26 Water dynamics of epiphytic vegetation in a lower montane cloud forest: fog interception, storage, and evaporation

C. Tobón
Universidad Nacional de Colombia, Medellin, Colombia

L. Köhler
University of Göttingen, Göttingen, Germany

K. F. A. Frumau and L. A. Bruijnzeel
VU University, Amsterdam, The Netherlands

R. Burkard and S. Schmid
University of Bern, Bern, Switzerland

ABSTRACT

Epiphytic vascular plants and bryophytes constitute an important component of cloud forest canopies. Because of their different characteristics compared with leaves and other tree structural elements, epiphytes can be expected to behave differently in terms of their ability to intercept and store rain and cloud water, whereas losses through evaporation and drip may also occur at different rates. The water dynamics of epiphytes were studied in a windward lower montane cloud forest in northern Costa Rica. The exposed site experienced frequent horizontal precipitation (fog and wind-driven rain) as well as strong winds. *In situ* epiphyte wetting experiments were conducted at different levels within the 20-m canopy during a series of fog events using pre-weighed branches with known epiphyte biomass, while making simultaneous measurements of fog density and drop-size spectrum on a tower extending above the canopy. Rates of water loss via evaporation from pre-wetted epiphyte-laden branches suspended at different heights within the canopy were determined on dry days. Storage capacities were determined by gravimetric means, both in the field and under controlled conditions. Total epiphyte biomass of the forest was estimated through systematic sampling of three emergent trees and five sub-canopy trees in combination with a diameter survey of four plots of 1000 m^2 each. Fog interception rates by epiphyte-laden branches differed with position in the canopy, with an average rate of 54.7 ml $hour^{-1}$ kg^{-1} of oven-dry biomass. Absorption rates were correlated with fog liquid water content and initial moisture content of the sample. Rates of water loss during dry conditions differed considerably – depending on sample exposition, ambient climatic conditions, and sample moisture content – but followed an exponential decline with time. Maximum water storage capacity values differed also, with higher values after artificial spraying than after exposure to natural fog, suggesting that the samples were not completely saturated under field conditions with fog-only.

INTRODUCTION

Cloud-forested headwater areas on the Atlantic (windward) slopes of northern Costa Rica exhibit very high runoff coefficients. This has been attributed to, *inter alia*, a combination of reduced evaporative losses in the cloud belt and extra ("occult") inputs of wind-driven cloud water captured by the vegetation (Zadroga, 1981). On the Pacific side of the Continental Divide,

Tropical Montane Cloud Forests: Science for Conservation and Management, eds. L. A. Bruijnzeel, F. N. Scatena, and L. S. Hamilton. Published by Cambridge University Press.

throughfall in a leeward cloud forest in the same area (Monteverde) was reported to be low (65% of incident rainfall) despite an estimated annual extra input of "fog water" of 886 mm (Clark *et al*., 1998). Epiphyte biomass in this forest was estimated at 33.1 t ha^{-1} (Nadkarni *et al*., 2004), more than twice the value derived by Köhler *et al*. (2007) for a nearby windward cloud forest at a similar elevation (see also Häger and Dohrenbusch, this volume).

The frequent fog incidence commonly associated with montane cloud forests is widely considered to be responsible for the abundance of epiphytes in these forests (Frahm and Gradstein, 1991; Wolf, 1993; Bohlman *et al*., 1995; Hemp, 2002; Gradstein *et al*., this volume; Mulligan, this volume). Because of their different characteristics compared with leaves, vascular epiphytes such as bromeliads, and non-vascular epiphytes such as mosses and filmy ferns, can be expected to behave differently in terms of their ability to intercept and store cloud water, whereas losses through evaporation may occur at a different rate as well (Veneklaas *et al*., 1990; Richardson *et al*., 2000; Köhler *et al*., this volume; Mulligan *et al*., this volume #25).

