Epiphyte biomass and its hydrological properties in old-growth and secondary montane cloud forest, Monteverde, Costa Rica

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Abstract

In a lower montane cloud forest near Monteverde, Costa Rica, biomass, distribution and composition of epiphytes were assessed on trees of different size classes in an old-growth forest and in a nearby 30-year-old secondary forest. Information on forest structure was used to derive stand-level estimates of epiphyte biomass of 16.2 t ha^{-1} in the old-growth forest and 1 t ha^{-1} in the secondary forest. In the old-growth forest epiphytes were dominated by mosses, which, together with crown humus, made up 84% of the total epiphytic biomass. In the secondary forest mosses were the dominant epiphyte fraction (92%) and nearly no crown humus was found. Water contents of epiphytic mosses and crown humus were determined *in situ* using gravimetric methods. Minimum and maximum water content of mosses were 36% and 418% of dry weight, respectively. Crown humus showed less fluctuation in water content than did mosses, with minimum and maximum values of 92% and 356%, respectively. The maximum water storage capacities at the stand level were estimated at 4.4 mm (mosses) and 0.55 mm (crown humus) in the old-growth forest, and at 0.36 mm (mosses) in the secondary forest where water storage of crown humus could be neglected.

Introduction

The epiphyte communities of tropical montane forests constitute a conspicuous feature of the canopy, particularly in cloud forests. Epiphytes are not only believed to reflect the prevailing micro-climatic conditions but are also expected to influence the interception of rainfall and cloud water. Of late, several studies of net precipitation in TMCF have reported very low values which were attributed to a high epiphyte load. Information on epiphyte biomass distribution, as well as on the associated water dynamics, is a prerequisite for obtaining a better understanding of the cloud and rainwater interception process in montane forests (e.g. through process modelling). However, quantitative studies of epiphyte biomass are extremely laborious and as a result such studies are comparatively rare and generally based on samples from a single or a very limited number of dominant trees at best. Therefore, relatively little is known of the standard errors of published biomass estimates. In the present study, the composition, biomass and (maximum) water storage capacities of the epiphyte biomass in both primary and 30 year old secondary forest are documented.

Methods

Study sites

The study was carried out between Febuary and July 2003 in two small headwater catchments within the Caño Negro drainage basin on the atlantic slopes of the Codillera Tilarán, Costa Rica. The two forest plots were located several km north-east of the town of Santa Elena at about 1450 m altitude asl. One plot were established in undisturbed lower montane cloud forest (primary forest – PF) another in a 30 year old secondary forest (SF) with individual remnants and trunk bases of the former old-growth forest.

In the PF plot the slope was steep (31.9°) and the aspect was west while the SF site showed a lower inclination (15.3°) with an north-west aspect. Epiphytic vegetation in PF was abundant while SF lags of great amounts of epiphytes. The climate, geology and vegetation of the area have been summerized by LAWTON & DRYER (1980) and LAWTON (1980).

Stand structure

In both stands height of all trees (dbh ≥ 5cm) as well as height of their stems within 1000 m² (PF) and 330 m² (SF) were determined direct by climbing of the trees or with laser measurement technique (LaserAce 300, MDL). Diameter at breast height (dbh) was assessed by measuring circumferences at a height of 1.30 m. For trees with table roots circumference was measured above. Before the measurements stems were cleaned of epiphytes and climbers. Additional information of the stand structure (number of tree ferns, palms as well as number of trees with strongly deformed crowns) was recorded.

Epiphyte sampling and analysis

a) Distribution and composition of epiphytes

In total 265 epiphyte samples were collected on 9 individual trees in PF and 6 trees in the SF plot. Trees were chosen upon accessibility of the crown and representability of epiphyte biomass. They were belonging to different tree species and different dbh-groups which were representing different forest layers in the primary forest. Group dbh > 60 cm: sampled trees dbh 99, 99, 76 cm; Group dbh 20 - 60 cm: sampled trees dbh 58, 44, 30 cm; Group dbh 5 - 20 cm: sampled trees dbh 17, 14, 12 cm. In the secondary forest dbh of sampled trees were 25, 20, 18, 13, 8, 7 cm. Trees were climbed by using single-rope techniques (PERRY 1978) or by ladder for smaller trees. The sampled trees were stratified into major sections (trunk, inner branches, middle branches, outer branches). In the secondary forest and the smallest trees of the PF no middle branch section was distinguished. Epiphyte dry weight-to-substrate surface area ratios were obtained by collecting five samples of each crown section per tree from areas circulating the branches. To sample the outer branch section it was necessary to cut off the branches which were subsequently also used for the estimation of total epiphyte biomass. From each trunk epiphyte samples were taken by stripping off all epiphytes within a band circulate the trunk at 3 different heights. For trees of bigger dbh-classes all epiphytes within 4 rectangular sample areas (20 x 30 cm, expositions N, S, W, O) were collected at 3 different heights of the trunk. The samples were taken to the laboratory and subsequently separated into the following fractions: bryophytes, lichens, ferns, bromeliads, remaining vascular plants as well as crown humus. Samples were oven-dried at 70°C for 48 h to obtain the epiphytes dry weight. (Additional data on the water contents of the different epiphyte components were collected but will not be presented within this report).

