



DEPARTMENT OF BIOLOGICAL AND
ENVIRONMENTAL SCIENCES

AN INVESTIGATION ON LEAF WATER ECONOMY TRAITS IN TREES WITH VARYING CLOUD IMMERSION IN THE WAYQECHA ANDES REGION



Panagiotis Boukouvalas

Degree project for Master of Science (120 hec) with a major in Biology

BIO797, Degree Project in Conservation Biology (60 hec)

Second cycle

Semester/year: Autumn 2025- Spring 2026

Supervisor: Johan Uddling, Department of Biological and Environmental Sciences

Hampus Holmberg, Department of Biological and Environmental Sciences

Examiner: Daniel Zuleta, Department of Biological and Environmental Sciences

Table of contents

Abstract	3
1. Introduction	5
1.1 Tropical montane cloud forests	5
1.2 Leaf water economy traits	6
1.2.1 Foliar water uptake (FWU).....	6
1.2.2 Leaf water retention	6
1.2.3 Minimum stomatal conductance (g_{min})	6
1.3 Main threats	7
2. Aims	8
3. Materials and methods	8
3.1 Sampling sites.....	8
3.2 Study species	10
3.3 Foliar water uptake (FWU)	12
3.4 Leaf water retention angle	13
3.5 Minimum stomatal conductance g_{min}	13
3.6 Community composition	13
3.7 Statistical analysis	13
4. Results	14
4.1 Foliar water uptake (FWU)	14
4.1.1 Cloud gradient.....	14
4.1.2 Cloud curtain plots.....	15
4.2 Leaf water retention angle	16
4.2.1 Cloud gradient.....	16
4.2.2 Cloud curtain plots.....	18
4.3 Minimum stomatal conductance (g_{min}).....	18
4.3.1 Cloud gradient.....	18
4.3.2 Cloud curtain plots.....	20
4.4 Community composition	20
5. Discussion	22
5.1 Species acclimation and adaptation capacity	22
5.2 Community composition	23
6. Conclusion	24
7. Acknowledgements	24
8. References	25

Appendix 1 30

Appendix 2 32

Abstract

Tropical cloud forests (TCFs) are characterized by high levels of humidity due to the frequent presence of clouds, creating a unique ecosystem type. With the imminent threats of climate change, land-use change and deforestation, understanding how cloud immersion affects plants' water economy is imperative for conservation. In this study, we investigate three key leaf water economy traits exhibited by 26 tropical tree species, foliar water uptake (FWU), minimum conductance ($g_{\min}$) and leaf water retention angle, along a natural cloud gradient in the Wayqecha Andes region in Peru. Two other plots established by the Wayqecha Amazon Cloud Curtain Ecosystem Experiment (WACCCE) were used, where an artificial barrier reduces the fog levels received by the treatment plot in comparison to the control. For FWU measurements, all samples were subjected to standardized wetting treatment, where leaves were submerged for two hours under controlled conditions. Leaf water retention angle was measured by recording the angle at which water moves when the leaf is tilted. For $g_{\min}$ determination, leaves were dried for four hours while mass loss, relative humidity and temperature were recorded regularly. The results showed significant large species differences for the three traits, with mean values between species exhibiting a 15-fold difference for FWU, a twofold difference in leaf water retention angle and a nine-fold difference for $g_{\min}$. There was no significant within species difference in trait values of trees growing in the different cloud regimes or under the experimental cloud removal plot. Community-weighted trait averages of FWU and $g_{\min}$ did not differ between High, Medium and Low cloud level plots in the cloud gradient. However, leaf water retention angle was higher in Low cloud level plots, suggesting an improved capture and use of intercepted water under potentially more water-limited conditions. This study indicates that FWU and $g_{\min}$ might not be the most important traits in shaping tree community composition under varying cloudiness levels, but that leaf surface characteristics influencing the retention of intercepted fog water may play a role.

1. Introduction

The planet's rising temperature as a result of the ongoing climate crisis affects myriads of ecosystems across the globe. Tropical forests pose no exception, as changes in precipitation patterns along with increasing warming levels lead to extended drought periods (Intergovernmental Panel on Climate Change (IPCC) 2023) and as a result, the risk of ecosystem degradation increases significantly (Calvin et al. 2023). More specifically, tropical montane cloud forests (TMCFs) which are characterized by their high humidity deriving from clouds or mist due to their presence inside the cloud condensation layer (Karger et al. 2021), face direct threats caused by the lifting of the cloud bank and reductions in cloud persistence due to rising land temperatures. Moreover, upwind forest degradation and deforestation may reduce cloud immersion in these forests altogether. A decline in cloud immersion is linked to altered hydrological cycles along with species decline and, possibly, extinction in TMCFs (Nadkarni and Solano 2002).

1.1 Tropical montane cloud forests

Tropical montane cloud forests (TMCFs) are unique ecosystems, formed by their special microclimatic conditions, derived from the perpetual cloud (alternatively referred to as fog) immersion and them being located at least 500 meters above sea level, where the low clouds in which the vegetation canopy is immersed provide a large portion of total precipitation, also called occult precipitation (Los et al. 2021). The term is generally used to differentiate this particular type of forest from other cloud forest variants to account for the hydrological and ecological functional differences that occur as the climatic conditions become cooler and wetter, through the transition from the lower montane to the sub-alpine belts and upper montane belts (Bruijnzeel, Mulligan, and Scatena 2011). They occupy approximately 0.4% of the planet's surface, but account for 16% and 20% of Earth's vertebrae and plant diversity respectively (Ray et al. 2006). Trees in TMCFs having shorter heights and denser stems, as well as a more stunted or gnarled appearance in forests located in higher elevations (Los et al. 2021), higher root to shoot ratios, low above-ground production and leaf nutrient concentrations, as well as the characteristically lush epiphytic growths (Fahey, Sherman, and Tanner 2016).

Water plays a vital role in TCFs, as cloud immersion affects every aspect of the forest, promoting speciation and endemism, hosting species that would otherwise be outcompeted and hence are sensitive to climatic changes (Foster 2001a). TMCFs provide a variety of ecosystems services, acting as biodiversity hotspots, carbon sinks and regulators of freshwater supplies moving downstream in drier areas (Bartholomew et al. 2026). It is precisely their uniqueness that makes these ecosystems vulnerable to anthropogenic threats and the effects of global warming, as will be discussed at a later section.

The exact effects of fog/cloud immersion on tree species leaf water economy have been studied little, leaving gaps in our understanding. Recent evidence from a novel experimental field study, the Wayqecha Amazon Cloud Curtain Ecosystem Experiment (WACCCE) where wide mesh curtains were employed in order to intercept fog droplets and lower fogginess downwind, has shown marked decrease in leaf wetness, slight decrease in vapor pressure deficit (VPD), and a slight increase in above canopy air temperature (Metcalf et al. 2025). It was also found that trees in the cloud curtain plot had leaves and branches with lower content of non-structural carbohydrates compared to trees in the control plot (personal communication with Daniel Metcalfe). How variations in fogginess exert selection pressures on leaf water economy traits or directly affect these traits through acclimation is largely unknown and need to be explored deeper to understand how

changes in cloud immersion shape tree water economy and tree community composition in TMCFs. This will in turn improve projections of TMCFs in a changing climate.

1.2 Leaf water economy traits

Water plays an essential role in the survival and proliferation of tree species, hence the importance of studying traits related to its regulation. Especially in the context of TMCFs, the additional moisture coming from the frequent cloud immersion, allows plant species to take advantage of certain physiological traits to a higher degree compared to other systems. For the purpose of this study, three key leaf water economy traits were chosen: foliar water uptake, leaf water retention and minimum conductance.

1.2.1 Foliar water uptake (FWU)

The process of foliar water uptake (FWU) describes the uptake of water that is intercepted by the leaf surface and absorbed through them, into the water potential gradient that exists between liquid water outside the leaf and the leaf interior. It has been shown to improve plant water status and reduce water deficit (Goldsmith, Matzke, and Dawson 2013a) and the level of dependence on this process differs among species. Experiments on *Drimys brasiliensis*, a species commonly found in TMCFs, have shown that 42% of total foliar water content came from direct water diffusion from fog inputs (Eller, Lima, and Oliveira 2013). Similarly, it has been shown that species that exhibit a higher capacity for FWU risk the loss of leaf turgor under lack of cloud immersion during drought periods, since leaf wetting events are more scarce and hence FWU is being limited (Eller, Lima, and Oliveira 2016a). Nevertheless, it is evident that FWU is useful for trees as it combats the effects of drought and improves carbon balance (Chin et al. 2023).

1.2.2 Leaf water retention

Leaves have a certain capacity at retaining water on them, which is connected to various morphological traits, such as leaf wettability, trichome morphology and distribution, stomatal size, etc. (Wang et al. 2023). The amount of water leaves can retain is especially important when taking into consideration processes like FWU, allowing water to be absorbed into the leaves more easily. Evapotranspiration demands are also more easily met, with external leaf surface water evaporating first, before transpiration takes place (Cao et al. 2026). Species studied in TMCFs have been found to exhibit low leaf water repellency – the capacity of leaves to repel water from their surface – observations consistent with other tropical forests with high precipitation rates (Goldsmith et al. 2017). Along with a leaf's water repellency, the other important factor that dictates how easily water is shed from the leaf is the inclination of the leaf surface. Both of these parameters are captured but the concept of drop retention angle, which is the angle at which a drop of water starts to roll off a surface when the surface is gradually tilted (Lenz, Bauer, and Ruxton 2022).

1.2.3 Minimum stomatal conductance (g_{min})

One of the key traits in determining a tree species capacity to withstand drought stress is minimum stomatal conductance (g_{min}), which describes the loss of water through closed or leaky stomata and cuticle of the leaf (Duursma et al. 2019a). Temperature is the key driving factor determining the water loss pathways between closed stomata transpiration and cuticular transpiration (Garen and Michaletz 2025) and despite the relative shortage of studies in TMCFs, in other tropical tree

species, $g_{\min}$ has been found to be an important factor determining the time required for them to reach critical desiccation thresholds and species with lower $g_{\min}$ values were able to maintain turgor and structural integrity during prolonged dehydration (Sunny et al. 2026). The measure of $g_{\min}$ could be a factor of importance for TMCF species during the dry periods, especially in low cloud immersion conditions.

1.3 Main threats

Climate change is one of the main drivers of negative change in TMCFs. Rainfall and temperature changes are expected to shift climatic optimum altitudes for mountain ecotones by hundreds of meters by the time CO_2 levels have doubled (Foster 2001b). Presence of significant warming in TMCFs was documented across the globe (Los et al. 2021), and although a certain buffering capacity of these forests has also been found, prolonged droughts crucially affect humidity levels (Newell, Ausprey, and Robinson 2022). Thus, their highly specialized plant communities are particularly vulnerable, due to their small hydraulic safety margins (Oliveira et al. 2014). The ‘lifting cloud base hypothesis’ is another primary result of the changing climate, as projected by a multitude of numerical model analyses, and entails the increase of the base height of the stratocumulus level within which the cloud forests grow, as a result of the increase in surface temperature as a result of global warming (Guerra et al. 2025). With the above considered, it is no surprise that the majority of TMCF ecosystems in Neotropical ecoregions are expected to experience pronounced cloud immersion declines and increased drought levels in the future (Helmer et al. 2019a).