The exact role of epiphytes in the canopy water balance is still incompletely understood but arguably assumes extra importance given the major difficulties associated with the accurate quantification of total water inputs to these forests. Under the prevailing windy conditions the separation of "ordinary" precipitation from wind-driven (horizontal) rain and fog is particularly difficult (cf. chapters by Frumau *et al*., Giambelluca *et al*., Häger and Dohrenbusch, Holwerda *et al*. #29, and Schmid *et al*., this volume). This calls for novel approaches, including process-based modeling (Murakami, 2006) and stable isotope techniques (Scholl *et al*. this volume; cf. Rhodes *et al*., 2006). Hölscher *et al*. (2004) used a running-water balance model to assess the contribution by epiphytes to total rainfall interception in an upper montane forest not subjected to significant fog inputs in the Cordillera de Talamanca of Costa Rica. To apply a similar approach under conditions of mixed precipitation (i.e. rain and fog), separate information is required on the wetting and drying characteristics as well as the storage capacities of leaves and epiphytes.

Previous studies of fog interception by epiphytes have mostly used disturbed samples. Epiphytes have been collected from branches and placed in plastic nets or racks inside the forest or in the open and have been exposed to rainfall and fog, or sprayed with water to determine the maximum storage capacity (e.g. Veneklaas *et al*., 1990; Chang *et al*., 2002; Hölscher *et al*., 2004; Mulligan *et al*., this volume #25). However, such approaches are likely to change the structure and composition of epiphyte arrangements on individual branches (Van Leerdam and Zagt, 1989). Moreover, upon entering a forest, fog is typically moving in a spatially heterogeneous manner according to spatial changes in wind speed and canopy density (Lovett, 1984). As a result, fog interception and evaporation rates will vary depending on position in the canopy and exposure to the prevailing winds and radiation. To take these considerations into account the present study used suspended branches with their epiphytes still in place at different heights within the canopy. The samples were exposed to the elements during foggy or dry conditions whilst determining the corresponding changes in weight and recording ambient weather variables.

This work was carried out as part of a larger project aiming to evaluate the hydrological impacts of cloud forest conversion to pasture in the Monteverde area of Costa Rica (Bruijnzeel, 2006).

STUDY SITE

The studied windward lower montane cloud forest was situated on the Atlantic slope in the Tilarán range at *c*. 1460 m.a.s.l., near Santa Elena, Monteverde, north-western Costa Rica (10° 21′ 33″ N, 84° 48′ 5″ W). Rainfall input between 1 July 2003 and 30 June 2004 was about 6000 mm with a somewhat less rainy period between February and April. Due to the prevailing strong winds, horizontal precipitation occurred frequently (both in the form of wind-driven rain and fog). Measured horizontal precipitation for the July 2003–June 2004 period was 2740 mm. Average temperature in 2003 was 17.0°C (monthly range 15.4–17.7°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). The main canopy reached a height of *c*. 20 m, with epiphyte-laden emergents extending from the canopy by several meters. Common trees in the upper canopy included *Ficus crassiuscula, Elaeagia auriculata, Weinmannia wercklei*, and various Myrtaceae (Lawton and Dryer, 1980). Tree ferns and palms of ~4 m height dominated the understorey. Epiphytic vascular plants and bryophytes were abundant and represented an estimated biomass of 16.2 t ha^{-1} (Köhler *et al*., 2007).

METHODOLOGY

Branch sections of *c*. 0.5 m length and diameters of 1.0–5.0 cm were collected from several trees using rope climbing techniques. The branches were covered with bryophytes, lichens, and small ferns, which were left in place. To measure epiphyte fog interception or evaporation rates, sample branches were placed on open trays at three different heights within the canopy (6, 15, and 22 m) using arms extending from a 25-m tall canopy access tower. Wind speed (A100 cup anemometers, Vector Instruments, UK), temperature and humidity (HMP45C sensors, Vaisala, Finland) were measured at these same heights, and solar radiation (CM7, Kipp and Zonen, the Netherlands) above the canopy. Occurrence of horizontal precipitation was recorded at all four heights as well using wire harps and cylindrical louvered screen gages (Frumau *et al.*, this volume) whereas fog liquid water content (*LWC*) was derived from above-canopy measurements of fog drop-size spectrum made with a cloud-particle spectrometer (Burkard *et al.*, 2003; cf. Schmid *et al.*, this volume).

