BRYOPHYTES IN THE HYDROLOGICAL CYCLE AND CLIMATE CHANGE IMPLICATIONS: A CASE STUDY OF LA RÉUNION CLOUD FOREST.

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Trees covered in epiphytic bryophytes in the cloud forest of La Réunion.

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Dissertation presented in partial fulfillment of the requirements for the degree of Bachelor of Science (Honours) in the Department of Botany at the University of Cape Town, 2012.

Contents:

Methods

Results

Abstract

Bryophytes are able to intercept atmospheric water over the entire surface of their shoot and, once intercepted, this water forms a vital part of the hydrological cycle of their surrounding ecosystems. To investigate the role of bryophytes in the hydrological cycle, our study, conducted in the biodiversity hotspot of the tropical montane cloud forest of La Réunion, focused on two leafy liverwort species, *Mastigophora diclados* and *Bazzania decrescens*. We evaluated liverwort biomass, water storage capacity, atmospheric or cloud water interception, and photosynthetic response to desiccation. We found that *B. decrescens* stored approximately double the mean and maximum litres of water per hectare despite occupying less than half the volume of *M. diclados*. Despite this decreased water storage capacity, we found that *M. diclados* had a greater ability to intercept atmospheric moisture than *B. decrescens,* which had similar interception ability to the control. These interception abilities affected water flux in the two liverwort species. We found that this variation in water flux had an effect on photosynthesis. Both species displayed a significant relationship between photosynthesis and water content. We found that both species showed a loss of photosynthesis at very low and very high water contents with the optimal water content for photosynthesis corresponding to the *in situ* water content of the liverworts. The abundance of both species and their cloud water interception ability together with the wide range of photosynthetic tolerance of *M. diclados* and the large water storage capacity and slow desiccation rate of *B. decrescens* make both liverwort species ecologically important in the forest's hydrological cycle. Anthropogenic climate change threatens this ecosystem as the cloud that these species are so dependent on is predicted to lift. Our findings tie the liverworts very closely to their environment and therefore show support for the idea that bryophytes are excellent early warning signals for predicted climate changes.

Key words

Bazzania decrescens - climate change - cloud water interception - La Reunion - *Mastigophora diclados* - tropical montane cloud forest

Abbreviations

CWI: Cloud water interception
ETR: Electron transport rate
Mini-PAM: Miniature pulse-amplitude modulated photosynthetic yield analyser
TMCF: Tropical montane cloud forest

Introduction

Cloud forests are widely defined as “forests that are frequently covered in cloud or mist” (Stadtmüller, 1987). One of the most notable characteristics of tropical montane cloud forests (TMCFs) is their abundance of epiphytes, particularly epiphytic bryophytes which form up to 75% of the epiphyte community (Gradstein *et al.*, 2010; Lakatos, 2011). Bryophytes are poikilohydric meaning that their water content is changeable with that of the atmosphere (Lakatos, 2011). Associated with poikilohydry is the lack of specialised organs for the absorption of water or prevention of water loss (Lakatos, 2011). Bryophytes therefore store most of their water externally (Hietz, 2010) and are able to take up water and nutrients over the whole surface of their shoot which allows them to efficiently intercept solutes in rainwater, cloud and mist droplets, and airborne dust (Proctor, 2000).

The ability of bryophytes to intercept and store water suggests that they may be linked to a complex system of hydrological interrelations in these TMCFs (Lakatos, 2011). In a Tanzanian cloud forest epiphytes intercepted 724 mm of water per year, which represents 18% of annual precipitation (Pócs, 1980). This is likely an underestimation as cloud water interception (CWI) was not included and has been shown to contribute 2% to 61% of total water in the central cordillera of Panama (Cavelier *et al.*, 1996) and 10% to 93% in elfin cloud forests in Venezuela and Colombia (Cavelier & Goldstein, 1989). The ability to intercept cloud water is crucial to the survival of bryophytes and is highly developed in this group; for example, in pendent mosses, interception of as little as 0.5 mm of cloud water is sufficient to recharge their water holding capacity (Leon-Vargas *et al.*, 2006).

Once intercepted from the atmosphere, the water that bryophytes hold is a vital part of the hydrological cycle in cloud forests as this water is released into the canopy in frequent drying and re-wetting cycles (Lakatos, 2011). The water captured by bryophytes contributes significantly to maintaining the high humidity in the canopy and understory when atmospheric water inputs are absent (Veneklaas *et al.*, 1990). Bryophytes often store 500% to 1400% of their dry weight in water (Pócs, 1980) and have been shown to evaporate water up to 250% of their dry weight in three days in a cloud forest (Köhler *et al.*, 2007). In temperate coniferous rainforests the contribution of epiphytes to forest water vapour has been estimated to be as high as 25% of total ecosystem evaporation (Barbour *et al.*, 2005). Although CWI occurs on many forest components, such as stems, leaves and branches, the canopy water storage value tends to be much lower in forests where epiphyte biomass is less (Köhler *et al.*, 2010; Lakatos, 2011). The role that bryophytes play in the hydrological cycle is undoubtedly important and the importance of cloud water in TMCF water budgets has been acknowledged for some time (Kerfoot, 1968; Zadroga, 1981). Despite this, how such cloud-affected ecosystems function hydrologically is still largely unresolved (Scholl *et al.*, 2010; Bruijnzeel *et al.*, 2005; Giambelluca *et al.*, 2010). Specifically, the quantification of fog and cloud as a moisture source during rainless periods is needed to elucidate the water balance of cloud forests, especially since these usually occur in hydrologically important areas (Scholl *et al.,* 2010; Mulligan *et al.*, 2010).

Tropical forests contain around half of the world's bryophyte diversity, with cloud forests specifically being considered "hotspots of diversity" (Frahm & Gradstein, 1991). A better understanding of these forests worldwide has become even more pressing in recent years as predicted climatic changes are likely to affect bryophyte species distribution, community composition, and biomass (Scholl *et al.*, 2010). Most importantly for cloud forests, predicted climate changes include reduced input by cloud water (Still *et al.*, 1999). Their physiological dependence on water and nutrients from clouds and rain makes epiphytic bryophytes specifically vulnerable to changes in cloud water deposition in TMCFs (Nadkarni, 2010). As a result of this vulnerability, epiphytes in cloud forests have been shown to be useful indicators of even subtle changes in climate (Nadkarni, 2010). Considering that bryophytes affect or dominate a significant portion of terrestrial ecosystems (Lakatos, 2011), the predicted impact of these changes on the associated systems should be a research priority.

In addition to the threats posed by a changing climate, cloud forests also have to contend with land use change. Due to their cloudy, wet and difficult terrain, TMCFs have historically had some protection against degradation relative to other tropical forests (Scatena *et al.*, 2010). By the late 1970's and early 1980's this protection started to diminish and the forests started becoming increasingly fragmented and converted, so much so that by the early 1990's TMCFs moved high on the list of the world's most endangered ecosystems (Scatena *et al.*, 2010). Despite their late entry into the game of tropical forest destruction, by 1990/1991 TMCF's were being lost at a rate significantly greater than tropical lowland forests (1.1% per year vs 0.8% per year) (Doumenge *et al.*, 1995). The threat of land use change combined with predicted climate changes, the two biggest threats to global biodiversity, makes research on bryophytes in cloud forests all the more necessary.

Our study was done on the TMCF of La Réunion. La Réunion's TMCF is hugely valuable as it covers 6% of the island (National Park of La Réunion, 2012), is a biodiversity hotspot containing the peak of richness for corticulous bryophyte diversity (Ah-Peng *et al.*, 2012), and offers many benefits, including but not limited to hiking tourism. While the TMCF on the island has been a National Park since 2007, the limits of the forest are under pressure to be converted into agriculture and housing developments as the population of the island is ever expanding. We suspect that the forest plays a significant role in the hydrological cycle of the island due to its large bryophyte populations.