To consider the great abundance of tree ferns in the PF-plot whose stems showed a dense epiphyte cover while their "crowns" generally were free of epiphytes the stems of three tree ferns were sampled additionally by collecting all epiphytes in three different heights of the trunk.

b) Total epiphyte biomass

For the estimation of total epiphyte biomass from each individual tree one branch was sawn off and lowered to the forest floor (same branches as used before for the epiphyte sampling of the outer crown - see above). Lowering of branches was not possible for the trees of dbh-group > 60 cm. But before cutting off branches the forest floor beneath was cleaned from fallen epiphytes. Loss of epiphytes from fallen branches was assumed to be very low. Total epiphyte cover of the three different branch sections was removed and weighted in the field. A subsample taken from each section was oven-dried to obtain the dry weight. Total epiphyte biomass of the crown was calculated by multiplying epiphyte biomass of the single branches by the total number of branches within the crown. Epiphyte biomass of the trunks was obtained by multiplying the epiphyte dry weight-to-substrate surface area ratios with the stem surface area. To calculate the total stem surface area, the stem was divided into segments of varying lenght which were assumed to be cylinders. From each segment length and mid-segment diameter was measured and surface area was determined. Stems often showed a dense cover of climbers which are in contrast to the epiphytes rooting in the ground. Differentiation whether plants have a connection to the ground or are real epiphytes often was impossible. In this study only clearly cognizable epiphytes were sampled, therefore the epiphyte biomass obtained for the trunks is a conservative estimation. However, in the crown only few climbers occur so the differentiation between epiphytes and climbing plants was much more easy.

Results of determinations of average epiphytic biomass of single trees were extrapolated to estimate epiphyte biomass at stand level. Therefore single tree values were multiplied by the number of stems within each dbh – group. For trees with a strong crown deformation only the average epiphyte biomass on the trunks were taken into account. For tree ferns only the stem section was considered. Palms were frequently free of epiphytes and therefore assumed not to contribute epiphytic biomass to the overall estimation.

Water content of the epiphytic moss vegetation and crown humus

The water content of epiphytic mosses and crown humus was monitored *in situ* during a period of five months (March-July) including the dry and rainy season. In total more than 600 samples were collected. Samples of entire moss mats were taken from different branches of the inner crown section (inner branches) of 1 to 4 individual trees of the upper canopy (6 samples for each tree) 15 – 20 m above ground level. Additionally in each tree two samples of crown humus were separately collected. Samples were stored in plastic bags and transported to the lab. Water content was determined gravimetrically by measuring fresh weight and reweighting after drying and expressed as percent of dry weight:

$$\text{Water content} = ((\text{fresh weight} - \text{dry weight}) / \text{dry weight}))*100$$

Sampling was always carried out between 9 a.m. and 1 p.m. To estimate the maximum water storage capacity of epiphytes (mosses and crown humus) their biomass at the stand level was multiplied by the maximum water storage (difference between lowest and highest water content of epiphytic mosses and crown humus observed in the field).

To obtain information of the differences (spatial variability) of water contents of epiphytic mosses for three individual days additional samples of bryophytes from the base of the trunk, the trunk and the outer branches were taken and the water content was determined as described above.

Results and Discussion

Stand structure

The height of the upper tree layer was 22 to 25 m in the PF plot. Highest (emergent) trees often showed exposed crowns which were not building up a uniform upper canopy layer. The stem density (dbh ≥ 5cm) was 1890 ha^{-1} after correction for the slope. Tree ferns and palms were abundant (22.8% and 19.6%, respectively). 5.3% of the trees possessed a strongly deformed crown. For a incomplete list of tree species identified in and close to the primary forest plot see Appendix 1.

Table 1: Data on the stand structure of a primary and a 30 year old secondary montane cloud forest in Monteverde, Costa Rica.

	Primary forest	Secondary forest
Plot size [m²]	1000	330
Age [yr]	____	30
Average height [m]	22 - 25	9
Average inclination [°]	31.9	15.3
Exposition	W	NW
Number of stems (dbh ≥ 5cm) [n ha $^{-1}$]	1890	2152
Tree ferns [%]	22.8	2.8
Palms [%]	19.6	2.8
Trees with crown deformation [%]	5.3	2.8

The SF plot showed a higher stem density (2152 stems ha^{-1} after slope correction). The mean height of the upper tree layer was approximately 9 m with several trees reaching up to 12 m. Single outstanding individual trees of the former primary forest showed similar heights as the upper canopy trees of the PF plot. The woody vegetation of the SF was characterised by a high percentage of Melastomataceae (26.8%). Tree ferns and palms were present only by single individuals (2.8% each). Bamboo (*Chusquea* ssp.) was abundant but not considered due to its low dbh less than 5 cm. 2.8% of the trees had a strongly deformed crown. Table 1 summerizes the main results of the structure analysis of the two forest plots.