Rates of fog water absorption by the epiphytes were determined by exposing three pre-weighed and air-dried sample branches per measurement height and sampling occasion to passing fog, and recording changes in weight on an hourly basis using portable weighing equipment. Samples were exposed throughout the daytime (07:00–17:00 h) as long as conditions with fog (but not rain) lasted. Care was taken to avoid that samples received water dripping from other samples in higher positions. In total, 67 sample branches were used during 11 fog events. On dry days, rates of water loss via evaporation were determined using three pre-wetted samples per measurement height and run. Drying experiments were carried out during daytime conditions on 19 days between February 2003 and February 2004 without fog or rainfall, involving a total of 102 samples. After each absorption or drying experiment, all epiphytes were collected per branch, weighed to the nearest 0.1 g and dried at 70°C for 48 hours. Branch volume, surface area, and length were also determined. The observed hourly differences in sample weight and oven-dry weights allowed computation of the corresponding (net) fog absorption or evaporation rates. Water contents were expressed as percentages of dry weights.

Similar epiphyte-covered branches ($n = 53$) as used in the field experiments were used for the laboratory determination of the maximum water storage capacity. Samples were sprayed with water until saturation, covered with plastic against evaporation and suspended for about 30 min until drainage finished. Next, the epiphytes were separated from the branch and gravimetric moisture contents determined as described above. The mean gravimetric water content for all samples was taken to represent the maximum epiphyte water storage capacity. The value of total epiphyte biomass for the forest as derived by Köhler *et al.* (2007) was used to extrapolate fog water absorption and evaporation rates (ml hour^{-1} kg^{-1} of dry biomass) and storage capacity values (%) to the stand level (in mm hour^{-1} and mm, respectively).

Between March and July 2003, bryophytes and crown humus were also sampled frequently (though irregularly) from 0.5-m branch sections located in the inner crowns at 15–20 m height to determine day-to-day variations of *in situ* gravimetric water content ($n = 600$; Köhler *et al.*, 2007). The observed difference in maximum and minimum water contents during this period was multiplied times the corresponding biomass to obtain an estimate of the *in situ* water storage capacity associated with dry biomass of epiphytes and canopy humus at the stand level (Köhler *et al.*, 2007).

Simple and multiple regressions were used to investigate to what extent fog absorption rates, epiphyte storage capacity, and fog *LWC* were correlated, and to assess the influence of different climatic parameters on fog absorption and evaporation rates (Pearson correlation coefficients).

Epiphyte absorption and evaporation rates at different measurement heights were compared on the basis of geometric means, minimum and maximum values, Pearson correlation coefficients as well as coefficients of variation and an ANOVA test.

RESULTS AND DISCUSSION

Fog interception by epiphytes

Fog events occurred throughout the year, mostly together with wind-driven rain. However, during the drier February–April period, fog events often occurred separately from rainfall. During 11 such events – which represented a wide range of intensities – epiphyte-covered branches were exposed to passing fog. Fog absorption increased asymptotically with time (Figure 26.1), and in individual events reached 88% of sample oven-dry weight. Overall average fog absorption was 5.6% (± 3.0) of dry weight hour^{-1} or 54.7 ml hour^{-1} kg^{-1}. *Net* absorption rates (i.e. gross absorption minus concurrent evaporation, see below) at 15 and 22 m were not significantly different at *c*. 5% of dry epiphyte weight hour^{-1}, but the average rate of 6.8% at 6 m height was significantly higher ($p < 0.03$) (Table 26.1, Figure 26.1). Therefore, net fog absorption efficiency increased from the top of the canopy downward. In addition, during some hours with low-intensity fog, samples were observed to lose weight

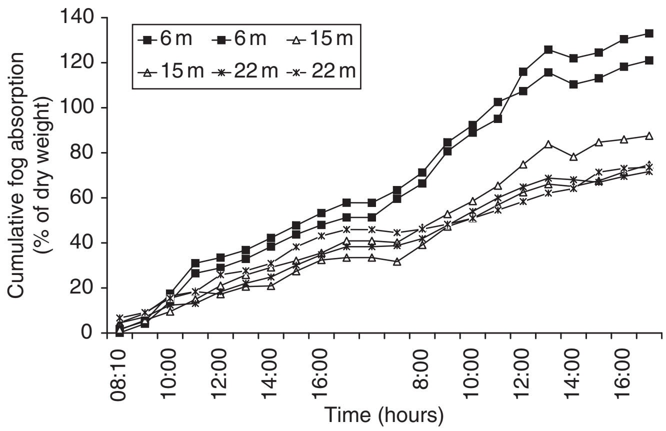

Figure 26.1. Cumulative daytime absorption (% of dry weight) of fog water by epiphytes exposed to foggy conditions in a windward lower montane cloud forest, Monteverde. Epiphyte samples were positioned at 6, 15, and 22 m above ground level.