Despite an increase in knowledge on the Neotropical TMCFs, the Asian and African TMCFs remain largely mysterious as studies have been few and isolated (Scatena *et al.*, 2010). Currently, major gaps in our understanding of TMCFs have been identified as, *inter alia*, information on plant physiology, information on the hydrological and ecological consequences of converting TMCF to other forms of land use and information on the influence of land use and climate on the biodiversity and ecological functioning of TMCF (Scatena *et al.*, 2010).

This study will work towards filling these gaps by addressing i) How much bryophytic biomass is in this TMCF and how much water is this mass storing? ii) How much cloud water are the bryophytes intercepting in this cloud forest and how much cycles through the bryophytes in a day? As well as iii) given that predicted climate changes include the lifting of the cloud belt, which would decrease cloud water input, how does bryophyte photosynthesis react to changes in water content? We focused on two bryophyte species, *Mastigophora diclados* and *Bazzania decrescens*.

Materials and Methods

Study site

The study was conducted on La Réunion (55^{o}39’E; 21^{o},00’S), a French overseas department in the Mascarene Archipelago in the Indian Ocean, 300 km East of Madagascar and 200 km off the coast of Mauritius, its nearest neighbour. La Réunion is a biodiversity hotspot and is unique in the sense that, unlike other oceanic islands, it still has large areas of its tropical rainforest intact (Ah-Peng *et al.*, 2007). The bryological flora of the island has high species diversity, with 405 moss species and 245 liverwort species discovered to date (Ah-Peng & Bardat, 2005). The climate on the island is tropical with summer rainfall (1500 mm to >8000 mm p.a.) (Ah-Peng *et al.*, 2007). The study took place from 10 to 21 April 2012 (decimal day of year 101 to 112). The study site (Figure 1), in TMCF on the dormant volcano Piton des Neiges (3070 m.a.s.l.), was within the Bébour forest near the Sentier de la Rivière walking trail within the Parc National de La Réunion. Two plots of 10 m x 10 m were identified at 1350 m.a.s.l. and had GPS coordinates of 55^{o},34’,36”E; 21^{o}04’,33”S and 55^{o}30’23”E; 21^{o}04’33”S. Despite the weather being sometimes sunny with no clouds, the site was inundated at least once every day by heavy cloud, and sometimes this cloud persisted throughout the day and was accompanied by rain.

Figure 1: Picture of the study site (1350 m.a.s.l) in the Bebour Cloud Forest on the dormant volcano Piton des Neiges on La Réunion. Note the extensive epiphytic bryophyte coverage of the tree branches.

Study species

Two species were studied, *Mastigophora diclados* (Brid. ex F.Webber) Nees. and *Bazzania decrescens* (Lehm. & Lindenb.) Trevis. These two species were selected as they formed the bulk of the bryophyte biomass in our study site.

M. diclados is a leafy liverwort of the Mastigophoraceae. It is a yellowish- to reddish-brown or dark brown plant that grows in mats or cushions (Wigginton, 2004). Its fronds are well developed and can grow up to 10 cm long and are regularly pinnate or bipinnate (Wigginton, 2004). The main axes are straight, rigid and 0.6-1.0 mm wide with branches that are distant, regularly spaced, arched and much more slender than the main axes, often attenuate becoming flagelliform (Wigginton, 2004). It grows in mossy forests at moderate elevations on branches, trunks and roots of forest trees and on the trunks of tree ferns (Wigginton, 2004). It can be a habitual canopy species (Wigginton, 2004). By inspection *in situ* at our study site it was noticeable that *M. diclados* grew in the understory and canopy of the forest, but generally did not grow as near the ground as *B. decrescens*. The gametophytes tended to grow in large loosely packed masses that covered tree branches or trunks, often hanging in large “balls” from tree branches both low and high up in the canopy (Figure 2).

B. decrescens is also a leafy liverwort but of the Lepidoziaceae. Its strong green shoots are 1.5-2.5 mm wide with stems 0.15-0.20 mm wide and leaves that are not divided into lobe and lobule but are plane to deeply concave (Wigginton, 2004). It occurs from sea level to the sub-alpine region, growing in abundance on the trunks, bases, and large branches of trees as well as on stumps, logs, and rotten wood (Wigginton, 2004). By inspection *in situ* at our study site it was noticeable that *B. decrescens* is generally restricted to growing in the forest understory, usually on rocks and fallen logs that are moist all of the time. The gametophytes are relatively small and grow in dense flat mats (Figure 2).

Determining water content, water storage capacity and biomass

The methods laid out by Köhler *et al.* (2010) for determining water content of epiphytes were used. For each species of liverwort a small monospecific sample of approximately 10 cm x 10 cm was cut from the liverwort cushion and placed immediately into a sealed plastic bag of

Figure 2: *Mastigophora diclados* (i-iii) and *Bazzania decrescens* (iv-vi). Individual gametophytes (i and iv), gametophytes *ex situ* (loosely packed in (ii) and in a dense mat in (v)) and habit (large loosely packed masses that covered tree branches or trunks, often hanging in large "balls" from tree branches both low and high up in the canopy in (iii) and dense flat mats in the forest understory near the floor in (vi)).

known mass. Collections were made on three days at two different times of day, either the morning or the mid- to late afternoon, and in different weather conditions - two days were sunny and one was rainy. In total 72 samples of each species were collected. Samples were weighed (Denver Instrument, accurate to 1mg) in the plastic bag to include any water adhering to the bag. The difference between this weight and the known weight of the plastic bag gave the weight of each sample *in situ*. Samples were then removed from the bags, saturated with water using a spray bottle, and weighed again to determine their saturated weight before being dried in an oven at 70 °C for 48 hours, after which they were weighed a third time to determine their dry weight. The difference between the dry weight of each sample and the *in situ* weight of each sample was taken to be the *in situ* water content of each sample, in grams of water per gram of dry weight (g H_2O g dry weight^{-1}). The difference between the saturated weight and the dry weight of each sample was taken to be the maximum water storage capacity of the sample, in g of H_2O g of dry weight^{-1} (g H_2O g dry weight^{-1}). The dimensions of each sample were also measured, giving *in situ* and maximum water storage of the samples in grams of water per cm^3 (g H_2O cm^{-3}). Two-sample t-tests were used to determine if the two species differed significantly ($p<0.05$) in water storage capacity.

Bryophyte biomass was estimated in three plots of 10 m x 5 m within the study site. In each plot the diameter at breast height of every tree present was recorded. Each tree was then divided into approximately cylindrical sections and each section's length and diameter was measured. On each of these sections the percentage cover by bryophytes was estimated visually and categorized as *Mastigophora diclados* cover, *Bazzania decrescens* cover or other bryophyte cover. The thickness of bryophyte cover in each category on each section was then measured three times per section per species using a metal ruler pushed horizontally into the bryophytes until it touched the wood of the tree underneath.

The biomass estimates were then converted to biomass per cm^3 according to standard surface area and volume relationships. These values were converted into kg of dry mass per hectare (kg dry mass ha^{-1}) and litres of water per hectare (litres H_2O ha^{-1}) using the cm^3 to gram of dry mass and cm^3 to gram of water relationships determined in the water content analysis above. The grams of water and grams of dry mass per cm^3 were log-normally distributed and thus the geometric mean was used in estimation of biomass and water storage capacity (Limpert *et al.*, 2001). In order to account for compounded error rates, the standard deviation was corrected using standard techniques for error propagation (Limpert *et al.*, 2001).