Human encroachment is the other key issue faced by TMCFs. Land-use change, usually defined as the transformation of cloud forest landscape to agricultural land and pastureland, or its destruction through fires and logging, have adverse effects on TMCFs’ natural processes and plant communities, with a loss in forest cover estimated to be 55-60% (Los et al. 2021). Studies have shown altered hydrological cycles that result in higher annual streamflow in TMCF converted pasturelands, due to lower rainfall interception (Muñoz-Villers and McDonnell 2013), with soil degradation in intensely managed pasturelands resulting in reduced water infiltration capacity (López-Ramírez et al. 2020). Besides that, model estimations suggest that deforestation in lowland tropical forests reduces evapotranspiration, resulting in lower moisture content in the air mass that flows towards the adjacent mountains. In turn, this causes a lift in the condensation level and thus the cloud formation zone (Lawton et al. 2001), further exacerbating the pressure of climate change on these ecosystems.

A direct result of the effects of both land-use change and climate change is the reduction in biodiversity for these fragile forest ecosystems. Evidence shows a reduction in taxonomic, ecological and functional diversity in degraded land compared to preserved forest areas (Castillo-Campos et al. 2024). Mesoamerican cloud forests exhibit a mean upslope shift of 1.8-2.7 meters annually in a long-term study of a multitude of plant species across different taxa since 1979, driven by the less thermophilic species (Ramírez-Barahona et al. 2025), indicating not only their vulnerability, but also the general need for further research and monitoring of these systems’ capacity for acclimation.

2. Aims

My primary aim is to evaluate whether the benefits of cloud immersion on many cloud forest tree species according to previous studies derive from traits controlling leaf water economy. The main questions I am looking to answer are the following:

- How do trees of a given species differ in their leaf water economy traits (leaf water uptake, leaf minimum conductance to water loss and leaf water retention) when growing in locations with more versus less cloud immersion? Is there any capacity for acclimation and/or local adaptation (ecotypes) for species growing in a natural cloud gradient? We expect leaf water uptake to show increased levels in higher fog immersion, as previous findings indicate a connection between high cloud immersion frequency and foliar water uptake (Goldsmith, Matzke, and Dawson 2013b). Considering the above, we expect differences between species in various cloud immersion conditions.
- Are the trees able to acclimate these traits to differences in cloud immersion? Plant species in TCFs have exhibited a certain degree of reliance on foliar water uptake during dry periods in order to maintain their leaf turgor, thus less leaf-wetting events – as a result of less cloud immersion – could have adverse effects on these species (Eller, Lima, and Oliveira 2016b). We anticipate that some form of acclimation could be possible in conditions with substantial experimental cloud level reduction.
- To what extent do these traits shape the species composition of tree communities, manifested through significant differences in community-weighted trait mean values along the natural cloud gradient? According to previous studies, differences in species functional traits in tropical montane cloud forests compared to other lowland tropical forests, are conceptually linked to their unique hydroclimatic conditions, and thus shaping distinct communities (Eller et al. 2020a). We anticipate a similar trend with community compositions along the natural cloud gradient.

3. Materials and methods

3.1 Sampling sites

Data collection was conducted in the Kosñipata Valley Andes region in the department of Cusco, in southeastern Peru. Using atmospheric models to determine the foggiest levels for each site, 15 plots were selected along a natural cloud gradient at a similar altitude. These were separated into three categories depending on fog density: High, Medium, and Low. Half of the plots had been established within the borders of the Wayqecha Biological Station area, situated at the southern edge of the Manu National Park, while the rest were inside the borders of the park, in relative proximity (Figure 1). All 15 plots are on the same elevation (between 2800-2950m).

Table 1 – List of the plots along the cloud gradient, including their number, cloud level category, geographical coordinates, elevation (m), annual cloud input (mm/yr) and cloud water percentage of the annual precipitation (cloud water (mm) / precipitation (mm)).

Plot	Fog	Latitude	Longitude	Elevation (m)	Annual Cloud Input (mm/yr)	Cloud Water %
1	Low	-13.163838	-71.619662	2882	85.7	19.9
2	High	-13.166022	-71.619662	2927	151.8	22.6
3	High	-13.165766	-71.613651	2874	155.3	26.5
4	Medium	-13.164976	-71.607044	2891	118.0	27.3
5	Low	-13.171714	-71.606413	2842	93.6	28.1
6	Medium	-13.180076	-71.611754	2928	122.4	21.7
7	Low	-13.183811	-71.610604	2884	88.48	19.3
8	High	-13.185449	-71.6096	2895	156.4	21.7
9	Medium	-13.185937	-71.607829	2909	116.0	18.2
10	High	-13.180823	-71.605498	2853	145.8	18.5
11	High	-13.175248	-71.592041	2891	155.6	24.4
12	Medium	-13.175139	-71.586713	2927	127.8	27
13	Low	-13.178233	-71.584674	2895	77.5	20.3
14	Medium	-13.186429	-71.585453	2896	130.4	32
15	Low	-13.19081	-71.586128	2919	92.7	27.3

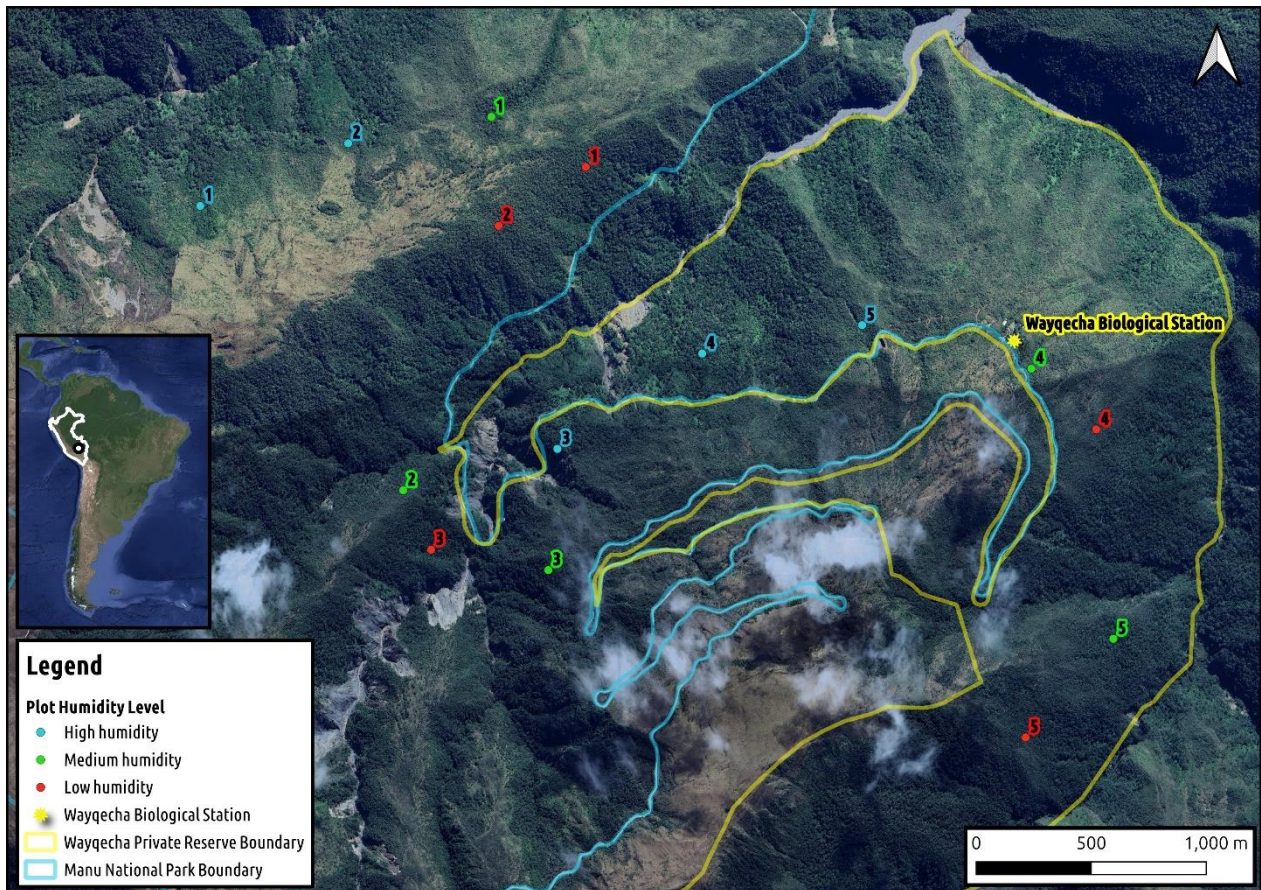


Figure 1. Map of the area of study showing the 15 cloud gradient plots. Low cloud level plots (red dots) experience fog precipitation < 100 mm/year, Medium cloud level plots (green dots) experience a precipitation of 100 - 140 mm/year, and High cloud level plots (blue dots) experience a precipitation > 140 mm/year. Map elaborated by the Alejandro Romero using QGIS version 3.34.

An additional site was included in the sampling process, created in a previously established experimental project, the Wayqecha Amazon Cloud Curtain Ecosystem Experiment (WACCCE). Large mesh panels were installed 1 km away from the biological station and two plots were created: the experimental plot (Fog Exclusion, FE), whose forest canopy was lower than the top of the panels, with the aim that it should receive lower amounts of fog due to the presence of the curtain that intercepts the water droplets as the clouds move up the forest valley. The control plot (CON) was set up approximately 50m upslope from the FE plot, and they were similar in canopy structure and biomass, as well as species composition, and secure from any human disturbances (e.g. logging) (Metcalf et al. 2025). Estimating the efficiency of the fog exclusion treatment is challenging due to lack of widespread metrics. During nighttime, the WACCCE infrastructure was able to reduce annual relative humidity up to ~7%, which are considered to be relatively severe fog reduction levels, as according to (Helmer et al. 2019b) any reduction in relative humidity above 3% is classified as severe cloud reduction.