Distribution and composition of epiphytes

Within all dbh-groups and all sections of trees in the primary forest mosses are the dominating epiphyte fraction (Figure 1). The trees (dbh ≥ 60cm) show a relatively low percentage of bryophytes on the inner branches (49%), whereas their portion is increasing towards the middle (59%) and the outer branches (78%). A similar pattern of epiphytic moss distribution was found by other authors and can be explained by the fact that bryophytes are early colonizers on young branches, covering them rather quickly, while most vascular epiphytes need dead organic matter, bryophytes and more time to establish (FREIBERG & FREIBERG 2000). The findings of the present study, that smaller and consequently younger trees show even a higher percentage of mosses, supports this hypothesis.

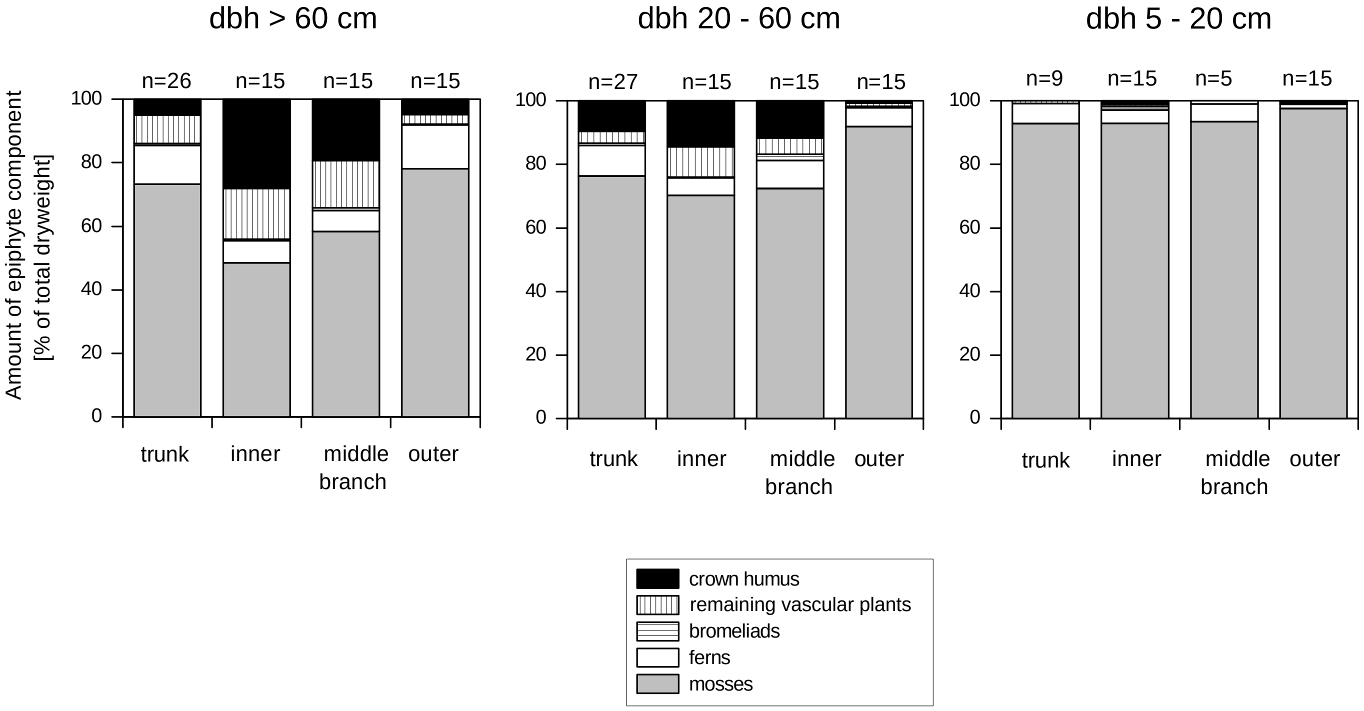

Figure 1: Distribution and composition of epiphytic biomass in the primary forest plot in Monteverde. Trees are divided into in three dbh-groups.

Other studies (e.g. INGRAM & NADKARNI 1993) found lower percentages of epiphytic mosses because only living bryophytes were considered and sampling was carried out on dominating trees only. Crown humus shows a reverse distribution than mosses with a high percentage on the inner branches and lower values on the middle and outer branches. Smaller and younger trees presents relatively low values of crown humus since time was insufficient for humus accumulation. The remaining vascular plants show a similar distribution as the crown humus with higher percentage on the inner branches and declining values towards the middle and outer branches. Ferns, which were often dominated by filmy ferns, show a relatively high percentage (14%) on the outer branches compared to the inner and middle branches of the biggest trees. Other epiphyte components within the tree crowns contribute only to a small percentage (< 10%) to the total epiphyte biomass. Lichens were found only in very few samples and their biomass was to low to determine. The stems of the biggest trees despite of their high age show a relatively high percentage of mosses but low values of crown humus and remaining vascular plants because of the steep inclination of the stem surface which is less favourable for the humus accumulation and establishing of higher plants. However, percentages of vascular plants on the stems are probably somewhat underestimated due to the fact that only plants clearly identified as epiphytes and no climbers were taken into account in this study. Tree ferns, which were all within the dbh - group 5-20 cm, were sampled separately from trees. Epiphytes which were only found on their trunks were dominated by mosses (82%).