Investigating cloud water interception and water flux

This was done using the same weighing lysimeters as the study by Maphangwa *et al.* (2012). The weighing lysimeters were originally developed for quantifying evapotranspiration, but have subsequently been used for recording fog and dew accumulation and evaporation from soil surfaces (Maphangwa *et al.*, 2012). The lysimeters consist of a metal pan attached to a sensitive scale linked to a data logger (Maphangwa *et al.*, 2012). They are able to directly measure gains, losses, and residence times of water (Maphangwa *et al.*, 2012). Three lysimeters, one for each study species and one as a control, were set up underneath a rain exclosure at one of our study sites and set to log weight every 15 minutes. A temperature and relative humidity logger (Madgetech, RHTemp1000) as well as a tipping rain gauge (HOBO 8000 event data logger) were set up adjacent to the rain exclosure. In each lysimeter pan a mat of bryophyte gametophytes (approximately 240 mm in diameter) from each species was placed on an upturned plastic container which served to elevate the mat above the lip of the pan, therefore eliminating any boundary layer effects the lysimeter itself may have imposed on the water fluxes of the bryophytes. The experimental set-up is shown in Figure 3. Since the bryophyte mat was sheltered from rain, any changes in weight of the mat must result from cloud water interception and evapotranspiration and thus the flux of cloud-derived water through the species can be determined. The data gathered consisted of three environmental measurements, rainfall events (mm), temperature (^{o}C) and relative humidity (%) as well as the weight of bryophyte mat (g) associated with a given time of day. When plotting weight gain and loss against time and examining it in conjunction with our three environmental measurements, it was suspected that three different climatic conditions were causing three distinct responses in the liverwort species. The presence of these three climatic states was confirmed by plotting each day's weight change responses on the same time of day axis, which allowed the level of overlap between days of similar weather conditions to be seen. The days were separated into a) days with high humidity, relatively mild temperatures and little rainfall, presumably with a relatively average amount of cloud cover (decimal day of year 102, 111 and 112), b) relatively dry days where humidity dropped below 100 %, temperature showed higher peaks and little to no rain fell (decimal day of year 103, 104, 106, 107 and 110) and c) very wet days where rainfall was very high and humidity remained high and temperature low the entire day (decimal day of year 108 and 109). Water flux was calculated as the difference between each lysimeter reading and the reading preceding it. These differences were then summed, separating the negative from the positive differences (negative indicating water out and positive indicating water in), to give water flux out of and in to each treatment per day in milliliters of water per day (ml H_2O day^{-1}). The average water flux values for each type of day (climatic conditions a-c above) and their standard errors were calculated. A factorial analysis of variance (ANOVA) was used to establish which flux estimates were significantly different ($p<0.05$) from each other (Statistica v10, StatSoft, Inc., 2011).

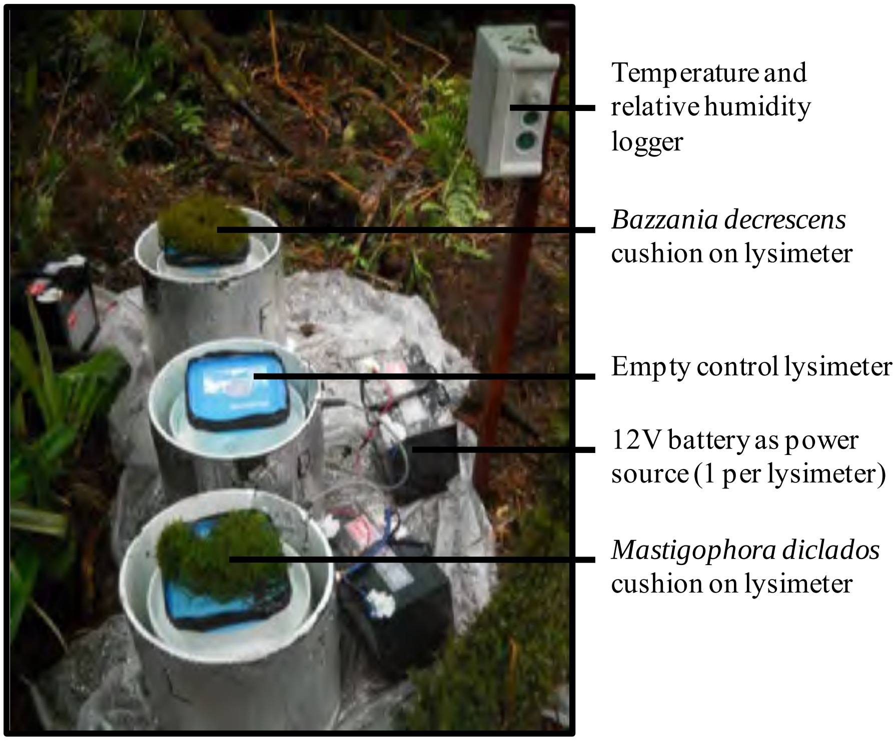


Figure 3: Experimental set-up at the site in the La Réunion Cloud Forest, rain excluded from set-up by tarpaulin (not seen) and rainfall measured outside of exclosure by tipping rain gauge (not seen).

Photosynthetic response to desiccation

Photosynthesis was measured using a miniature pulse-amplitude modulated photosynthetic yield analyser (Mini-PAM) following the recommended sampling process for bryophytes (Mini-PAM; Walz, Effeltrich, Germany). The Mini-PAM, in conjunction with the Leaf Clip Holder 2030-B (Mini-PAM; Walz, Effeltrich, Germany), was able to estimate electron transport rate (ETR), a measure of photosynthetic carbon fixation and photorespiration, which was used in our analyses as a measure of photosynthesis (see Lakatos *et al.* 2012). The sampling of the bryophytes for photosynthetic activity took place during the oven drying stage, with the drying temperature during this process reduced to below 30 ^{o}C in order to avoid damage to the bryophyte's photosynthetic apparatus. Each sample was dried for 15 minutes, removed from the oven and allowed to cool for 5-10 minutes in order to acclimate, weighed to determine its water content and then tested with the Mini-PAM to establish its photosynthetic activity at that particular water content. These measurements were done during the day in ambient sunlight. The process was repeated every 15 minutes until the samples stopped losing weight and were completely dry. The Mini-PAM is able to give false low ETR readings due to uncontrollable factors, like a passing shadow or sample leaves not lying perfectly flat underneath Leaf Clip Holder 2030-B, but is not able to give false high readings. Since false low readings will affect any model used on the data, six replicates were done for each sample at each given water content and the highest of these six readings was used in the analyses. This gave a better representation of the biological process occurring. The data collected were not homoscedastic, normal or assymetrical, thus a spline model, which requires none of these conditions to be met, was used to evaluate the form of the relationship between ETR and water content. 95 % confidence intervals were also calculated for the model using a non-parametric bootstrapping method. These analyses were performed in R (v2.15.1, R Core Team, 2012).

Results

All data used in analyses are shown in the appendix.

Water content, water storage capacity and biomass of the bryophytes

B. decrescens had a significantly higher maximum water storage capacity and *in situ* water storage than *M. diclados*, however both species had relatively high water storage capacities (maximum of over 1000 % of dry weight) (Table 1). The dry biomass per hectare of *M. diclados* was less than that of *B. decrescens* (Table 2) despite *M. diclados* having more than double the volume (mean ± standard error, 127.7 ± 51.8 vs 58.2 ± 30.0 m^3 ha^{-1}). This larger biomass combined with its larger water storage capacity (mean ± standard error, 6.5 ± 0.22 vs 4.7 ± 0.09 g water g dry $weight^{-1}$) resulted in *B. decrescens* holding approximately double the volume of water per hectare than *M. diclados* (equivalent to mean ± standard deviation of 1.17 (± 0.90) mm vs 2.29 (± 0.52) mm of rainfall, see Table 3).

Table 1: Maximum and *in situ* water storage capacities of *Mastigophora diclados* and *Bazzania decrescens* as determined by gravimetric analysis on samples collected in the La Réunion cloud forest. All values are the mean grams of water stored per gram of dry weight (± standard error). * indicates a significant difference was found between the two species in a two-sample t-test.

	Mean maximum water storage (mean g H_2O g dry $weight^{-1}$ ± standard error) * (p<0.001)	**Mean water storage *in situ*** (mean g H_2O g dry $weight^{-1}$ ± standard error) * (p<0.001)
Mastigophora diclados	7.20 (± 0.16)	4.67 (± 0.09)
Bazzania decrescens	10.74 (± 0.30)	6.34 (± 0.22)

Table 2: Mean biomass (kg of dry mass per ha) of *Mastigophora diclados* and *Bazzania decrescens* in three 10 m x 5 m plots in the cloud forest of La Réunion. Mean biomass per plot (50 m^2) was calculated as the product of cm^3 of bryophyte volume per 50 m^2 plot and grams of dry weight per cm^2 (determined from samples collected in the forest). The standard deviation is corrected for error propagation. The large standard deviation is a product of the high variability in estimation of biomass in only three plots. This biomass estimation is likely below the actual biomass value of bryophytes in the forest as liverworts and other bryophytes that were not one of our two study species were not included.