3.2 Study species

The study species were selected based on three categorization criteria: 1) ecosystem dominance, consisting of the three most abundant species, *Weinmannia bangii*, *Weinmannia crassifolia* and *Clethra cuneata*, based on basal area across all plots, 2) plot encounters, consisting of the three species that occurred in the largest number of plots, *Myrsine coriacea*, *Cavendishia bracteata* and *Weinmannia crassifolia*; 3) specific plot dominance, selecting the three most dominant species in each plot. The five species *Weinmannia bangii*, *Weinmannia crassifolia*, *Clethra cuneata*, *Myrsine*

coriacea and *Cavendishia bracteata* were thus sampled whenever they were present in any of the plots. Due to overlaps between species in categories 1-3 in different plots, or the absence of species, usually 5-6 species were sampled per plot with a replication of six trees per species, leading to an average of 30-42 samples (branches) collected during each sampling day.

Table 2 Complete list of all the 26 species sampled along cloud gradient (High: HCF-01-02-03-04-05, Medium: MCF-01-02-03-04-05 and Low: LCF-01-02-03-04-05) and the WACCEE plots (Control: CON, Experimental: FE).

Species	Sampled plots
<i>Bejaria aestuans</i>	MCF-05
<i>Cavendishia bracteata</i>	HCF-02, HCF-03, HCF-04, HCF-05, LCF-01, LCF-02, LCF-04, LCF-05, MCF-01, MCF-03, MCF-04, MCF-05
<i>Clethra cuneata</i>	HCF-02, HCF-05, LCF-04, MCF-02, MCF-04, MCF-05
<i>Clethra revoluta</i>	CON, FE, LCF-03
<i>Clusia alata</i>	HCF-02, HCF-03, LCF-01, LCF-02
<i>Clusia flaviflora</i>	LCF-04, LCF-05, MCF-03, MCF-05
<i>Clusia trochiformis</i>	HCF-03, HCF-04, LCF-03
<i>Cyathea caracasana</i>	HCF-01
<i>Gaultheria reticulata</i>	MCF-04
<i>Hedyosmum cuatrecasum</i>	HCF-01, LCF-03, MCF-01
<i>Hedyosmum goudotianum</i>	LCF-01
<i>Hesperomeles ferruginea</i>	LCF-04, MCF-02, MCF-04
<i>Meliosma frondosa</i>	CON, FE, MCF-01
<i>Miconia adinantha</i>	LCF-02
<i>Miconia micropetala</i>	HCF-04
<i>Myrsine coriacea</i>	CON, FE, HCF-02, HCF-03, HCF-04, HCF-05, LCF-01, LCF-02, LCF-04, LCF-05, MCF-01, MCF-02, MCF-03, MCF-04, MCF-05
<i>Ocotea andina</i>	HCF-04
<i>Ocotea glabriflora</i>	CON, FE, MCF-03
<i>Oreopanax cuspidatus</i>	HCF-01
<i>Podocarpus oleifolius</i>	HCF-04, LCF-01, LCF-05, MCF-03
<i>Prunus integrifolia</i>	CON, FE
<i>Sciodaphyllum allocotanthum</i>	LCF-04
<i>Symplocos baehni</i>	HCF-05
<i>Weinmannia bangii</i>	CON, HCF-01, HCF-02, HCF-03, HCF-04, LCF-03, MCF-01, MCF-05
<i>Weinmannia crassifolia</i>	HCF-01, HCF-02, HCF-03, HCF-05, LCF-01, LCF-02, LCF-04, LCF-05, MCF-01, MCF-02, MCF-03, MCF-04, MCF-05
<i>Weinmannia reticulata</i>	CON, FE, LCF-02

3.3 Foliar water uptake (FWU)

Foliar water uptake capacity was measured utilizing the methods described by (Limm et al. 2009), with certain adjustments that were required due to time constraints. Depending on the height and accessibility of the tree sampled, branches of varying sizes with at least six sun exposed leaves in suitable conditions were collected (one from each tree sampled) between 8:00 am and 15:00 pm. After the cut, the bottom of the branch was covered with Vaseline to prevent water loss, tagged and placed in moist double bags (a wet paper towel was placed in each small bag, and a thoroughly wet cotton towel was placed in the big plastic bags used for transport to be brought back to the lab area. The samples remained in the moist and black colored bags overnight.

The following day, samples were opened and their water potential (Ψ) was sporadically measured until they reached a value within a -0,5 MPa to -1,2 MPa interval. In instances when the water potential value was above the -0,5 MPa threshold, samples were bench dried in ambient room-temperature and measured again after 30 min have passed. The measurements were conducted with the use of a Scholander-type pressure chamber (Model 1505D PMS Instrument Company, Albany, OR, USA). Certain species, e.g. *Clusia alata*, secreted latex or other viscous substances that interfered with the measurements. To mitigate this issue, in species that exhibited such features, water potential was measured once a slight meniscus of water was formed on the petiole cut, to allow any viscous substance to overflow and ensure that water is not pushed outside of the leaf because of its mechanical pressure. Water potential measurements were important to measure FWU as a similar driving force and verify the robustness of the results. The FWU conductance (g_{FWU}) was used for that purpose and was calculated using the equation below:

$$g_{FWU} (mmol\ m^{-2}\ s^{-1}\ MPa^{-1}) = \frac{FWU\ (mmol\ m^{-2}\ s^{-1})}{\Psi\ (MPa)}$$

Once leaves were within the desired Ψ range, they were weighed, their petiole was sealed with parafilm, and they were subsequently submerged in regular water for 2 hours, whilst ensuring that the petiole remained above the water surface to prevent water intrusions through the cut petiole. After the two hours had passed, leaves were removed from the water and thoroughly patted dry with absorbent tissues and weighed. Leaves were then bench-dried for at least 15 min, weighed again, briefly dipped in water and then patted dry to be reweighed. Foliar water uptake was measured using the standardization method below:

Foliar water uptake (g)

$$\begin{aligned} &= (Mass\ after\ two\ hours\ of\ submersion - Initial\ mass) \\ &- (Mass\ after\ 1\ second\ of\ submersion \\ &- Mass\ before\ 1\ second\ of\ submersion) \end{aligned}$$

This method was utilized to correct for any potential excess water that was not removed during the manual pat drying after submersions.

Lastly, leaves were photographed to calculate their leaf area using ImageJ software US National Institutes of Health, Bethesda, MD). Samples were then oven-dried for 48 hours and reweighed.

3.4 Leaf water retention angle

As mentioned in section 1.2.2, drop retention angle is an intuitive way to capture all the important parameters pertaining to the leaf water retention capacity of leaf surfaces. For the purpose of our results, this concept will be referred to as “leaf water retention angle” from this point onwards. In the lab, a leaf was taken from the ones stored in the zip log bags during the previous sampling day. The leaf was held at a horizontal position and using a Pipette, a 50µL droplet of regular water is applied on the adaxial side of the leaf. Gradually, the leaf angle was changed by slowly turning the leaf point downwards, until water movement was observed. Using a digital protractor phone app, the angle of the leaf was noted down (Goldsmith et al., 2017).

3.5 Minimum stomatal conductance g_{min}

During sampling days, leaves were removed from the same branch used for the FWU protocol and stored separately in moist zip log bags that were stored in a portable cooler. The day after collection, one leaf from each sample was taken and nail police was applied on the cut end of the petiole to prevent water loss. To calculate g_{min} , evapotranspiration (E) and vapor pressure deficit (VPD) values had to be measured for each leaf, according to the equation below:

$$g_{min} = \frac{E}{VPD}$$

For that purpose, each leaf was weighed and the time the measurement was taken was noted, and temperature and relative humidity were recorded to get VPD. The leaf was then placed on chicken wire with a fan pointing towards it. This process was repeated until all leaves were measured. Same measurements mass, temperature and relative humidity were repeated again every 30 minutes had passed from the previous ones, for at least 4 hours, to get the mass loss for all the leaves after the previous round. Subsequently, leaves were photographed for leaf area calculations, oven-dried for 48 hours and then reweighed.

3.6 Community composition

Using diameter at breast height (dbh) data from previous field operations, the basal area (BA) of all the trees in the plot was calculated. The BA values of the sampled trees, whose IDs were recorded throughout the sampling process, were combined with the average values for each of the three traits for every species sampled in the cloud gradient, creating community-weighted trait averages (means) for the trees in the cloud gradient plots, to determine the contribution of these characteristics to the community composition in varying cloud immersion.

3.7 Statistical analysis

All of the data sorting, graph construction and statistical tests, and analyses were conducted in Excel and RStudio, using R version 4.5.3 (R Core Team, 2026). To examine the differences of the chosen traits (FWU, g_{min} and leaf water retention) along the plots in the natural cloud gradient for all the sampled species, a linear mixed model was employed: Trait ~ Species * Cloud level(Plot), where Species and Cloud level are the fixed factors and Plot is the random factor, nested inside the Cloud level fixed factor. A Type III mixed effects model with Satterthwaite's method was used to determine the significance of the effects.

To test for possible differences between the cloud curtain experiment plots (CON and FE), a standard two-way fixed-effects factorial ANOVA model was used, including replication.

Both Cloud treatment and Species are fixed factors, regarding trees as independent experimental replicates in this case.

Upscaling and examining whether community-weighted traits differ between cloud levels in the cloud gradient, basal area measurements of the species were combined with data for each trait to provide the percentages occupied by each species in the plot communities as described previously. To test the significance of the relationships, a One-Way ANOVA was employed, where Cloud level was considered as the fixed factor and the input data were plot-level values of community-weighted trait averages.

All the assumptions of normality and homoscedasticity were met by all the models. Since some of the values for the FWU were negative, a fixed positive value of +0.10 was added to all FWU datapoints and subsequently log-transformed, to minimize errors due to larger variation in the high values of the dataset.

4. Results

4.1 Foliar water uptake (FWU)

4.1.1 Cloud gradient

Species differences in FWU were prevalent in the cloud gradient and were found to be significant after analysis ($p = 0.011$; Figure 2). A 15-fold difference was found between the species with the lowest mean value for FWU (*Ocotea andina*) and the one with the highest (*Sciodaphyllum allocotanthum*) However, cloud cover did not appear to affect FWU across all species ($p = 0.92$; Figure 3) and there was no significant interaction between the species and cloud level ($p = 0.365$).

