia	UMCF	3,700		44,000	Hofstede et al. 1993
Puerto Rico	ECF	1,000	Windward	7,360	Weaver 1972
Puerto Rico	ECF	1,015	Ridgetop	4,350	Weaver 1972
Puerto Rico	ECF	930	Leeward	4,750	Weaver 1972
Costa Rica					
Costa Rica	LMCF	1,480	Leeward	33,100	Nadkarni et al. 2004
Costa Rica	ca. 50 yr	1,480	Leeward	200	Nadkarni et al. 2004
Costa Rica	ECF	1,700		4,730	Nadkarni 1984
Costa Rica	UMRF	2,900	Leeward	3,400	Köhler 2002
Costa Rica	10–15 yr	2,900	Leeward	160	Köhler 2002
Costa Rica	40 yr	2,900	Leeward	520	Köhler 2002
OGF	LMCF	1,490	Windward	16,215	This study
SF	30 yr	1,620	Windward	1,035	This study

total epiphyte mat weight at 33,100 kg ha^{-1}, which consisted mainly of dead organic matter (63%) accumulated on branch junctions in dominant trees. No branch junctions were sampled at our sites since no such preferential accumulation was recognizable.

There do not seem to be many data on epiphyte mat weight at the stand level for secondary tropical montane forests except for the study by Nadkarni et al. (2004) who derived a value of 200 kg ha^{-1} for a ca. 50-year-old forest at Monteverde. Their estimate is rather low considering the age of the stand but this can probably be explained by the drier climatic conditions prevailing on the leeward side of the Continental Divide compared to the currently studied windward plots. However, in both studies the biomass of epiphytes and canopy humus was much lower in secondary than in OGF (Table 5). This finding most likely reflects the young age of the secondary stands since epiphytes often exhibit slow growth rates (Jacobsen 1978) whilst their biomass generally increases during succession (Hale 1967 in Coxson and Nadkarni 1995).

Site factors that typically promote the abundance of epiphytes in tropical montane forests include high atmospheric humidity and fog incidence, low temperatures and high precipitation. Poikilohydric non-vascular epiphytes are particularly sensitive to prolonged dry periods and depend on sufficiently frequent wet periods for their survival (Benzing 1998; Wolf 2005). As indicated previously, long-term climatic data for the higher parts of the Atlantic slopes of the Cordillera de Tilarán are not available but precipitation totals measured at the two study sites for the period July 2003–June 2004 were ca. 6,000 and 4,385 mm at the old-growth and SF site, respectively. To this should be added the very substantial contributions by wind-driven rain and fog (determined at 2,740 and 5,085 mm, respectively; Bruijnzeel et al. 2006). In addition, the seasonal distribution of precipitation is favourable for epiphyte growth in the San Gerardo/Monteverde region. During 3 months in the dry season of 2003 (February through April), 53% of the days had no measurable vertical rain. However, 72% of the days had measurable amounts of horizontal precipitation (K.F.A. Frumau, unpublished data). The duration of the longest dry spell in terms of rainfall only observed was eight days (4 days when taking horizontal precipitation into account; K.F.A. Frumau, unpublished data). With respect to epiphyte mat water dynamics (see below) it can be assumed that rewetting of epiphytic vegetation and canopy humus normally takes place within a few days (cf. Fig. 3).