In the secondary forest plot mosses contribute to a high percentage (83% - 97%) to the total epiphytic biomass (Fig. 2). The pattern of distribution of the mosses is similar to the distribution found in the primary forest with lower values on the inner branches compared to the outer branches. The high portion of epiphytic mosses suggests that bryophytes are early colonizers not only in primary but also in secondary forests. As for the smaller trees in the primary forest remaining components of epiphytes are only found in a very low percentages. Only ferns show be a little higher values up to 11% on the inner branches.

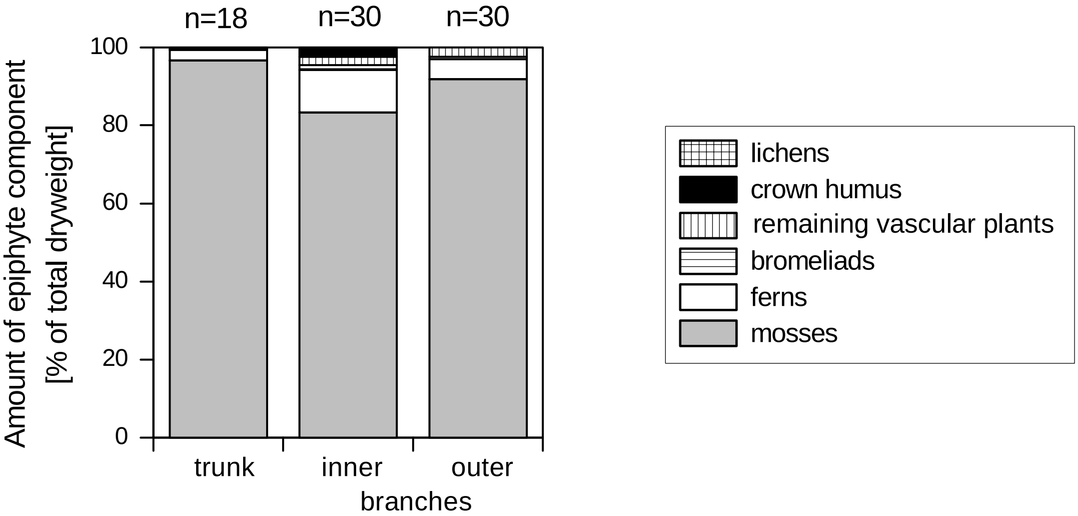

Figure 2: Distribution and composition of epiphytic biomass in the secondary forest plot in Monteverde.

Epiphytic biomass at the stand level

The average epiphyte biomass per tree (dbh > 60 cm) in the primary forest was estimated at 140.9 kg (n=3, standard deviation 103.1 kg) (Table 2). This value is nearly identical to the epiphyte biomass reported by NADKARNI (1984) (141.9 kg) for dominating trees in elfin forest of Monteverde. Trees with dbh 20 – 60 cm showed a lower average epiphyte biomass of 36.6 kg per tree (n=3, standard deviation 18.9 kg). The lowest epiphyte biomass was found for the smallest trees (dbh 5 - 20 cm) with an average value of 1.8 kg per tree (n=3, standard deviation 0.6 kg). Due to the more simple structure of the secondary forest and the fact that no correlation between tree size an epiphytic biomass has been found, no different dbh-groups of trees were distinguished. The average epiphyte biomass per tree was estimated at 0.49 kg (n=6, standard deviation 0.37 kg). The average values of epiphytic biomass were multiplied by the number of stems within each dbh – group to obtain total epiphyte biomass for each group on stand level. For trees with a strong crown deformation or without a crown only the average epiphyte biomass on the trunks were taken into account.

Table 2: Epiphytic biomass in the primary and the secondary forest, Monteverde. Standard deviation in parenthesis. * not included are palms (n = 370 ha^{-1}).

	Primary forest					**Secondary forest**
	dbh – groups [cm]			Tree ferns		dbh [cm]
	> 60	20-60	5-20		**sum**	5-25
Average epiphyte biomass per tree [kg] n=3	140.9 (103.1)	36.6 (18.9)	1.8 (0.6)	0.05 (0.01)		0.49 (0.37)
Number of stems (trees with crown) [n ha^{-1}]	50	210	730*	430	**1420**	2090
Number of stems (trees with crown deformation) [n ha^{-1}]	0	50	50	0	**100**	62
Total epiphyte biomass [kg ha^{-1}]	7045	7814	1334	21.5	**16215**	1035
Biomass of epiphytic mosses [kg ha^{-1}]	4136	6078	1273	17.5	**11505**	944
Biomass of crown humus [kg ha^{-1}]	1381	705	6	0	**2092**	7
Biomass of remaining epiphyte fractions [kg ha^{-1}]	1528	1031	55	4	**2618**	84