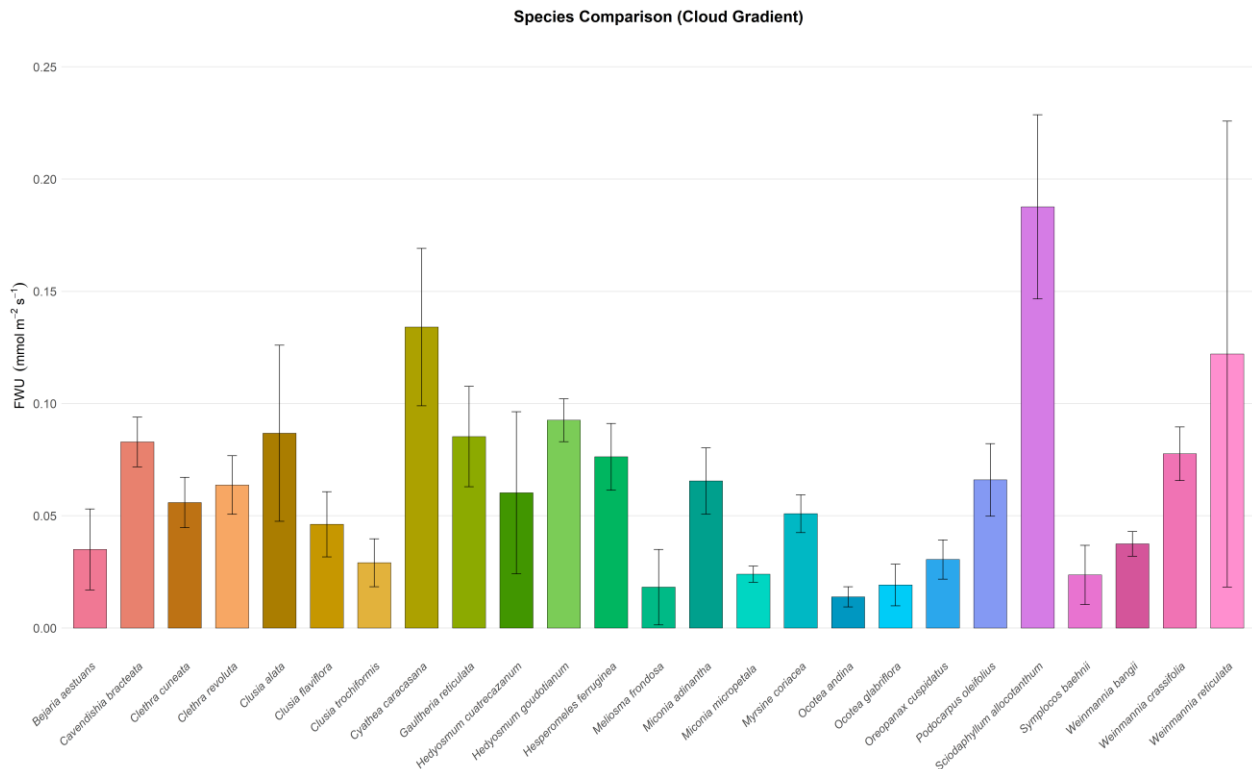


Figure 2. Species comparison for foliar water uptake (FWU, mmol m⁻² s⁻¹) in the cloud gradient shown with standard errors (SE).

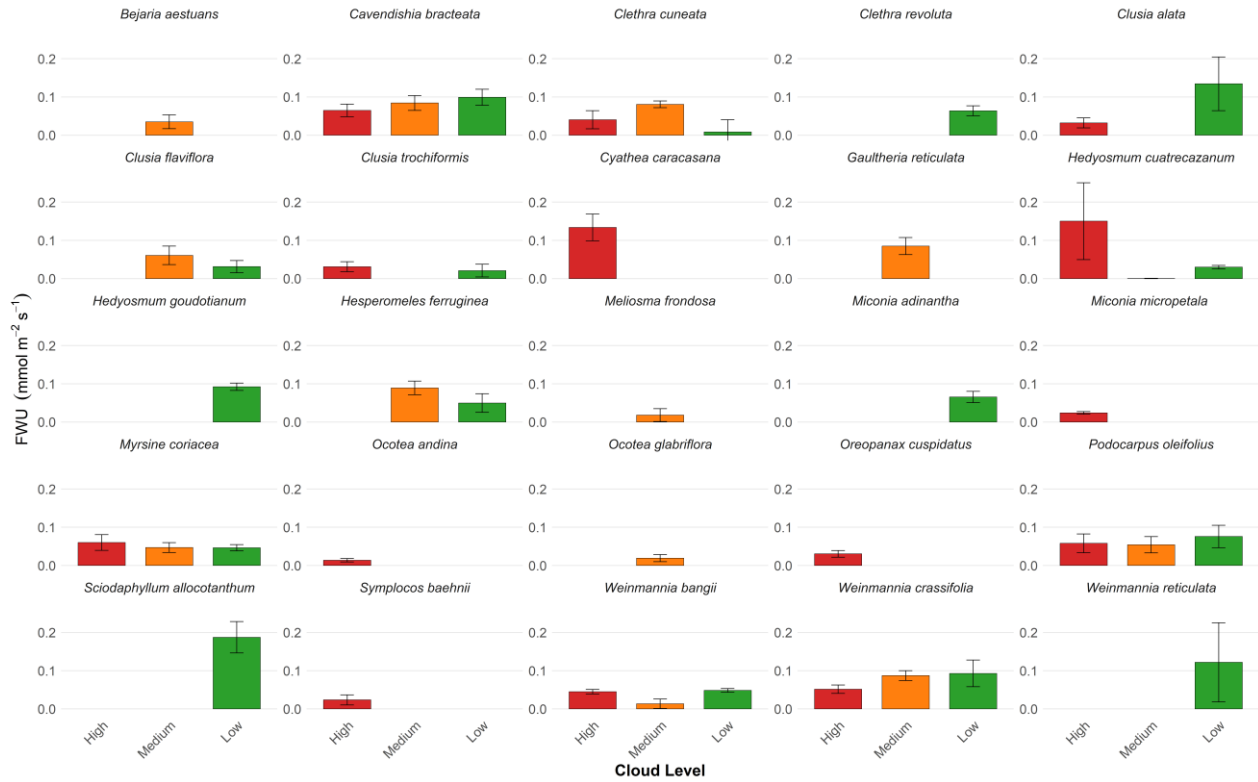


Figure 3. Cloud cover level plot comparison within each of the 25 species sampled along the cloud gradient for foliar water uptake (FWU, $\text{mmol m}^{-2} \text{s}^{-1}$) shown with standard errors (SE). The three cloud levels are (in order of appearance): High (red), Medium (green) and Low (blue). It is important to note that not all species are present across all plots, hence the lack of data for some cloud levels in some species.

4.1.2 Cloud curtain plots

Although always being slightly higher in control plots, there was no significant effect of the experimental treatment effect of reduced fog immersion on the FWU of the plots of the WACCEE ($p = 0.184$; Figure 4). As for the species difference, the result was ambiguous, with a $p = 0.052$, marginally insignificant. No specific species interactions with the treatment were found to be significant ($p = 0.999$).

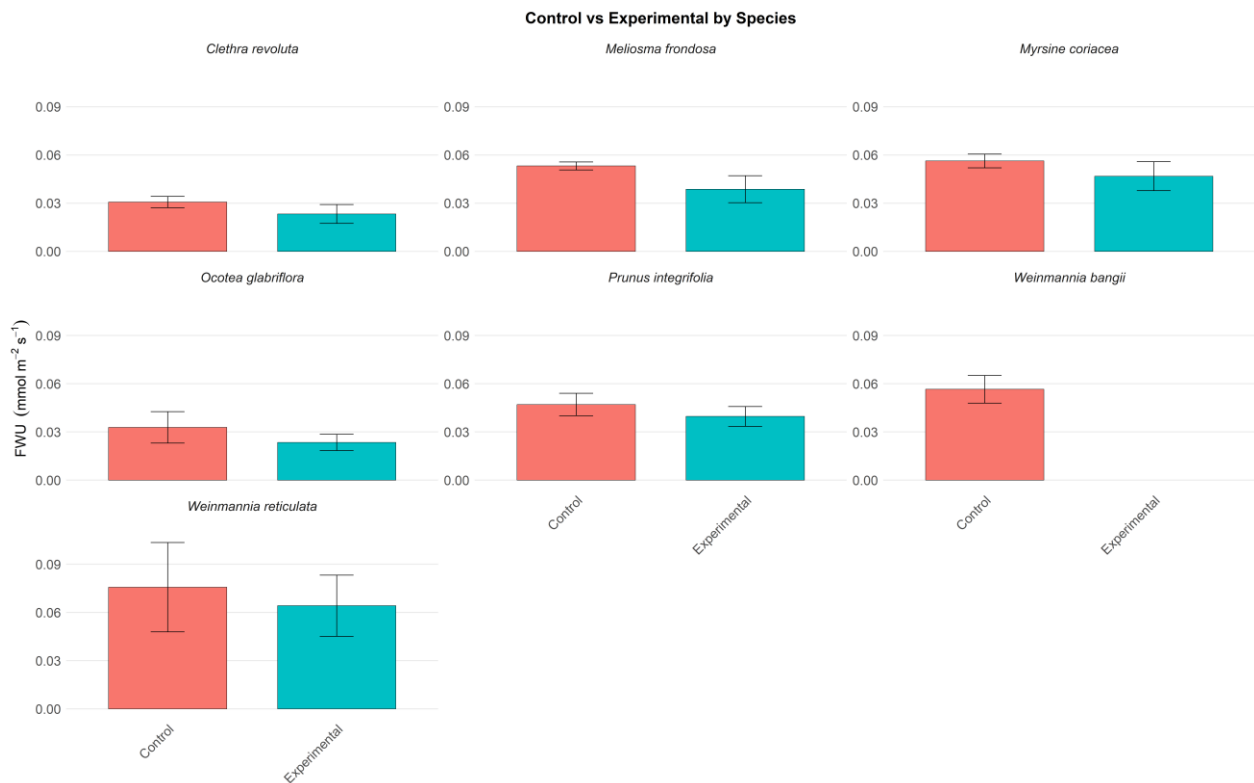


Figure 4. Comparison of foliar water uptake (FWU, $\text{mmol m}^{-2} \text{s}^{-1}$) between the control (red) and experimental (blue) plots of the WACCEE for each of the species measured shown with standard errors (SE). The species *Weinmannia bangii* was present only on the control plot.

The results for g_{FWU} can be viewed in the Appendix 2 (Figures A1, A2 and A3).

4.2 Leaf water retention angle

4.2.1 Cloud gradient

Leaf water retention angle followed similar trends to FWU. Species was the most significant factor that described the data variance ($p = 0.0002$; Figure 5), with a twofold difference between the species with the lowest mean trait value (*Podocarpus oleifolius*) and the one with the highest (*Sciodaphyllum allocotanthum*). Cloud level as a general effect was not a significant contributor ($p = 0.47$; Figure 6). There were, however, significant species by cloud level interactions with the cloud cover level ($p = 0.027$) indicating species-specific divergent influences of cloud level.