Table 26.1 *Average and maximum values of fog absorption and evaporation rates (standard deviations between brackets) of epiphytes at three different heights within a windward lower montane cloud forest, Monteverde*

	22 m	15 m	6 m
Net fog absorption rate			
(gain as % of dry weight hour^{-1})			
Average	4.8 (± 3.0)	5.2 (±2.4)	6.8 (±3.2)
Maximum	13.4	13.2	16.2
Interception rate (ml hour^{-1} kg^{-1})	49.4 (± 31.4)	52.6 (± 27.1)	62.3 (± 34.7)
Evaporation rate			
(loss as % of dry weight hour^{-1})			
Average	13.3 (± 10.3)	12.7 (± 10.8)	10.0 (± 8.8)
Maximum	55.4	45.1	36.5

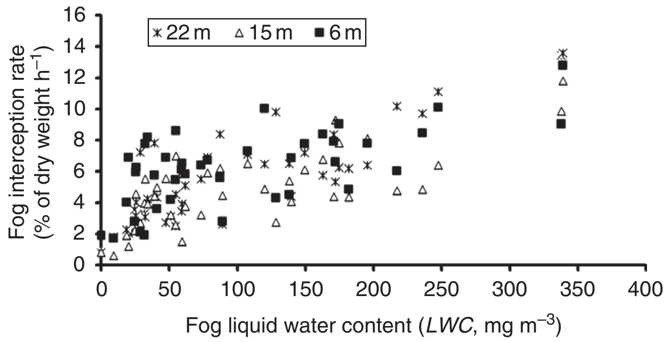

Figure 26.2. Relationship between fog liquid water content (mg m^{-3}) and hourly absorption of fog water by epiphytes (% of dry weight) exposed at three different heights in a windward lower montane cloud forest, Monteverde.

again – especially in the more exposed and ventilated upper third of the canopy. Conversely, at 6 m (i.e. below the main canopy) the air remained near-saturated, whereas radiation levels were low and ventilation poor (Table 26.1).

When exposed to consecutive fog events, samples accumulated on average up to 133% of their dry weight (Figure 26.1), with the largest increases noted at the lowermost position. Of the samples that were exposed to continuous fog for three days in a row, some began to drip on the second day after their weight had reached about 180% of the dry weight. However, consecutive measurement showed that all samples continued to increase their weight throughout the duration of the fog event (Figure 26.1). Visual inspection revealed that even when the sample surface was almost saturated, the inside was still partially dry. Thus, part of the surface excess water dripped to the forest floor while wetting of the inner part of the moss sample continued. According to Chang *et al*. (2002), fog absorption by bryophytes is controlled by surface wetness. However, the present results indicate that absorption is only partly influenced by the degree of surface wetness; increases in weight, even when the surface is completely saturated, occur due to continued movement of water from the outside to the inside of the sample.

The presently found average values of fog absorption (49.4–62.3 ml hour^{-1} kg^{-1}) are much lower than those reported by Chang *et al*. (2002) in Taiwan but considerably greater than those obtained by Mulligan *et al*. (this volume #25) in a sheltered Colombian LMCF. This may be related to differences in sampling methodology and duration of sample exposure, as well as the prevailing fog density and wind speeds. In the present study, the samples were undisturbed and may have mimicked actual conditions rather better than disturbed and repacked samples. Also, the largest increases in sample weight were observed at the beginning of the experiments, which further explains the larger values found by Chang *et al*. (2002) who exposed completely dry samples during very short periods only (up to 1.5 hours). The very low rates of fog absorption reported for the Colombian forest may reflect the very low wind speeds and reduced fog density prevailing beneath the canopy at Tambito (see discussion in Mulligan *et al*., this volume #25).

