Effects of altered precipitation regimes on bryophyte carbon dynamics in a Peruvian tropical montane cloud forest

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Effekter av förändrade nederbördsregimer på mossors koldynamik i en peruansk tropisk bergmolnskog

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Abstract

Tropical montane cloud forests (TMCF) are unique ecosystems that are frequently surrounded by clouds which increase humidity and promote the growth of bryophytes. Several dimensions of humidity are important for the carbon dynamics of bryophytes. Climate change is therefore projected to have a large impact on them as well as on the TMCF itself. The present study aimed to investigate the effects that changing precipitation regimes will have on bryophyte carbon dynamics. Specifically changes in precipitation amounts, frequency and type i.e. if the precipitation falls as rain or is brought by cloud mist were studied through three experiments; (1) a blocked, full factorial experimental set-up tested for the effect of the three precipitation factors on bryophyte net photosynthesis and respiration, (2) the bryophyte photosynthetic performance was also measured on this set up and (3) on a second experimental set up the response of bryophyte carbon dynamics to re-wetting after increasing desiccation periods was measured. The results of the first experiment showed that precipitation amount had the clearest effect on bryophyte carbon dynamics where net ecosystem exchange (NEE) decreased most in high amount treatments. A slightly lower decrease in NEE was found with low amounts of mist compared to low amounts of rain, although the difference between the types was not significant. Furthermore, an effect from frequency was found on respiration where the effect differed most between amounts and types for the high frequency treatments while the difference was smaller for medium and low frequencies. However no interactions with frequency were found for NEE or gross primary production (GPP). In the second experiment, bryophytes generally reached a saturated photosynthesis at relatively low light levels ($400 \, \mu$mol photons m^{-2} s^{-1}). At these light intensities or higher, the samples watered with low amounts of mist at high frequencies led to the highest maximum photosynthetic rate (P_{max}) while the samples watered with high amounts of mist at low frequency gave the lowest P_{max}. Thus, low amount, high frequency mist was generally most beneficial for carbon uptake. However at lower light intensities ($200 \, \mu$mol photons m^{-2} s^{-1}) the carbon gain for the samples of low amount treatments was lower compared to samples of high amount treatments. In the third experiment, there was a clear decrease in GPP and NEE, i.e. carbon uptake, with increasing desiccation length. No trend for the respiratory response to increasing desiccation length was determined. In summary, bryophytes in TMCF seem to be well adapted to the environment they live in today, where desiccation periods are short and where low amounts of precipitation, probably in the form of mist are beneficial to bryophyte carbon uptake. This also suggests that projected changes in climate conditions in TMCF will influence bryophyte carbon dynamics negatively, leading to a decrease in carbon accumulation. Since bryophytes provide a number of important ecosystem services, a negative change in their carbon dynamics could result in biodiversity loss as well as changes in the hydrologic cycle and carbon dynamics of the TMCF. This in turn could have large scale effects on both downslope ecosystems and the people living there, as well as an impact on the world's biodiversity.

Keywords: Bryophytes, Peru, Tropical mountain cloud forest, Climate change, Precipitation, Carbon dynamics, Respiration, Net ecosystem exchange, NEE, Photosynthesis, Gross primary production, GPP, PAR, Desiccation

Sammanfattning

Tropiska bergmolnskogar (eng: Tropical montane cloud forests; TMCF) är unika ekosystem som frekvent omges av moln vilka ökar fuktigheten och gynnar tillväxt av mossor. Koldynamiken hos mossor påverkas av fukt över flera dimensioner. Det är därför projicerat att klimatförändringen kommer få en stor påverkan på dem samt även på de TMCF. Målet med denna studie var att se hur effekterna av förändrade mängder och frekvenser av nederbörd och om den nederbörden föll som regn eller kom direkt från molnen (dimma), påverkar mossors koldynamik. Detta utfördes genom tre experiment; (1) ett grupperat fullfaktoriellt experiment där responsen på de tre nederbördsfaktorerna mättes genom skillnader i mossornas respiration och nettoutbyte av koldioxid vid fotosyntes, (2) vidare studerades fotosyntes vid varierande ljusintensiteter under de olika nederbördsregimerna samt (3) hur mossors koldynamik svarade på varierande uttorkningsperioder. Resultaten från det första experimentet visade att nettoutbytet av koldioxid minskade mest med höga mängder nederbörd. En något mindre minskning i nettoutbyte förekom med låga mängder dimma jämfört med låga mängder regn, skillnaden mellan de två nederbördstyperna var dock inte signifikant. Vidare hittades också en effekt från nederbördsfrekvens på mossornas respiration där hög frekvens visade störst skillnader mellan mäng och typ av nederbörd medan medium och låg frekvens visade mindre sådana skillnader. Ingen interaktion med frekvens hittades för bruttoproduktionen eller netto utbyte av koldioxid. Det andra experimentet visade att mossor generellt uppnådde sin maximala fotosyntetiska kapacitet vid en relativt låg ljusintensitet (400 µmol fotoner m^{-2} s^{-1}). Vid denna eller högre ljusintensitet gav låga mängder dimma med hög frekvens den högsta maximala fotosyntesen (P_{max}) medan höga mängder dimma med låg frekvens gav den lägsta P_{max}. Det verkar därmed som att låga mängder dimma med hög frekvens var mest fördelaktigt för mossors kolupptag. Vid lägre ljusintensitet (200 µmol fotoner m^{-2} s^{-1}) var kolupptaget dock lägre i prover vattnade med låga mängder nederbörd jämfört med höga. I det tredje experimentet visade både bruttoproduktionen och nettoutbytet av koldioxid en linjär nedåtgående trend med längre uttorkningsperiod. Respiration visade dock ingen klar trend. Sammanfattningsvis verkar mossor i TMCF vara väl anpassade till den miljö de lever i idag med korta uttorkningsperioder och där låga mängder nederbörd, troligtvis i form av dimma är mest fördelaktigt för mossors kolupptag. Detta tyder också på att projicerade förändringar i nederbördsregimer tyder på att deras kommer påverka mossors koldynamik negativt och att deras kolupptag kommer vara mindre än idag. Då mossor utför viktiga ekosystemtjänster kan en negativ förändring av deras koldynamik leda till förlust av biodiversitet och förändringar av hydrologin och kolcykeln i TMCF. På en större skala skulle detta i sin tur påverka ekosystem på lägre altituder och de människor som bor där samt få en stor påverkan på världens biodiversitet.

Content

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List of abbreviations

CO_2	Carbon dioxide
GPP	Gross primary production
NPP	Net primary production
NEE	Net ecosystem exchange
TMCF	Tropical montane cloud forest
UMCF	Upper montane cloud forest
LMCF	Lower montane cloud forest
SACF	Subalpine cloud forest
VPD	Vapour pressure deficit
RH	Relative humidity
LCP	Light compensation point
E_0	Quantum efficiency
k	Half saturation constant
P_{max}	Light saturated or maximum photosynthesis
R_{auto}	Autotrophic respiration
R_{hetero}	Heterotrophic respiration
°C	Degrees Celsius
SALLJ	South American low level jet stream
DW	Dry weight
RWC	Relative water content
IRGA	Infrared gas analyser
MAT	Mean annual temperature
LT	Local time
PAR	Photosynthetically active radiation
RMSE	Root mean square error
ANOVA	Analysis of variance
AL	Low amount
AM	Medium amount
AH	High amount
F1	High frequency
F2	Medium frequency
F4	Low frequency
M	Mist
R	Rain

1. Introduction

The world is projected to experience a rapid climate change during this century driven by the increase of atmospheric greenhouse gases like carbon dioxide (CO_2), due to anthropogenic emissions from the burning of fossil fuels (IPCC 2013). But, CO_2 is also the main component in natural ecosystem processes through which carbon is cycled. By photosynthesis the vegetation takes up CO_2 and binds the carbon as biomass and by the energy gaining process of respiration vegetation releases CO_2 back to the atmosphere again (Chapin et al. 2011). Since both photosynthesis and respiration are affected by a number of climatic factors like water, light and temperature, the cycling of carbon will be affected by climate change (Chapin et al. 2011). It is therefore important to quantify the global carbon cycle and to understand the mechanisms by which it is affected in order to understand the climate change impact on the world's ecosystems. One of the ecosystems which are most threatened by climate change are tropical montane cloud forests (TMCF; Aldrich et al. 1997).

The TMCFs are unique ecosystems that are frequently surrounded by clouds which provides a continuous water input in the form of both rain and from the cloud mist itself (Clark et al. 2014). TMCF thereby have a large impact on the hydrologic cycle and this unique environment give rise to a very high biodiversity (Gentry 1992; Leo 1995; Brujinzeel et al. 2011; Clark et al. 2014). The frequent cloud cover and high atmospheric humidity of TMCFs is also highly beneficial for the occurrence of tree anchoring epiphytes like bryophytes (Benzing 1998). The bryophytes in turn provide important ecosystem services by collecting and retaining cloud water and nutrients as well as contribute to the aboveground biomass and biodiversity of TMCFs (Veneklaas et al. 1990; Gentry 1992; Weathers and Likens 1997; Benzing 1998; Köhler et al. 2007; Horwath 2012).

The bryophytes are however very sensitive to changes in atmospheric humidity. In contrast to vascular plants, bryophytes does not have a protective epidermis or stomata to regulate water loss. Water is instead exchanged through their whole surface which leads to rapid loss when the atmospheric humidity is lower than optimal. To cope with this bryophytes have evolved a tolerance to desiccation i.e. they can survive drying out to equilibrium with the air. During this time both photosynthesis and respiration are suspended but is resumed to normal function again upon rewetting (Proctor et al. 2007a). One challenge with this strategy is that the bryophytes need to be able to retain a long-term positive carbon balance, or take up more carbon through photosynthesis than they lose by respiration. Since the respiratory carbon losses are generally larger than the photosynthetic gain during the dehydration and rehydration stages, changes in humidity in TMCFs are therefore important for bryophyte carbon dynamics (Hanson ad Rice 2014). Several vital humidity dimensions for bryophytes have been identified; for example the frequency of the bryophytes wet dry cycles, for how long they are hydrated and both the length and intensity of desiccation (Norris 1990; Wagner et al. 2014a).

Because of the high dependency on the occurrence of clouds, climate change is expected to have a large impact on the TMCFs of the world and especially on the sensitive bryophytes (Benzing 1998; Foster 2001). Changes in both precipitation regimes and temperature will be of importance but one aspect that will have a particularly large impact is the projected rise in cloud base height and decrease in cloud cover (Still et al. 1999: Halladay et al. 2012b). This could

potentially change all the humidity dimensions that are important for bryophytes which could lead to negative effects on their carbon dynamics. Changes in bryophyte carbon dynamics could in turn result in biodiversity loss and changes of the carbon dynamics and the hydrologic cycle of the TMCF itself.

Despite being important and unique ecosystems, it is only in the last decade that studies on TMCFs have increased in numbers and the impact from climate change is therefore largely unknown (Brujinzeel et al. 2011). The same goes for bryophytes which are generally understudied compared to vascular plants and particularly so the ecophysiology of tropical bryophytes and how they will be affected by climate change (Proctor et al. 2007a; Hanson and Rice 2014). The study presented in this thesis therefore aimed to provide a better understanding of the effects that changes in precipitation regimes will have on bryophyte carbon dynamics and photosynthetic performance as well as how the carbon dynamics of bryophytes will cope with increasing desiccation periods. Specifically this was investigated for a Peruvian TMCF by answering the three questions:

1) How is bryophyte carbon dynamics affected by altered precipitation regimes, specifically by different amounts, frequencies and types of precipitation?
2) How is bryophyte photosynthetic performance affected by altered precipitation regimes?
3) How do bryophyte carbon dynamics respond to and recover from desiccation?

2. Background

2.1 Carbon exchange between land and the atmosphere

Photosynthesis and respiration

Carbon is cycled between land and the atmosphere through the continuous uptake and release of CO_2 performed by the vegetation. Photosynthesis is the process where vegetation takes up CO_2 from the atmosphere and uses it to create carbohydrates (sugars). There are different variations of how the photosynthetic pathway functions but the most common is called the C_3 pathway and as good as all bryophytes perform this type of photosynthesis (Chapin et al. 2011; Glime 2007). There are some indications that other pathways might occur in bryophytes in rare cases, however it has not been completely determined yet (Glime 2007). The following section will therefore only describe the C_3 pathway. Photosynthesis is performed in plant leaves in the cell organelles called chloroplasts, which contains the pigment chlorophyll. When sun rays hit the leaves, this pigment absorbs the light energy which is transformed into chemical energy and the by-product oxygen. The chemical energy is further used to fixate CO_2 into three-carbon compounds (thereof the pathway name C_3) which are subsequently used to produce glucose. So by using the suns energy, plants can take up carbon from the atmosphere and at the same time perform the important ecosystem service of releasing oxygen for us to breath. The produced glucose is then further used by the plants to build up and maintain biomass and to take up nutrients. To be able to do this the plants does however also need energy. This energy does not come directly from the sun but is gained from the performance of mitochondrial respiration. In this process some of the glucose is converted back into energy in the cell organelles called mitochondria with the by-product of CO_2. This way carbon is released back into the atmosphere again. The type of organisms that gain its energy from the sun and uptake of CO_2 instead of from eating other organisms are called primary producers or autotrophs (Chapin et al. 2011).

Although the processes of photosynthesis and respiration are related in the sense that the products from one is used in the other, and vice versa, they are however not directly correlated. For example, the respiration rate is highly dependent on temperature, the vegetation need for growth, maintenance or ion uptake is variable during seasons and life spans and since photosynthesis is only performed when light is available it can only occur at daytime, while respiration continues through the night as well (Chapin et al. 2011). Consequently, increased photosynthesis does not necessarily lead to increased respiration. However, cells with a high capacity to photosynthesise also have a large quantity of enzymes which are involved in the photosynthetic process. This in turn means they have a larger need to perform maintenance respiration to keep the enzymes operational. A higher photosynthetic capacity thus potentially leads to a larger respiratory loss (Reich et al. 1998).

Adjacent to photosynthesis, the process of photorespiration also occurs in the chloroplasts. In this process some of the produced sugars are directly converted back to CO_2 again where between 20 to 40% of the uptake is instantly released back into the atmosphere. This contra productive process is believed to be a remnant function from when the atmosphere contained much lower concentrations of oxygen compared to today. However, photorespiration still fills

important functions by acting as a step in restoring necessary photosynthetic enzymes as well as protects the chlorophyll from damaging oxygen radicals. After photorespiration has occurred, the release of CO_2 by mitochondrial respiration has been shown to be around 50 to 60 % of the CO_2 uptake by photosynthesis, across different ecosystems. This means that around 40 to 50 % of the CO_2 fixated by photosynthesis is bound as plant biomass (Chapin et al. 2011).

Carbon budgeting

The vegetation carbon balance between land and the atmosphere or the carbon accumulation on land, can be determined by quantifying the CO_2 uptake and release from photosynthesis and respiration. This can be done on several different scales. On a cellular or leaf level the carbon accumulation is determined by the difference between photosynthesis and respiration, also referred to as net photosynthesis. The net photosynthesis can of course also be calculated on a larger scale. The total vegetation production of an ecosystem through photosynthesis is called gross primary production (GPP). The net primary production (NPP) is then calculated by subtracting the total vegetation respiration from the GPP. Consequently the NPP comprises of the produced plant biomass (plus the soluble and volatile organic compounds also needed for plant functions; Chapin et al. 2011). However, for a whole ecosystem, CO_2 is also released back to the atmosphere by heterotrophic respiration. The heterotrophic respiration is performed by secondary producers or heterotrophic organisms which gain their energy by eating other organism. Heterotrophic organisms are for example decomposers like bacteria and fungi which perform respiration when they break down dead organic material from dying leaves and plants or other fauna which respires when they eat and digest plants. The total net exchange between the atmosphere and the biosphere, or the difference between GPP and autotrophic plus heterotrophic respiration, is called the net ecosystem exchange (NEE; Equation 1; Chapin et al. 2011).

$$NEE = GPP - (R_{auto} + R_{hetero})$$ *Equation 1*

However, when the actual plant biomass gain is not considered, NEE can also be used when only measuring the net CO_2 exchange by vegetation (not including the heterotrophic respiration). In this study NEE thus represent only the net exchange of CO_2 by the bryophytes, or the GPP - R_{auto}.

CO_2 chamber measurements

There are several different methods to quantify the CO_2 exchange through the processes of photosynthesis and respiration, or NEE, between the vegetation and the atmosphere. When measuring NEE over a small scale, for example a single plant, it is common to use a closed chamber method (Laurila et al. 2005). In this study a closed chamber method with a dynamic system connected to an infrared gas analyser (IRGA) was used. With this method a clear chamber is placed over the sample to be measured and sealed to minimize erratic mixing with the outside air. Two tubes then connect the chamber to the IRGA so that air can be circulated between them. As the sample is hit by light through the clear chamber it performs photosynthesis and consequently takes up CO_2 from the air inside the chamber. The IRGA then detects the change in the CO_2 concertation of the circulating air and logs the change at

predetermined time intervals. If on the other hand the chamber is covered with a cloth, placing the plant in the dark, photosynthesis shuts down and the plant only respires. Consequently the CO_2 concentration increases in the chamber instead. The rate at which the plant photosynthesises or respires can then be calculated from the increase or decrease in CO_2 concentration over time (Campbell and Norman 1998).

Depending on if a study focuses on the atmosphere or the biosphere the meaning of the signage of NEE usually differs. When studying the atmosphere the interest lies in if the CO_2 concentration of the atmosphere increases or decreases, thus a positive NEE usually means that the CO_2 concentration in the atmosphere increased while a negative NEE means the concentration decreased. On the other hand if the biosphere is to be studied a positive NEE usually means the vegetation has taken up CO_2 from the atmosphere and increased its biomass while a negative NEE means the vegetation has released CO_2 and decreased in biomass. Since the study presented in this report focused on the carbon dynamics of bryophytes the second signage approach was employed, i.e. positive NEE means a net uptake of CO_2 by the bryophytes from the atmosphere and a negative NEE means a net release of CO_2 to the atmosphere.

Modelling photosynthesis

Photosynthesis usually follows a rectangular hyperbola shape called a light response curve. This curve represents the photosynthetic response in autotrophs with increasing light intensity (Figure 1; Chapin et al. 2011). From the light response curve four parameters can be determined; the light compensation point (LCP), the quantum efficiency (E_0), the maximum photosynthetic rate (P_{max}) and the half saturation constant (k). The
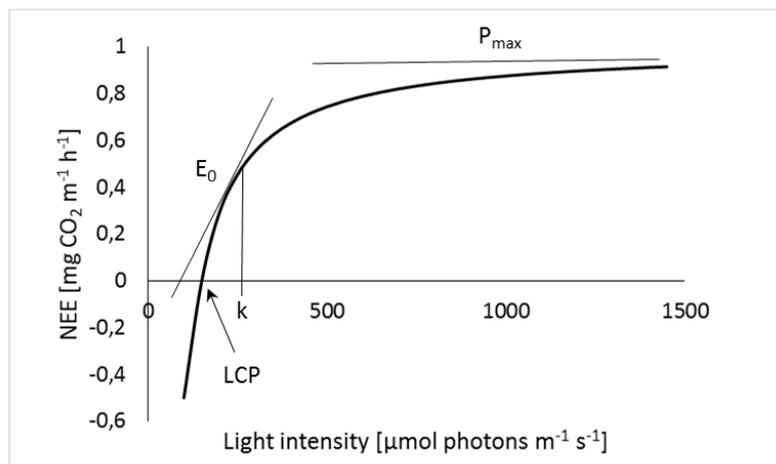
Figure 1. Light response curve showing P_{max} (maximum photosynthetic rate), k (half saturation constant), E_0 (quantum efficiency) and LCP (light compensation point). Modified from Chapin et al. (2011).