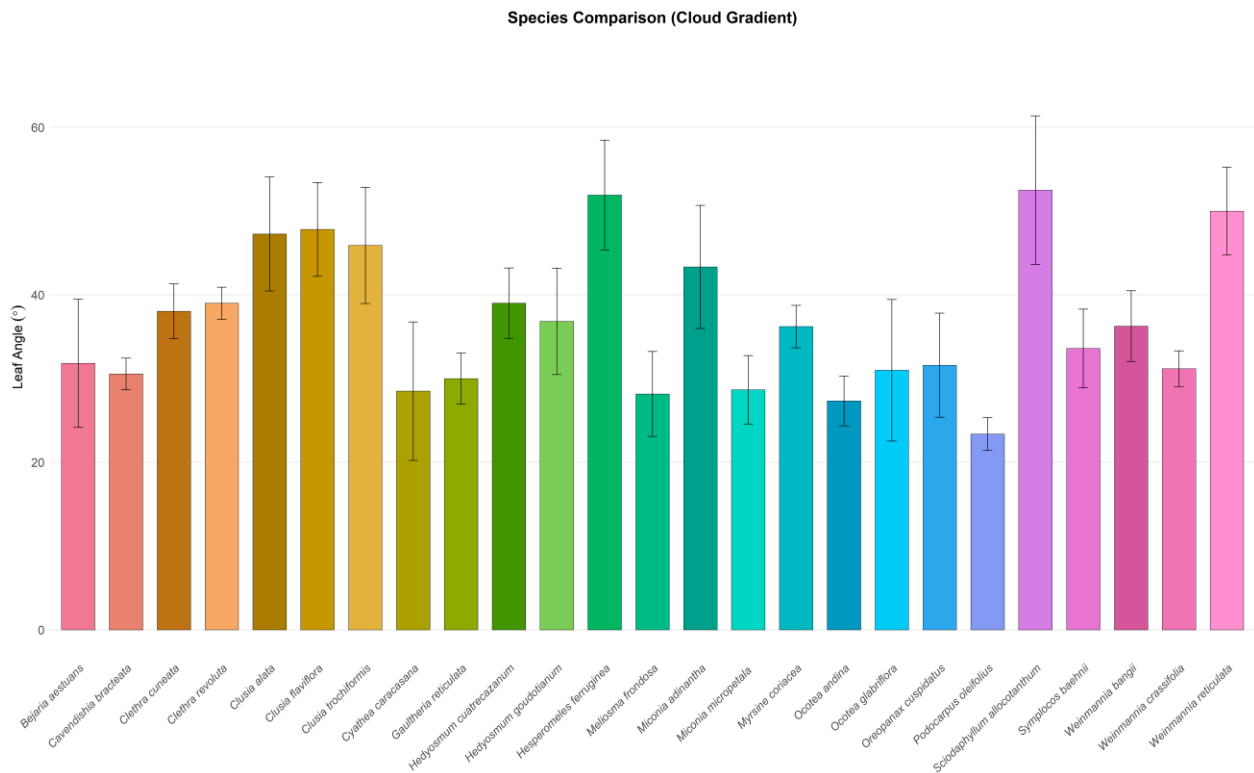


Figure 5. Species comparison for leaf water retention angle (°) in the cloud gradient shown with standard errors (SE).

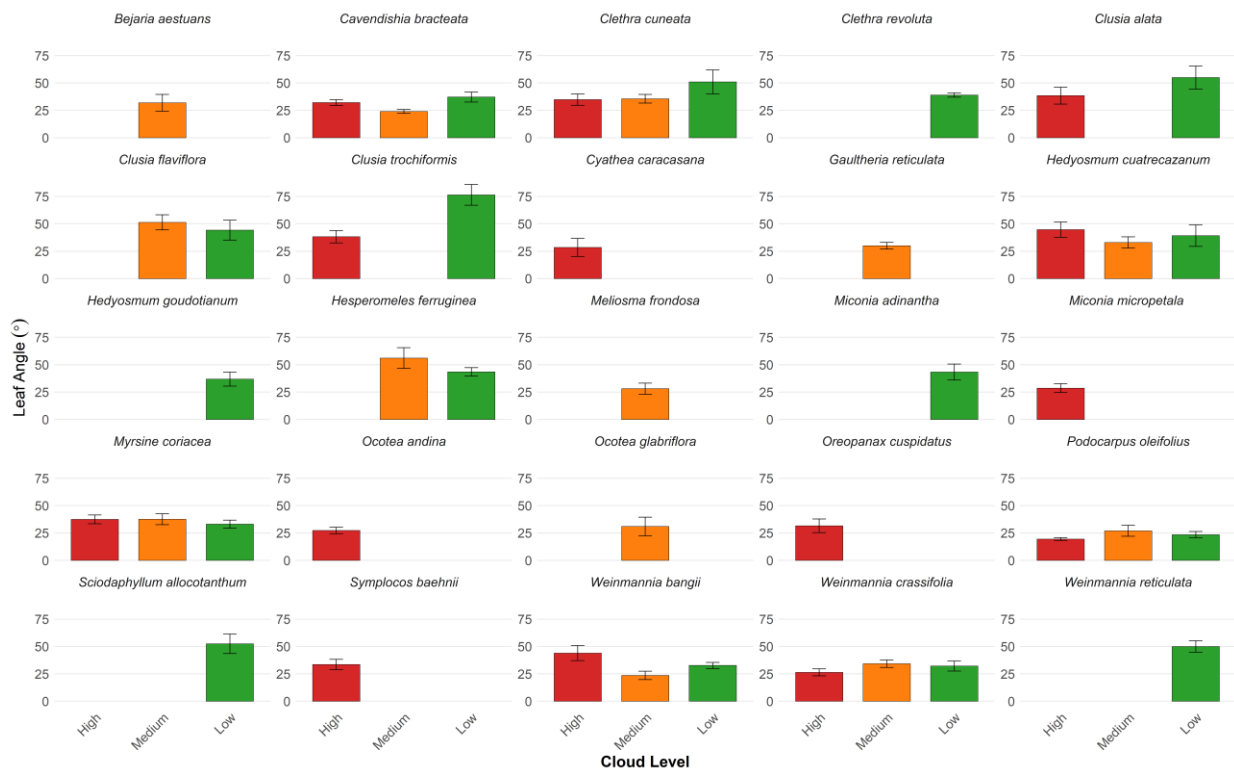


Figure 6. Cloud cover level plot comparison within each of the 25 species sampled along the cloud gradient for leaf water retention angle (°) shown with standard errors (SE). The three cloud levels are (in order of appearance): High (red), Medium (green) and Low (orange).

Low (blue). It is important to note that not all species are present across all plots, hence the lack of data for some cloud levels in some species.

4.2.2 Cloud curtain plots

Regarding leaf water retention angle, none of the factors explored appeared to have any significance in defining the trait. Neither species ($p = 0.662$), nor treatment ($p = 0.759$; Figure 7) could explain data variance, and no relevant species by cloud level interactions ($p = 0.465$) were found. Such observations allude to a potential lack of trait plasticity, similar to FWU.

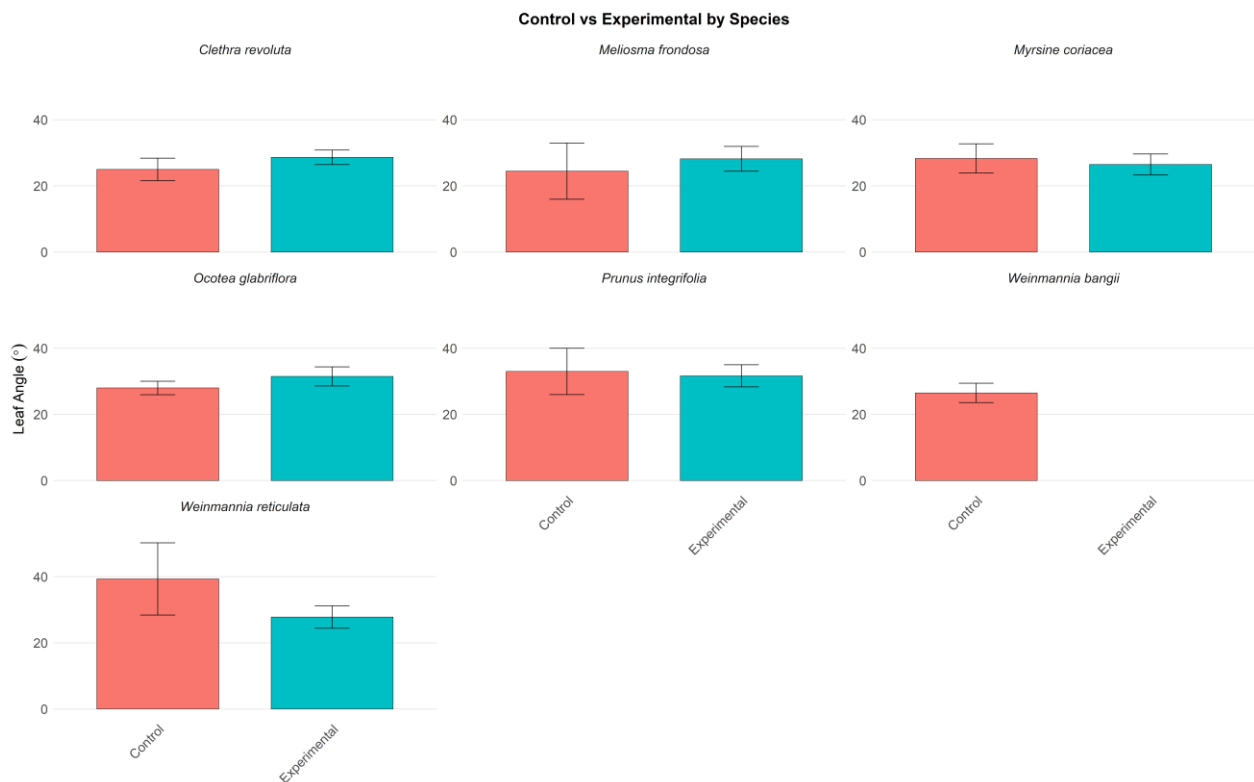


Figure 7. Comparison of leaf water retention angle (°) between the control (red) and experimental (blue) plots of the WACCEE for each of the species measured shown with standard errors (SE). The species *Weinmannia bangii* was present only on the control plot.

4.3 Minimum stomatal conductance (g_{min})

4.3.1 Cloud gradient

Similar to the other two traits, species differences in the cloud gradient were significant ($p < 0.0001$; Figure 8), exhibiting a 9-fold difference between the species with the lowest mean trait value (*Clusia trochiformis*) and the one with the highest (*Cyathea caracasana*). Cloud level by itself was not significant ($p = 0.512$; Figure 9). However, similar to leaf water retention angle, interactions between cloud level and species were significant ($p = 0.019$), suggesting that certain species might react differently to the changing cloud level.