Amounts of fog absorption by the epiphytes correlated rather poorly with climatic parameters that would be expected to be of importance, such as atmospheric humidity or wind speed ($r^2 < 0.24$). This is due to the fact that during fog events relative humidity at all heights was close to saturation anyway, whereas wind speeds were highly variable. No relationship with average wind speeds was found either. However, absorbed amounts of fog water correlated better ($r^2 = 0.56$) with fog *LWC* (Figure 26.2). Furthermore, the multi-factor ANOVA revealed a significant relation ($p < 0.05$) between epiphyte fog absorption rate, fog *LWC* and (to a much lesser degree) wind speed (Figure 26.3).

Generally, the rate of fog absorption was somewhat larger at the beginning of the experiments – when the samples were still air-dry – implying an inverse correlation between the rate of fog absorption (ml hour^{-1} kg^{-1}) and sample gravimetric moisture content (%, Figure 26.4). The epiphytes were capable of absorbing more than twice their own dry weight below the main canopy (at 6 m) though smaller values were attained at higher positions in the canopy (Figure 26.4).

Evaporation from epiphytes

Figure 26.5 shows the exponential decreases in epiphyte water content during four consecutive dry days (1–4 February 2004) at 22, 15, and 6 m height, respectively. The surfaces of the samples generally dried within 4 hours but most samples remained moist inside even after several days of exposition to dry conditions (e.g. >100% gravimetric moisture; Figure 26.5). The continued supply of moisture from the inner to the outer parts is thought to

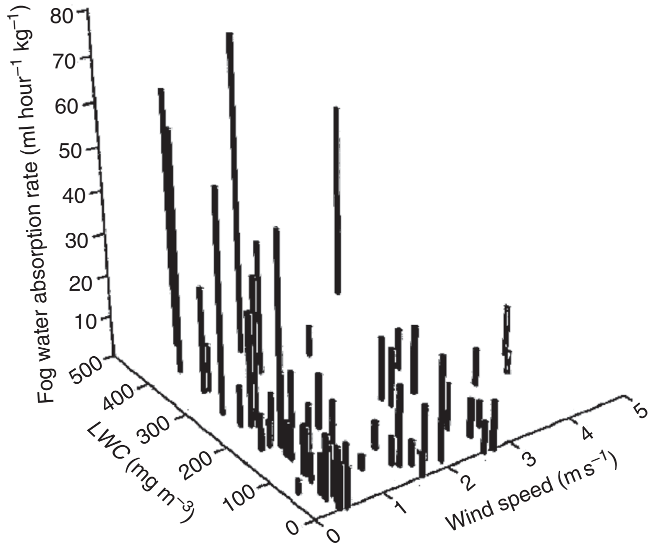

Figure 26.3. Dependence of fog absorption (ml hour^{-1} kg^{-1}) by the epiphyte surface layer on fog liquid water content (*LWC*, mg m^{-3}) and wind speed (m s^{-1}) in a windward lower montane cloud forest, Monteverde.

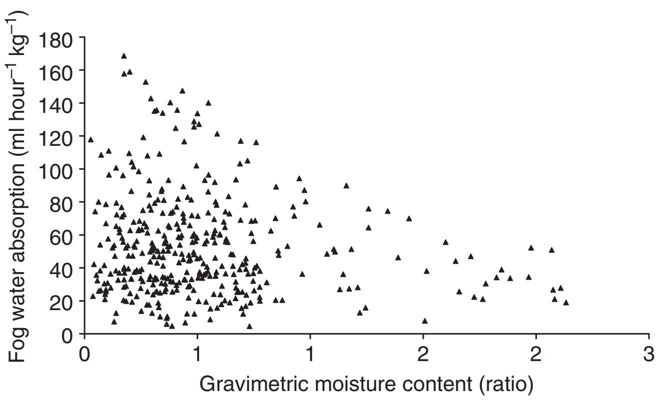

Figure 26.4. Fog water absorption by epiphytes (ml hour^{-1} kg^{-1}) vs. epiphyte gravimetric water content (% of dry weight) in a windward lower montane cloud forest, Monteverde.

sustain epiphyte physiological processes and to ensure survival during dry conditions (cf. Hietz, this volume).

Average evaporation rates and total loss of water by epiphytes located at the top of the tree crowns were much higher than inside the forest ($p < 0.05$; Table 26.1). Evaporation was related ($r^2 = 0.47$) to gravimetric water content of the sample (Figure 26.6) and to net radiation as measured at the top of the canopy ($r^2 = 0.43$; epiphytes at 22 m only), but not to the Penman reference evaporation equivalent ($r^2 = 0.18$) as determined for above-canopy conditions.