	Mean biomass per 50m^2 plot (mean kg dry mass ha^{-1} ± standard deviation)
Mastigophora diclados	2 541(± 8 965)
Bazzania decrescens	3 667 (± 5 198)
Total	6 208 (± 14 162)

Table 3: Mean water storage (litres of water ha^{-1}) of *Mastigophora diclados* and *Bazzania decrescens* in the cloud forest of La Réunion. The standard deviation is corrected for error propagation. Water storage was calculated by combining volume of liverwort species per hectare in three 50 m^2 plots and g of *in situ* water stored per cm^3 of collected samples.

	Mean water storage per hectare (mean litres H_2O ha^{-1} ± standard deviation)
Mastigophora diclados	11 707 (± 8 965)
Bazzania decrescens	22 862 (± 5 198)
Total	34 569 (± 14 162)

Cloud water interception and water flux in the bryophytes

Both species and the control show diurnal weight change patterns, with the amplitude of this change larger in the liverworts than the control (Figure 4a). Both species differ from the control with regards to their weight change patterns over time and the two species responses diverge from each other most when relative humidity is consistently high and rainfall shows a sharp increase in volume (Figure 4a). During this divergence, *M. diclados* shows a very steep increase in weight while *B. decrescens* increases less steeply, in a manner more similar to the control (Figure 4 a & c). During decimal days of year 101, 102, 108, 109, 111 and 112 *M. diclados* shows weight fluctuations similar to that of the control, but shows a daily gain in weight that exceeds any gain seen in the control (Figure 5). On decimal days of year 103, 104, 106, 107, 108, 109 and 110 *M. diclados* loses more weight and gains less weight than the control, causing a continuous decrease in weight relative to the control (Figure 5). A similar pattern of continuous decrease relative to the control is seen in *B. decrescens* throughout the study period (Figure 5). On a cloudy day the weight loss by both *M. diclados* and *B. decrescens* is relatively small and similar to loss by the control (Figure 6a). When rainfall increases, the two species responses diverge from each other and *M. diclados* gains weight at a fast rate, exceeding its original weight at the start of the day, while the control and *B. decrescens* both show little weight gain and do not regain the weight lost during the day (Figure 6a). On a dry day (Figure 6b) the two species responses are similar to each other and the control throughout the day. However, *M. diclados* diverges from *B. decrescens* and the control with a rapid weight loss towards the middle of the day, accompanied by a rise in temperature and a drop in relative humidity. On a wet day (Figure 6c), the difference in response to atmospheric moisture between the two species is most clear. While *B. decrescens* and the control show relatively little weight gain throughout the day, *M. diclados* gains in excess of 50 g (Figure 6c).

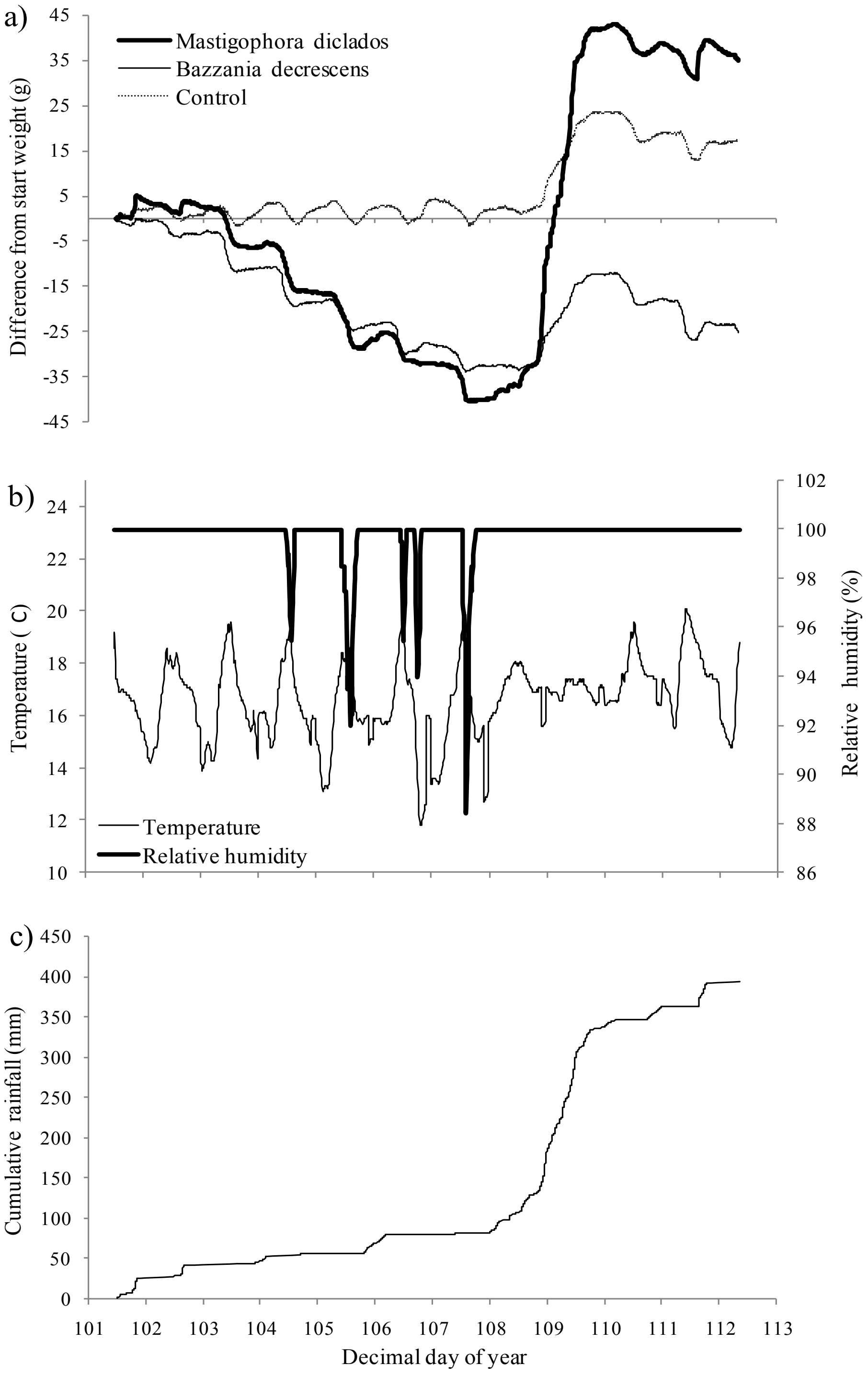


Figure 4: Weight change in *Mastigophora diclados, Bazzania decrescens* and the control over time (a), relative to selected environmental variables temperature (b), relative humidity and rainfall (c) in the cloud forest of La Réunion. A weight gain represents cloud water interception while a loss of weight indicates evapotranspiration. Although rain was excluded from the lysimeter enclosure, an increase in rainfall will be accompanied by an increase in cloud, thus the increase in weight that corresponds to increased rainfall is a result of cloud water interception rather than rain water interception.