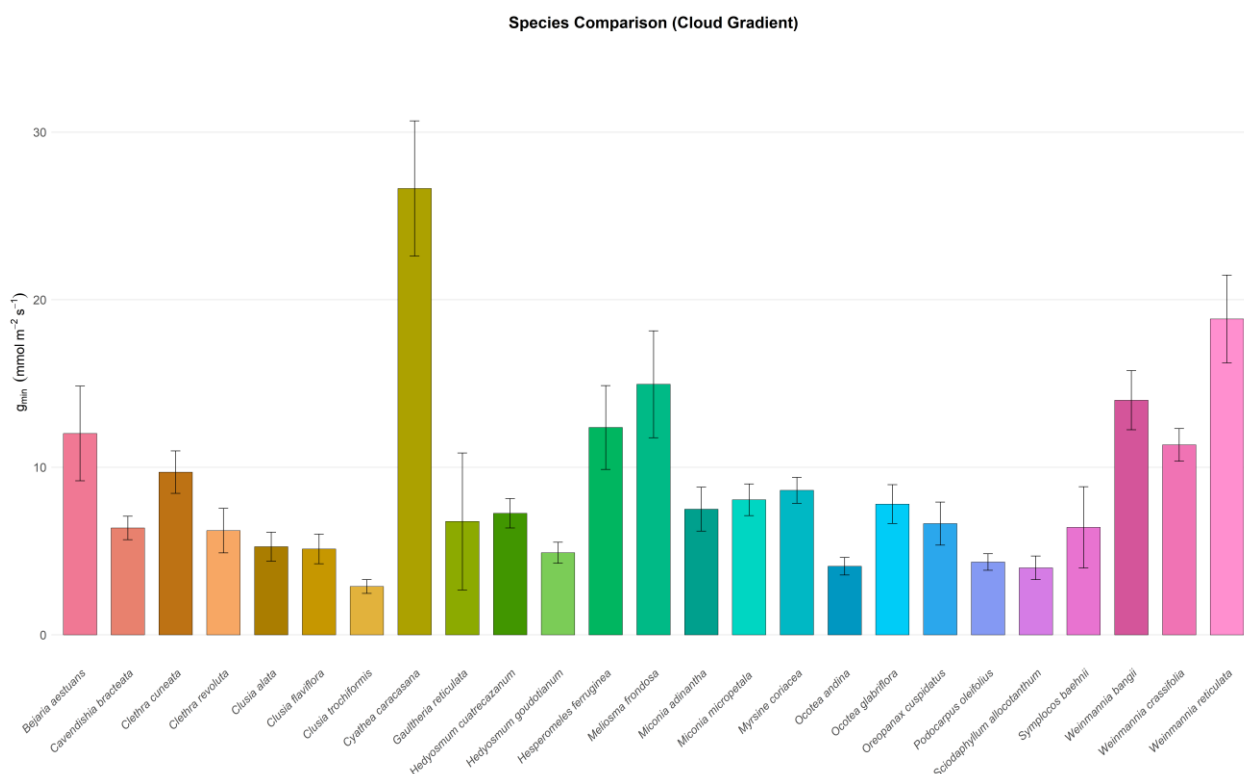


Figure 8. Species comparison for foliar water uptake minimum conductance (g_{min} , mmol m⁻² s⁻¹) in the cloud gradient shown with standard errors (SE).

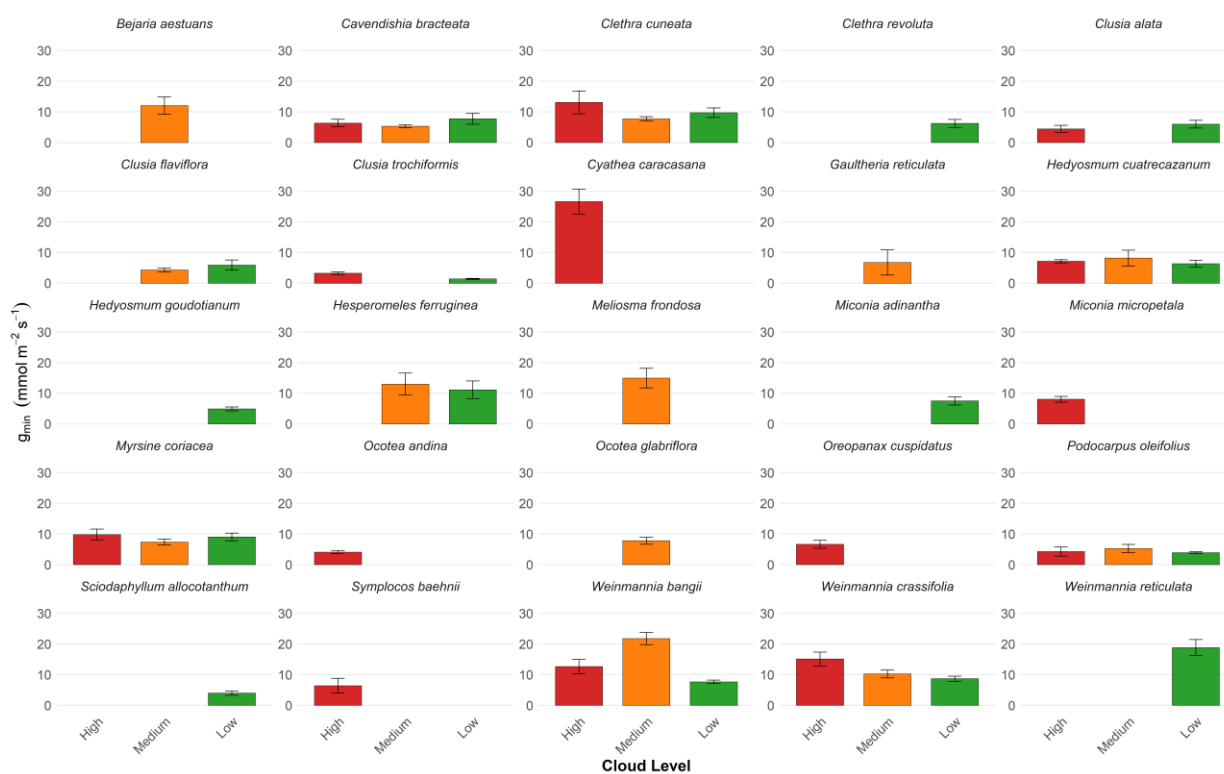


Figure 9. Cloud cover level plot comparison within each of the 25 species sampled along the cloud gradient for minimum conductance (g_{min} , mmol m⁻² s⁻¹) shown with standard errors (SE). The three cloud levels are (in order of appearance): High (red), Medium (green) and Low (blue). It is important to note that not all species are present across all plots, hence the lack of data for some cloud levels in some species.

4.3.2 Cloud curtain plots

Species difference in $g_{\min}$ in the experimental WACCEE plots was found to be significant ($p = 0.018$; Figure 10), while the treatment effect as a factor was found to have an insignificant impact ($p = 0.750$). There were also no relevant interactions between species and the treatment ($p = 0.747$).

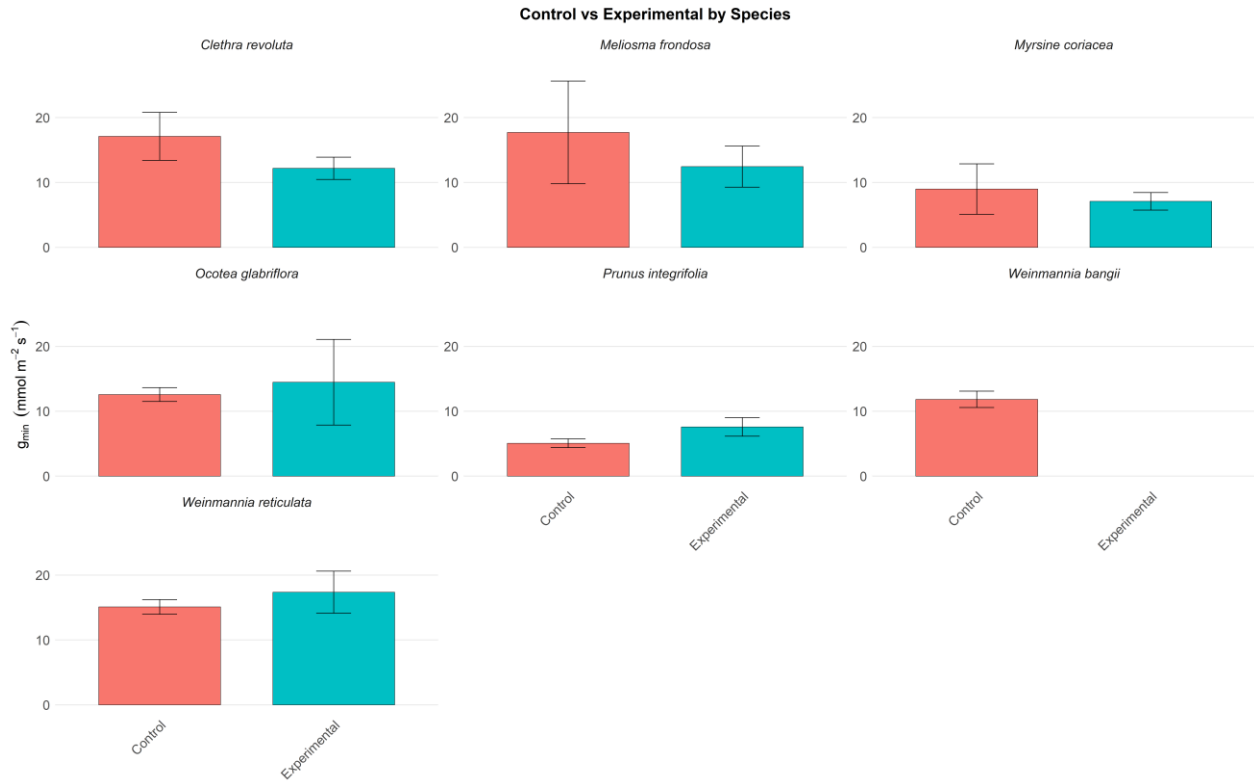


Figure 10. Comparison of minimum conductance ($g_{\min}$, $\text{mmol m}^{-2} \text{s}^{-1}$) between the control (red) and experimental (blue) plots of the WACCEE for each of the species measured shown with standard errors (SE). The species *Weinmannia bangii* was present only on the control plot.

4.4 Community composition

After getting the community-weighted average trait values by accounting for the basal area for all the plots in the cloud gradient, the one-way ANOVA showed no significant effects of two of the three selected traits (FWU: $p = 0.358$, $g_{\min}$: $p = 0.786$), while it showed a strongly significant effect of leaf water retention angle ($p = 0.009$). Low cloud level plots appeared to have the highest mean trait values for FWU and leaf water retention angle amongst the three cloud level categories, and the lowest $g_{\min}$ values (Figures 11).