LCP is the light intensity where photosynthesis and respiration balance each other out, i.e. where the plant carbon accumulation is zero. As light intensity increases the net photosynthesis initially increases resulting in a rate of amount of carbon gained per unit light which is called the quantum efficiency (E_0). At high light intensity the net photosynthesis eventually becomes limited by the plant's capacity to utilize the light and the photosynthetic rate reaches its maximum (P_{max}), or photosynthesis becomes light saturated (Chapin et al. 2011). The light intensity at which the photosynthetic rate is at half speed is called the half saturation constant (k; Street et al. 2007). In a high light environment plants often produce a large amount of photosynthetic enzymes to be able to take advantage of the abundance of light. With high photosynthetic capacity the respiratory loss is also higher due to the increased requirement of maintenance. This usually leads to a higher LCP in high light environments compared to in low

light since a larger carbon uptake is needed before zero net accumulation is reached. In a low light environment plants often produce a lower amount of photosynthetic enzymes and therefore the photosynthetic capacity and the maximum photosynthesis is usually also lower here (Chapin et al. 2011).

The Michaelis-Menten equation can be used to describe the light response curve (Equation 2; Johnson and Goody 2011).

$$V = \frac{(V_{max} * S)}{(S + K_m)}$$ *Equation 2*

Where V is the process rate, V_{max} is the maximum process rate at a saturated substrate concentration, S is the concentration of a required substrate for the process to occur and K_m is the substrate concentration needed to reach half the maximum process rate (Johnson and Goody 2011). When modelling photosynthesis this means that V is the rate of photosynthesis, V_{max} is the light saturated photosynthetic rate, S is the light intensity and K_m is the light intensity needed to reach half the light saturated photosynthetic rate.

When measuring the CO_2 exchange between the vegetation and atmosphere, it is not possible to directly measure the photosynthesis because respiration is always performed simultaneously by the plant. The change in CO_2 concentration during light conditions consequently only show the net exchange of CO_2 from these two processes or the NEE Chapin et al. (2011). By re-arranging Equation 2 and using measurements of NEE over several light intensities and respiration, it is possible to model the photosynthetic pattern according to Equation 3.

$$NEE = R - \frac{P_{max} * I}{I + k}$$ *Equation 3*

Where NEE is net ecosystem exchange rate, R is the respiration rate, P_{max} is the rate of light saturated photosynthetic rate, I is light intensity and k is the light intensity needed to reach half the light saturated photosynthetic rate.

If a start value of P_{max} and k is set, NEE can be modelled for each measured light intensity. An initial root mean square error can then be calculated by taking the difference between the measured and modelled NEE samples, squaring those differences, summing them up and finally taking the root of the sum. The RMSE is thus a measurement of the average variance, or residual between the measured and modelled values. By changing the parameters P_{max} and k iteratively the RMSE between the modelled and measured NEE can then be minimized resulting in optimized values of P_{max} and k for each sample respectively. Using the optimized P_{max} and k the NEE can then be modelled for a larger range of light intensities to show the photosynthetic pattern or light response curve (Figure 1).

2.2 Tropical montane cloud forests

Tropical montane cloud forests are defined as montane forests which are frequently surrounded in clouds situated in the tropical areas of the world (Bubb et al. 2004; Brujinzeel et al. 2011). Despite being important and unique ecosystems TMCF have long been understudied and the

mechanisms which governs their distribution as well as the impact from climate change are still not fully understood (Brujinzeel et al. 2011). TMCF have a large impact on the hydrologic cycle due to their ability to capture and retain moisture and slowly release it in a steady flow during both wet and dry seasons (Table 1). The TMCF of the Andean mountains also contributes with a disproportionally higher amount of discharge and an important input of dissolved carbon and nutrients to the Amazon River. The reason for this high contribution is the location of these forests on steep slopes at high altitudes which receive large amounts of precipitation both in the form of rain and cloud mist (Clark et al. 2014). The steady supply of water discharge from TMCF areas is important for use in irrigation, generating hydropower and provides drinking water. The forest cover also reduces soil erosion and shallow landslides (Brujinzeel 2004; Brujinzeel et al. 2011). In addition TMFC are hot spots for biodiversity which harbours a diverse flora and fauna. The isolated nature of these forests promotes speciation or the evolution of new species, many of which are endemic, hence can only be found in one single area in the world (Gentry 1992). For example around 30 % of the birds, mammals and amphibians that are endemic to Peru are primarily found in cloud forests (Leo 1995). The Andean cloud forests are also home to a large diversity of epiphytes, or arboreal flora as they are called, which grow in the trees by anchoring to them but without exploiting them (Gentry 1992; Benzing 1998).

Table 1. Ecosystem services performed by TMCF

Ecosystem service	Description	Reference
Hydrologic cycle	Capture precipitation for hydropower, irrigation, drinking water	(Brujinzeel et al. 2011; Clark et al. 2014)
Biodiversity	Large diversity and endemism of bryophytes in TMCF	(Gentry 1992; Leo 1995)
Amazon river	Brings dissolved load to the Amazon river	(Clark et al. 2014)
Erosion	Reduce soil erosion and shallow landslides	(Brujinzeel 2004)

Definition and extent of TMCF

TMCFs are generally found in the tropical montane areas across the globe (Stadtmüller 1987; Bubb et al. 2004). Following an altitudinal gradient upwards in a tropical montane area, lowland rainforest gives way to lower montane rain forest, upper montane rain forest and finally subalpine rain forest (Grubb et al. 1963; Grubb 1977). High elevation grasslands called Punas, can be found above the treeline (Rapp and Silman 2012). TMCF occur in the lower, upper and subalpine montane rainforest zones in areas where clouds are more frequently occurring compared to adjacent areas (Grubb and Whitmore 1966; Stadtmüller 1987; Brujinzeel et al. 2011). Some indication of what is meant by a frequent cloud cover could be given by Jarvis and Mulligan (2011). They found that 40 to 60 % of 477 cloud forest locations situated at an altitude between 0 and 2000 meters above sea level were covered by an average cloud cover of more than 50 %. The number of sites with the same cloud cover fraction then increased to around 100 % between 2000 to 3000 m. a. s. l.

TMCF have been suggested to occur within a roughly defined altitude range of 1000 to 3500 m. a. s. l. (Figure 2; Stadtmüller 1987; Brujinzeel et al. 2011). In inland high montane areas the transition from lowland rain forest to lowland montane cloud forest (LMCF) occurs around 1200-1500 m. a. s. l. (Kitayama 1995). The lowland cloud forest then shifts into upper montane cloud forest (UMCF) where the frequency of clouds increases notably, roughly at between 2000

and 3000 m. a. s. l. (Grubb and Whitmore 1966; Grubb 1977; Kitayama 1995). The last transition to the subalpine tropical cloud forest (SACF) occurs somewhere between 2800 and 3200 m. a. s. l. (Kitayama 1995; Brujinzeel et al. 2011). However due to the Massenerhebung effect, also called the telescoping effect, these ranges are more applicable on inland situated cloud forests. On islands or in locations closer to the ocean these ranges have been shown to shift downward such that the ecotones are compressed and sometimes even excluded. This effect is not yet fully understood but is believed to be caused by the occurrence of clouds (Grubb and Whitmore 1966; Brujinzeel et al. 1993). Closeness to the ocean can also have an effect on the size and shape of the cloud forest areas. Banded areas of TMCF generally occur in montane areas whereas island or locations closer to the ocean are usually typified by smaller and more isolated patches of cloud forests (Hamilton et al. 1995). However all TMCF are generally considered being isolated since they only occur in the narrow areas which are controlled by the prevailing cloud cover (Horwath 2012).
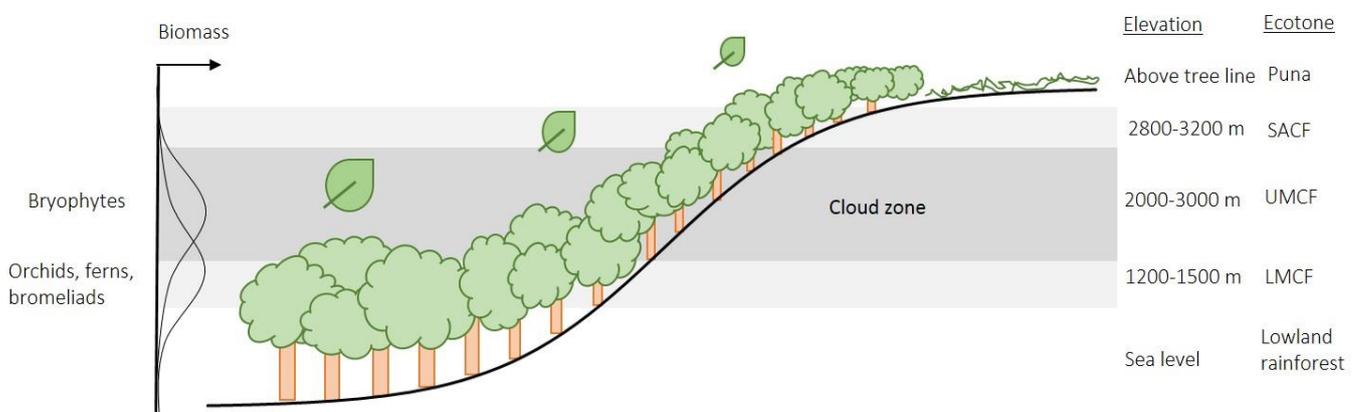
Figure 2. Zonal distribution of TMCF showing changes in vegetation physiognomy and relative change in epiphyte biomass. (Modified from Benzing 1998; Foster 2001; Horwath 2012)

A compilation of the global distribution of tropical montane cloud forests by UNEP-WCMC resulted in 605 locations in 41 countries within the tropics (Aldrich et al. 1997). However the total area of these locations was never calculated and the global extent of cloud forests have since proven difficult to determine. In many parts because of variation in previously mentioned factors like definition of frequent cloud cover and generally applicable altitude ranges. By defining forested areas and using set altitude ranges, areas where cloud forests most likely occur were determined to comprise around 380 000 km^2. This is about 2.5 % of all tropical forests in the world (Bubb et al. 2004). Using a different approach defining cloud forest areas by hydro-climatic boundaries instead, Mulligan (2010) greatly increased this area to 2 210 000 km^2 worldwide, or 14.2 % of all tropical forest. However, this approach also includes forests which are frequently covered by clouds or fog at over 70% of the time, thereby including forests with different appearance compared to TMCF. Mulligan (2010) therefore define these areas as "significantly cloud-affected forests" rather than tropical montane cloud forests.

The vegetation of TMCF

Following a gradient from lowland rainforest up to SACF the forest vegetation changes from rainforest to montane forest and the stature of the forest decreases (Figure 2). The area of the leaves also decreases and they become thicker with a xeromorphic appearance, meaning they

have the ability and appearance of plants that can withstand drought. Towards altitudes with UMCF and SACF the trees even grow stunted (Foster 2001). The reasons for this stunted and xeromorphic appearance are not completely understood but are most likely connected to the dominating climate and cloud cover which limits light availability, affects temperature and humidity and brings rain which all affects the forest stature and form (Rapp and Silman 2012). Water shortage due to saturated soils and consequently poor root systems could be one explanation for the xeromorphic appearance of the leaves (Brujinzeel and Proctor 1995).

Another characteristic trait of TMCF is that they are covered in tree anchoring epiphytes which are estimated to make up around 25 % of the TMCF species (Benzing 1998; Foster 2001). From the lowland montane forest to the LMCF, epiphytic species like bromeliads, ferns and orchids dominates but with increasing altitude the bryophytes dominates instead (Benzing 1998). In the UTMC the bryophyte cover have been found to make up around 60-90 % of the total epiphytic cover and this is why cloud forests are sometimes also referred to as mossy forests (Stadtmüller 1987; Benzing 1998: Horwath 2012). Bryophytes is the collective name for the three divisions: *Bryophyta* – mosses, *Marchantiophyta* – liverworts and *Anthocerophyta* – hornworts (Glime 2007). Liverworts usually dominates in the wet environment of TMCF but mosses have adapted to them as well. Hornworts on the other hand usually grow on soils in more open areas and are therefore unusual in TMCF (Horwath 2012).

The bryophytes of a cloud forest provides many services for the forest and its fauna (Table 2). In a Peruvian cloud forest the epiphytic biomass and associated dead organic matter was around 15 tonnes dry weight hectare^{-1} corresponding to 30 % of the aboveground biomass (Horwath 2012). Similar values of epiphytic biomass (mostly bryophytes), 12 and 16 t DW ha^{-1}, was found in cloud forests in Colombia and Costa Rica (Veneklaas et al. 1990; Köhler et al. 2007). Besides adding to above ground biomass, the bryophytes play an important part of the cloud forest dynamics (Benzing 1998). Most important is their effect on the hydrologic cycle. Bryophytes intercept cloud water and add to the total through fall from the tree crowns to the ground (Veneklaas et al. 1990; Horwath 2012). Besides capturing water, bryophytes also have a large water holding capacity of up to 2000% of their dry weight (but varying between species; Proctor 2009). When scaling up, the 16 t DW ha^{-1} bryophytes in Costa Rica could hold so much as 44.000 L/ha corresponding to retaining 4.4 mm rainfall (Köhler et al. 2007). In addition cloud water has been found to contain higher amounts of nutrients like NH_4^+ and NO_3^- compared to rain and by increasing the uptake of this water bryophytes therefore increases the forest nutrient pool (Weathers and Likens 1997). Since cloud forests are usually quite isolated many of the epiphyte species are endemic and contributes to the large biodiversity of TMCFs (Gentry 1992). Finally the mats of bryophytes function as a moist and protected germination bed for seeds from other species as well as being homes to many animals (Benzing 1998).

Table 2. Ecosystem services performed by bryophytes in TMCF

Ecosystem service	Description	Reference
Biomass	Contributes to increase aboveground biomass	(Veneklaas et al. 1990; Horwath 2012)
Nutrient pool	Increases nutrient input by capturing cloud water	(Weathers and Likens 1997)
Biodiversity	Large diversity and endemism of bryophytes in TMCF	(Gentry 1992)
Help other species	Acts as nursing bed for seeds and home for fauna	(Benzing 1998)
Hydrologic cycle	Captures, stores and releases cloud water and rainfall	(Veneklaas et al. 1990; Köhler et al. 2007; Proctor 2009)

2.3 Physiology of bryophytes

Although there has recently been an increasing interest for studying bryophytes they are generally understudied compared to vascular plants and especially so the ecophysiology of tropical bryophytes (Proctor et al. 2007a; Hanson and Rice 2014). However this chapter will describe the most recent view of the bryophytes tolerance to desiccation and factors governing their photosynthesis and respiration.

Desiccation tolerance in bryophytes

Bryophytes were among the first plants to colonize land. To deal with their new drier environment they developed the feature of being desiccant tolerant, which is functionally different from being drought tolerant. Drought tolerance occurs in vascular species which have developed root systems and conducting tissues for upwards water transport. Water loss is then inhibited by the leaf epidermis and regulated through the stomata openings. Plants adopting this strategy are called homeohydric. When vascular plants regulate water loss by closing stomata they also become limited from taking up CO_2 which decreases their photosynthetic rate. Despite this trade-off many vascular species have adapted well to drier conditions. But there are still few species that can survive the water stress from a relative water content below 30 to 40 % (Proctor et al. 2007a). Bryophytes on the other hand, which are desiccation tolerant or have adopted a poikilohydric strategy, can survive loss of all free water in their cells without dying. Instead, they go into a dormant stage where photosynthesis and respiration are downregulated. Only in the short transition period from full turgor to desiccation are the bryophytes experiencing water stress. When rewetted again by dew or rainfall (however not only by atmospheric humidity) bryophytes can regain full photosynthetic capacity (León-Vargas et al. 2006; Proctor 2000). These two different strategies were developed by inherently different species, over the same course of evolution and one of them should therefore not be seen as superior to the other (Proctor et al. 2007a).

A structural difference between bryophytes and vascular plants is that the bryophytes do not have roots which can be used to take up water, but they do have root-like tissues called rhizoids which anchor them to the substratum. Another difference is that bryophytes do not have vascular tissue or stomata but instead take up water directly through their whole surface (Dilks and Proctor 1979). This gives the benefit of fast uptake of water when available. However if too much water covers the surface it becomes a physical hinder for gas uptake and thereby reduces the possibility to take up CO_2 for photosynthesis (Tuba et al. 1996). The large surface to volume ratio of bryophytes also induces fast dehydration. However as long as there is liquid water available for capillary uptake the bryophyte cells can remain at full turgor pressure (Dilks and Proctor 1979; Proctor et al. 2007a). Bryophytes have external capillary spaces which can hold additional water and support turgor pressure for longer but without decreasing gas exchange by covering the surface (Dilks and Proctor 1979; Léon-Vargas et al. 2006; Tuba et al. 1996). The differing life forms of bryophytes also helps to deal with capturing and reducing loss of moisture. For example bryophytes growing in tufts reduce water loss by being compact but at the same time the surface exposed to the sun and potential for CO_2 uptake decreases. Pendant bryophytes are instead more exposed to sunlight and have less physical hindrance for taking up CO_2 and water however in dry conditions they risk rapid dehydration compared to

more compact species (Bates 1998; Zotz et al. 1997). By being small, bryophytes are also at an advantage since they only become subject to the slower exchange of heat, water, carbon dioxide and oxygen by diffusion in the boundary layer close to their surface and hence avoid the amplified loss of the mixing of the free air above them (Proctor 1990).

Despite these adaptations to retain water there will eventually be times when there is no more available liquid water and the bryophytes will lose turgor and dry out. In a dry habitat this can happen rather quickly. Without precipitation or other water additions from dew or mist the internal storage of bryophytes at 22° C and 50% relative humidity (RH) will be lost through evaporation in around one hour while in a cloud forest at 15° C and 85 % RH the storage can last for around five hours (León-Vargas et al. 2006). Hence the buffer time is rather short and it is therefore always an advantage for bryophytes to be desiccant tolerant, independent of habitat features (Proctor et al. 2007a). Nonetheless the degree of desiccation tolerance varies between species. For example species which grow in wet areas with little sun exposure or even under water where desiccation periods are few and short have a lower desiccation tolerance. On the opposite side are species which grow in dry and open sun exposed areas which must be highly desiccation tolerant (Proctor 2001). Epiphytic bryophytes are usually somewhere in between these two extremes. The bryophytes growing on tree branches dry out relatively fast compared to the ones on the more shaded trunks, but are still not as exposed as the most extreme species (Proctor et al. 2007a).