At the stand level trees (dbh >60) were estimated to carry a epiphyte load of 7045 kg ha^{-1}. Trees (dbh 20-60 cm) showed a much lower epiphyte biomass per tree but were more abundant and consequently their contribution to the total epiphyte biomass of the primary forest plot was high (7814 kg ha^{-1}). The smallest trees (dbh 5-20) cm showed a high stem density but their epiphytic biomass per tree was very low resulting in a low contribution to the stands epiphyte biomass (1334 kg ha^{-1}). For tree ferns that occurred exclusively within the lowest dbh-group epiphytic biomass was estimated separately which results in only 21.5 kg ha^{-1}. This shows the importance to treat tree ferns separately from normal trees because the application of single tree biomass to all stems (including tree ferns) would have resulted in a overestimation of epiphytic biomass within this dbh-group. Palms which were as well abundant in the lowest dbh-group but frequently free of epiphytes were assumed to contribute no epiphytic biomass to the overall estimation. The approach described above results in an overall estimation of epiphytic biomass of 16215 kg ha^{-1} for the primary forest plot. This falls in the wide range reported for montane tropical forests (0.37 - 44 t ha^{-1}; overview in Köhler, 2002) but it is more than three times higher than the epiphytic biomass reported by NADKARNI (1984) for a elfin forest in Monteverde. However, the studied elfin forest was very different in structure and, as in other studies on epiphyte biomass, the estimation was based on epiphyte sampling on a limited number of dominating trees only. In the SF the total epiphyte biomass was estimated at 1035 kg ha^{-1} for the whole stand. Data on the epiphytic biomass of tropical secondary forests are extremely rare. Values found in Monteverde are higher than epiphytic biomass reported from 10-15 and 40 year old secondary forest in the Cordillera Talamanca, Costa Rica (Köhler 2002) and are believed to reflect the more humid climatic conditions (higher cloud incidence) in Monteverde.

In PF for trees of dbh group > 60 cm the contribution of the different tree sections to the total biomass of epiphytes has been 45% (inner branches), 30% (middle branches), 20% (outer branches) and 5% (trunk). For trees of the dbh group 20 – 60 cm only 18% were found on the inner branches, 47% on the middle branches, 28% on the outer branches and 7% on the trunks. On the smallest trees (dbh 5 – 20 cm) most epiphytic biomass was found on the outer branches (56%) whereas 22% were contributed by the inner branches and the trunk each. A middle branch section was not distinguished within the lowest dbh - group. In the SF the contribution of the different tree sections has been 33% (inner branches), 31% (outer branches) and 36% (trunk). A middle branch section was not distinguished in this stand. The distribution of epiphytic biomass within the different tree sections suggests a stronger accumulation of epiphytes towards the inner parts of the crown with increasing tree age whereas younger trees show relatively high amounts of epiphytes on their trunks and in the outer or middle parts of their crowns.

For each tree section the amount of epiphytic mosses and crown humus was calculated by applying the data of epiphytes composition and distribution (Figure 1) to the epiphytic biomass values. For example 45% of the epiphytic biomass of the trees (dbh > 60 cm) were found on the inner branches (= 3170 kg ha^{-1}). Mosses making up 48.6%, crown humus 28.0% which corresponds with 1553 kg ha^{-1} for mosses and

888 kg ha^{-1} for crown humus. In the same way the amounts of mosses and crown humus were calculated for the remaining tree sections and dbh-groups which results in a total amount of 11505 kg ha^{-1} for epiphytic mosses and 2092 kg ha^{-1} for crown humus in the primary forest. Applying the percentages of mosses (Figure 2) to the different tree sections results in a total amount of 944 kg ha^{-1} for epiphytic mosses in the secondary forest. Crown humus was only found in very few samples within the inner crown and was estimated at only 7 kg ha^{-1} for the whole stand. Because of the low number of tree ferns and palms in the secondary forest they were not taken into account separately within this study.

Water content of the moss vegetation and crown humus

In the present study the monitoring of water contents of epiphytes focused on epiphytic mosses and crown humus because a) they are known to have a high water storage capacity, and b) they made up a high percentage of the total epiphyte biomass of the investigated stands (84% in the primary forest, 92% in the secondary forest). Between march and July 2003 water contents of mosses fluctuated between 36% of dry weight in the dry season and 418% of dry weight in the rainy season (Figure 3). The low value can be assumed to represent the driest point of moss vegetation within the observation period quite well. The maximum water content was derived from samples collected after heavy rain and epiphytes were still dripping during collection therefore are assumed to be saturated. Probably water contents of mosses can exceed this values momentarily during events of rainfall or heavy fog but the measured maximum value is within the published range of maximum water storage capacity for mosses (200-500%; PÓCS, 1980; NADKARNI, 1984; FRAHM, 1990, KÖHLER 2002).