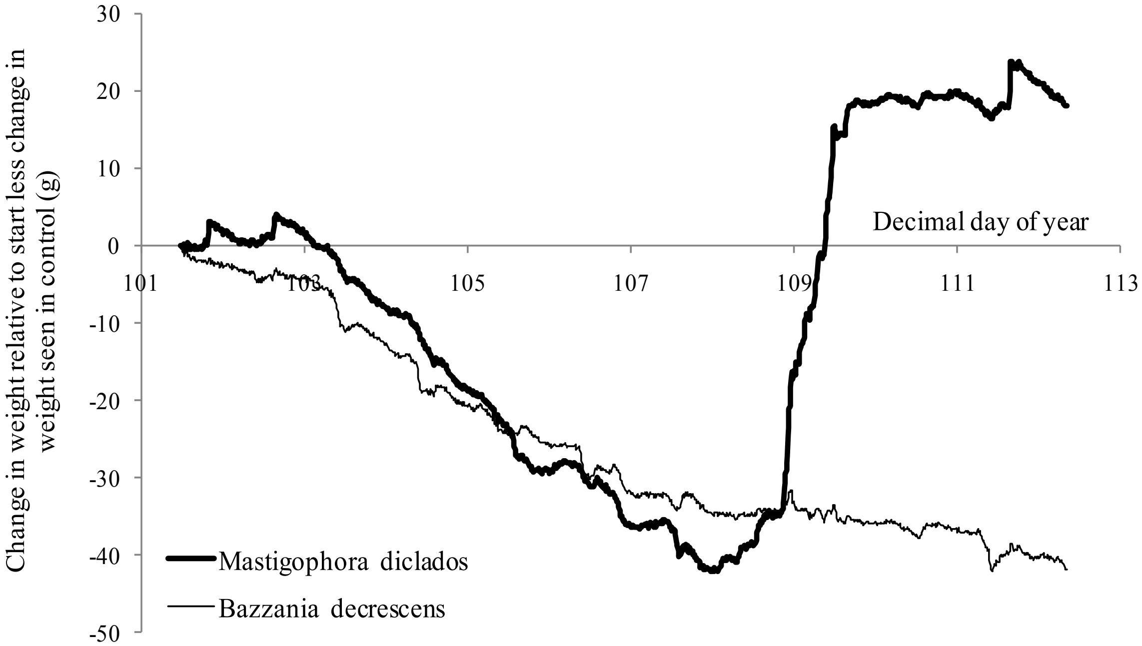
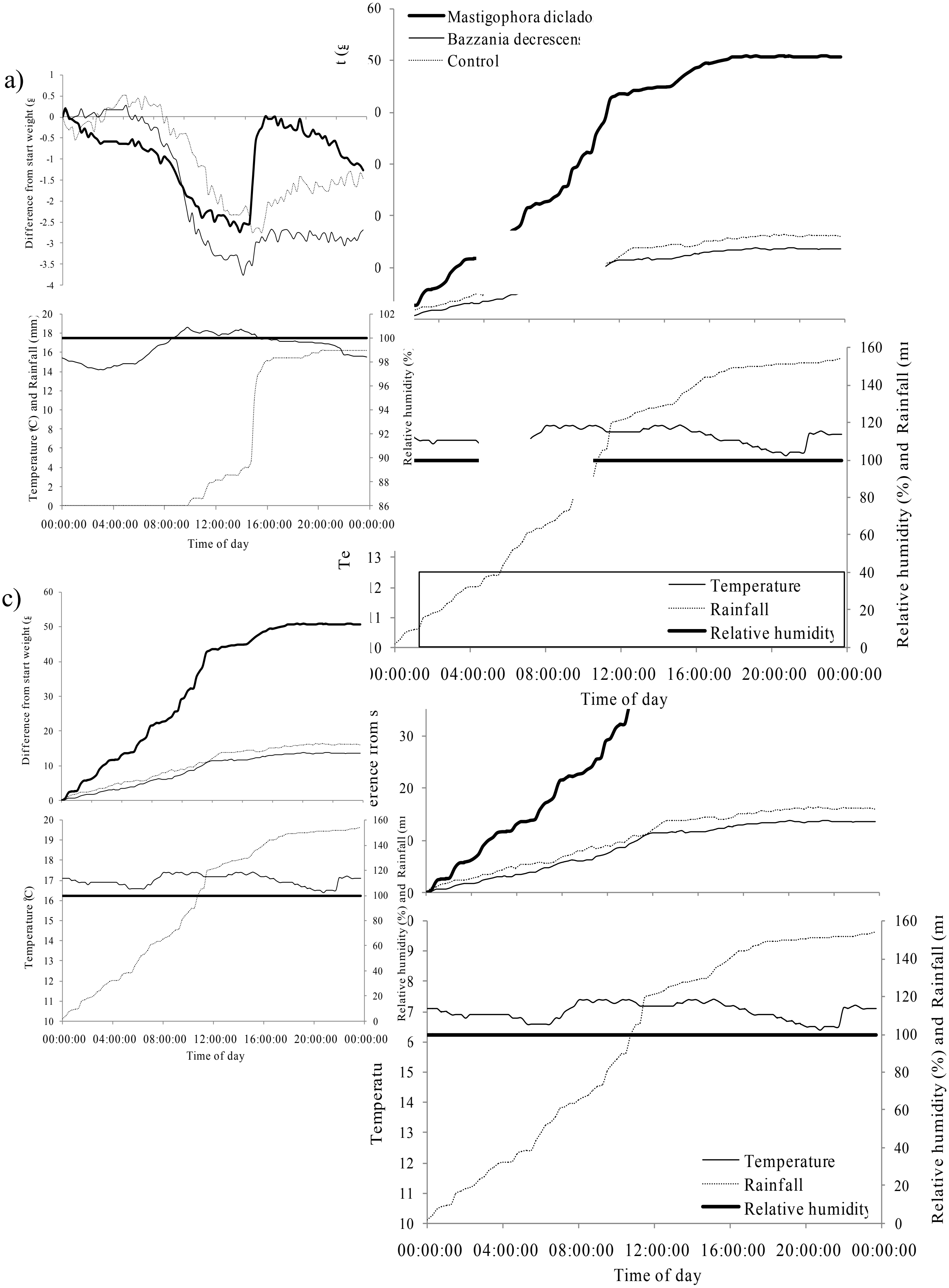


Figure 5: Weight change in *Mastigophora diclados* and *Bazzania decrescens* over time relative to the weight change seen in the control lysimeter in the cloud forest of La Réunion. Weight change was calculated as the difference from start weight for each species less the difference from start weight of the control. Note that while *M. diclados* exceeds the weight gain seen in the control at certain times during the study period, *B decrescens* does not.



a)
Difference from start weight (g
Temperature (°C) and Rainfall (mm)
Relative humidity (%)
Time of day
00:00:00 04:00:00 08:00:00 12:00:00 16:00:00 20:00:00 00:00:00
Mastigophora diclado
Bazzania decrescens
Control
Temperature
Rainfall
Relative humidity
Relative humidity (%) and Rainfall (mm)
c)
Temperature (°C)
Relative humidity (%) and Rainfall (mm)

A factorial ANOVA (appendix) was performed on the water fluxes of *M. diclados, B. decrescens* and the control for the three factors: i) whether flux was in or out, ii) which of the two species or control the flux was measured in and iii) what the climatic conditions were on the day. All factors as well as all interaction terms had a significant effect on the water flux value estimated ($p<0.0005$ and $\beta<0.02$ in all cases). On cloudy days with low levels of precipitation the water flux in is not significantly different to the water flux out in either species or the control and none of the flux values differed significantly from the control (Figure 7a). The lack of significant difference here may be a result of the exceptionally small sample size as only two days were cloudy with low levels of precipitation (Figure 7a). On days when humidity fell below 100% and precipitation was low, *M. diclados* had a significantly greater water flux in than out (Figure 7b). The same trend holds for *B. decrescens* despite the non-significant difference between flux in and out, as the non-overlapping error bars suggest that failure to find significance might be due to lack of statistical power (Figure 7b). On this day the control shows no significant difference between water flux in and water flux out (Figure 7b). On very wet days with high levels of precipitation the water flux in seen in *M. diclados* is significantly greater than its water flux out as well as significantly greater than any other flux throughout the study period (Figure 7c). On this day *B. decrescens* and the control show similar in and out fluxes to one another (Figure 7c). On these days all treatments lost very low amounts of water by flux out (Figure 7c). Maximum total water flux in by *M. diclados* was 51.57 ml for the approximately 240 mm diameter lysimeter sample while the equivalent sample of *B. decrescens* had a maximum in flux of 14.38 ml, which was less than the maximum in flux of the control (18.69 ml). The maximum CWI based on in flux of water was therefore 17.28 ml h^{-1} kg of biomass^{-1} or 1054 litres per day per hectare of average biomass for *M. diclados,* 4.33 ml h^{-1} kg of biomass^{-1} or 381 litres per day per hectare of average biomass for *B. decrescens*. These maximum interceptions values all occurred on decimal day year 109, the highest rainfall day of the study period.