Factors controlling bryophyte photosynthesis

Bryophytes photosynthesise through the C_3 pathway in the same manner as most vascular plants do (Proctor 2000; Chapin et al. 2011). However the poikilohydric nature of bryophytes affects the photosynthesis differently. Below follows a short summary of the most important factors for bryophyte photosynthesis; light, moisture and temperature. Of course other factors usually affecting photosynthesis, like CO_2 concentration and nutrients, also influences bryophyte photosynthesis. However since information on them are scarce for tropical bryophytes (Wagner et al. 2014a) as well as their subordinate relevance to this study they will not be discussed here.

<u>Light</u>

The maximum photosynthesis for bryophytes are usually relatively low compared to vascular plants and it has been suggested bryophytes are shade plants, i.e. have low photosynthetic capacity and thereby a low light compensation point (Glime 2007; Marschall and Proctor 2004). Gabriel and Bates (2003) found photosynthetic saturation at low light intensities of between 20 and 69 µmol m^{-2} s^{-1} for bryophyte species found in shady to sun exposed habitats while Zotz et al. (1997) found saturation at between 200 and 400 µmol m^{-2} s^{-1}. Gabriel and Bates (2003) concluded that the generally low light intensities needed for saturation of bryophyte photosynthesis suggests they are indeed shade plants. However Marschall and Proctor (2004) found higher light saturations on average at around 300 to 500 µmol m^{-2} s^{-1} in bryophytes from shady respectively sun exposed habitats and a few species which saturated at a much higher light intensities from 600 to above 1000 µmol m^{-2} s^{-1}. Marschall and Proctor (2004) therefore concluded that bryophytes generally act as shade plants however not necessarily all species are since some only saturate at light levels above 1000 µmol m^{-2} s^{-1}.

Although bryophyte photosynthesis generally saturates at low light levels, light could still be a limiting factor. Bryophytes easily dry out when exposed to high light intensities for longer periods which might lead to desiccation and downregulation of photosynthesis. This means that the most favourable times for bryophytes to photosynthesise are usually during cloudy conditions when the light intensity is low (Marschall and Proctor 2004).

Moisture
One challenge with the poikilohydric strategy of bryophytes is that they need to be able to retain a long-term positive carbon balance, or take up more carbon through photosynthesis than they lose by respiration, through day- and night-time and when shifting between wet and dry stages. During the dehydration and rehydration stage the respiratory losses are mostly larger than the carbon gain. To make up for the loss a high photosynthetic performance is therefore required when the conditions are favourable (Hanson and Rice 2014). Lange et al. (2004) found that the moisture and light conditions affecting photosynthesis were seldom optimal at the same time and that light was usually limiting during or after rain when water was usually not. It has been suggested this absence of optimal conditions is a reason for the lower biomass of bryophytes in lowland forests. The higher temperature and rain during the night leads to large respiratory losses and the low light intensity during rain or otherwise high light intensity which induce desiccation, limits photosynthetic gain during the day (Richards 1984; Wagner et al. 2014a). However these difficulties are not only problematic for bryophytes in lowland forest but also influences bryophytes at higher altitudes (Wagner et al. 2014a). There are five important dimension regarding the timing and duration of favourable conditions for bryophytes to gain a positive carbon uptake; timing of precipitation, hydration length, frequency of dry wet cycles, desiccation length and desiccation intensity (Norris 1990; Wagner et al. 2014a).

1. Timing of precipitation

The timing of when precipitation falls and when light is available influences both the carbon loss and gain. If bryophytes are wet during the night they will perform respiration but no photosynthesis due to the absence of light and consequently suffer a carbon loss. If the morning is then sunny and warm the bryophytes will dry out rather quickly before mid-day. Because of this they will downregulate photosynthesis and lose the opportunity to gain biomass. But if the bryophytes instead receive rain or mist in the morning, which is usual in cloud forest they will be wet at mid-day and photosynthesis will be favoured (Richards 1984; Zotz et al. 1997; Wagner et al. 2014a).

2. Hydration length

To be able to photosynthesise the bryophytes need to be hydrated. Proctor et al. (2007b) found that, following desiccation, photosynthesis in *Polytrichum formosum* declined at a continuous rate during dehydration from a relative water content of 100 to 60 %. The rate then decreased a bit slower down to a RWC of around 40 % after which photosynthesis ceased completely. The ability to capture and retain moisture depends on the life-form of the bryophytes; for example pendulous species are good at capturing moisture however it is also rapidly lost again. Turfs on the other hand are better at retaining the moisture but it takes a larger amount of water to rehydrate a turf once desiccated (Bates 1998; Zotz et al. 1997). However the retention of moisture is also determined by the humidity of the surrounding air. High humidity decreases the saturation deficit of the air, or the amount of water needed to fully saturate the air, which

decreases the gradient from the bryophyte cells to the atmosphere and thus the rate at which they dry out. The bryophyte surface resistance is however most likely minor (Proctor 1982).

3. Frequency of wet dry cycles

Proctor et al. (2007b) showed that directly following re-wetting the bryophytes lose carbon through increased respiration and low photosynthetic capacity. Upon rewetting desiccated *P. formosum* the recovery of respiration started within a minute and increased for about 4 to 10 minutes before it decreased again returning to a normal respiration rate. Photosynthesis however recovered more slowly and needed 15 to 20 minutes to regain net carbon dioxide exchange (Proctor et al. 2007b). During re-wetting the bryophytes also lose carbon through leaching of organic compounds however it is uncertain to what degree it harms them. A faster transition from hydrated to dehydrated or vice versa could therefore be important to reduce carbon loss (Wagner et al. 2014a). How frequently bryophytes dry out and rehydrate is therefore also important, more frequent transitions suggests increased carbon loss.

4. Desiccation length

Species which grow in a more shaded and wet habitat are more sensitive to desiccation and are damaged faster and to a higher degree compared to species which grow in a drier and more sun-exposed habitat (Proctor 2001). Proctor et al. (2007b) showed that after being desiccated for a longer period (18 days) *P. formosum* needed 2 to 3 days to fully recover their photosynthetic capacity. The *Anomodon viticulosus* however recovered photosynthesis fully within 3 to 4 hours after desiccation lengths up to 15 days. But when desiccated for longer the recovery was less complete and after 40 to 45 days the NEE was negative i.e. the bryophyte did not take up carbon anymore but only suffered respiratory loss (Hinshiri and Proctor 1971). León-Vargas et al. (2006) found that several bryophyte species from a cloud forest only survived a few days of desiccation before showing signs of damaged photosynthetic capacity. The higher tolerance towards longer desiccation periods in Proctor et al. (2007b) and Hinshiri and Proctor (1971) could possibly be explained by the differing climate of the species habitats; a drier English woodland exposed to larger seasonal climate fluctuations compared to a cloud forest.

5. Desiccation intensity

The relative humidity of the air at which the bryophytes are desiccated is also important for their recovery. León-Vargas et al. (2006) found that cloud forest species generally recovered better from desiccation if they were kept dry in air at high relative humidity (74-85%) compared to low (20-43%). But, this finding seem to differ between species and what type of habitat they grow in. For example the highly desiccation tolerant *Tortula ruralis* found in for example open rocky areas or dry sand-steppe grasslands did not survive when being kept at high humidity for more than a few days likely due to continued respiratory losses but no photosynthetic capacity (Mayaba et al. 2001; Tuba et al. 1996; Proctor 2001). There is a discussion regarding if recovery of the photosynthetic capacity after desiccation is due to reactivation of already existing components within the bryophyte cells or if it is induced by acclimation, hardening and/or repair of these components (Mayaba et al. 2001; Proctor 2007b). Mayaba et al. (2001) argued that bryophytes of moist habitats most likely are adapted to the reactivation of already pre-existing components and Proctor et al. (2007b) showed that the downregulation and reactivation of these components occurred through morphological changes of the cells. Proctor et al. (2007b) also suggest that the increased risk of bryophyte mortality when drying out very quickly could be

caused by too little time to make these necessary morphological changes, but conclude this is a further step to investigate in order to better understand the desiccation of bryophytes.

Temperature

Like for other plants, an increase in temperature leads to exponentially increased respiration and increased photosynthesis along an optimum curve in bryophytes (Wagner et al. 2014a). The influence of temperature on carbon dynamics is however likely less extensive compared to moisture and light. Although as Richards (1984) found, for lowland species temperature can have an impact on the respiratory loss. In concurrence Frahm (1990) found a carbon loss at 30° C compared to a carbon gain at 15° C in tropical montane bryophyte species (Frahm 1990 in Wagner et al. 2014a). However in contrast, Wagner et al. (2013) did not find that higher temperature alone explained the higher respiratory loss in lowland species compared to higher altitude species. They suggested that the higher temperature may have an indirect effect by causing a higher evaporation rate leading to desiccation of the bryophytes and a decreased carbon gain from photosynthesis.

Plants can acclimatize to temperature increases and hence reduce temperature driven respiratory losses. However such acclimatization in TMCF bryophytes have not been proven yet. A transplant study where bryophyte samples were moved from 1200 and 500 m. a. s. l. to 500 and 0 m. a. s. l. respectively showed that the bryophytes generally suffered large carbon losses and the mortality was high. Although a few samples seemed to cope with the new conditions. However, as the authors point out, further studies with lower temperature- and altitude differences are necessary to reveal if bryophytes are really able to acclimatize to increased temperatures. They also discussed the confounding effect of varying moisture availability between the original and new habitats (Wagner et al. 2014b). Such an effect from moisture was found in a similar study where epiphytes were also transplanted to lower sites (Nadkarni and Solano 2002).

2.4 Climate change in TMCF areas

Past and future projected climate change

Pollen records from a lake in a lower montane cloud forest in southern Peru showed that this area underwent strong climate changes during the Pleistocene (records span from 48.000 years ago to present) but still remained a high biodiversity ecosystem. Although this could indicate that climate change is not a risk for present ecosystems the past rate of temperature increase was gradual; 1° C per millennium compared to today's rate which is projected to be between 2 and 4° C on average for the whole world by 2100 (Bush et al. 2004; IPCC 2013). The TMCF in this area did migrate during past climate changes but remained strong due to the slow rate of climate change which provided enough time for the ecosystem to adapt. Something which is not certain to happen today (Bush et al. 2004). Especially not when considering that mountainous areas are projected to experience an even higher rate of increasing temperature compared to the rest of the world (Bradley et al. 2004). Since TMCF are closely coupled to the hydrologic cycle, climate change will likely have an impact on their vegetation structure and function. How the TMCF will change is however still very uncertain. Partly because the microclimatic patterns will change differently in different TMCF regions and because they are

poorly projected in global climate circulation models due to low model resolution for high topography regions. But also because the combined effects of changes in different climatic factors could lead to varying vegetation changes depending on where the change occurs and on the species composition of that area (Oliveira et al. 2014). However species with narrow altitude ranges will likely be most affected as they risk being shifted out of their optimal habitat in just a few generations (Bush et al. 2004).

Still et al. (1999) presented one of the first hypothesis of a rising cloud base in a TMCF in Monteverde, Costa Rica as a response to climate change. They used relative humidity (RH) as a proxy for cloud base height and modelled climate change forced by a doubling of the CO_2 concentration (from 345 to 690 ppm). In response the RH was found to generally shift upwards during the northern hemisphere winter and downwards during the summer. For the Monteverde cloud forest, this would mean a 200 meter rise of the cloud base in the dry season when the forest needs the input from cloud water most. Indications of a rising cloud base in Monteverde have already been found by Pounds et al. (1999). They connected a demographic change of amphibians, lizards and birds and a sudden amphibian population crash to a decrease in dry season cloud mist frequency. The decrease in cloud mist occurred due to an increase in sea surface temperatures (ENSO fluctuations accounted for; Pounds et al. 1999). Changes in the cloud cover over the eastern slope of the Andes have also been detected. Halladay et al. (2012a) found that between 1983 and 2008, the cloud cover in TMCF areas showed a decrease of 4 % in March and in lowland areas the decrease was somewhat larger at 8 % in January, March and September. Halladay et al. (2012a) hypothesize that a reduction in cloud cover would have the largest effect on TMCF areas during the dry season when the mean cloud cover and rainfall are low but not as great during the wet season when moisture is abundant.

Using the HADCM3 and ECHAM5 global circulation models Mulligan (2010) projected climate change for tropical montane cloud forest areas by 2050. The two models projected a concordant average temperature increase of between 2 to 5° C and 1.3 to 4.2° C respectively for all cloud forest areas. By using a regional climate model which better represent the complex topography, Urrutia and Vuille (2009) projected that temperatures will increase with around 3.5 to 4.5 degrees at 3000 meters by 2100 in the Andes and also that the lapse rate will decrease from -0.57° C 100 m^{-1} to -0.49° C 100 m^{-1}. The lapse rate is the rate of decrease in temperature with altitude and determines at what height condensation and cloud formation occurs (given the same air humidity; Ahrens 2013). The decrease in lapse rate would therefore mean that the air cools down to the point of condensation at a slower rate and could therefore lead to an increased cloud base height (Still et al. 1999).

For rainfall there was a larger disagreement between the HADCM3 and ECHAM5 models and also a larger range of the changes. The HADCM3 projected that some areas (for example Colombia and Central Africa) will receive increasing precipitation of 100-1000 mm per year while other areas (for example Peru and Madagascar) could see a decrease in precipitation within the same range. The ECHAM5 on the other hand projected increasing rainfall of a few hundred mm year^{-1} for all cloud forest areas except some in South East Asia and Madagascar. Large uncertainties thus surround the future changes in rainfall while temperatures seem to increase in most cloud forest areas (Mulligan 2010). For the Andes, Urrutia and Vuille (2009) projected that south of 12° S at high elevations precipitation will generally decrease possibly due to a weakening of the upper tropospheric wind flow which brings in the moist easterlies

from the Amazon. However north of 12° S the high elevations will generally see an increase in precipitation. But the changes in precipitation was somewhat uncertain for the regional model as well and the model generally overestimated precipitation on the eastern slope of the Andes (Urrutia and Vuille 2009; Table 3).

Table 3. Summary of observed and projected climate changes in the Andes

Climate factor	Observed and projected climate change in the Andes	Reference
Cloudiness	Lower lapse rate - rise of cloud base height	(Still et al. 1999; Urrutia and Vuille 2009)
	Observed decrease in cloud cover over the Andes	(Halladay et al. 2012)
Temperature	Increase in temperatures (2-5° C)	(Urrutia and Vuille 2009; Mulligan 2010)
	More rapid warming compared to past changes	(Bush et al. 2004)
	Amplified warming in mountainous areas	(Bradley et al. 2004)
Precipitation	Precipitation patterns will likely change and both increases and decreases in rainfall is projected	(Urrutia and Vuille 2009; Mulligan 2010)
	However uncertainties surround precipitation changes	(Urrutia and Vuille 2009; Mulligan 2010)

Other threats to TMCF

Besides the direct climate change impacts there are also other threats to TMCF. Rather high average migration rates due to climate change have been reported; Parmesan and Yohe (2003) found a global range shift rate of 6.1 meter in elevation per decade while Chen et al. (2011) found an even higher rate of 11.0m in elevation per decade. Chen et al. (2011) also found varying individualistic range shifts for different species. Reasons for variation could be due to a time lag for some species which are dependent on different climate thresholds, like a minimum or maximum temperature, to occur at a certain phenological stage before being able to migrate. Furthermore if species are specialist rather than generalists their migration ability depends on if suitable habitats occur in the near surroundings (Warren et al. 2001). For cloud forests which are home to many specialists and endemic species, generalists from below which migrate faster or are better competitors could therefore possibly pose a threat (Oliveira et al. 2014).

Feeley and Silman (2010) evaluated the risk of extinction for Andean vegetation and found that when assuming the montane forests can migrate upslope at the same rate as temperatures increase, there is a good chance of development of new habitats. However the recorded migration rates in the Andes during the last decades are lower than those for temperature and migration projections with these rates instead pointed to some minor population decreases. When also taking into account the anthropogenic impact from fire and animal grazing on the Puna zones above cloud forests this substantially limited upslope migration and increased the extinction risk for many populations (Feeley and Silman 2010). The anthropogenic influence on these areas could therefore contribute largely to limiting the survival of the shrinking cloud forests due to climate change.

Other anthropogenic threats to cloud forests, besides the direct deforestation of them, is the deforestation and conversion to agriculture occurring below them. These type of land use changes reduces evapotranspiration because crops does not have as deep roots as forests and consequently cannot take up as much water (Lawton 2001). The loss of large areas of lowland Amazon forests will result in multiple feedbacks on climate factors like decreased cloudiness, and changes in convection and precipitation regimes (Lawton 2001; Malhi et al. 2008).

3. Method

3.1 Study site

The study site was an upper tropical mountain cloud forest at the Wayqecha biological station situated at 2900 m. a. s. l. in the Kosñipata catchment, Andean Peru (13°11'09.9"S, 71°35'16.3"W; Figure 3). The Kosñipata catchment is situated on the eastern slope of the Andes where the vegetation changes over an altitude of 2500 meters, from lowland rainforest to TMCF and last Puna (Clark et al. 2014).
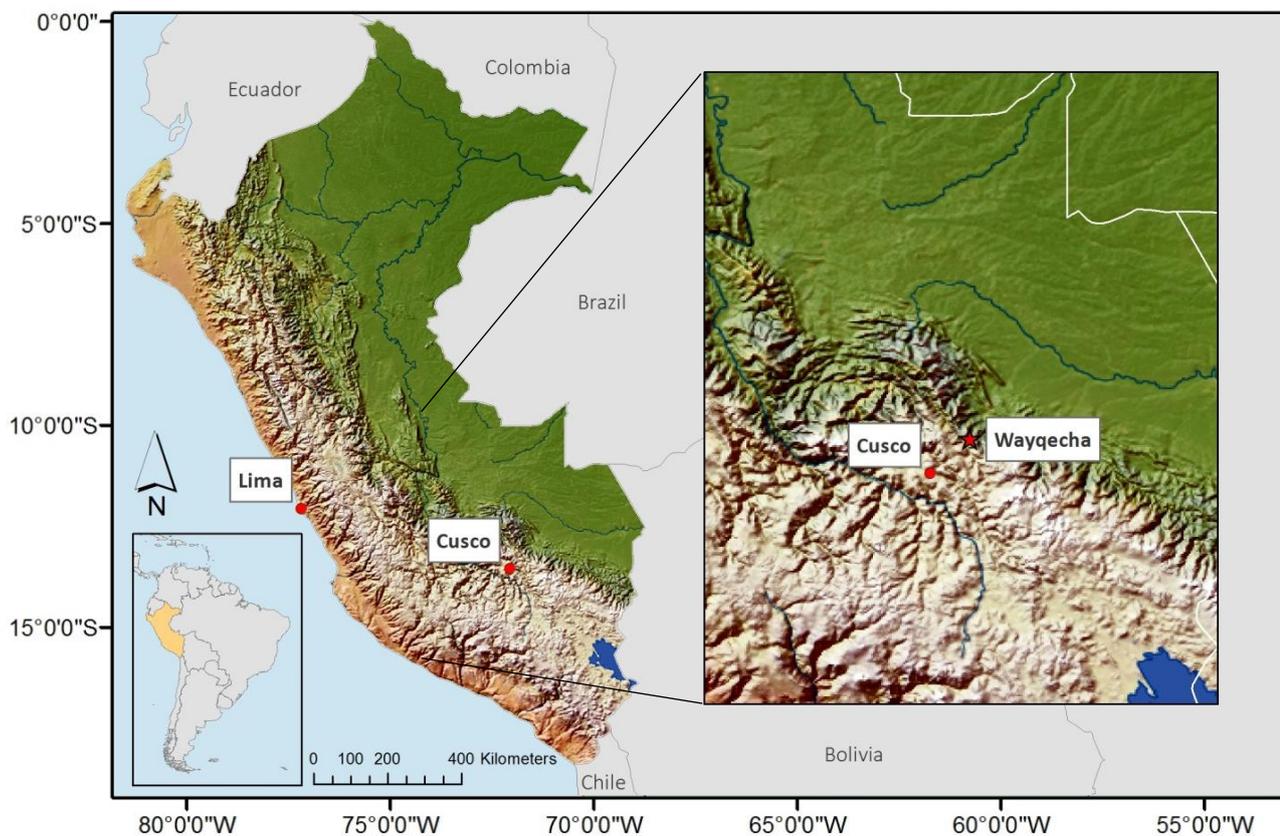
Figure 3. Location of the study site at Wayqecha biological station, Andean Peru. Made with Natural Earth data. Free vector and raster map data at www.naturalearthdata.com.