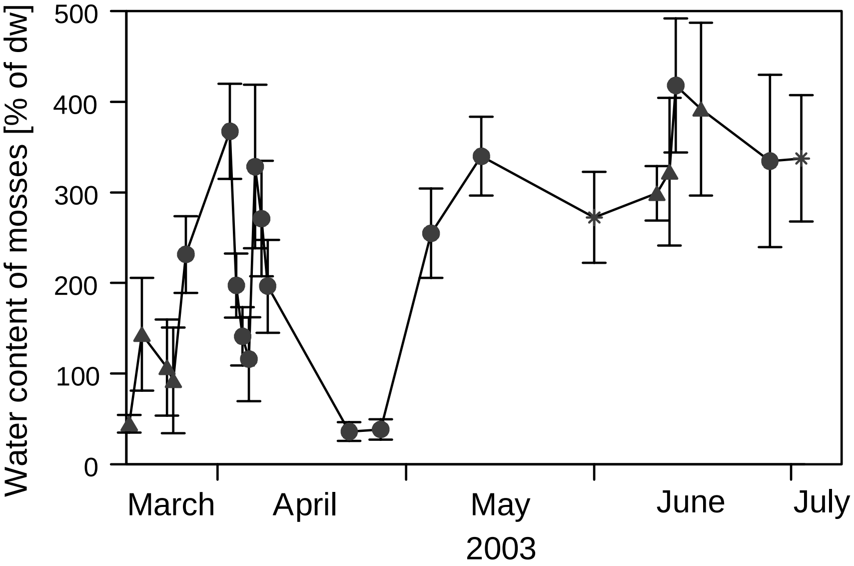

Figure 3: Water contents of epiphytic mosses within the tree crowns of a primary forest in Monteverde. Number of sampled canopy trees: ▲: n = 1, ●: n = 3, ✳: n = 4. Number of moss samples n = 6 per tree.

To estimate the maximum water storage capacity of the investigated forest stands the potentially available water storage capacity of epiphytic mosses (382%, difference between the minimum and maximum water content) was applied to the biomass of epiphytic mosses. In the secondary forest (epiphytic mosses: 944 kg ha^{-1}) this results in a maximum water storage capacity of 0.36 mm. This low value is a consequence of the low epiphytic biomass of this stand. For the primary forest (epiphytic mosses: 11505 kg ha^{-1}) the associated maximum water storage capacity was 4.4 mm at the stand level. This is a high value compared to the water storage capacity of 3 mm (epiphytic mosses only) reported for a elfin forest in Tanzania (PÓCS 1980). On the other hand, actual amounts of rainfall interception by mosses will be determined by actually available rather than potential storage capacities as determined by weather conditions. Following the results of an analytical interception model (HÖLSCHER et al. 2003), the importance of the mossy epiphyte layer for total rainfall interception by a montane forest in the Cordillera Talamanca, Costa Rica was relatively low despite its considerable maximum water storage capacity. The main reason was that under high rainfall conditions only a fraction of the total storage is actually available in the beginning of the next rainfall. However, the cited study was conducted in an upper montane rainforest on the sheltered pacific slopes of the Cordillera Talamanca, Costa Rica which was characterised by a limited cloud incidence and much lower biomass of epiphytic vegetation, and results have to be tested for different forest types before generalisation can be drawn . Therefore the present study provides the important *in situ* database necessary for the modelling of the cloud and rainwater interception process for a different forest type under contrasting climatic conditions in Monteverde.

Between march and July 2003 water contents of crown humus fluctuated between 92% of dry weight in the dry season and 356% of dry weight in the rainy season (Figure 4). Also the curve shape is similar to that of epiphytic mosses the fluctuation of the water contents is much lower. The potentially available water storage capacity of crown humus (264%) was applied to the biomass of humus. In the secondary forest only 7 kg ha^{-1} crown humus were found and therefore the associated water storage can be neglected. In the primary forest the biomass of crown humus (2092 kg ha^{-1}) corresponds with a maximum water storage capacity of 0.55 mm. It can be assumed that likewise the mossy epiphytes the contribution of crown humus to total rainfall interception is less than what could be expected from its water storage capacity.

Crown humus is known to be subject to higher fluctuations of moisture in comparison to forest floor soils (BOHLMAN ET AL. 1995). However, in comparison to epiphytic bryophytes crown humus can keep a considerable amount of water during dry periods if mosses are already dried out and shows less variability of its water contents than mosses. Therefore crown humus might function as an important resource of humidity for canopy organisms during dry periods which following the results of the present study needed more than 30 years of secondary succession for his development.