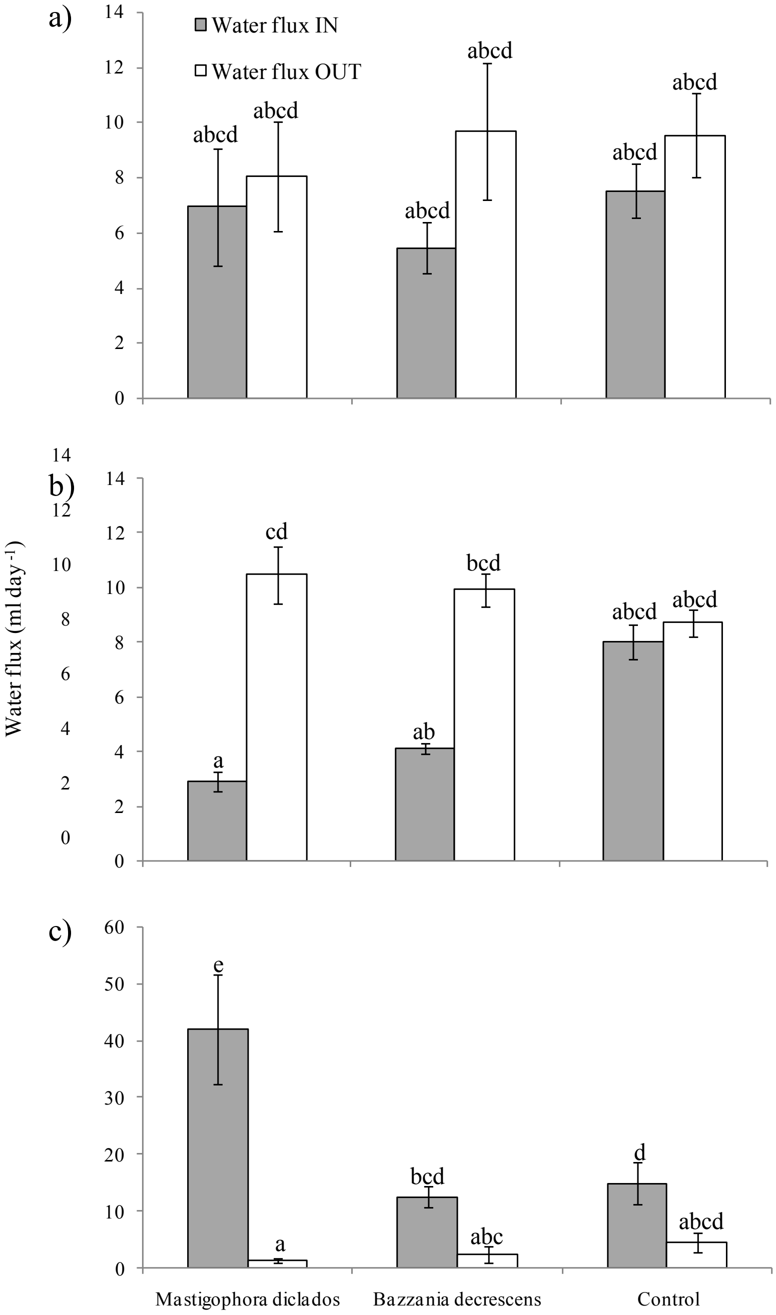


Figure 7: Water flux in and out *M. diclados*, *B. decrecens* and the control in the cloud forest of La Réunion. Flux data are divided into 3 climatic conditions: a) cloudy days with high humidity and little rain, b) relatively dry days when rainfall and relative humidity were low and c) relatively wet days when rainfall and relative humidity were high Letters a-e above the flux bars show which flux values are significantly different ($p<0.05$) from each other according to a factorial ANOVA. Flux bars sharing the same letter are not significantly different from each other. Error bars show standard error. The error bars are large on a) and c) due to the small sample size. Water flux was calculated as the difference between two consecutive lysimeter measurements, summed over the course of a day, separating negative and positive differences for IN and OUT fluxes.

Photosynthetic response to desiccation

According to the spline model, each species showed a significant relationship between photosynthesis, measured as electron transport rate (ETR), and water content (Figure 8). Both species show an optimal water content for photosynthesis according to the fitted spline model, *M. diclados* at approximately 4.5 g of water per g of dry weight and *B. decrescens* at approximately 5.8 g of water per g of dry weight (Figure 8). This optimum corresponds closely to the *in situ* water content of both species (mean ± standard error) 4.67 (± 0.09) g H_2O g dry weight^{-1} for *M. diclados* and 6.34 (± 0.22) g H_2O g dry weight^{-1} for *B. decrescens.* According to the spline model, *B. decrescens* has an ETR at least half of its expected maximum ETR over a range of approximately 8.1 g water g dry weight^{-1} and has a relatively pronounced peak in ETR (Figure 8). *M. diclados* has a narrower range of observed water contents but has a more consistent ETR than *B. decrescens* and has an ETR at least half of its expected maximum ETR at all measured water contents except 0 g water g dry weight^{-1} (Figure 8). The rise in ETR at high water contents seen in both species is a result of the lack of data points at very high water contents and does not represent a biological phenomenon (Figure 8). The two species have similar maximum photosynthetic values (at approximately 7.8 µmol m^{-2} s^{-1}) (Figure 8).