Largescale controls of cloudiness

The occurrence of tropical montane cloud forests on the eastern slopes of the Andes is unusual since most cloud forests are situated in areas influenced by coastal climates. The prevailing wind patterns and the influence of the South American low level jet stream (SALLJ) does however enable the cloud forests to thrive in this area. The trade winds coming from the North East bring moist air from the Atlantic Ocean in over the Amazon area where it warms up. When the air reaches the Andes it is stopped by both the mountain range and the subsidising cold air coming in from the west. This forces the warm air from the east to rise and then turn south forming the SALLJ. The topography and alternate influence from the SALLJ and the dry air to

the west affects the vegetation in the Andes and gives rise to dry, humid and super-humid areas where tropical montane cloud forests are found in the super-humid areas (Killeen et al. 2007). In the Kosñipata catchment a zone of high cloud cover (60 %) is found between 1500 and 3500 m. a. s. l. with the highest mean annual cover (80%) between 2000 and 3500 m. a. s. l coinciding with the upper tropical montane cloud forest. The UMCF experience a wet season between October and April and a dry season between May and September with the highest cloud cover in January and the lowest in June. The seasons are controlled by the north-south movement of the intertropical convergence zone, a zone around the equator where air rises due to convection. However a band of cloudiness around 60 % still covers the eastern slope in the dry season due to the constant easterly trade winds bringing in moist air over the area. In addition, sun heating of the slope and air over the lowland areas also creates upslope winds bringing with them moisture and promotes orographic cloud formation (Halladay et al. 2012a).

At the TMCF zone the daily change in cloud cover shows the largest variation in the dry season. In the morning (7.00-10.00 local time) the cloud cover is around 50-60 % and then increase in the afternoon (13.00 LT) to about 80 %. During the night it then decreases again to around 60 %. The change in cloud cover could be due to winds flowing downslopes from the west during the night. In the wet season the cloud cover is less variable and shifts from 80% during night and in the morning, up to around 90 % in the afternoon. The cloud patterns found in this TMCF area are different from the ones found at the lowland below and at the Puna zone found above, were cloud cover is less frequent and show slightly different daily and seasonal variations (Halladay et al. 2012a). The cloudiness of this area is correlated with anomalies of sea surface temperatures in areas in the Pacific Ocean, the Tropical North Atlantic and the Indian Ocean, where the Pacific SSTs has the strongest influence on the TMCF zone. An increase in the Pacific SSTs leads to a decrease in cloud cover in the TMCF zone (Halladay et al. 2012b).

Rainfall

The TMCF area typically receives rising warm and moist air during the morning which leads to rainfall in the afternoon. When the air then sinks back downslopes during the night, moist air at lower elevations are displaced which causes convection and additional rainfall during the night (Rapp and Silman 2012). The maximum precipitation in the Kosñipata catchment occurs at around 1000 m. a. s.
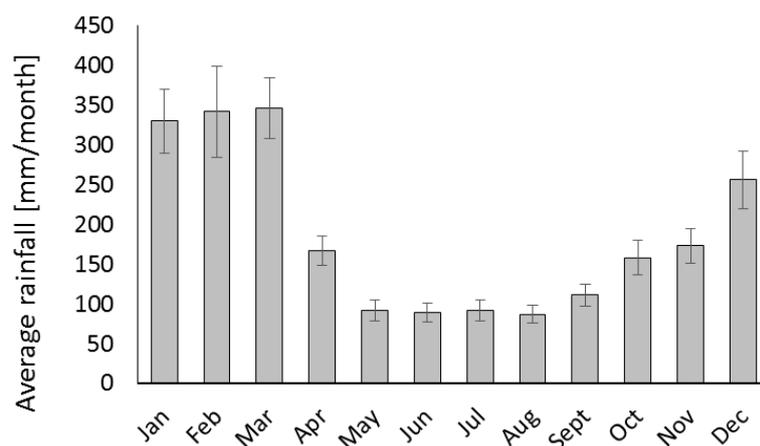
Figure 4. Average monthly rainfall at Wayqecha station. The figure is based on data for 1988 to 2012 published in supplement to Clark et al. 2014. Error bars show two standard errors.

l. and the rainfall then decrease linearly with an increase in altitude (Horwath 2012). Besides normal rainfall the Kosñipata catchment also receives additional precipitation from intercepted cloud water. Of the annual input 90.8 % or 3112 mm (±16.5 % or 414 mm; one standard deviation error) comes from rain and 9.2 % or 316 mm (±3.6 % or 116 mm) from clouds. Over

a year the rainfall peaks during the wet season and reaches a low during the dry season (Figure 4: Clark et al 2014).

Humidity

The mean annual relative humidity of the Kosñipata catchment at 3000 m. a. s. l. is around 98 % and on a microclimate scale, the humidity from the forest floor to the canopy is affected by the cloudiness of the area (Horwath 2012). Another way of measuring air humidity is through the vapour pressure deficit. The vapour pressure is the pressure the water exerts in the air and the deficit is the amount of additional water the air can hold before it becomes saturated. This measurement better represents the force exerted on the vegetation which drives transpiration. Rapp and Silman (2012) found that the VPD above the canopy is largest in the mornings of the dry season (0.4 kPa) and lower during the evening and night (0.1 kPa) and during the wet season it is low the whole day (0.1 kPa; Rapp and Silman 2012). In the understory however the deficit is very low throughout the whole year (< 0.05 kPa) with only a slight deficit during the morning of the dry seasons (0.1 kPa; Horwath 2012; Rapp and Silman 2012). Since vegetation normally does not experience water stress until VPD above 1 kPa it means the humidity is high throughout the whole year (Rapp and Silman 2012).

Temperature

The mean annual temperature (MAT) in the Kosñipata catchment at 3000 m. a. s. l. is 11° C with a MAT day time temperature of 12.7° C and a MAT night time temperature of 9.5° C. However the understory temperature is usually between 1 and 2° C lower. Generally the temperatures are lower in the dry season and higher in the wet season but the difference between the seasons are usually less than 4° C. The diurnal temperature fluctuation is larger in the dry season compared to the wet season (Rapp and Silman 2012).

Light

Light intensity is usually very low in TMCF due to the frequent cloud cover (van de Weg et al. 2012). Rapp and Silman (2012) found that the above-canopy photosynthetically active radiation (PAR; light with a wavelength of 400-700 nm or visible light) was fairly even throughout the year at higher altitudes (2720-3400 m. a. s. l.). It varied between 500 to 750 µmol photons m^{-2} s^{-1} except for in September when it increased to around 1000 µmol photons m^{-2} s^{-1}. Below the canopy the light intensity decreased with the light extinction coefficient of 0.34 m^{-1} (van de Weg et al. 2012). If starting with 1000 µmol photons m^{-2} s^{-1} and a leaf area index of 4.15 (van de Weg et al. 2012) it would result in a decrease in light intensity to around 243 µmol photons m^{-2} s^{-1} in the understory (calculated according to Aubin et al. 2000). In accordance Léon-Vargas et al. (2006) found that the light intensity in a Venezuelan cloud forest was around 50 to 100 µmol photons m^{-2} s^{-1} in the understory but could reach 200 µmol photons m^{-2} s^{-1} closer to the canopy top.

Vegetation

The trees of this TMCF area are mainly from the families *Asteraceae*, *Cunoniaceae*, *Melastomataceae*, *Rosaceae* and *Rubiaceace* and bamboo from the *Cusquea* genus is also common. The forest has a closed canopy with sparse understory made up of shrubs and herbs. The tree branches on the other hand are covered in epiphytes to some degree by the vascular

ferns, orchids, bromeliads and the *Ericaceae* family, but it is the non-vascular bryophytes that dominates (Gibbon et al. 2010). Over a gradient from 950 to 3600 m. a. s. l. in the Kosñipata catchment 227 species of bryophytes were found and of them 80-85% were liverworts and the remaining 15-20% mosses (no hornworts were found). The highest diversity was found between 1500 to 3000 m. a. s. l. were over 100 species per study site (comprising of only three trees) were found. Half of all species came from the families *Lejeuneaceae, Plagiochilaceae* and *Lepidoziaceae* (all liverworts; Horwath 2012) of which the last two were found in this study


Figure 5. Bryophytes found at the study site at Wayqecha biological station a) Thick layer of Plagiochila sp. covering a branch b) Lepidozia cf. caespitosa c) Plagiochila sp. d) Plagiochila sp. covered in dew. All photos: Jenny Ahlstrand

(Figure 5).

3.2 Precipitation experiment

Experimental design

Multiple species of moist bryophytes were collected, taking care to exclude the rhizoids. In this study no hornworts were collected therefore further reference to the group bryophytes includes only mosses and liverworts. Since the bryophytes were to be placed on a flat surface for the experiment, only species growing on horizontal branches at breast height were collected to minimize changing their natural conditions. The bryophytes were washed in tap water to remove any remaining soil, thoroughly and randomly mix species whilst at the same time ensuring all bryophytes were equally moist. The bryophytes were then left to drain for one hour and divided into containers. Each container held 10.0 grams wet weight of bryophytes and it was ensured that the species were interspersed randomly in each sample. A subset of bryophyte samples were collected, air dried and sent to Dr Jasmín A. Opisso Mejía, at Universidad Nacional Mayor de San Marcos, Lima, Peru, for species determination (Appendix 1).

A blocked full factorial experimental design was employed to test the effects of three different hydrological factors; amount, frequency and type of precipitation on bryophyte carbon dynamics (Oehlert 2000). The amount and frequency factors had three levels each and the type factor had two levels. Specifically, three different amounts of precipitation; low (AL), medium (AM) and high (AH), three different frequencies i.e. how many days between each precipitation event; low (F4; number representing days between events), medium (F2) and high (F1) and two different types of precipitation, mist (M) and rain (R), were used in the model. The model set up thus resulted in 18 different treatment regimes with four replicates each leading to a total of 72 samples (Figure 6 & 7; Table 1). Containers were randomly assigned to treatments.
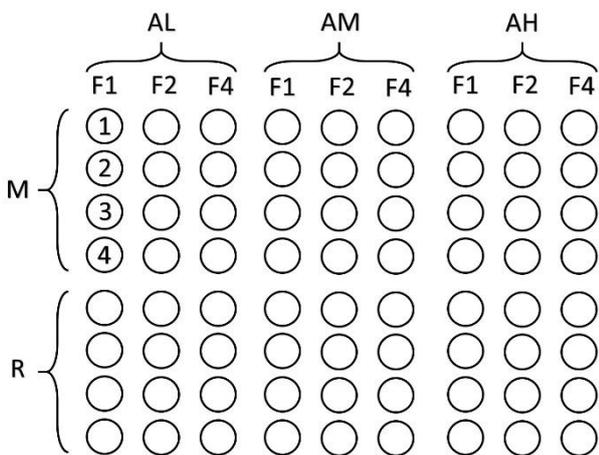
Figure 6. Experimental design with 18 treatments combining three precipitation amounts; low (AL), medium (AM) and high (AH), three frequencies; low (F4; number representing days between events), medium (F2) and high (F1) and two precipitation types; mist (M) and rain (R).

Figure 7. Model set up at Wayqecha biological station. Photo: Robinson Palomino Paz

The three treatment frequencies between precipitation events were calculated using daily precipitation data from Wayqecha for the years 2009 and 2010 (Girardin et al. 2014). The daily frequency of precipitation events during the dry season (July, August and September) were used

to calculate the low frequency treatment (1 event every 4 days), the mean annual daily frequency of precipitation events for the whole period was used for the medium frequency treatment (1 event every 2 days) and the daily frequency of precipitation events during the wet season (January, February and March) was used for the high frequency treatment (1 event every day). The number of days with rain in each period were divided by the total number of days in each period respectively.

The three treatment amounts of precipitation were calculated from precipitation data for the dry seasons (July, August and September), wet seasons (January, February and March) and whole period of the years 1998 to 2012, published in Clark et al. (2014). The average amount of rain per period was divided by the number of days per periods to calculate mean daily precipitation amount. In the treatments with different frequencies but the same amount of precipitation, the amount was divided by the number of events every four days so that the samples were given the same total amount of water after four days. For example in the case of the lowest amount of precipitation, the samples with low frequency received 56 ml every four days, medium frequency received 28 ml every second day and high frequency received 14 ml every day (Table 4). This meant that over four days, each sample received 56 ml in total.

The two types of precipitation included in this study was mist and rain. Mist was produced by spraying the samples with a spray bottle, using a funnel to ensure the full water amount reached the sample and rain was produced by dripping water over the samples with a syringe.

Table 4. The 18 precipitation treatments used in this study, divided by type, amount and frequency of precipitation. The first row show amount of precipitation in ml. The second row in italic within parenthesis is the key for the treatments. The first letter represents the type of precipitation; mist (M) and rain (R), the second letter the amount; low (L), medium (M) and high (H) and the last number the frequency; watered every day (1), every second day (2) and every fourth day (4).

		Watered every day			Watered every second day			Watered every fourth day		
Mist	Amount (ml)	14 *(ML1)*	27 *(MM1)*	50 *(MH1)*	28 *(ML2)*	54 *(MM2)*	100 *(MH2)*	56 *(ML4)*	108 *(MM4)*	200 *(MH4)*
Rain	Amount (ml)	14 *(RL1)*	27 *(RM1)*	50 *(RH1)*	28 *(RL2)*	54 *(RM2)*	100 *(RH2)*	56 *(RL4)*	108 *(RM4)*	200 *(RH4)*

The treatments were then applied over eight weeks (Appendix 2). Rain water was used to water the samples to avoid unnatural mineral build up in the bryophytes (Bates 2009) To replicate natural precipitation events during the course of treatment application, the bryophyte samples were watered with between 3 and 10 ml, each 15 to 60 minutes over five hours between 8 am and 1pm. The different times between watering events depended on the total amount the samples were to be given. The containers had drainage holes to remove excess water and stood at a slightly tilted table to increase drainage, again replicating as well as possible drainage patterns in natural bryophyte communities.

All samples were kept equally moist during the collection day. The next day the samples were again watered equally and the initial respiration and NEE were measured in all samples. To ensure normal photosynthetic capacity and no physical hindrance for CO_2 uptake the measurements always started two hours after the bryophytes were last watered (Tuba et al. 1996; Romero et al. 2006). Respiration and NEE were then measured in all samples every eight

days, which meant that all samples had been watered that same day to control for short-term differences in moisture content (Appendix 2).

The respiration and NEE measurements were carried out with an infrared gas analyser (EGM-4, PP systems, Amesbury, MA, USA; accuracy ±1ppm) connected to a closed, clear plastic chamber of 550 cm³. During the respiration measurements the chamber was covered by an opaque cloth to block out all light and thereby stop photosynthesis. During the NEE measurements a LED light (SL 3500 C, Photon Systems Instruments, Brno, Czech Republic) was used to ensure maximum photosynthesis was reached and that all measurements of photosynthesis across samples were made under identical light levels. The light was set to 1400 µmol photons m^{-2} s^{-1} which was recorded using a PAR sensor (photosynthetically active radiation; PAR-1/PAR Sensor, PP systems, Amesbury, MA, USA) within the clear plastic measurement chamber. Each sample was placed under the light one minute before the measurement to acclimatize it to the high light condition. Initially the acclimatization time was determined by placing a bryophyte sample under the light and measuring the time it took to reach a steady photosynthetic rate and one minute was then consequently used for all measurements. No acclimatization time for respiration was used. Instead the respiration was measured over a longer period since the concentration change needed more time to stabilize. After sealing each sample within the clear chamber, The CO_2 concentration within the chamber, starting from ambient levels (~400 ppm) was measured every four seconds for 60 seconds for NEE and for between 60 to 90 seconds for respiration.
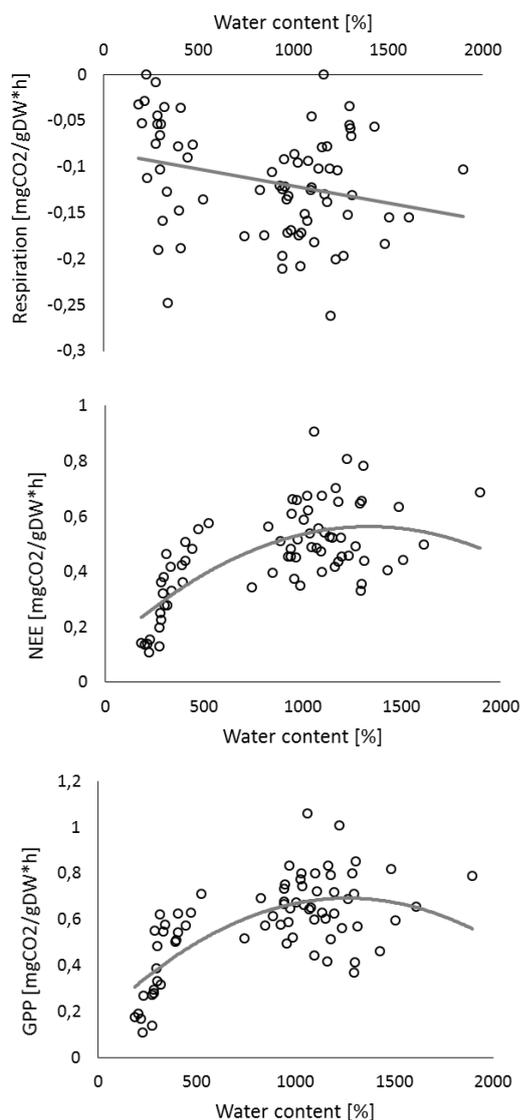
Figure 8. The response of respiration, NEE and GPP to water content of the bryophytes (FW/DW*100). The solid line describes the relationship. The relationship for respiration is showed with a linear model and for NEE and GPP with a non-linear (quadratic) model.

The indoor temperature was measured at the days when respiration and NEE was measured. The temperature ranged between 12.1 and 21.6° C (average 17.6° C) throughout the experiment, with one exceptionally high reading of 26.9° C registered the first day. Temperature was not found to be correlated with respiration, NEE or GPP meaning the temperature variation should not have had an effect on the measurements (data not shown).