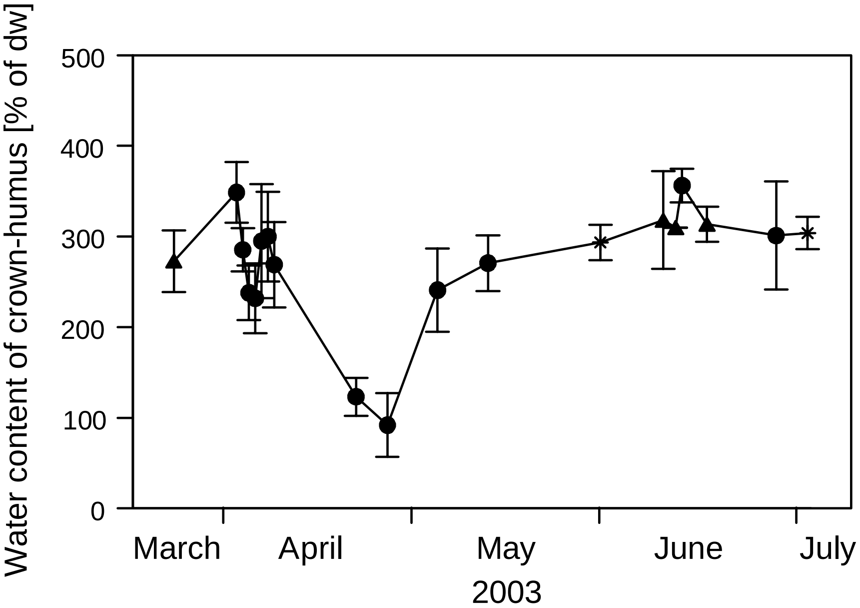

Figure 4: Water contents of crown humus within the tree crowns of a primary forest in Monteverde. Number of sampled canopy trees: ▲: n = 1, ●: n = 3, ✳: n = 4. Number of humus samples n = 2 per tree.

So far nearly no information exists about the time scale in which drying and wetting processes of epiphytes are taking place although those data are a important requisite for the understanding of epiphytes water dynamics. A on week detail of the observation period presented above, where water contents were determined on a daily basis (03.04 – 09.04.03) provides better information of the water dynamic of epiphytic mosses an crown humus (Figure 5). On 03.04. after 3 days with heavy rain, both, mosses and humus showed high water contents of 367% and 348% respectively. During the following three day of sunny weather conditions without rain or fog mosses and crown humus were drying out and water contents were falling for 251% (mosses) and 117% (humus). On the 07.04. a rewetting took place (probably mainly through heavy fog) and water contents nearly reaching the initial values. During the following two days with lighter fog events mosses were drying out again whereas water contents of crown humus was still increasing before declining the following day. This data suggests a delayed, reaction of crown humus to wetting and drying and less dynamic in comparison to epiphytic mosses. Even for mosses the dying process to reach low water contents lasts several days under sunny conditions. So it can be assumed that in Monteverde mostly rewetting through rain and/or fog takes place before epiphytes totally dried out. Drying can take place even under conditions of light fog (8/9.04) if epiphytes water contents are high enough. But exact data on rain and fog precipitation for the sampling period still have to be evaluated, before more detailed statements can be made.

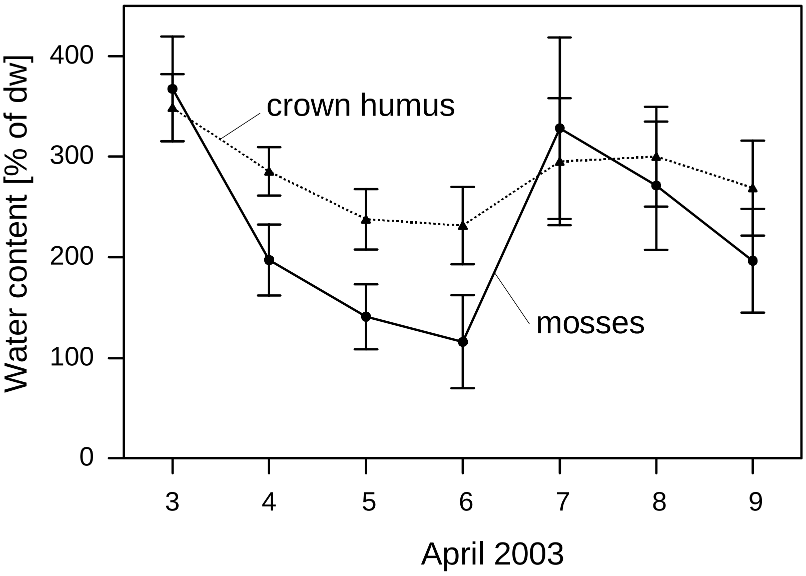

Figure 5: Water contents of epiphytic mosses and crown humus within the inner crown of 3 dominating trees of a primary forest in Monteverde. Mosses n = 6 per tree, humus n = 2 per tree.

That heavy fog can strongly influence the water contents of epiphytes and therefore might be an important factor who effects the interception process by epiphytes was shown during two days without rain but heavy fog (Figure 6). Mosses collected on the wind exposed and fog effected side of the trunk of a dominating tree showed more than 5 times (6.03.2003) and 3 times (8.04.2003) higher water contents than mosses sheltered by wind and fog.