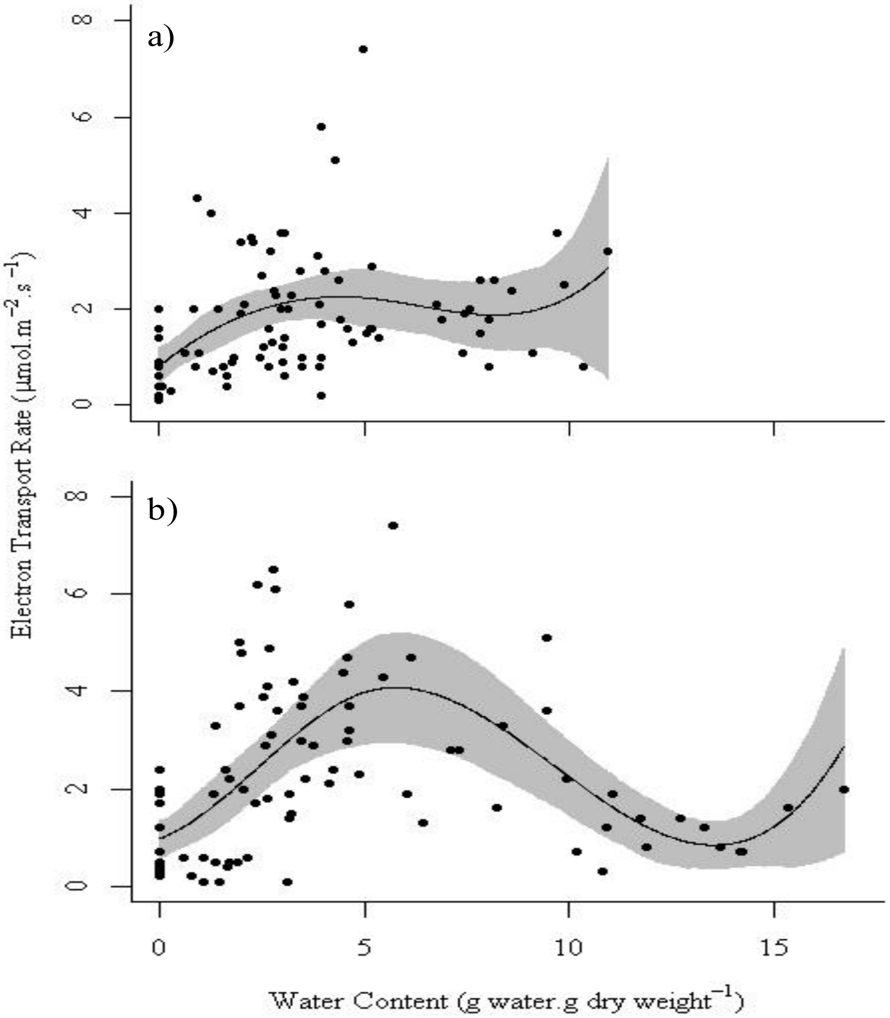


Figure 8: Electron transport rate (ETR) as a function of water content in a) *Mastigophora diclados* (R^2=0.137, p=0.0001) and b) *Bazzania decrescens* (R^2=0.346, p<0.0001) in the cloud forest of La Réunion according to the fitted spline model. The shaded area shows 95 % confidence bands as determined by non-parametric bootstrapping. The black line represents the spline model that was fitted to the data. The increase in ETR in both species at very high water contents is a product of the statistical model used, which estimated an increase at high water contents only because of the lack of data points at these high water contents and not as a result of an underlying biological phenomenon.

Discussion

Bryophytes intercept and store atmospheric water which then fluxes in and out of the plant to varying degrees depending on the climatic conditions and the species. Predicted climate changes are likely to affect the interception, storage and water flux of bryophytes in cloud forests, possibly with profound biological implications.

Differences in architecture and habit of the two study species, *B. decrescens* and *M. diclados*, explained many of their differences in water content and water storage. The architectural and habit attributes of *B. decrescens* resulted in it having greater external water storage relative to *M. diclados* and therefore higher maximum water storage capacity and *in situ* water storage capacity. *B. decrescens* had underleaves which formed cup-like structures and were connected at their base to the main leaves. This distinctive structure allowed the underleaves to hold intercepted water and keep the main leaves moist using water drawn from the underleaves to the main leaves via capillary forces. The main leaves of *B. decrescens* were overlapping, which further enhanced the water holding capacity as surface tension prevented the water from running off the shoot. Furthermore, *B. decrescens* grew in dense colonies that formed mats close to the ground which reduced water loss as external water holding capacity was increased by the gaps created between shoots. Unlike *B. decrescens, M. diclados* had dissected leaves that stored water by creating many small capillary spaces in the shoot. *M. diclados* also grew in less dense colonies that formed loose masses as opposed to the tight mats of *B. decrescens*. Despite its lower water storage capacity when compared with *B. decrescens* (~720 % vs ~1070 % storage per gram of dry weight), *M. diclados* still held a large amount of water relative to other species as past estimates of saturated or maximum water storage capacity have shown that bryophytes store 500 to 1400 % of their dry weight in water (Pócs, 1980).

The differences in architecture, habit and water storage attributes between *M. diclados* and *B. decrescens* were so pronounced that although *M. diclados* occupied more than double the volume (127.7 vs 58.2 m^3 ha^{-1}), it stored less than half the volume of water per hectare (11 707 vs 22 862 litres H_2O ha^{-1}) and had a lower biomass (2 541 vs 3 667 kg dry mass ha^{-1}) per hectare than *B. decrescens.* Our dry biomass estimates gave a combined contribution to total biomass by our study species of 6 208 kg ha^{-1}. This estimate was within the expected range as a study in a

Colombian lower montane cloud forest estimated 5 600 kg ha^{-1} of epiphyte biomass (Mulligan *et al.*, 2010) and epiphyte biomass in a Costa Rican old growth cloud forest was estimated at 3400 kg ha^{-1} (Köhler *et al.*, 2010) while other studies have estimated the range of epiphyte biomass in lower montane cloud forests to be between 2 100 kg ha^{-1} (in a stunted ridge top Jamaican forest) and 33 100 kg ha^{-1} (for a tall leeward cloud forest on the Pacific slope near Monteverde, Costa Rica) (reviewed by Köhler *et al.*, 2007). These values were likely an underestimation of the true epiphytic bryophyte biomass in the cloud forest of La Réunion as we only estimated biomass of two bryophyte species in the forest. When evaluating water storage in conjunction with biomass estimates, the combined water storage capacity of *B. decrescens* and *M. diclados* (22 862 and 11 707 *l* ha^{-1} respectively) was 34 569 *l* ha^{-1}, or 3.46 mm of rainfall. While one must acknowledge that the majority of this water was being stored in *B. decrescens* and this species is likely to play an important ecological role in the forest, the high volume of *M. diclados* must not be overlooked and this species is also ecologically important.

In addition to differing in their capacity to store water, *M. diclados* and *B. decrescens* also differed in their ability to intercept atmospheric moisture. *M. diclados* had a greater ability to intercept atmospheric moisture than *B. decrescens,* which had a similar interception ability to the control. When examining the change in weight of the two species relative to the change in weight of the control, *M. diclados* was the only species to gain more weight than the control over the study period. Furthermore, over the same amount of surface area, *M. diclados* intercepted a maximum of 51.57 ml while *B. decrescens* and the control intercepted a maximum of 14.38 ml and 18.69 ml respectively. When scaled up according to biomass estimates, these interception values represented a maximum interception of 17.28 ml h^{-1} kg of $biomass^{-1}$ in *M. diclados* and 4.33 ml h^{-1} kg of $biomass^{-1}$ in *B. decrescens.*

These cloud water interception (CWI) values fitted into the range expected based on previous studies as, on average, CWI by epiphytes was 8.1 ml h^{-1} kg of $biomass^{-1}$ in a Columbian cloud forest (Mulligan *et al.,* 2010) and 54.7 ml h^{-1} kg of $biomass^{-1}$, with a maximum over 32 times this when exposed to consecutive fog events, in a windward Costa Rican lower montane cloud forest (Tobón *et al.*, 2010). These values for CWI were lower than one's intuition might suggest based on the high water storage capacity of the bryophytes. However, it has been hypothesized that the actual contribution of non-vascular epiphytes to cloud water and rainfall interception may be low as epiphytes that are frequently wetted have little available storage despite their large potential storage (Mulligan *et al.*, 2010; Hölscher *et al.*, 2004). This low available storage explained the reduced CWI ability of *B. decrescens* relative to *M. diclados* as the mat-like architecture of *B. decrescens* dried out less readily than the loose masses of *M. diclados*, which left *B. decrescens* with less space available for capturing new atmospheric moisture.

The variation in water flux pattern of the liverworts was due to different biological processes dominating under differing environmental conditions. On cloudy days with high humidity and low rainfall, both species' weight remained fairly constant and water loss was kept to a minimum throughout the day. Since the control showed a similar water flux pattern to both species, the lack of water loss in the two species was more likely the result of low temperature and high humidity reducing the evaporative gradient rather than evidence of an evolved strategy to prevent desiccation. On these cloudy days, as soon as rainfall increased, presumably accompanied by an increase in cloud density, *M. diclados* intercepted cloud water at a faster rate than *B. decrescens.* This interception caused *M. diclados* to exceed its original weight at the start of the day while *B. decrescens* and the control showed some ability to intercept cloud but did not exceed their initial start weight. Cloud water was only intercepted when rainfall increased. An increase in rainfall was accompanied by an increase in cloud density as the clouds that bring rain are heavier and fuller than those that do not. Regular cloud inundation by non-rain giving clouds may be enough to save the liverworts from complete desiccation but, in order to increase externally stored water and thus maintain healthy water relations, denser rain-giving clouds are needed by the liverworts.