On average, rates of water lost by evaporation were 1.5–2.8 times higher than rates of net fog water absorption (Table 26.1). As such, the large losses of water from thoroughly wetted

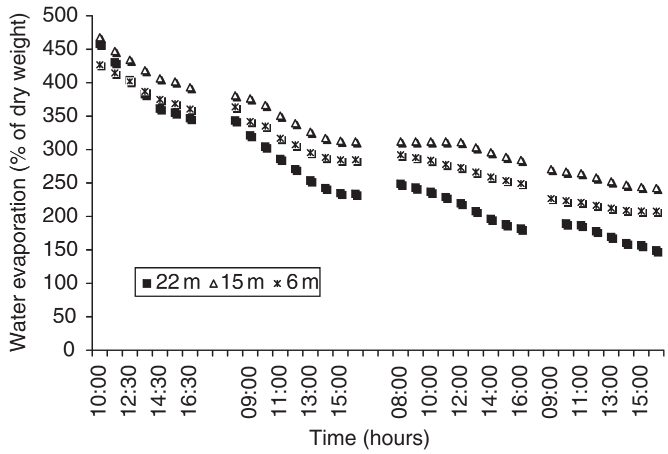

Figure 26.5. Decrease in daytime water content (% of dry weight) of nine epiphyte samples at three heights each ($n = 27$) during four consecutive dry days, in a windward lower montane cloud forest, Monteverde.

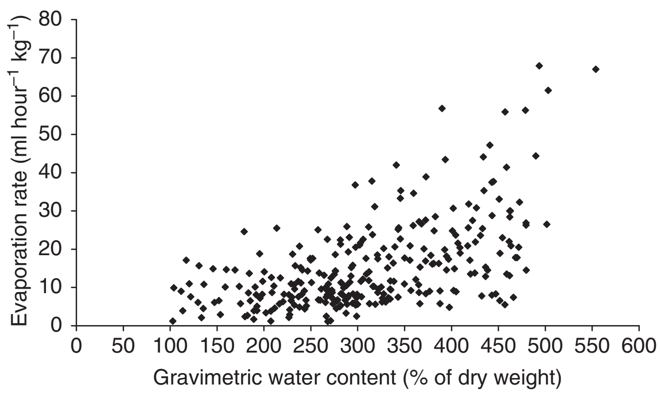

Figure 26.6. Relationship between daytime weight loss through evaporation from epiphytes (ml hour^{-1} kg^{-1}) and epiphyte water content (% dry weight) in a windward lower montane cloud forest, Monteverde. Data from three different heights were pooled.

epiphytes were not compensated by fog inputs, and additional water must be derived from rainfall. The situation is less critical at lower levels in the canopy where epiphytes retained greater quantities of water in between fog or rainfall events (Figure 26.5) and where net absorption rates were higher (Figure 26.1). These wetting and drying patterns have important implications for the throughfall dynamics of cloud forests. Often, the epiphytes will still be partially wet upon the start of a rainfall event and less water will be required to replenish epiphyte water storage capacity. This, in turn, is expected to result in more water passing through the canopy and reaching the soil surface. The different wetting and drying characteristics of epiphytes compared to those of leaves also render the modeling of overall canopy interception much more complex (cf. Murakami, 2006; Hölscher *et al.*, 2004).

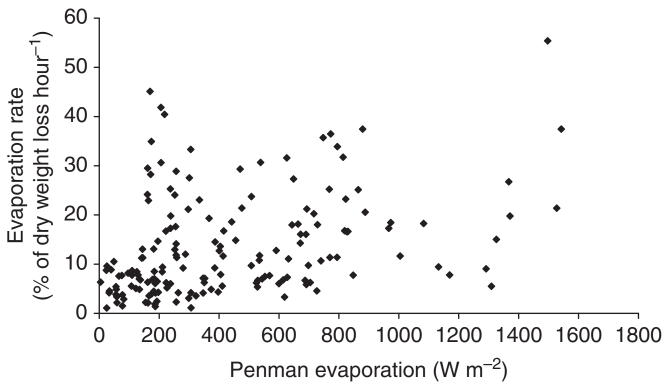

Figure 26.7. Cumulative weight loss through evaporation from epiphytes and canopy humus as measured *in situ* at 15–20 m height in a windward lower montane cloud forest at Monteverde, during three consecutive rainless days in April 2003.