Measurements of respiration and NEE were also performed on the second last day of the treatment period. At this point the high frequency samples had been watered that same day. However the medium frequency samples were only watered the day before and it was three days since the low

frequency samples were watered. The varying water contents of the bryophytes enabled exploration of the response of respiration, NEE and GPP to water content over a larger water content range compared to if only the recently watered samples had been used as otherwise in the precipitation experiment. The water content of each sample was calculated by taking the fresh bryophyte weight divided by the dry bryophyte weight and the multiplied by 100. Linear and non-linear (quadratic) regressions were then used to determine the relationship between bryophyte water content and respiration, NEE and GPP respectively (see *Statistical method* section below for explanation of method). Respiration showed a small increase with water content ($p = 0.025$; Figure 8). At lower water amounts the NEE and GPP increased with increasing water amount after which the response levelled out and even decreased slightly at very high water amounts ($p = < 0.001$ and < 0.001 respectively) which is in accordance with Tuba et al. (1996) and Romero et al. (2006).

At the end of the eight week study the bryophyte samples were dried in an oven at 65°C for 60 hours and then weighed to quantify dry biomass.

Data analysis

The first four CO_2 values of each measurement were excluded to avoid variation due to initial pressure equalization. The rate of change in CO_2 concentration over time within the sealed chamber was calculated for each measurement respectively by fitting a linear trend line to all remaining CO_2 values and calculating the slope and R^2. R^2 values were used to identify outliers, however at low flux rates (with low slope) the use of R^2 was not appropriate for this purpose. Hence, outliers were identified by plotting the slopes against the R^2 values (Appendix 3). If the slope was > 0 & < 0.1 ppm sec^{-1} for respiration and < -0.1 ppm sec^{-1} for NEE, a low R^2 value was accepted if the CO_2 change was steady. All slopes > 0 & < 0.1 ppm sec^{-1} with a low R^2 value showed steady changes in CO_2. Two slopes > 0.1 ppm sec^{-1} did however stand out with low R^2 values. On closer inspection, they were the result of a sudden large increase in CO_2 possibly due to a chamber leakage and/or erratic air mixing within the chamber so was consequently removed. Two respiration rates turned out positive, however the values were extremely small (0.005 ₐand 0.05 ppm sec^{-1}) and most likely were so low that they were on the edge of the EGM-4 measurement resolution (±1 ppm). Both values were therefore considered erroneous and changed to zero, i.e. no respiration occurred. The R^2 values for the trend lines of the NEE measurements were mostly high ($R^2 > 0.9$) however two samples showed R^2 values of around 0.8. They were likely the result of chamber leakage and/or erratic air mixing within the chamber. In each case the nonlinear portion of the change in CO_2 concentration over time was excluded and the measurements were kept (Appendix 3). In total 1008 samples were measured meaning only 0.6 % of them were removed or altered.

Respiration and NEE rates were calculated in mg CO_2 per gram bryophyte (dry weight) and hour according to Equation 4 derived from the ideal gas law (Campbell and Norman 1998).

$$\frac{k*P*V*M_{(CO_2)}*1000}{R*T*DW}$$

Equation 4

Where k is the slope of the linear trend line fitted to the CO_2 measurements [ppm area of container^{-1} h^{-1}], P is pressure [atm], V is total chamber volume [m^3], $M_{(CO2)}$ is molar weight of

CO_2 [g mole^{-1}], R is the ideal gas constant [atm m3 mol^{-1} K^{-1}], T is temperature [K] and DW is bryophyte dry weight [g].

The total volume of the chamber was calculated by taking the volume of the chamber, tubes and airspace within the EGM-4 and subtracting the volume of the chamber and the bryophytes (dry mass + water content). The volume of the chamber and tubes were calculated with a volume equation for cylinders, the airspace within the EGM-4 was 4,2 ml (Andrew Lintz, PP systems support, pers. comm.) and the volume of the container holding the bryophytes was calculated by taking the weight divided by the density of the container. To my knowledge there is no figure of bryophyte dry weight density in the literature. Instead an average dry weight density of leaves (0.41 gDW cm^{-3}; Niinemets 1999) was used to estimate the volume of the dry bryophyte biomass. By subtracting the dry bryophyte biomass from the weight of each sample at each measurement occasion the amount of water held by the bryophyte biomass was used to calculate the volume of the water of each sample.

Two samples (RL24 and ML43) were lost during transport, so the dry weights for them could not be determined. Instead the average percentage of dry weight per fresh weight of the remaining three replicates within the same treatment group were multiplied with the fresh weight of the missing sample to derive an estimated dry weight. This estimated weight was credible since it was very close to the average dry weight of the three other samples within that group; RL24 estimated weight was 1.78 g compared to group average 1.81 g and 1.99g for ML43compared to group average 1.94 g.

The GPP was then calculated by simply adding the respiration to the NEE (Chapin et al. 2011). To account for any initial sample variation the differences between the last and first (pre-treatment) measurements of respiration, NEE and GPP respectively were calculated and used in the statistical analysis.

Statistical method

Full factorial three-way ANOVAs were performed in the statistical analysis software SPSS (IBM SPSS Statistics for Windows, version 23, IBM Corp., Armonk, N.Y., USA) to compare the main and interactive effects of amount, frequency and type of precipitation on the difference between the last and the first measurements of the dependent variables (respiration, NEE and GPP). As mentioned above, amount included three levels (low, medium and high), frequency included three levels (every day, every 2nd day and every 4th day) and type of precipitation included two levels (mist and rain).

In a three-way ANOVA each treatment effect is tested separately to show main effects of the treatments; for example the increased amount of precipitation shows the response of respiration rate at each precipitation level but at an average precipitation frequency and the increase in frequency shows the response at each frequency level but at an average precipitation amount. This is essentially what a one-way ANOVA does as well (Gotelli and Ellison 2013). However an advantage of the three-way ANOVA is that interactive effects between treatments are also tested. The interactive effects shows the response in respiration rate to a combination of the two treatments, for example both low amount and low frequency could together show a different response compared to from just low amount or low frequency when considered separately. The

null hypothesis for the ANOVA is that there is no difference between treatment groups and it is accepted if the variance within groups is larger compared to the variance between groups. If on the other hand the variance between groups is larger compared to the variance within groups the null hypothesis is rejected and the alternative hypothesis is instead accepted i.e. the groups are significantly different from each other (Gotelli and Ellison 2013). The ANOVA is based on a model for which some assumptions must be fulfilled (Oehlert 2000);

1) The residuals (or the errors of the samples) must show equal variance
2) The residuals must follow a normal distribution
3) The residuals must be independent

The assumptions behind the full factorial ANOVAs were thoroughly tested. To check for normally distributed residuals a visual examination of histograms and Q-Q plots of the standardized residuals were performed. The equality of variance and linearity of the model was determined by plotting the standardized residuals against predicted values from the model, checking for that the residuals were evenly spread with increasing predicted values. The respiration data set fulfilled this assumptions sufficiently while both NEE and GPP showed some deviations from equal variance. These two data sets were consequently transformed by first adding 1 and then taking the logarithm of all values. Afterwards the assumptions were again evaluated and found to be sufficiently fulfilled. The ANOVA is not designed to show which groups that are actually different from each other (Oehlert 2000). Post-hoc Tukey's HSD tests were instead performed to determine this.

The relationships between respiration, NEE and photosynthesis to air temperature and bryophyte water content, i.e. the percentage fresh weight of dry weight, were examined with linear and non-linear regression (Figure 8). Linear regression tests the hypothesis that the change in a response variable is caused by the change in a predictor variable and describes this relationship using a linear model. A quadratic, or non-linear regression tests the same hypothesis but described the relationship using a quadratic model. Both models are based on some assumptions which must be fulfilled (Gotelli and Ellison 2013);

1) The functional relationship between the response and predictor variables should be explained by the chosen model, i.e. linear or non-linear
2) The residuals must show equal variance
3) The residuals must follow a normal distribution
4) The residuals must be independent

These assumptions were tested for all data sets however some deviations regarding equal variance occurred for NEE and GPP. It was not possible to transform the data set due to the occurrence of both positive and negative values. However regression is quite robust against some deviation from the assumption of equal variance hence the regressions were still performed (Gotelli and Ellison 2013). Nevertheless the results could be affected by these deviations and should therefore be interpreted with caution.

3.3 Light experiment

Experimental design

At the end of the 8 week treatment period, additional measurements covering different light conditions were conducted on the samples of the hydrology experiment above, to determine if the photosynthetic light response patterns differ with different precipitation regimes. NEE was measured under four different light intensities created by setting the LED-light to 200, 400, 800 and 1400 µmol photons m^{-2} s^{-1} respectively. Respiration was also measured to be able to calculate GPP (Chapin et al. 2011). Due to time constraints all measurements could not be performed on the same day, however measurements at the same light level were recorded at the same time.

To determine if photosynthetic light response patterns were affected by changing precipitation regimes a range of response descriptors - P_{max}, k, E_0 and LCP - were modelled for each sample using the measured NEE, respiration and PAR described above. Equation 5 was used to model P_{max} and k (Street et al. 2007). A start value of P_{max} of 100 and k of 1 were set to first model NEE. The initial root mean square error was then calculated by taking the difference between the measured and modelled NEE samples, squaring those differences, summing them up and finally taking the root of the sum. The RMSE is thus a measure of the average variance, or residual between the measured and modelled values. By changing the parameters P_{max} and k iteratively using the Solver Add-In in Excel, the RMSE between the modelled and measured NEE was minimized resulting in optimized values of P_{max} and k for each sample respectively.

$$NEE = R - \frac{P_{max}*I}{I+k}$$ *Equation 5*

Where NEE is net ecosystem exchange [mg CO_2 gDW^{-1} h^{-1}], R is respiration [mg CO_2 gDW^{-1} h^{-1}], P_{max} is the rate of maximum photosynthesis [$mgCO_2$ gDW^{-1} h^{-1}], I is PAR [µmol photons m^{-2} s^{-1}] and k is the half-saturation constant [µmol photons m^{-2} s^{-1}].

Using the optimized P_{max} and k in Equation 6 the E_0, quantum efficiency or the initial slope of the curve [mg CO_2 $µmol^{-1}$ photons m^{-2} s^{-1}], was calculated for each sample respectively (Street et al. 2007).

$$E_0 = \frac{P_{max}}{k}$$ *Equation 6*

Using the optimized P_{max} and k and measured respiration in Equation 7 the LCP, light compensation point [µmol photons m^{-2} s^{-1}], was calculated for each sample respectively (Street et al. 2007).

$$LCP = \frac{R*k}{P_{max}-R}$$ *Equation 7*

Data analysis

Since the respiration and NEE values at 1400 µmol photons $m^{-2}\,s^{-1}$ were the same measurements as in the hydrological experiment, one outlying value was removed. No further values from the measurements at 200, 400 or 800 µmol photons $m^{-2}\,s^{-1}$ were removed.

Measurements from ten samples did not result in typical light response curves but were of a more arbitrary nature because the model in equation 2 did not result in realistic P_{max} and k values. The optimization of the parameters led to negative values for k (the half saturation constant, indicating when the photosynthetic rate is half of P_{max}) for these ten samples and they were consequently removed from further analysis. One other sample was also removed since the respiration value of this sample was erroneous due to a sudden large increase in CO_2 as explained above (see method section in the hydrology experiment).
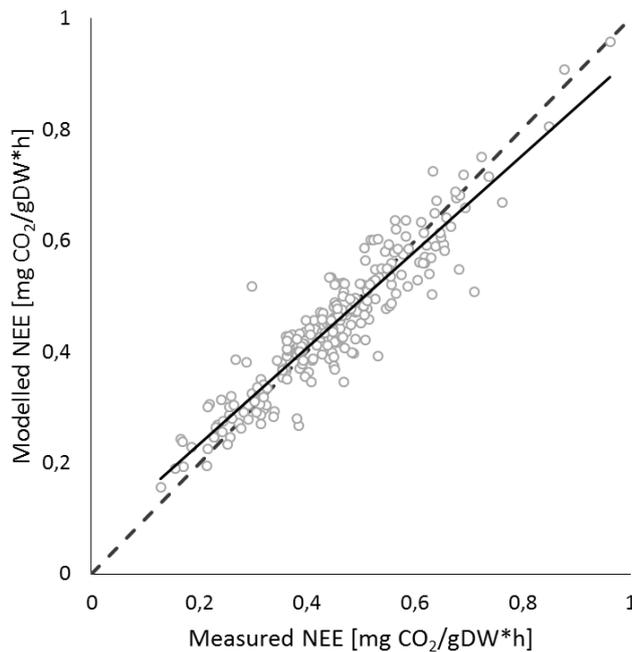

Figure 9. All modelled values are plotted against all measured values to show the average bias of the model. The dashed line is the one-to-one line and the solid line show the linear relationship between the measured and modelled values. Low values of NEE are slightly overestimated while high values are slightly underestimated by the model.

The modelled values of NEE were plotted against the measured values of NEE for each sample to determine how well the model predicted NEE. For all samples the NEE was slightly overestimated at low measured values and slightly underestimated at high values (data not shown). A general evaluation of all modelled values plotted against all measured values show the average bias of the models (Figure 9), which is similar to the bias for each respective sample, i.e. slightly overestimated at low measured values and slightly underestimated at high values. The RMSE for all samples ranged between 0.0011 and 0.12 mg CO_2 gDW^{-1} h^{-1} with an average RMSE at 0.042 mg CO_2 gDW^{-1} h^{-1}. The total variance for all models had an R^2 value of 0.87.

Statistical method

Full factorial three-way ANOVAs were performed in SPSS to compare the main effects: amount, frequency and type of precipitation as well as the interactive effects on the dependent variables P_{max}, k, E_0 and LCP respectively. As described above 11 samples were removed. This led to that all samples within one of the 18 treatment groups were removed and the performed ANOVAs were therefor not balanced. When the assumptions of an ANOVA was tested all parameter data sets showed some deviations from them. All data set were hence transformed by taking the logarithm of all values. The assumptions were then tested again and deemed sufficiently fulfilled. Post-hoc Tukey's HSD tests were performed to determine which groups that were significantly different from each other.

3.4 Desiccation experiment

Experimental design

Mixed species of bryophytes were collected, washed and put into containers in the same manner as described for the hydrology experiment. In the desiccation experiment, eight different treatments were used with four replicas of each treatment, leading to a total of 32 samples. Respiration and NEE were measured, as described for the hydrology experiment, for all the samples before the treatments started. The samples were then left to air dry until reaching atmospheric equilibrium after which respiration and NEE were again measured for all samples. During the drying out period the bryophytes were weighed roughly four times per day to determine when they were completely dry (Figure 10).
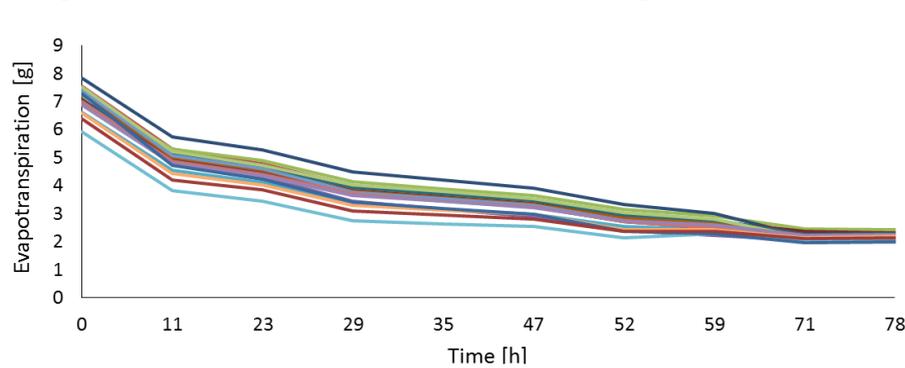
Figure 10. The desiccation rate were similar for all samples (indicated by one solid line per sample). It took between 70 and 80 hours for the samples to dry to atmospheric equilibrium.

The samples were then left dry for 0, 3, 6, 9, 12, 15, 18 and 21 consecutive days respectively after which they were measured a third time. Then they were rewetted over three days (within a 53 hour period), with a total of 50 ml water per day spread over five hours. The 53 hour recovery time is consistent with findings of Proctor et al. (2007b). Respiration and NEE were finally measured again (Figure 11; Appendix 4).
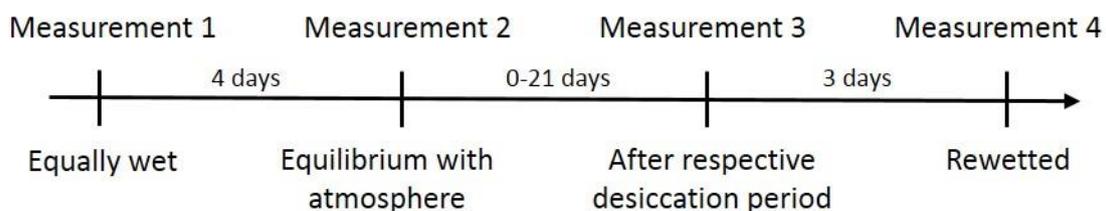
Figure 11. Time line of the four measurements on each sample indicated above the line (where respiration, NEE and GGP were measured each time) and the stage in the drying and rewetting process is indicated below the line.

Data analysis

The first four CO_2 values of each measurement were excluded to avoid variation due to initial pressure equalization. The rate of change in CO_2 concentration over time was calculated and outliers were identified by correlating the slopes with the R^2 values as described in section 3.2 under Data analysis.

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One respiration slope > 0.1 ppm sec^{-1} stood out with a low R^2 value. This was the result of a sudden large increase in CO_2 possibly due to a chamber leakage and/or erratic air mixing within the chamber so was consequently removed (Appendix 3). Two respiration rates turned out positive, however the values were extremely small (0.008 and 0.03 ppm sec^{-1}) and most likely were so low that they were on the edge of the EGM-4 measurement resolution (± 1 ppm). Both values were therefore considered erroneous and changed to zero, i.e. no respiration occurred. In total 128 measurements were made meaning only 2.3 % of them were removed or altered.

At the end of the eight week study the bryophyte samples were dried in an oven at 65°C for 60 hours and then weighed to quantify dry biomass.

The GPP was then calculated by adding the respiration to the NEE (Chapin et al. 2011). The variation in respiration, NEE and GPP between the eight desiccation lengths (in days) and over the four measurement times (before treatment (1), after drying (2), after completed treatment (3) and after re-wetting (4); Figure 11) was most prominent after re-wetting, while the three first measurements were relatively similar to each other. Hence only the last measurements after re-wetting (4), were further investigated (Appendix 5). The percentage recovery of respiration, NEE and GPP after desiccation was calculated by dividing the last measurement (4) with the first measurement (1; Figure 11) and then multiply by 100.

Statistical method

The responses of the absolute values and the percentage recovery of respiration, NEE and GPP to desiccation length were determined using linear regression. The assumptions behind a linear regression were tested as described above. There was a small tendency of unequal variance in the two NEE data sets however regression is quite robust against this and the assumptions were therefore deemed to be sufficiently fulfilled (Gotelli and Ellison 2013).