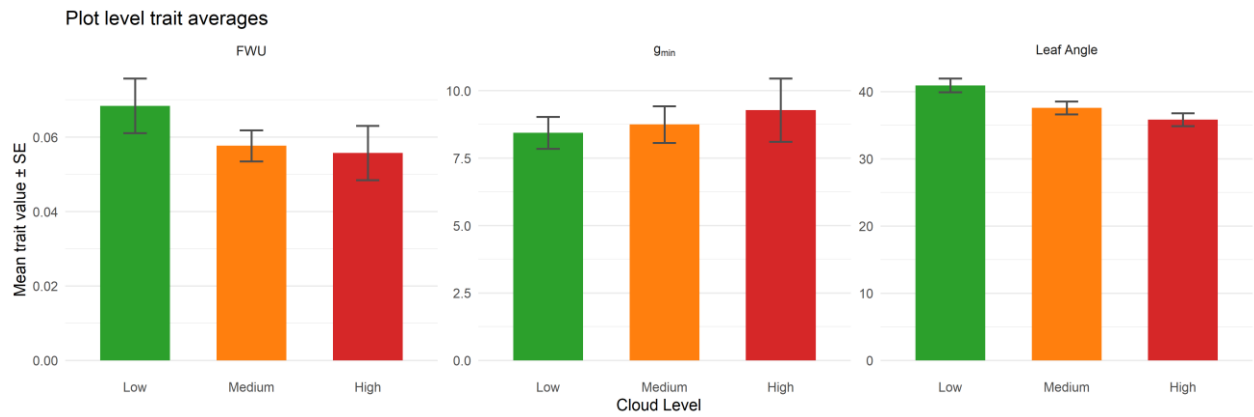


Figure 11. Comparison of the community-weighted average values for all three selected traits (FWU, g_{min} and leaf water retention angle) made basal area data for each tree in the cloud gradient plots, shown with standard errors (SE). The three distinct cloud cover levels are (in order of appearance): Low (green), Medium (orange) and High (red).

Table 3 List of the 25 cloud gradient species averages for basal area (BA, cm^2) and their water potentials (Ψ , MPa) prior to submersion for FWU measurements. BA averages were calculated from the total number of trees sampled in all the plots, while Ψ was calculated based on the sampled trees as per Table 2.

Cloud gradient species	Average species basal area (BA, cm^2)	Average water potential (Ψ , MPa)
Bejaria aestuans	137	-0.75
Cavendishia bracteata	59.2	-0.6
Clethra cuneata	179	-0.65
Clethra revoluta	1072	-0.90
Clusia alata	277	-0.6
Clusia flaviflora	136	-0.61
Clusia trochiformis	1368	-0.59
Cyathea caracasana	139	-0.89
Gaultheria reticulata	529	-1.13
Hedyosmum cuatrecasum	215	-0.62
Hedyosmum goudotianum	50	-0.70
Hesperomeles ferruginea	134	-0.76
Meliosma frondosa	59.4	-0.58
Miconia adinantha	84.3	-0.66
Miconia micropetala	77.9	-0.59
Myrsine coriacea	58.9	-0.81
Ocotea andina	270	-0.56
Ocotea glabriflora	631	-0.51
Oreopanax cuspidatus	99.4	-0.52
Podocarpus oleifolius	431	-0.51
Sciodaphyllum allocotanthum	11.1	-0.62
Symplocos baehnii	7.39	-0.75
Weinmannia bangii	734	-0.76
Weinmannia crassifolia	101	-0.64

Weinmannia reticulata	848	-0.65
-----------------------	-----	-------

5. Discussion

5.1 Species acclimation and adaptation capacity

Despite the data from previous studies showing that cloud immersion is in fact beneficial for plant and tree species present in TMCFs, studies on the acclimation and adaptation capacity of these species to varying cloud immersed conditions are scarce. According to the results of this experiment, for the three traits tested, two main points are indicated for the tree species growing in the cloud gradient: I) large species differences for all three traits and II) lack of within species variation between the different cloud level categories. The latter indicates that neither acclimation and/or local adaptation (existence of ecotypes) causes the significant within-species variation. This in turn implies a low capacity for the three leaf water economy traits examined to adjust to changing cloud immersion levels.

As for the fog exclusion experiment examined in the cloud curtain plot, substantial reduction in fog input did not have any significant effects on any of the three traits. This suggests a lack of acclimation capacity for these three leaf water economy traits in the examined species, at least in the conditions of reduced cloud immersion. Plasticity for leaf water economy traits in general has not been documented, especially in the context of TMCFs. While FWU is found to be frequent in ecosystems with higher wettability events, little is known for the capacity of species to acclimate in changes to cloud immersion. Fog reduction treatment had a negative impact on the capacity for FWU in eight species in a Peruvian TMCF (Anders et al. 2025), however there is a distinct lack of findings for tree species, despite the widespread occurrence of FWU across all ecoregions on the planet (Schreel and Steppe 2020). In temperate tree species, the response to drought on FWU was species specific (Schreel et al. 2019), which points towards individual species strategies being of potentially great importance for tropical tree species likewise.

A study on five water-use traits including g_{min} in 20 tropical species in Rwanda has shown not only large within species differences in g_{min} , but also a high degree of thermal plasticity. The site with the lowest annual mean temperature had 68% higher g_{min} values in most of the species compared to the one with the highest (Wittemann et al. 2024), consistent with previous drought acclimation reports that have shown a tendency for decreased g_{min} values in plants acclimated to drought stress (Duursma et al. 2019b). However, that study used plots in an elevational gradient, which should be considered when drawing comparisons, since all the plots in our study were on same elevation as mentioned in section 3.1. Other studies focus on stomatal conductance (g_s) and crown conductance (g_c), rather than g_{min} , which the leaf conductance after stomata have closed as much as possible. Conifers in a temperate cloud forest in USA, have shown that g_s was significantly higher under cloud immersion and exponentially declined as the leaf-to-air vapor pressure deficit increased in conditions with less or no cloud cover (Reinhardt and Smith 2008). An attempt to model the responses of g_s to varying degrees of cloud immersion was met with limitations in the case of cloud immersion caused by the great variation tied with environmental factors affecting g_s , and a lack of understanding on the water status and stomatal conductivity relationships for cloud forest vegetation (Lowman and Dil Godoy 2020).

One important parameter that should be taken into consideration when reviewing our results is the nature of the method that was chosen for the division of plots into the three distinct categories. As stated in the Materials & methods section 3.1, atmospheric models that estimated annual precipitation and fog input data were used to divide the 15 plots of the cloud gradient into

High, Medium and Low cloud levels, and not wetness data from on field sensors. Considering the emerging patterns discussed in the Results section that it appears the majority of species in the cloud gradient exhibit either the highest or lowest values in the Medium cloud level plots (Figures 3, 6 & 9), there is a possibility that after collecting humidity and precipitation data from installed sensors on site, it is shown that certain plots were mischaracterized and, hence, altering the results and interpretations. This in turn could possibly reveal differences in the significance of the effects of the cloud level to the examined traits and within species interactions, hence our results should be taken with a certain degree of caution.

On a final note, a recently published review of the findings on the responses of American tropical forests to the shifts in temperature and precipitation caused by climate change, indicate that although tree community compositions do change to account for these shifts, this change happens at a much lower rate to what would be necessary to acclimate or adapt (Aguirre-Gutiérrez et al. 2025). According to the review, changes in TMCFs are even slower compared to lowland forests. This lack of changes are given with the assumption that there is no acclimation or local adaptation capacity, which aligns with our own findings. This is, naturally, further corroborated by the lack of acclimation of tree species to fog exclusion treatment.

5.2 Community composition

Despite the fact that trait differences between species were found to be significant, that did not translate into the community-weighted averages for the community composition for FWU and g_{min} , as they appeared to have no effect on the species distribution in the plots of the cloud gradient. That was not the case for leaf water retention angle, as it significantly differed for the tree species compositions along the cloud gradient, with Low cloud level plots showing greater values than the other two categories. This suggests that trees in Low cloud level plots are better at holding water, which is beneficial for trees in these environments where water is presumably scarcer than areas with more foggy and rainy conditions. Additionally, despite the insignificance of differences in FWU and g_{min} , the patterns shown in Figure 10 show higher mean FWU values and lower g_{min} in Low cloud level plots compared to the other two categories, implying improved leaf water economy under both moist and dry conditions. Combined with our significant findings on leaf water retention angle, it is implied that Low cloud level plots have a better leaf water economy regulation, perhaps to account for the lower fog input. However, it should be noted that in denser fog environments, the capacity for FWU is higher than in less foggy conditions, and thus trees could benefit from higher capacity for leaf water retention, but the results of community-weighted means analysis suggest the opposite effect.

Some studies regarding leaf water repellency have shown a distinct lack of correlation between that and the morphological features of plants, and importantly, a great variation between species across different forest ecosystems (Holder 2011), while others have shown that leaf water repellency in cloud forests is lower compared ones in the lowlands (Holder 2007). Leaf water repellency is directly linked to the capacity of leaves to retain water on their surfaces, indicating that TCMF plant species have a higher capacity for leaf water retention.

According to results from other TMCFs, these environments might be considered arid during the dry seasons they experience, and as a result, plants would require additional mechanisms to deal with potential water or atmospheric stress. Due to this, fog exposure acts more like a buffer, rather than a solution to stress under drought (Bittencourt et al. 2019). Interestingly, drought strategies usually play an important role in tree species compositions, as has been seen in the past with species having different drought strategies, with certain tree species having higher g_{min} values and hence lower drought tolerance compared to others that had lower g_{min} values and were better

at preventing water loss under dryer conditions (Wittemann et al. 2024). This is in line with the mean value distribution for g_{min} that can be seen in Figure 10.

Traits such as leaf morphology and wood tissue have been linked to species growing in TMCFs, as a response to increased water availability through fog immersion (Andrés-Hernández and Rodríguez-Ramírez 2025). Moreover, there are many environmental filtering factors that interact and impose restrictions on the growth capacity of lowland species, allowing the formation of communities that contain species specially adapted for these unique conditions, from increased root production through carbon allocation, to lower specific leaf area and unique leaf morphology (Eller et al. 2020b). Such input from prior studies makes further research imperative to determine whether the trait interactions with the cloud levels found along natural gradients are perhaps linked to only specific traits and whether other climatic and geomorphological factors contribute to the shaping of TMCF communities. Furthermore, our results might imply that FWU and g_{min} are not the most important leaf water economy traits shaping tree community composition under varying cloud regimes. Good leaf water economy seems more important at low cloud levels; significantly so for water retention angle, and insignificantly but following that same direction for FWU and g_{min} .

6. Conclusion

In the context of a rapidly changing climate, understanding how leaf traits related to water acquisition and efficiency function and shape plant communities, will provide deeper insights on how vulnerable ecosystems like TFCs are able to adapt to changes in their local climate, as droughts become more frequent and the cloud bank slowly rises. This study showed that tree species in TMCFs had large trait value differences between them and that cloud level immersion had no significant effect on within-species differences in varying cloud immersion, or in the fog exclusion treatment, indicating a lack of acclimation capacity for tree species in TMCFs. It also produced significant evidence on the importance of leaf water retention on tree communities of different cloud immersion and potentially an improved capture capacity and use of intercepted water under more water-limited conditions. Our findings imply a stronger need for good leaf water economy in low cloud level areas. There is a definite need for further investigation into other water economy traits for tree species of this ecotype, including more species and considering different factors of leaf morphology, exploring alternative anatomical pathways for water uptake, such as bark water uptake, as well as the effect of epiphytic communities who are prevalent in these environments and their potential interference. A deeper insight will provide more efficient and targeted approaches for future conservation efforts.