Evaporation from epiphytes sampled *in situ* from the inner parts of tree crowns at 15–20 m height during three consecutive rainless days in April 2003 amounted to 251% of dry weight in the case of bryophytes and 117% for less exposed canopy humus (Figure 26.7). This finding agrees with the observation during the branch weighing experiments that the outside parts of epiphyte samples dried out much faster than the insides. Although, strictly speaking, the two evaporation data-sets (*in situ* sampling vs. suspended branches) are not fully comparable, the similarity in results is striking.

Water storage capacity of epiphytes

The average maximum water storage capacity of epiphyte samples (laboratory wetting tests) was determined at 323 ± 106% of dry weight. The high standard deviation reflects the variable composition of epiphytic species on the sample branches. Although the bulk of the epiphytes consisted of mosses with an intrinsically high storage capacity, the presently found storage value falls in the lower part of the range reported for various cloud forests (Kershaw, 1985; Shaw and Goffinet, 2000) and is much lower than the value derived by Pypker *et al*. (2001) for a Douglas fir forest in the Pacific North-West using very small (3 g) undisturbed epiphyte samples. Such differences may be related to differences in size, composition, and shape of the samples used in the various studies. The presently used samples were much larger and consisted of a mixture of bryophytes, ferns, and bromeliads rather than bryophytes only.

Combining the maximum water storage capacity of 323% with the total epiphyte biomass of 16 215 kg ha^{-1} derived for this mature cloud forest by Köhler *et al*. (2007) allowed an estimation of the (maximum) amount of water that can be held by the epiphytes at the stand scale as 5.24 mm. Kőhler *et al*. (2007) derived a very similar value of 4.95 mm for the same forest based on the maximum variation in epiphyte water content as measured *in situ* in the crowns at 15 and 20 m. However, because of the considerable amounts of water actually retained by the epiphytes (cf. Figure 26.5), the actually available storage capacity will be much lower and variable, depending on antecedent weather conditions (cf. Hölscher *et al*., 2004; Köhler *et al*., 2007).

CONCLUSIONS

Amounts of cloud water absorbed by epiphytes suspended at different levels within the canopy of a windward lower montane cloud forest in Costa Rica were positively related to fog liquid water content, whereas absorption rates decreased as epiphyte water content increased. Net fog absorption rates were always higher below the main canopy (6 m) than at the canopy level (22 m), whereas evaporation rates were persistently lower at 6 m. Evaporation losses on dry days were typically 150–280% of average fog absorption rates, depending on canopy position. Therefore, epiphyte water content within the canopy was both higher and varied less with time than in the top of the canopy. Evaporation followed a logarithmic decay pattern and was inversely related to remaining water content of the sample. Although both laboratory and *in situ* tests suggested a maximum water storage capacity value associated with epiphytes of *c*. 5 mm at the stand level, *in situ* evaporation experiments also indicated that epiphytes did not fully dry out between precipitation events, not even after three to four consecutive dry days. This implies that in practice a much smaller amount of rainfall may be required to replenish epiphyte storage capacity depending on previous wetting and drying cycles. As a result, amounts of throughfall will be enhanced accordingly, also because epiphytes were observed to start dripping during dense fog events before full saturation was reached.

ACKNOWLEDGEMENTS

Financial support from the Forestry Research Programme of the Department for International Development of the UK (FRP-DFID project R7991) is gratefully acknowledged. The views expressed here are not necessarily those of DFID. Dr. Peter Hietz is thanked for reviewing the draft manuscript. Special thanks go to Eulogio Jimenez of the San Gerardo Lodge for site permission and help, and to the FIESTA field team for their assistance.

REFERENCES

Bohlman, S.A., T.J. Matelson, and N.M. Nadkarni (1995). Moisture and temperature patterns of canopy humus and forest floor soil of a montane cloud forest, Costa Rica. *Biotropica* **27**: 13–19.

Bruijnzeel, L.A. (2001). Hydrology of tropical montane cloud forests: a reassessment. *Land Use and Water Resources Research* **1**: 1.1–1.18.