Water dynamics of epiphytes and canopy humus

The high maximum water contents of bryophytes measured at the OGF site (OGF: 418% of dry weight) are in accordance with other studies that have reported values between 200% and 500% (Pócs 1980; Nadkarni 1984; Frahm 1990). Thus, bryophytes can significantly increase the overall water storage capacity of montane forest canopies. Canopy storage values of 0.75–1.2 mm are typically found for lowland rain forests with low epiphyte mass (e.g., Calder et al. 1986; Lloyd and Marques 1988; Jetten 1996). For two upper montane cloud forest stands in Colombia water storage capacities of 2–5 mm have been reported, with the highest values pertaining to a stand with high epiphyte biomass (Veneklaas and Van Ek 1990). Pócs (1980) estimated the water storage capacity of the total epiphytic vegetation of an elfin forest in Tanzania at 5 mm, of which bryophytes alone accounted for 3 mm. In the present study the maximum stand water storage of non-vascular epiphytes alone was estimated at 4.4 mm in the OGF. The corresponding value for the SF (0.36 mm) was an order of magnitude lower. However, despite the high potential storage capacity of epiphytic vegetation the actual storage capacity may be much smaller, depending on the balance between previous precipitation inputs (both rainfall and fog) and losses via evaporation and drip (Veneklaas and Van Ek 1990). Based on results obtained with an analytical interception model for an upper montane rain forest in the Cordillera de Talamanca, Costa Rica (Hölscher et al. 2004), the contribution by non-vascular epiphytes to overall rainfall interception is relatively low (6%) despite their considerable water storage capacity. The main reason for this is that during the rainy season the epiphytes are usually close to saturation and hence only a fraction of the potential storage is actually available at the beginning of the next rainfall. Although the epiphytes were almost completely dry during the dry season (Hölscher et al. 2004), the actual effect was small as there was little rain to be accommodated anyway. The epiphytic mat weight and associated stand water storage capacity in the OGF were much higher compared to the Cordillera de Talamanca (3,400 kg ha^{-1} and 0.81 mm, respectively; Köhler 2002). Following the results of the model application of Hölscher et al. (2004) at the Talamanca site and taking into account the fact that rainfall is both higher and more evenly distributed in the San Gerardo/Monteverde area, it is highly likely that the influence of the epiphyte vegetation on overall rainfall interception at Monteverde will also be much lower than expected on the basis of its high potential water storage capacity. This was confirmed by the observations of in situ water dynamics of non-vascular epiphytes in the OGF (Fig. 3). The drying out of nearly saturated epiphyte mats in the inner crown (where a major part of the epiphyte biomass is found) took more than 3 days even during sunny conditions. During a 1-year period, the longest period without rain or fog at the San Gerardo site was 4 days. Also, on days with rain or fog there is often more than one event per day. Thus, it can be assumed that rewetting by rain and/or fog will usually take place before the epiphytes dry out completely, although drying may continue even under conditions of light fog (as on April 8th and 9th) as long as epiphyte water content is high enough. Furthermore, longer-term in situ measurements of water contents of bryophytes during the rainy season (May–July; Fig. 2a) showed little variation and high values averaging ca. 330% (n = 9 sampling days). This is in accordance with the results of the analytical interception model (Hölscher et al. 2004) which suggested that in the Cordillera de Talamanca epiphytes stayed close to saturation during the rainy season.

Nearly no information is available on the water storage capacity and dynamics of canopy humus in tropical montane forests. In an old-growth leeward cloud forest at Monteverde, Bohlman et al. (1995) compared moisture and temperature patterns in canopy humus and the soil of the forest floor. Canopy humus showed greater fluctuations in moisture content compared to the forest floor. Values (expressed as percentage of fresh weight) ranged between 27% and 79%. Expressing the presently measured water contents of canopy humus in the OGF in the same way gives a range from 47% to 78%. Thus, maximum water contents derived by the two studies are nearly identical, whereas minimum values were lower in the leeward forest compared to the more exposed OGF. Bohlman et al. (1995) reported a maximum water loss from canopy humus of 30% of the total water content within a week. In the present study, the fastest decline in canopy humus water content was 3.8% within a single day (again expressed as percentage of fresh weight) which gives a similar value (26.3%) when extrapolated to a one-week period. However, the water content of canopy humus showed less variation than that of epiphytic bryophytes (Figs. 2, 3). Also, canopy humus is able to retain a considerable amount of water during dry periods when bryophytes are largely dehydrated (Fig. 3). Therefore, it can be expected that the difference between actual and potential water storage capacity of canopy humus is even greater than for non-vascular epiphytes.

Conclusions

The present results suggest that at this Costa Rican study site it may take more than a century for epiphyte mat weight and associated hydrological functions to reach values found in local OGFs.

Despite the high potential water storage capacity of epiphytic bryophytes and canopy humus in montane cloud forest, the actually available storage is likely to be much smaller, depending on antecedent rainfall and evaporative conditions. This contention needs to be tested further in different forest types before generalizations can be made.

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