4. Results

4.1 Precipitation experiment

To account for pre-existing variation among samples, the change in respiration, NEE and GPP were calculated by taking the respective rates at the end of two months of the treatments minus the rates before the treatment. A positive change in respiration thus indicated a decrease in respiratory carbon loss from the bryophytes while a negative change indicated an increased respiratory loss over the treatment period (Figure 12). A positive change in NEE indicated a larger net uptake of carbon by the bryophytes while a negative change indicated a decrease in the net uptake over the treatment period. The same applied to GPP; a positive change in GPP meant a larger uptake of carbon while a negative change meant a lower uptake over the treatment period.

Table 5. Results from ANOVAs (F and P values) testing for the effects of precipitation type, amount and frequency on the change in respiration, NEE and GPP respectively over the treatment period. Significant results (p <0.05) are marked in bold.

	Respiration				NEE				GPP			
	df	*F* value	*P* value	R^2 *	df	*F* value	*P* value	R^2 *	df	*F* value	*P* value	R^2 *
Full Model	17	4.88	**< 0.001**	0.49	17	1.92	**0.036**	0.18	17	2.35	**0.009**	0.25
Type	1	40.2	**< 0.001**		1	0.95	0.334		1	10.0	**0.003**	
Amount	2	0.08	0.924		2	10.9	**< 0.001**		2	7.84	**0.001**	
Frequency	2	0.21	0.811		2	1.63	0.206		2	1.17	0.319	
Type*Amount	2	9.46	**< 0.001**		2	1.04	0.360		2	1.18	0.315	
Type*Freq.	2	0.20	0.820		2	0.07	0.934		2	0.05	0.954	
Amount*Freq.	4	1.36	0.261		4	0.16	0.956		4	0.46	0.765	
Type*Amount*Freq.	4	4.23	**0.005**		4	0.96	0.438		4	1.72	0.160	

* Showing the adjusted R^2

The overall model for the change in respiration was statistically significant (p < 0.05) and showed a three-way interaction between type, amount and frequency (Table 5). The interactive effect showed that mist consistently resulted in a significantly larger decrease in respiration loss compared to rain (Figure 12). It also showed that the decrease in respiratory loss was highest with low amount of mist and then decreased with increasing amount. Although, high amount of mist still resulted in decreased respiratory losses. In contrast, low amount of rain resulted in increased respiratory losses. With medium and high amounts of rain the respiratory losses changed only slightly, resulting in both small increases and decreases of respiratory losses. The treatment group receiving high amounts of rain at low frequencies however resulted in a decreased respiratory loss of similar size to those with high amounts of mist. The interaction with frequencies was more complex. The high frequency seemed to have the largest effect which together with low amounts resulted in a larger decrease in respiratory loss in samples watered with mist compared to a large increase in samples watered with rain.

The overall model for the change in NEE was statistically significant (p < 0.05) and showed one main effect - amount (Table 5). The high amounts resulted in a larger decrease in NEE over the treatment period compared to low and medium amounts irrespective of type or frequency,

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i.e. the net uptake of carbon was lower in samples watered with high precipitation amounts (Figure 12). However NEE was positive for all samples, meaning there was still a net carbon uptake by the bryophytes (Appendix 6).

The overall model for the change in GPP was statistically significant ($p < 0.05$) and showed two main effects – type and amount (Table 5). Mist resulted in a larger decrease in GPP compared to rain over the treatment period meaning the bryophyte uptake of carbon decreased more when watered with mist. The samples watered with high amount of both mist and rain also resulted in a larger decrease in GPP compared to low and medium amounts (Figure 12).
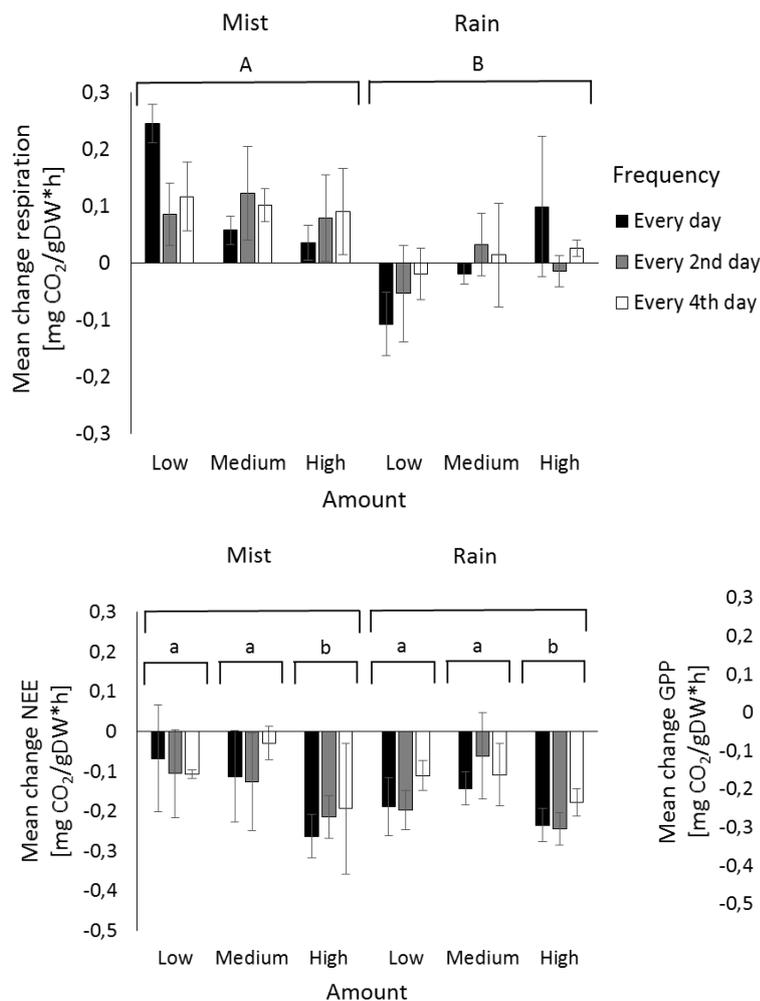

Figure 12. Upper case letters indicate significant differences between effects of varying precipitation types and lower case letters indicate significant differences between effects of varying precipitation amounts on the change in respiration, NEE and GPP following a three way ANOVA. No significant effects of precipitation frequencies were found. Error bars show one standard deviation.

4.2 Light experiment

From visually evaluating the average light response curves for the 18 treatments respectively, the general trend was that low amounts of precipitation (green lines) resulted in higher maximum photosynthesis (P_{max}) compared to medium (orange lines) and high (blue lines) amounts (Figure 13). Generally high frequency (darkest lines) showed a higher P_{max} while low frequency (lightest lines) showed a lower P_{max}.
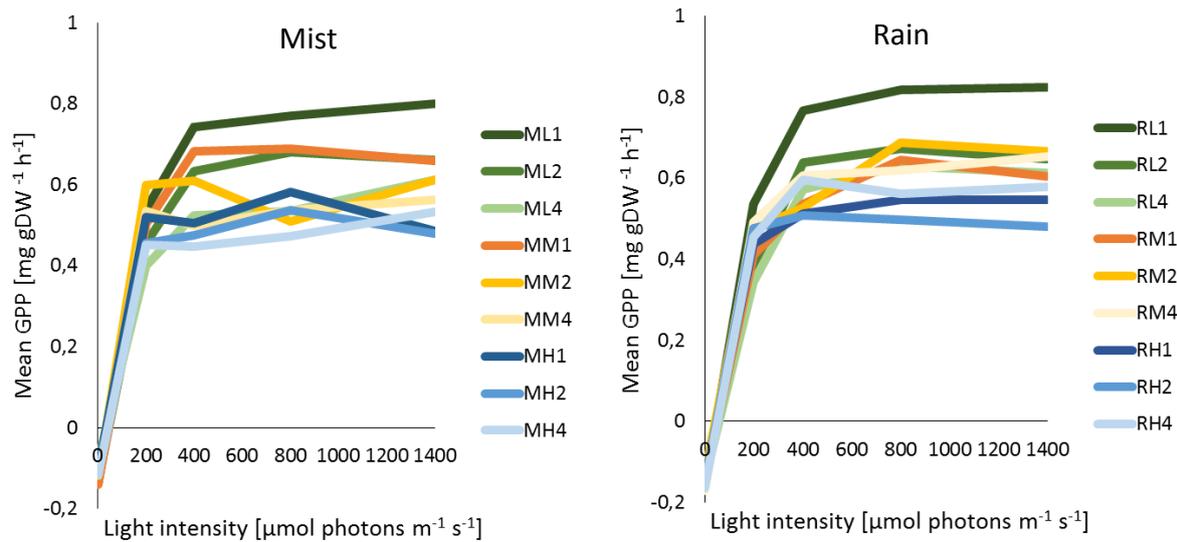

Figure 13. Average light response curves for the 18 treatments split into two graphs showing samples watered with mist to the left and the samples watered with rain to the right. Treatment keys in legend as explained in Table 4.

All four performed ANOVAs were overall significant (p < 0.05; Table 6). The two explanatory variables amount and frequency had significant effects on light saturated photosynthesis (P_{max}; Table 6) where P_{max} decreased with increasing precipitation amount however increased with increasing precipitation frequency (Figure 14). No effects from precipitation type nor any interactive effects between the three factors were found for P_{max}.

Table 6. Results from three-way ANOVAs (F and P values) testing for the effects of precipitation type, amount and frequency on P_{max}, k, E_0 and LCP respectively. Significant results (p <0.05) are marked in bold.

		P_{max}				k				E_0				LCP		
	df	F value	P value	R² *	df	F value	P value	R² *	df	F value	P value	R² *	df	F value	P value	R² *
Full Model	17	4.689	**< 0.001**	0.511	17	3.287	**0.001**	0.393	17	2.662	**0.005**	0.320	17	2.824	**0.003**	0.341
Type	1	2.715	0.107		1	2.746	0.105		1	2.017	0.163		1	11.905	**0.001**	
Amount	2	25.549	**< 0.001**		2	13.434	**< 0.001**		2	8.206	**0.001**		2	7.652	**0.001**	
Frequency	2	3.729	**0.032**		2	2.890	0.066		2	2.472	0.096		2	2.034	0.143	
Type*Amount	2	0.131	0.878		2	3.265	**0.048**		2	3.484	**0.040**		2	1.892	0.163	
Type*Freq.	2	1.101	0.342		2	0.271	0.764		2	0.193	0.825		2	0.878	0.423	
Amount*Freq.	4	1.843	0.138		4	1.141	0.350		4	1.689	0.170		4	1.227	0.314	
Type*Amount*Freq	4	0.720	0.583		4	2.977	**0.030**		4	3.063	**0.026**		4	2.164	0.089	

* Showing the adjusted R²

A significant three-way interactive effect between type, amount and frequency were found for the half-saturation constant (k; Table 6). Decreases in k were found with increasing amount and generally k was higher in samples watered with rain compared to with mist (Figure 14). The effect from frequency was more difficult to determine; low frequency had an increasing effect at low amounts of both mist and rain while medium frequency decreased k at medium amounts of mist and high amounts of rain.

The two explanatory variables amount and type were found to have significant effects on the light compensation point (LCP; Table 6) where LCP decreased significantly with increasing precipitation amount but was higher when watered with rain compared to with mist (Figure 14). No effect from precipitation frequency nor any interactive effects were found for LCP.

A significant three-way interactive effect between type, amount and frequency were found for the quantum efficiency (E_0; Table 6). An increase in E_0 was found with increasing precipitation amount (Figure 14). E_0 also increased with decreasing frequency in medium and high amounts of mist but only in high amounts of rain.
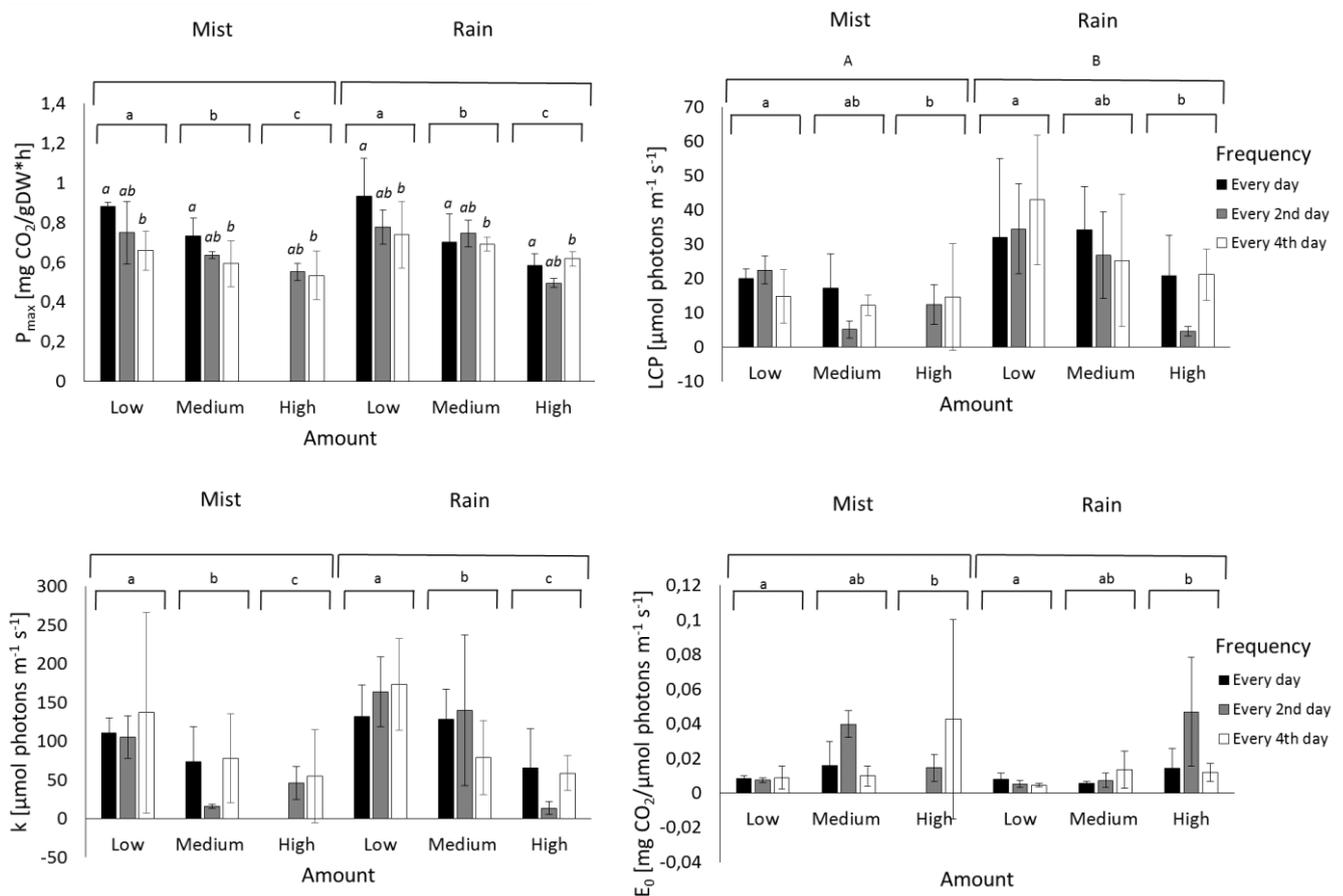
*Figure 14. Upper case letters indicate significant differences between the effects of varying precipitation types , lower case letters indicate significant effects of varying precipitation amounts and lower case italic letters show significant effects of varying precipitation frequencies on P_{max}, k, LCP and E_0 respectively following a three-way ANOVA. Error bars show one standard deviation.*

4.3 Desiccation experiment

Upon visual inspection the respiration after rewetting showed some weak trend towards being higher with a very short desiccation length (to atmospheric equilibrium and then immediately re-wetted again). Then respiration first seemed to decrease in samples desiccated for 3 and 6 days respectively after which it increased again to a steady level regardless of desiccation length. Although a non-linear regression could provide a better model to fit to this data a linear regression was still chosen to describe it since the exact functional relationship between desiccation length and respiration was not known. There was no significant ($p < 0.05$) linear relationship between respiration and desiccation length (Table 7; Figure 15).

NEE on the other hand showed a more distinct pattern connected to the increasing length of desiccation where it significantly ($p < 0.05$) decreased as the desiccation length increased (Figure 15). The model explained 72 % of the variation ($R^2 = 0.72$; Table 7). In a similar manner to NEE, GPP also decreased significantly ($p < 0.05$) as the desiccation length increased (Figure 15). The model explained 80 % of the variation ($R^2 = 0.80$; Table 7).

Table 7. Results from linear regression (F and P values) testing for relationship between respiration, NEE and GPP and treatments of varying desiccation length (1, 3, 6, 9, 12, 15, 18 and 21 days). Significant results (p <0.05) are marked in bold.

|	Respiration					NEE					GPP			
df	*F* value	*P* value	R	R²	df	*F* value	*P* value	R	R²	df	*F* value	*P* value	R	R²
1	0.054	0.82	0.042	0.002	1	76.3	**< 0.001**	0.85	0.72	1	117.6	**< 0.001**	0.89	0.80
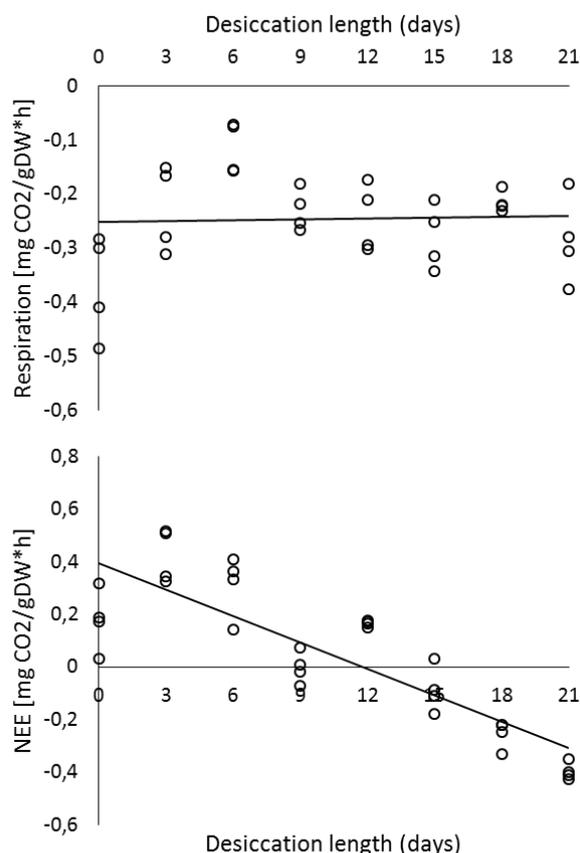
Figure 15. Responses of respiration, NEE and GPP respectively to desiccation length (1, 3, 6, 9, 12, 15, 18 and 21 days) in absolute values. The solid lines explains the relationships between respiration, NEE and GPP respectively to desiccation length.

Since the first measurements of respiration, NEE and GPP respectively were relatively similar to each other (Appendix 5), the percentage recovery of respiration, NEE and GPP compared to before treatment rates (Figure 16) showed a similar pattern as the absolute numbers (Figure 15).