On drier days with little to no rain and higher maximum daily temperatures, *M. diclados* had a significantly greater outward flux of water relative to its inward flux. The same trend held for *B. decrescens.* The control did not show this pattern and had the same inward as outward flux of water. This increased outward water flux in all the two liverworts indicated that increased temperatures combined with decreased humidity caused the vapour pressure deficit of the forest's air to increase, which placed a higher evaporative demand on the liverworts, hence they lost more water via evaporation. This loss via evaporation was particularly important as the low level of rainfall on these days was associated with a lack of dense clouds and thus no "recharging" of water stores was possible and desiccation became a real threat as the loss of the evaporated water was not recovered. In addition to evaporation, since the control had the same inward as outward flux of water while the two species had a greater outward than inward flux, there was evidence that transpiration by the liverworts was occurring in addition to evaporation.

The greatest differences in water flux between the two species and the control could be seen on wet days with consistently high humidity, low temperatures and large volumes of rain. On these days, *B. decrescens* and the control showed relatively little weight gain throughout the day while *M. diclados* could gain in excess of 50 g of water from CWI. *M. diclados* had an inward water flux significantly greater than under any other climatic conditions and than either *B. decrescens* or the control under the same conditions. This suggested that *M. diclados* had the ability to intercept cloud water efficiently, especially from dense rain clouds. This ability was what allowed it to occupy a broad range of microhabitats, from the forest understory into the frequently-desiccated canopy, while *B. decrescens* was restricted to wetter forest floor. This finding confirmed past studies which had found that faster and slower reactivation of liverworts by water vapour and fog corresponded to distribution patterns in the canopy between wetter and drier microsites (Lakatos, 2011). The differing patterns of CWI in our study species linked to the differences in water storage discussed above. The faster and more efficient CWI of *M. diclados* was associated with a lower water holding capacity and frequent day-time drying, evidenced by the rapid loss of water by evaporation in this species during periods of low humidity. Slower and less efficient CWI, as was seen in *B. decrescens,* was associated with a higher water holding capacity and frequently wet micro-sites.

Variations in water flux caused by varying climatic conditions caused the water content of the liverworts to vary, which had an effect on photosynthesis. The relationship between water content and photosynthesis provides the link between quantifying the amount of cloud water the liverworts are intercepting and understanding of the importance of clouds in the forest as it shows the role that the intercepted cloud water plays in the physiological processes of the liverworts.

There was a relationship between water content and photosynthesis, measured as electron transport rate (ETR), in both species. ETR was at its minimum at very low and very high water contents. The loss of photosynthesis at low water contents was as a result of bryophytes photosynthesis becoming inactivated by desiccation at relative water contents of below 15% to 20% despite full loss of turgor occurring at 60 % to 80 % of dry weight (Lakatos, 2011). The ability of bryophytes to maintain photosynthesis at such low water contents is one of their most unique and impressive features (Lakatos, 2011). The decrease in photosynthesis at very high water contents was due to the high diffusive resistance to CO_2 by water (Lakatos, 2011) as external water on bryophyte plants provides an extra liquid-phase diffusive resistance for CO_2 on its pathway into the leaf where it is used for photosynthesis (Proctor, 2000). This is especially problematic as CO_2 diffuses slower in water than in air (Proctor, 2000), therefore the more water the plant is holding externally the more photosynthesis suffers. The decreased level of photosynthesis at low water contents combined with the trade-off between water content and gas exchange at high water contents explained the shape of the response curves of photosynthesis as a function of water content. There was a decline of photosynthesis at very low water contents due to loss of cell activity and at very high water contents due to the suppression of gas exchange (Dilks & Proctor, 1979). The water content associated with the maximum predicted ETR was very close to the *in situ* water content of the species as bryophytes have evolved several strategies for mediating the conflict between water conduction and storage and free gas exchange for photosynthesis.

The shape of the spline curve fitted to ETR as a function of water content differed between the two species. *M. diclados* showed a relatively consistent photosynthetic response over its range of water contents with ETR remaining above half of its maximum predicted value for all water contents except when it was completely dry. *B. decrescens* showed a photosynthetic response that varied over its range of water contents and ETR was only above half of its predicted maximum for a part of this range. The ability to *M. diclados* to photosynthesise over its entire water content range allowed it to inhabit a wide range of habitats, from the wet forest understory to the frequently dry canopy. Conversely, *B. decrescens* was restricted in its habitat choice by its inability to effectively photosynthesise at all water contents. The differences between species' photosynthetic patterns should be interpreted with caution as the spline model used, despite being the best model available, does not necessarily accurately represent the true biological processes occurring in the liverworts. It is suspected that the Mini-PAM had an inability to deal with fluctuating environmental conditions, such as light intensity, despite being specifically designed for use in the field. This was especially problematic in *M. diclados* as its brown colour and erect gametophytes seemed to worsen the problem. Combined with the lack of data points at certain water contents, these factors may be distorting the shape of the spline model fitted. With increased sampling intensity and comparison with other methods for measuring ETR the differences between species could be further investigated.

Although the effects of anthropogenic climate change on cloud forests are largely unknown, climate change has been predicted to lead to an increase temperature (Foster, 2010), changes to the rainfall regime (Solomon *et al.*, 2007), and clouds shifting up by hundreds of metres during the dry winter season, incidentally when these forests rely most on cloud water (Still *et al.*, 1999). These changes will reduce cloud water input to the bryophytes while simultaneously increasing water loss. Climate change has already been implicated in changes in dry season cloud formation in two cloud forests, Monteverde, Costa Rica (Nair *et al.*, 2008) and Tenerife, Canary Islands (Sperling *et al.*, 2004). If the threats of climate change weren't enough, the cloud forest on La Réunion is also under pressure from local residents to be converted into housing and agricultural land. Considering that montane cloud forests represent 6 % of the island (National Park of Le Réunion, 2012), changes to the bryophyte communities of the forest are important. The desiccation and re-wetting cycles of bryophytes have profound impacts on the ecosystems they inhabit. Canopy epiphytes play a vital role in intercepting and retaining nutrients, providing a habitat for wildlife, serving as a carbon sink (Nadkarni, 2010), influencing biogeochemical cycling and vegetation-atmosphere exchanges, and absorbing and retaining atmospheric nutrients and water (Asbury *et al.*, 1994; Clark *et al.*, 1998; Feild & Dawson, 1998; Hafkenscheid, 2000; Hietz *et al.*, 1999; Lakatos, 2011; Nadkarni & Matelson, 1991). The loss of the bryophytes in the TMCF of La Réunion would have far-reaching ecosystem consequences for biodiversity, hydrological processes and biogeochemical cycling as even when these deforested areas are abandoned to be colonised by secondary forests, the colonization of these secondary forests by epiphytes may take decades (Köhler *et al.*, 2010).

Conclusion

The water store and associated water flux of liverworts in this cloud forests varied depending on climatic conditions and this variation had an effect on photosynthetic activity. These findings tie the liverworts very closely to their environment and therefore show support for the idea that bryophytes are excellent early warning signals for predicted future climate changes (Gignac, 2011; Nadkarni, 2010). The conversion of cloud forest into any other land use would have drastic negative impacts on the cloud forest ecosystems of La Réunion and should be avoided at all costs. While this study was on two common and widespread species, the cloud forest has a number of rare species. These species often have restricted ranges and are likely to require more specific microhabitat conditions than our study species and might therefore be more sensitive to climate changes than our study species.

Acknowledgements

-My supervisors, Terry Hedderson, Claudine Ah-Peng, Olivier Flores and Adam West, for their support and valuable input.

-Dominique Strasberg (University of La Réunion) for the equipment and use of the biological field station of Manelongue.

-MOVECLIM Research Program for covering the travel costs (with the support of the Agence Nationale de la Recherche, Conseil Régional de la Réunion, Conseil Régional de la Guadeloupe, Government of Azores and Government of Canaries under the framework of Net-Biome transnational first call)

-National Park of La Réunion (authorization number DIR/I/2011/064) for the collecting permit, assistance of David Fontaine and Pierre Stamenoff for biomass measurements, and Jo Minatchy for assistance in setting up.

-The South African Association of Botanists for partially funding my honours year.

-The National Research Foundation of South Africa for partially funding my honours year.

-Charles Musil and Stanley Sneiders at SANBI for loan of and assistance with the lysimeters.

-The Department of Botany at The University of Cape Town for their staff’s continued support.

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