Bruijnzeel, L.A. (compiler) (2006). *Hydrological Impacts of Converting Tropical Montane Cloud Forest to Pasture, with Initial Reference to Northern Costa Rica*, Final Technical Report DFID-FRP Project no. R7991. Amsterdam: VU University Amsterdam, and Aylesford, UK: Forestry Research Progamme of the UK, Department for International Development. Also available at www.geo.vu.nl/~fiesta.

Burgess, S.S.O, and T.E. Dawson (2004). The contribution of fog to water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. *Plant, Cell and Environment* **27**: 1023–1034.

Burkard, R., P. Bützberger, and W. Eugster (2003). Vertical fogwater flux measurement above an elevated forest canopy at the Lägeren research site, Switzerland. *Atmospheric Environment* **37**: 2979–2990.

Clark, K.L., N.M. Nadkarni, D. Schaefer, and H.L. Gholz (1998). Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. *Journal of Tropical Ecology* **14**: 27–45.

Chang, S.-C., I.L. Lai, and J. Wu (2002). Estimation of fog on epiphytic bryophytes in a subtropical montane forest ecosystem in north-eastern Taiwan. *Atmospheric Research* **64**: 159–167.

Frahm, J.-P., and S.R. Gradstein (1991). An altitudinal zonation of the tropical rain forest using bryophytes. *Journal of Biogeography* **18**: 669–678.

Hemp, A. (2002). Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro. I. Altitudinal distribution. *Plant Ecology* **159**: 211–239.

Hölscher, D., L. Köhler, A.I.J.M. van Dijk, and L.A. Bruijnzeel (2004). The importance of epiphytes in rainfall interception by a tropical montane rainforest in Costa Rica. *Journal of Hydrology* **292**: 308–322.

Kershaw, K.A. (1985). *Physiological Ecology of Lichens*. Cambridge, UK: Cambridge University Press.

Köhler, L., C. Tobón, K.F.A. Frumau, and L.A. Bruijnzeel (2007). Biomass and water storage of epiphytes in old-growth and secondary montane rain forest stands in Costa Rica. *Plant Ecology* **193**: 171–184.

Lawton, R., and V. Dryer (1980). The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* **18**: 101–116.

Lovett, G.M. (1984). Rates and mechanisms of cloud water deposition to a subalpine balsam fir forest. *Atmospheric Environment* **18**: 361–371.

Murakami, S. (2006). A proposal for a new forest canopy interception mechanism: splash droplet evaporation. *Journal of Hydrology* **319**: 72–82.

Nadkarni, N.M., D. Schaefer, T.J. Matelson, and R. Solano (2004). Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *Forest Ecology and Management* **198**: 223–236.

Pócs, T. (1980). The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Botanica Academiae Scientiarum Hungaricae* **26**: 143–167.

Pypker, T.G., B.J. Bond, and M.H. Unsworth (2002). *The Role of Epiphytes in the Interception and Evaporation of Rainfall in Old-Growth Douglas-Fir Forests in the Pacific Northwest*. Corvalis, OR: Oregon State University.

Richardson, B.A., M.J. Richardson, F.N. Scatena, and W.H. McDowell (2000). Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Tropical Ecology* **16**: 167–188.

Rhodes, A.L., A.J. Guswa, and S.E. Newell (2006). Seasonal variation in the stable isotopic composition of precipitation in the tropical montane forests of Monteverde, Costa Rica. *Water Resources Research* **42**, W11402, doi:10.1029/2005WR004535.

Shaw, A.J., and B. Goffinet (2000). *Bryophyte Biology*. Cambridge, UK: Cambridge University Press.

Van Leerdam, A., and R.J. Zagt (1989). The epiphyte vegetation of an Andean forest in Colombia: aspects of its hydrology and distribution in the canopy. M.Sc. thesis, University of Utrecht, Utrecht, the Netherlands.

Veneklaas, E.J., R.J. Zagt, A. van Leerdam, *et al*. (1990). Hydrological properties of epiphyte mass of a montane tropical rain forest, Colombia. *Vegetatio* **89**: 183–192.

Wolf, J. (1993). Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Garden* **80**: 928–960.

Zadroga, F. (1981). The hydrological importance of a montane cloud forest area of Costa Rica. In *Tropical Agricultural Hydrology*, eds. R. Lal and E.W. Russell, pp. 59–73. New York: John Wiley.