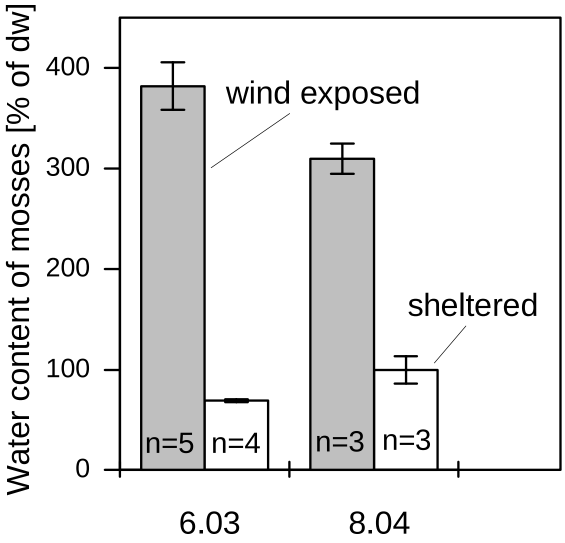

Figure 6: Water contents of epiphytic mosses in a primary forest in Monteverde. Samples were taken 10m above ground level on the wind exposed and sheltered side of the trunk of a dominating trees (*Ficus crassiuscula*) during dense fog conditions.

Difference of water contents of epiphytic mosses could also be observed between different sections of the trees (Figure 7). Water content of mosses collected on the stem bases were higher than for mosses sampled in the crown both, in dry and rainy season. Moss water contents within the crown showed less variation but values of mosses growing on the inner branches were somewhat higher than on the outer branches. Water contents of mosses growing on the stem showed low values in the dry season and intermediate values in the rainy season. For all sections water contents determined in the rainy season were many times higher than dry season values.

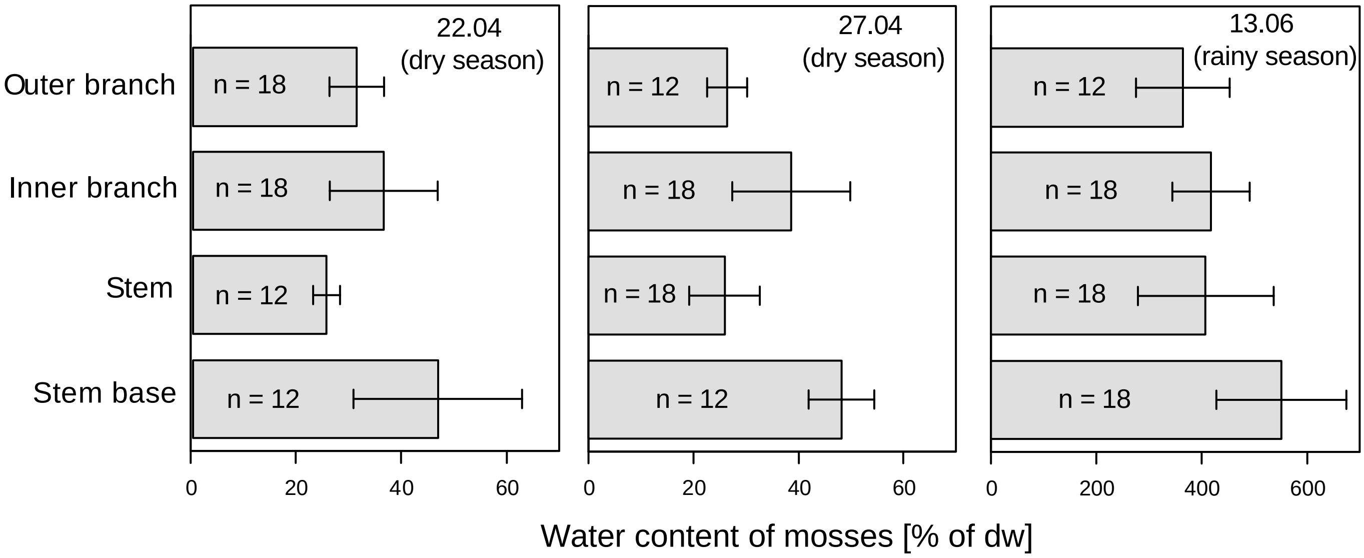

Figure 7: Water content of epiphytic mosses in a primary forest in Monteverde. Samples were collected in different sections of dominating trees (n=3 trees per sampling day) during two days in the dry season and one day in the rainy season .

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Appendix

Trees of the primary forest (incomplete list)

canopy trees

Panopsis costaricensis [Proteaceae]

Persea spec. [Lauraceae]

Ficus crassiuscula [Moraceae]

Meliosma vernicosa [Sabiaceae]

Weinmannia pinnata [Cunoniaceae]

Pouteria fossicola [Sapotaceae]

Guarea spec. [Melicaceae]

subcanopy trees

Cecropia cf. obtusifolia [Cecropiaceae]

Oreopanax xalapensis [Araliaceae]

Cojoba costaricensis [Fabaceae]

Elaeagia auriculata [Rubiaceae]

Prestoea acuminata [Arecaceae]

Guatteria oliviformis [Annonaceae]

Cosmibuena valerii [Rubiaceae]

understory treelets

Psychotria elata [Rubiaceae]

Siparuna spec. [Monimiaceae]

Guettarda poasana [Rubiaceae]

Chamaedorea tepejilote [Arecaceae]

Malvaviscus palmanus [Malvaceae]

Neomirandea angularis [Asteraceae]

Bactris dianeura [Arecaceae]