The percentage recovery of NEE and GPP therefore also showed similar significant responses to desiccation length as the absolute values. The models explained 71 and 76 % respectively of the variation ($R^2 = 0.71$ and 0.76; Table 8). Similarly as for the absolute values, a linear regression for respiration was not significant ($p < 0.05$; Table 8).

Table 8. Results from a linear regression (F and P values) testing for the effects of desiccation length (1, 3, 6, 9, 12, 15, 18 and 21 days) on percentage recovery of respiration, NEE and GPP respectively after completed treatment. Significant results (p <0.05) are marked in bold.

|	Respiration					NEE					GPP			
df	*F* value	*P* value	R	R²	df	*F* value	*P* value	R	R²	df	*F* value	*P* value	R	R²
1	2.1	0.16	0.26	0.068	1	73.7	**< 0.001**	0.84	0.71	1	96.9	**< 0.001**	0.87	0.76
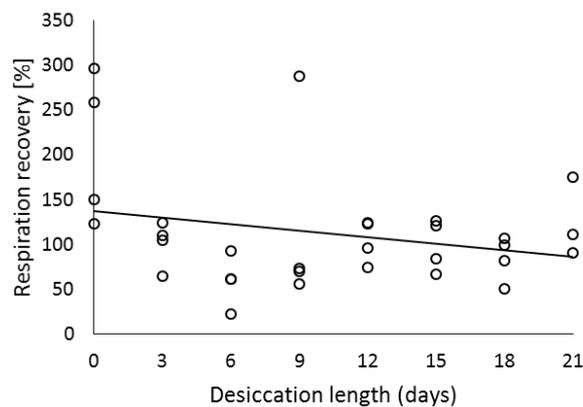
Figure 16. Responses of respiration, NEE and GPP respectively to desiccation length (1, 3, 6, 9, 12, 15, 18 and 21 days) in percentage recovery. The solid lines explains the relationships between percentage recovery of respiration, NEE and GPP respectively to desiccation length.
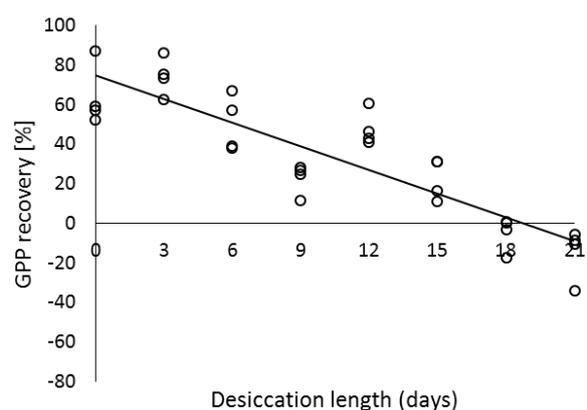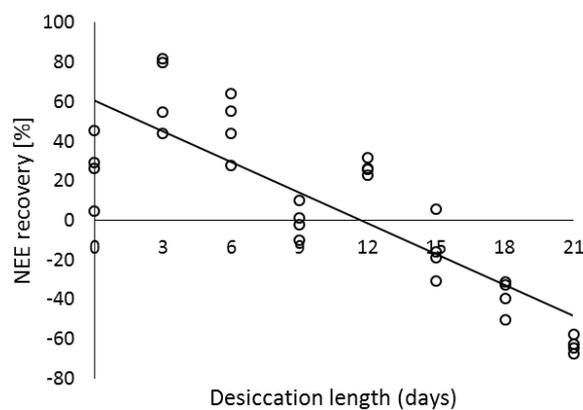
5. Discussion

Climate change is projected to have a large impact on the TMCF areas of the world (Still et al. 1999; Urrutia and Vuille 2009; Mulligan 2010; Oliveira et al. 2014). In the eastern Andes the temperatures are projected to increase with around 3.5 to 4.5° C at 3000 m.a.s.l by the year 2100. The precipitation patterns will also change however there is a larger uncertainty surrounding how and at what magnitude. The lapse rate is projected to decrease with 0.08°C 100 m^{-1} which could lead to an increased cloud base height (Urrutia and Vuille 2009; Still et al. 1999; Mulligan 2010). In addition decreases in the cloud cover have already been detected (Halladay et al. 2012b) On the basis of these projected climate changes which could lead to less frequent and lower amounts of cloud water input and also changes in rainfall in TMCF areas the effects of changing precipitation regimes on bryophyte carbon dynamics were studied.

5.1 Precipitation experiment

After the two month treatment period, the respiratory loss decreased most in samples watered with low amounts of mist. On the contrary the respiratory losses increased when watered with low amounts of rain. With medium and high amounts the changes in respiration were more similar between the precipitation types and showed decreased losses for both, however of a slightly greater extent for mist compared to rain. Since the photosynthetic capacity impacts the respiration rate (Chapin et al. 2011) these changes could possibly be explained by the changes in gross primary production i.e. lower respiration is expected with lower GPP and vice versa. In accordance the GPP rate in samples watered with low amounts of mist decreased more compared to in samples watered with low amounts of rain. This would suggest that the projected change from a high fraction of surrounding cloud cover to lower amounts of rain would actually have a more positive effect on bryophyte GPP.

Looking at the net ecosystem exchange the highest amount treatments generated the largest decreases in GPP and only showed slight decreases in respiratory loss meaning the NEE decreased most in high amount treatments. The increased respiratory loss in samples watered with low amount of rain was somewhat offset by a smaller decrease in GPP rate and the total effect on NEE was a slightly lower decrease compared to for the high amounts. This would suggest that higher amounts of precipitation, irrespective of type, results in the largest negative effect on bryophyte carbon uptake. Looking at the actual rates as well, the NEE resulted in a net carbon uptake by the bryophytes in all samples, but the GPP and NEE was higher in the low amount treatments compared to the high amount treatments irrespective of precipitation type (Appendix 6). So low amounts seem to be more beneficial to bryophyte GPP compared to high amounts. Also, although there was no significant effect from type on NEE the decrease in NEE was slightly lower for samples watered with low and medium amounts of mist compared to rain, contradicting with that rain should be beneficial for the total carbon balance of bryophytes.

One other thing to keep in mind is that the lower NEE with higher amounts could be an artefact of the poikilohydric strategy adopted by bryophytes; if the surface of the samples watered with the highest amount was still covered in a water film by the time of the measurements it could have prevented CO_2 uptake and photosynthesis to some extent (Tuba et al. 1996; Romero et al. 2006).

In any case it would seem that low amounts of precipitation in the form of mist is beneficial to bryophytes and this may very well be the case. The different effects from mist and rain (slightly lower decrease in carbon uptake with low amounts of mist compared to rain) is important to note and should be studied further as this is a major change the bryophytes stand to face with climate change. However it was very surprising to only find an interactive effect of frequency on respiration and not on NEE or GPP. Bryophytes are as discussed sensitive to too much water, but they are also sensitive to too little water (Proctor et al. 2007a). A climate which brings low amounts of precipitation but at a high frequency would therefore hypothetically be optimal. The change from mist to rain would therefore also seem to be less beneficial; the surrounding clouds would provide a much more frequent supply of low amounts of water compared to rainfall which would give larger amounts over a shorter time span and possibly with longer dry periods in between events. Since the TMCF areas are projected to experience longer periods with less frequent input from cloud mist and some like Monteverde and the eastern slope of the Andes already are experiencing it (Pounds et al. 1999; Halladay et al. 2012b), the effect of frequency on bryophyte carbon dynamics is an important aspect to study further.

The projected changes in precipitation patterns are generally more uncertain compared to the temperature changes (Urrutia and Vuille 2009; Mulligan 2010). How the diurnal precipitation patterns change will be of great importance for the bryophytes carbon dynamics. Cloud forest bryophyte species are today benefitted by the cold night temperatures and early morning precipitation which leads to low respiratory loss during night and optimal conditions for photosynthetic performance during daytime. If the timing of the precipitation will change to occur later in the day the bryophytes will be to wet to perform photosynthesis and the light intensity will also be lower during rainstorms possibly limiting photosynthesis (Tuba et al. 1996; Lange et al. 2004). Even if the timing of precipitation events does not change the bryophytes still risk lower carbon gain if temperatures increase because it could possibly lead to higher night time respiratory losses as well as quicker desiccation of the bryophytes during the day (Zotz et al. 1997; Wagner et al. 2014a).

In the TMCF areas where precipitation amounts will actually increase the bryophytes could still be put at a disadvantage. Oliveira et al. (2014) formed two critical questions to be answered for TMCF where precipitation and temperature will increase; will the increased amount of precipitation be enough to compensate for the increased temperatures and in that case will lowland species migrate upwards and compete with the specialised species over this changing habitat? Or will the increased precipitation be too low to sustain drought sensitive species with enough water to tolerate the increased temperature and subsequent increased evapotranspiration? The bryophytes are both drought sensitive and can be argued to be specialised to the wettest zones in TMCF since their abundance is by far largest in these areas (Benzing 1998; Foster 2001; Leon-Vargas 2006). So in any case it seems like bryophytes will not be favoured by changes in precipitation patterns. A transplant study by Jácome et al. (2011) also supports this hypothesis. They found that when moving whole branches covered in epiphytes from a cloud forest to lower elevation the most specialized species decreased and many disappeared while other more generalists survived changing the structure and function of the epiphytic cover. However, due to the survival of some species and to that other lower elevation species will likely move in, Jácome et al. (2011) hypothesized that the ecosystem function would not be lost however much of the high elevation biodiversity would be.

Jácome et al. (2011) monitored the changes in the transplanted bryophytes over two years and found that they were not abrupt but gradual in the communities over this time. The changes in bryophyte carbon uptake and respiration over the two month treatment time of this study could thus have been too short to show the full responses to the treatments. It would have been interesting to see if the samples would survive the observed lowered NEE or if they would eventually suffer such respiratory losses that they would die. Unfortunately it was not possible to measure the growth of the samples which could at least have indicated such net losses of biomass.

5.2 Light experiment

The light intensity above the canopy in the Kosñipata catchment varies between 500 and 1000 µmol photons m^{-2} s^{-1}, but below the tree canopy it is generally lower (Rapp and Silman 2012; van de Weg 2012). However the light intensity below a canopy also varies with how open or closed the canopy is (Denslow 1987). Vascular species in the tree canopies of cloud forests have been found to reach their saturated photosynthetic capacity at between 420 and 950 µmol photons m^{-2} s^{-1} while species lower down in the understory only needed an intensity of between 210 and 520 µmol photons m^{-2} s^{-1} to do so (Letts and Mulligan 2005).

In this study the bryophyte photosynthesis saturated quickly at a relatively low light intensity of 400 µmol photons m^{-2} s-1 in all samples regardless of the differing precipitation treatments, which is in accordance with León-Vargas et al. (2006). However the maximum photosynthesis (P_{max}) differed in response to precipitation amounts and frequencies. The samples receiving low amounts at high frequencies showed the highest P_{max} while high amounts at low frequencies resulted in the lowest P_{max} suggesting that the bryophytes are adapted to the climate they live in today.

Somewhat contradictory to the patterns of P_{max}, the half saturation constant (k) was lower, (meaning half of the light saturated photosynthetic rate was reached at lower light intensities) in samples treated with high amounts of precipitation compared to in samples treated with low amounts at low frequencies. But the interactive effect of precipitation amount and type also showed that k was lower with mist compared to rain over all amounts. Given the same quantum efficiency (E_0) the difference in k does not matter at low light intensities.

However the quantum efficiency decreased with low amounts of precipitation. In other words the carbon gain per unit light at low light levels was lower in samples watered with low amounts of precipitation. So at low light intensities the samples watered with low amounts were actually limited, and had a lower rate of carbon uptake compared to samples watered with high amounts. The interactive effect of precipitation amount and frequency also showed that the medium and low frequencies had an amplifying effect on the increase of E_0 for medium and high amounts of mist but only for high amounts of rain.

The increased light compensation point (LCP) with a decrease in precipitation amount also suggests a lower carbon gain at low light levels for samples watered with low amounts. The higher compensation point for rain compared to mist suggests mist improves the net carbon gain at lower light levels.

One explanation to the low photosynthetic rate at low light levels but higher light saturated photosynthesis in samples watered with low amounts, could be that these samples increased their photosynthetic capacity over the two month treatment period. Thereby they would reach a net carbon uptake later due to the high respiratory losses and also have a higher LCP (Reich et al. 1998; Chapin et al. 2011).

If disregarding the lower rates of carbon uptake at lower light intensities (200 µmol photons m^{-2} s^{-1}), together the changes in P_{max}, k, E_0 and LCP suggests that low amounts of mist at high frequencies are most beneficial for bryophyte carbon uptake in slightly higher light intensities (400 µmol photons m^{-2} s^{-1}). PAR measurements on a semi cloudy day showed the light intensity differed between 0 and 561 µmol photons m^{-2} s^{-1} at the collection site suggesting the bryophytes are benefitted by their environment today.

5.3 Desiccation experiment

The poikilohydric nature of bryophytes may seem like an advantage in the struggle to survive climate change. But for species adapted to very moist habitats it is likely not so.

The respiration showed an initial decreasing recovery from desiccation with increasing desiccation length. However for desiccation periods longer than 6 days the respiration then recovered to the same level in all samples irrespective of desiccation length. To be able to say anything more about this pattern the underlying mechanisms behind respiration recovery needs to be studied further. One possible explanation could be that the initial decrease in respiration is due to decreased GPP while the following increase in respiration could be due to an onset of decomposition in the samples which did not manage to recover well from desiccation. If this is in fact the underlying cause for the respiration pattern a logistic model could instead have been used to better describe this relationship with increasing desiccation length.

Clear negative trends in recovery of GPP as well as NEE with increasing desiccation length were found. This is in accordance with León-Vargas et al. (2006) who found that bryophytes in a Venezuelan cloud forest only survived a few days of desiccation before showing signs of damaged photosynthetic capacity. In contrast Hinshiri and Proctor (1971) and Proctor et al. (2007b) found that bryophyte photosynthesis recovered fully within 3 hours to 3 days after desiccation lengths up to 15 to 18 days. Not until after being desiccated for up to 40 to 45 days were the bryophytes so damaged that NEE never recovered to positive values i.e. they only suffered respiratory loss. However the higher tolerance towards longer desiccation periods found in Hinshiri and Proctor (1971) and Proctor et al. (2007b) could possibly be explained by the differing climate of the species habitats; a drier English woodland compared to a moist cloud forest (León-Vargas et al. 2006). Species which grow in a more shaded and wet habitat are more sensitive to desiccation and are damaged faster and to a higher degree compared to species which grow in a drier and more sun-exposed habitat (Proctor 2001). It thus seems like cloud forest species are not well equipped to survive the increasing desiccation periods which will follow with the projected less frequent cloud cover.

León-Vargas et al. (2006) approximated that the internal water storage of bryophytes can supply them for around 5 hours in a cloud forest while the same storage will only last for around one

hour in a drier and warmer environment since it will be evaporated faster in lower air humidity. The relative humidity of the air in which the bryophytes are desiccated is also important for their recovery. León-Vargas et al. (2006) found that cloud forest species generally recovered better from desiccation if they were kept dry in air at high relative humidity (74-85%) compared to low (20-43%). With the projected temperature increase in TMCF areas the air humidity will decrease and the water storage of cloud forest bryophytes will consequently last for a shorter time at the same time as the lower humidity can cause more severe damage to the bryophytes. The higher temperature may possibly also lead to a more rapid dehydration of the bryophytes. This could lead to less time for the bryophytes to adapt to the desiccated stage by performing necessary morphological changes of their cells also leading to larger damage from desiccation in the future (Mayaba et al. 2001; Proctor et al. 2007b).

In summary bryophytes in TMCF are desiccate tolerant to some degree and alleviated by internal water storage, however a lower air humidity and a more rapid desiccation rate influences this tolerance negatively. The projected climate change therefore suggests that bryophytes will be exposed to a more sever type of desiccation and in accordance with findings of this and other studies (León-Vargas et al. 2006) suffer from less complete or even no recovery of their photosynthetic capacity.

5.4 Statistical methods

Advantages and disadvantages of the three-way ANOVA

The main advantage of a three-way ANOVA is that besides the main effects from each treatment, the interactive effects between the treatments are also tested. Another advantage of using a three-way ANOVA instead of three separate one-way ANOVAs is that a three-way ANOVA is more efficient since less samples are needed to test multiple treatments on one set of samples instead of several sets. Therefore they could possibly also be more cost effective, depending on the sample and measurement costs. (Gotelli and Ellison 2013). However there are some disadvantages connected with multiway ANOVAs as well.

The p-value denotes the probability of finding large differences between groups if the null hypothesis was true. However using a threshold of 0.05 means that there is still a 5 % chance that the difference between groups could occur and that the null hypothesis is true, i.e. saying that there is a significant difference between groups when there is none or making what is called a Type I error. When accepting a null hypothesis that is not true, i.e. saying there is no difference between groups when there actually is, a Type II error is made. The Type I and II errors are inversely related to each other, when the risk of making one of them decreases the risk of making the other one usually increases instead (Gotelli and Ellison 2013; Smith et al. 2002).

When performing several ANOVAs the risk of these Type I and II errors increase. Using multiple predictor variables in an ANOVA and also testing for their interactive effects, increases the number of tests quickly and thereby also the risk of making errors. For a three-way ANOVA which has three treatments (A, B and C) with four possible interactions (AB, AC, BC, and ABC) this means seven F-tests are performed in total (Smith et al. 2002). Fletcher et al. found that 32 out 100 controlled three-way ANOVAs designed to have no main effects were still significant, i.e. the risk of making one or sometimes more Type I errors was 32%.

However a multiway ANOVA does have some protection against this. The overall F-ratio of the ANOVA is an average value of the individual F-ratios (between group variance divided by within group variance) between each compared group mean. Therefore if the overall F-ratio for the ANOVA is significant, all significant main and interactive effects cannot be Type I errors but some must be truly significant. On the other hand since there is a risk of making a Type I error in the overall F-ratio as well, the protection from these types of error is not complete. In accordance with this Fletcher et al. (1989) found that 6% of the overall F-ratios were significant using a p-value limit of 0.05 (so really only five out of a 100 samples should be significant). It should also be noted that when using real data sets the 0.05 limit does not always result in five Type I errors out of a 100 test, instead it should be considered to be the upper limit of errors that could be made and thus actually less than 1 out 20 tests could be a Type I error (Smith et al. 2002).

In accordance with this some of the significant results of this study could still be Type I errors. However only three-way ANOVAs which were overall significant was presented and thus there should only be a risk of a Type I mistake in 5 % or less of the cases. Still, significant main or interactive effects should be regarded with some care since several multiway ANOVAs was performed. Any Type II errors made in this study would not decrease the number of the presented significant results, only increase them.

Interactive effects

The main effect of different amounts or frequencies were not significant for respiration. Even so there was an interactive effect between type, amount and frequency. According to Oehlert (2000) and Gotelli and Ellison (2013) a multiway ANOVA can show significant interactive effects but without necessarily also resulting in significant main effects, simply because the differences between the levels in only one treatment could be too small on its own. For this reason it is often suggested that when significant interactive effects occur the significant main effects should not be considered. However if the main effects can explain some of the response they can still be considered (Oehlert 2000; Gotelli and Ellison 2013).

Effects of deviations from assumptions

Although the residual variance for NEE was slightly heterogeneous the assumptions of normality and equal variance were both sufficiently fulfilled for respiration, NEE and GPP (when NEE and GPP were transformed) in the precipitation experiment. The samples were also independent from each other in the respect of being initially equal and then randomly ascribed to a treatment. However they were not measured randomly but always in the same order; low amount samples with high to medium to low frequencies first, then medium amounts with high to medium to low frequencies and last large amounts with high to medium to low frequencies. This could have caused some measurement independence. The fulfilment of all three assumptions behind an ANOVA generally rarely apply to a collected data set. The models are also quite robust to slight deviations from the assumptions, more so when it comes to normality and equal variance but also for dependent samples when the dependency is random. However less so if the independence is not random (Oehlert 2000). But since the high amount

measurements were performed last, the effect of the measurement order would most likely be that the high amount treatments had more time to lose some of their water and therefore were more equal to the low and medium amount samples. Therefore this eventual measurement independence should not have any major impact on the results. One sample was removed from the respiration data set, and therefore also from the GPP data set, which led to that the ANOVAs testing these two responses were unbalanced (the sample size was not equal for all treatments). The effects of deviations from the ANOVA assumptions are generally more predictable when testing a balanced data set compared to an unbalanced data set. However in this case only one sample out of the 72 was removed and this should not complicate the outcome of the test (McGuiness 2002).

The problem with an unbalanced data set was slightly larger in the light experiment since the removal of 11 values resulted in that one whole treatment group was removed. Consequently although all data sets were transformed the deviations from the assumptions of an ANOVA were larger in this experiment compared to in the hydrology experiment. The variable P_{max} showed some deviation from normality while the other three were normally distributed. However P_{max} was the only variable which showed equal variance while the variance for k, LCP and E_0 was not fully equal. The results from the ANOVA should therefore be interpreted with caution. However there should be no such limitations of the actual measurements of respiration and NEE and the light response curves of the different treatment groups were therefore likely not implicated in any way.

Regression is based on the F-ratio (between group variance should be larger than within group variance) and for this the same assumptions apply as for ANOVAs (Gotelli and Ellison 2013). In the desiccation experiments the assumptions were not completely fulfilled since NEE showed some small deviation from the assumption of equal variance despite data transformations performed, however regression as well as ANOVA is quite robust against these deviations. The results should therefore be valid.

Improvements of experiment set up

One way to reduce the risk of making statistical errors and aid interpretation of results is of course to set up experiments in a way that enables the use of simpler statistical methods. However the world is not simple, but much more complex than what we want to make it. Since interactive effects do occur in nature more complex studies are needed to investigate them. Other improvements of this study could therefore instead have been to test more samples per treatment group and also perhaps over a longer time to see if the bryophytes would eventually suffer greater respiratory losses than what they could cover by photosynthesis. To reduce potential measurement dependency the samples could also have been measured randomly.

6. Conclusion

The precipitation experiment showed that amount had the clearest effect on bryophyte carbon dynamics. The highest amount treatments generated the largest decreases in GPP and only showed slight decreases in respiratory loss, meaning the NEE decreased most in high amount treatments. A slightly lower decrease in NEE was found with low amounts of mist compared to low amounts of rain, although the difference between the types was not significant. Furthermore, an effect from frequency was found on respiration where the effect differed most between amounts and types for the high frequency treatments while the difference was smaller for medium and low frequencies. However no interactions with frequency were found for NEE or gross primary production (GPP). It would thus seem that low amounts of precipitation probably in the form of mist, which is what they are adapted to today, is more beneficial to bryophytes. In the light experiment, bryophytes generally reached a saturated photosynthesis at relatively low light levels (400 μmol photons m^{-2} s^{-1}). At these light intensities or higher, the samples watered with low amounts of mist at high frequencies showed the highest maximum photosynthetic rate (P$_{max}$) while the samples watered with high amounts of mist at low frequency gave the lowest P$_{max}$. The light experiment thereby also pointed to that low amount, high frequency mist was generally more beneficial for carbon uptake. However at lower light intensities (200 μmol photons m^{-2} s^{-1}) the carbon gain for the samples of low amount treatments was lower compared to samples of high amount treatments. In the desiccation experiment, the trend of the respiratory response to increasing desiccation length was not possible to determine. However, there was a clear decreasing trend in GPP and NEE with increasing desiccation length. Thus, with increasing drought the accumulation of carbon by bryophytes is consequently at risk of being reduced.

In summary, bryophytes in TMCF seem to be well adapted to the environment they live in today with frequent input of low amounts of mist. The results therefore suggests that bryophyte carbon dynamics will be influenced negatively with projected changes in precipitation regimes, meaning their carbon accumulation will be lower compared to today. Since bryophytes provide a number of important ecosystem services a negative change in their carbon dynamics could result in both biodiversity loss and changes of the carbon dynamics and the hydrologic cycle of the TMCF as well. This in turn could have large scale effects on both downslope ecosystems and the people living there, as well as a global impact on biodiversity.

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Appendix 1

Table A-1. List of species included in this study

Division	Family	Species
Marchantiophyta	Plagiochilaceae	Plagiochila sp.
Marchantiophyta	Plagiochilaceae	Plagiochila sp.
Marchantiophyta	Lepicoleaeae	Lepicolea pruinosa
Marchantiophyta	Lepidoziaceae	Bazzania sp.
Bryophyta	Prionodontaceae	Prionodon densus
Marchantiophyta	Trichocoleaceae	Trichocolea pruinosa
Marchantiophyta	Radulaceae	Radula sp.
Bryophyta	Neckeraceae	Porotrichum mutabile
Bryophyta	Thuidiaceae	Thuidium peruvianum
Marchantiophyta	Plagiochilaceae	Plagiochila sp.
Bryophyta	Prionodontaceae	Prionodon densus
Bryophyta	Pterobryaceae	Pireella sp.
Marchantiophyta	Herbertaceae	Herbertus juniperoideus
Bryophyta	Meteoriaceae	Meteoridium remotifolium
Marchantiophyta	Porellaceae	Porella leiboldii
Marchantiophyta	Lepidoziaceae	Lepidozia cf. caespitosa

Appendix 2

Table A-2 Schedule for treatment and measurements in hydrology experiment

| Frequency (days)	1			2			4			
Amount	Low amount (ml)			Medium amount (ml)			High amount (ml)			Measurement
Day 0: Samples collected	Equally wet			Equally wet			Equally wet			
Day 1	Equally wet			Equally wet			Equally wet			Resp + NEE
Day 2	14	27	50							
Day 3	14	27	50	28	54	100				
Day 4	14	27	50							
Day 5	14	27	50	28	54	100	56	108	200	
Day 6	14	27	50							
Day 7	14	27	50	28	54	100				
Day 8	14	27	50							
Day 9	14	27	50	28	54	100	56	108	200	Resp + NEE
Day 10	14	27	50							
Day 11	14	27	50	28	54	100				
Day 12	14	27	50							
Day 13	14	27	50	28	54	100	56	108	200	
Day 14	14	27	50							
Day 15	14	27	50	28	54	100				
Day 16	14	27	50							
Day 17	14	27	50	28	54	100	56	108	200	Resp + NEE
Day 18	14	27	50							
Day 19	14	27	50	28	54	100				
Day 20	14	27	50							
Day 21	14	27	50	28	54	100	56	108	200	
Day 22	14	27	50							
Day 23	14	27	50	28	54	100				
Day 24	14	27	50							
Day 25	14	27	50	28	54	100	56	108	200	Resp + NEE
Day 26	14	27	50							
Day 27	14	27	50	28	54	100				
Day 28	14	27	50							
Day 29	14	27	50	28	54	100	56	108	200	
Day 30	14	27	50							
Day 31	14	27	50	28	54	100				
Day 32	14	27	50							
Day 33	14	27	50	28	54	100	56	108	200	Resp + NEE
Day 34	14	27	50							
Day 35	14	27	50	28	54	100				
Day 36	14	27	50							
Day 37	14	27	50	28	54	100	56	108	200	
Day 38	14	27	50							
Day 39	14	27	50	28	54	100				
Day 40	14	27	50							
Day 41	14	27	50	28	54	100	56	108	200	Resp + NEE
Day 42	14	27	50							
Day 43	14	27	50	28	54	100				
Day 44	14	27	50							
Day 45	14	27	50	28	54	100	56	108	200	
Day 46	14	27	50							
Day 47	14	27	50	28	54	100				
Day 48	14	27	50							
Day 49	14	27	50	28	54	100	56	108	200	Resp + NEE

Appendix 3
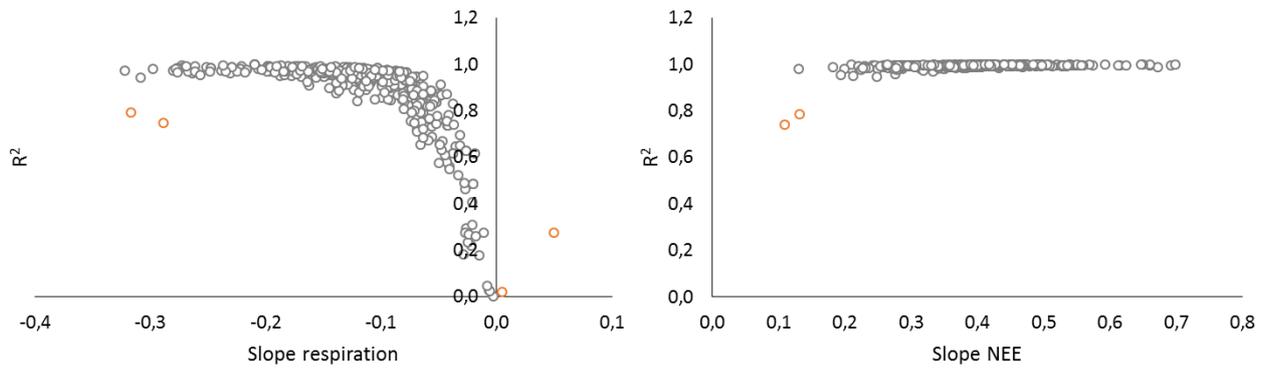
Figure A-1. Linear trend line slopes of changes in CO_2 concentration over time plotted against R^2 values of fitted trend lines for respiration and NEE from the hydrologic experiment. Orange circles mark values that were changed or removed.
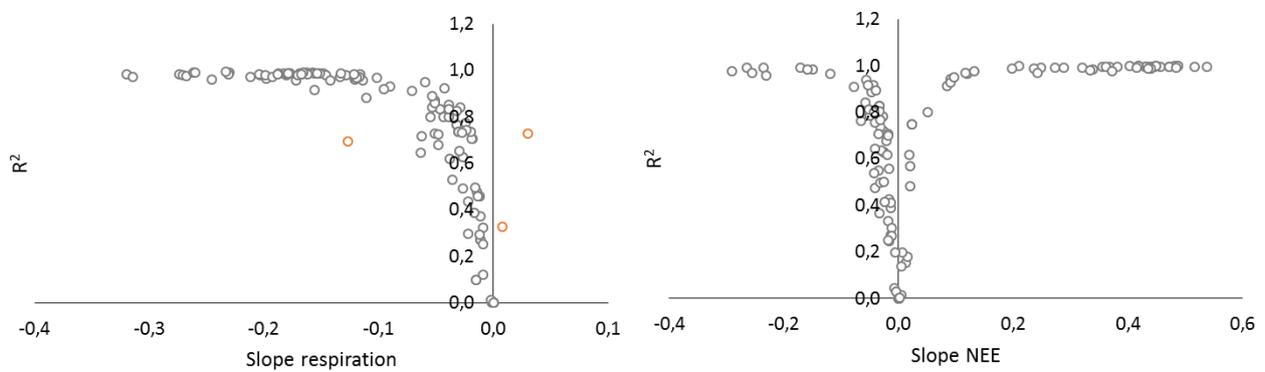

Figure A-2. Linear trend line slopes of changes in CO_2 concentration over time plotted against R^2 values of fitted trend lines for respiration and NEE from the desiccation experiment. Orange circles mark values that were changed.

Appendix 4

Table A-3 Schedule for treatment and measurements in desiccation experiment

|	Days samples were kept completely dry							
	1	3	6	9	12	15	18	21
	add water + measure	add water + measure	add water + measure	add water + measure	add water + measure	add water + measure	add water + measure	add water + measure
Day 0	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry
Day 1	measure	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry	weigh + wait for dry
Day 2	add water (50ml)							
Day 3	add water (50 ml)	measure						
Day 4	add water + measure	add water (50ml)						
Day 5	weigh + wait for dry	add water (50 ml)						
Day 6	weigh + wait for dry	add water + measure	measure					
Day 7	measure	weigh + wait for dry	add water (50ml)					
Day 8		weigh + wait for dry	add water (50 ml)					
Day 9		measure	add water + measure	measure				
Day 10			weigh + wait for dry	add water (50 ml)				
Day 11			weigh + wait for dry	add water (50 ml)				
Day 12			measure	add water + measure	measure			
Day 13				weigh + wait for dry	add water (50ml)			
Day 14				weigh + wait for dry	add water (50 ml)			
Day 15				measure	add water + measure	measure		
Day 16					weigh + wait for dry	add water (50 ml)		
Day 17					weigh + wait for dry	add water (50 ml)		
Day 18					measure	add water + measure	measure	
Day 19						weigh + wait for dry	add water (50 ml)	
Day 20						weigh + wait for dry	add water (50 ml)	
Day 21						measure	add water + measure	measure
Day 22							weigh + wait for dry	add water (50 ml)
Day 23							weigh + wait for dry	add water (50 ml)
Day 24							measure	add water + measure

Appendix 5

Figure A-3. Mean values of respiration, NEE and GPP for each of the eight desiccation treatments shown over the four measurement times (before treatment (1); after drying (2); after completed treatment (3); and after re-wetting (4); Figure x) was most prominent after re-wetting, while the three first measurements were relatively similar to each other. Hence only the last measurements after re-wetting (4), were further investigated

Table A-4. Results from ANOVAs (F and P values) testing for the effects of precipitation type, amount and frequency on the absolute values of respiration, NEE and GPP respectively. Significant results (p <0.05) are marked in bold.
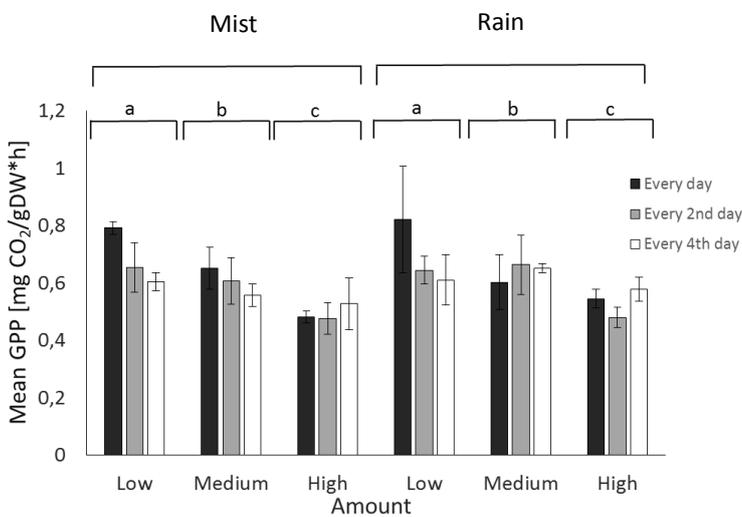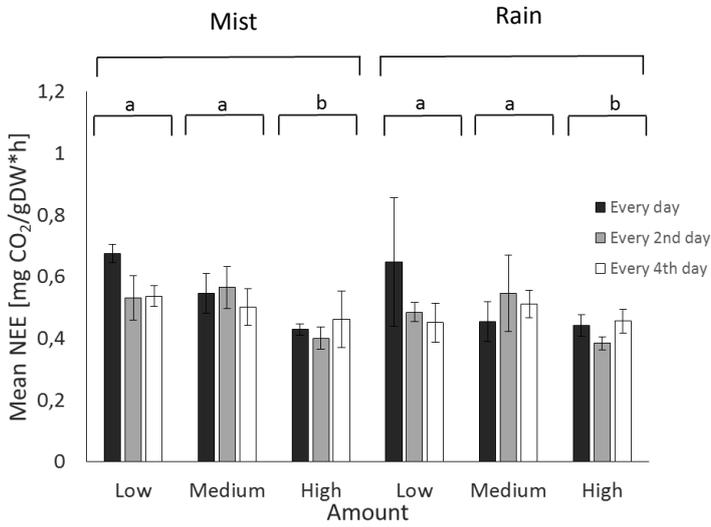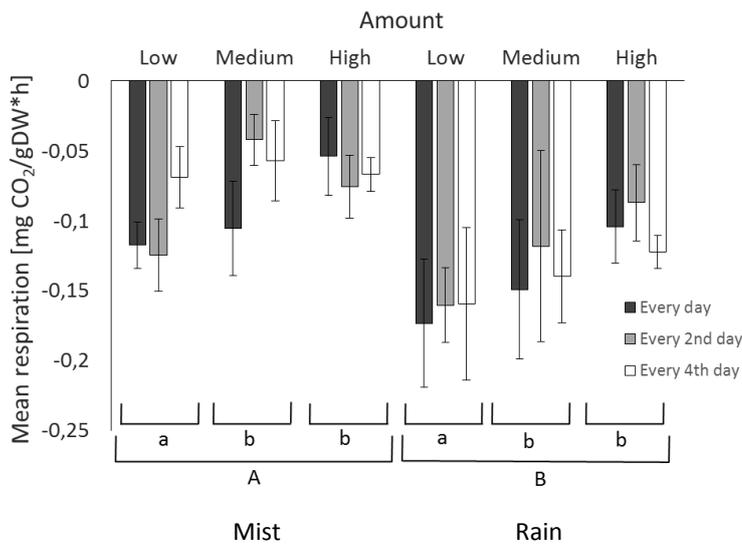
	Respiration				NEE				GPP			
	df	F value	P value	R²*	df	F value	P value	R²*	df	F value	P value	R²*
Full Model	17	4.166	**< 0.001**	0.435	17	3.262	**< 0.001**	0.351	17	4.916	**< 0.001**	0.487
Type	1	35.377	**< 0.001**		1	2.895	0.095		1	1.939	0.170	
Amount	2	9.377	**< 0.001**		2	14.763	**< 0.001**		2	26.926	**< 0.001**	
Frequency	2	1.209	0.306		2	1.821	0.172		2	3.265	**0.046**	
Type*Amount	2	0.830	0.442		2	0.791	0.458		2	0.520	0.598	
Type*Freq.	2	1.262	0.292		2	0.066	0.936		2	0.446	0.642	
Amount*Freq.	4	1.784	0.146		4	3.858	**0.008**		4	4.196	**0.005**	
Type*Amount*Freq.	4	0.497	0.738		4	0.559	0.693		4	0.818	0.519	

* Showing the adjusted R²

Figure A-4. Upper case letters indicate significant differences between the effects of varying precipitation types and lower case letters indicate significant differences between effects of varying precipitation amounts on the absolute values of respiration, NEE GPP following a three way ANOVA. Error bars show one standard deviation.

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