7. Acknowledgements

I would like to thank both of my supervisors, Johan Uddling and Hampus Holmberg, for their immense patience, gentle guidance and infinite trust by giving me the chance to work on a project of this magnitude and importance. A huge thank you to all our colleagues all over the world, who contributed to this project in any capacity: Dan, Walter, Scott and everyone else. A special thanks has to go to the members of our field team, Lou, Elias and Jimmy, for their incredible resilience and professionalism, their talent and the gentle care they showed us when we were sick or struggling. Gracias por todo! I would also like to thank the people of Paucartambo for welcoming us to their community and putting up with our peculiar restaurant orders. I extend my gratitude to the people running the Wayqecha Biological Station and the Manu National Park officials for granting us permission to work in the cloud forests and contribute our part to their protection. On

a personal level, I would like to thank my loved ones here in Sweden, for their support, understanding and love. Jule, Sam and Hannes, I'm giving a special shoutout to you: I wouldn't have been able to make it if it weren't for your companionship and support, in ways both practical and emotional. We did this together. I want to thank my family and friends back home, for keeping me sane and sending all their love and support, talking on the phone for hours and sending funny videos to chase the shadows away. Thank you mum for listening to my rants and putting up with my mood swings. Lastly, I want to dedicate this work to my two cats: to Munch, the funniest kitty alive and to Myrtle, the creature that taught me what love truly means.

8. References

- Aguirre-Gutiérrez, Jesús, Sandra Díaz, Sami W. Rifai, Jose Javier Corral-Rivas, Maria Guadalupe Nava-Miranda, Roy González-M, Ana Belén Hurtado-M, et al. 2025. "Tropical Forests in the Americas Are Changing Too Slowly to Track Climate Change." *Science* 387(6738): eadl5414. doi:10.1126/science.adl5414.
- Anders, Emily M., Sybil G. Gotsch, Matthew A. Vadeboncoeur, Daniel B. Metcalfe, David C. Bartholomew, Aline B. Horwath, Blanca Espinoza, Darcy Galiano, and Heidi Asbjornsen. 2025. "Trait Plasticity and Adaptive Strategies of Vascular Epiphytes to a Large-Scale Experimental Reduction of Fog Immersion in a Tropical Montane Cloud Forest." *American Journal of Botany* 112(5): e70042. doi:10.1002/ajb2.70042.
- Andrés-Hernández, Agustina Rosa, and Ernesto C. Rodríguez-Ramírez. 2025. "Does Climatic Variation Drive the Adjustment of Functional Traits? An Assessment of Tropical Montane Cloud Forest Tree Species." *Frontiers in Plant Science* 16. doi:10.3389/fpls.2025.1555607.
- Bartholomew, David C., Paulo R. L. Bittencourt, Darcy Galiano Cabrera, Roxana Sacatuma Cruz, Jimmy R. Chambi Paucar, Daniela Corrales Alvarez, Eric Cosio, et al. 2026. "Tropical Montane Cloud Forests Have High Resilience to Five Years of Severe Soil Drought." *Global Change Biology* 32(1): e70670. doi:10.1111/gcb.70670.
- Bittencourt, Paulo R. L., Fernanda de V. Barros, Cleiton B. Eller, Caroline S. Müller, and Rafael S. Oliveira. 2019. "The Fog Regime in a Tropical Montane Cloud Forest in Brazil and Its Effects on Water, Light and Microclimate." *Agricultural and Forest Meteorology* 265: 359–69. doi:10.1016/j.agrformet.2018.11.030.
- Bruijnzeel, L. A., Mark Mulligan, and Frederick N. Scatena. 2011. "Hydrometeorology of tropical montane cloud forests: emerging patterns." *Hydrological Processes* 25(3): 465–98. doi:10.1002/hyp.7974.
- Calvin, Katherine, Dipak Dasgupta, Gerhard Krinner, Aditi Mukherji, Peter W. Thorne, Christopher Trisos, José Romero, et al. 2023. *IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (Eds.)]. IPCC, Geneva, Switzerland*. First. eds. Paola Arias, Mercedes Bustamante, Ismail Elgizouli, Gregory Flato, Mark Howden, Carlos Méndez-Vallejo, Joy Jacqueline Pereira, et al. Intergovernmental Panel on Climate Change (IPCC). doi:10.59327/IPCC/AR6-9789291691647.

- Cao, Ashley J., Zeyin Li, Paul O. Seibert, and Cynthia Gerlein-Safdi. 2026. "The Role of Leaf Wettability and Morphology on Leaf Surface Water Storage: A Cross-Biome Synthesis." *Ecohydrology* 19(1): e70162. doi:10.1002/eco.70162.
- Castillo-Campos, Gonzalo, José G. García-Franco, M. Luisa Martínez, Gabriela Vázquez, Jesús J. Pale-Pale, Mirna R. Zamudio Pérez, and Octavio Pérez-Maqueo. 2024. "Assessing the Impact of Land Use Change on Different Components of Plant Diversity in a Tropical Montane Cloud Forest of Mexico." *Biodiversity and Conservation* 33(4): 1523–59. doi:10.1007/s10531-024-02814-z.
- Chin, Alana R. O., Paula Guzmán-Delgado, Anna Görlich, and Janneke HilleRisLambers. 2023. "Towards Multivariate Functional Trait Syndromes: Predicting Foliar Water Uptake in Trees." *Ecology* 104(8): e4112. doi:10.1002/ecy.4112.
- Duursma, Remko A., Christopher J. Blackman, Rosana López, Nicolas K. Martin-StPaul, Hervé Cochard, and Belinda E. Medlyn. 2019a. "On the Minimum Leaf Conductance: Its Role in Models of Plant Water Use, and Ecological and Environmental Controls." *New Phytologist* 221(2): 693–705. doi:10.1111/nph.15395.
- Duursma, Remko A., Christopher J. Blackman, Rosana López, Nicolas K. Martin-StPaul, Hervé Cochard, and Belinda E. Medlyn. 2019b. "On the Minimum Leaf Conductance: Its Role in Models of Plant Water Use, and Ecological and Environmental Controls." *New Phytologist* 221(2): 693–705. doi:10.1111/nph.15395.
- Eller, Cleiton B., Aline L. Lima, and Rafael S. Oliveira. 2013. "Foliar Uptake of Fog Water and Transport Belowground Alleviates Drought Effects in the Cloud Forest Tree Species, *Drimys Brasiliensis* (Winteraceae)." *New Phytologist* 199(1): 151–62. doi:10.1111/nph.12248.
- Eller, Cleiton B., Aline L. Lima, and Rafael S. Oliveira. 2016a. "Cloud Forest Trees with Higher Foliar Water Uptake Capacity and Anisohydric Behavior Are More Vulnerable to Drought and Climate Change." *New Phytologist* 211(2): 489–501. doi:10.1111/nph.13952.
- Eller, Cleiton B., Aline L. Lima, and Rafael S. Oliveira. 2016b. "Cloud Forest Trees with Higher Foliar Water Uptake Capacity and Anisohydric Behavior Are More Vulnerable to Drought and Climate Change." *New Phytologist* 211(2): 489–501. doi:10.1111/nph.13952.
- Eller, Cleiton B., Leonardo D. Meireles, Stephen Sitch, Stephen S. O. Burgess, and Rafael S. Oliveira. 2020a. "How Climate Shapes the Functioning of Tropical Montane Cloud Forests." *Current Forestry Reports* 6(2): 97–114. doi:10.1007/s40725-020-00115-6.
- Eller, Cleiton B., Leonardo D. Meireles, Stephen Sitch, Stephen S. O. Burgess, and Rafael S. Oliveira. 2020b. "How Climate Shapes the Functioning of Tropical Montane Cloud Forests." *Current Forestry Reports* 6(2): 97–114. doi:10.1007/s40725-020-00115-6.
- Fahey, Timothy J., Ruth E. Sherman, and Edmund V. J. Tanner. 2016. "Tropical Montane Cloud Forest: Environmental Drivers of Vegetation Structure and Ecosystem Function." *Journal of Tropical Ecology* 32(5): 355–67. doi:10.1017/S0266467415000176.

- Foster, Pru. 2001a. “The Potential Negative Impacts of Global Climate Change on Tropical Montane Cloud Forests.” *Earth-Science Reviews* 55(1): 73–106. doi:10.1016/S0012-8252(01)00056-3.
- Foster, Pru. 2001b. “The Potential Negative Impacts of Global Climate Change on Tropical Montane Cloud Forests.” *Earth-Science Reviews* 55(1): 73–106. doi:10.1016/S0012-8252(01)00056-3.
- Garen, Josef C., and Sean T. Michaletz. 2025. “Temperature Governs the Relative Contributions of Cuticle and Stomata to Leaf Minimum Conductance.” *New Phytologist* 245(5): 1911–23. doi:10.1111/nph.20346.
- Goldsmith, Gregory R., Lisa Patrick Bentley, Alexander Shenkin, Norma Salinas, Benjamin Blonder, Roberta E. Martin, Rosa Castro-Cossco, et al. 2017. “Variation in Leaf Wettability Traits along a Tropical Montane Elevation Gradient.” *New Phytologist* 214(3): 989–1001. doi:10.1111/nph.14121.
- Goldsmith, Gregory R., Nicholas J. Matzke, and Todd E. Dawson. 2013a. “The Incidence and Implications of Clouds for Cloud Forest Plant Water Relations.” *Ecology Letters* 16(3): 307–14. doi:10.1111/ele.12039.
- Goldsmith, Gregory R., Nicholas J. Matzke, and Todd E. Dawson. 2013b. “The Incidence and Implications of Clouds for Cloud Forest Plant Water Relations.” *Ecology Letters* 16(3): 307–14. doi:10.1111/ele.12039.
- Guerra, Juan C., Judit Carrillo, Hugo Rodríguez, and Silvia Alonso-Pérez. 2025. “Sinking of the Eastern North Atlantic Stratocumulus: Implications for the Macaronesian Cloud Forest.” *Earth Systems and Environment* 9(3): 1543–59. doi:10.1007/s41748-025-00655-6.
- Helmer, E. H., E. A. Gerson, L. Scott Baggett, Benjamin J. Bird, Thomas S. Ruzycki, and Shannon M. Voggesser. 2019a. “Neotropical Cloud Forests and Páramo to Contract and Dry from Declines in Cloud Immersion and Frost.” *PLOS ONE* 14(4): e0213155. doi:10.1371/journal.pone.0213155.
- Helmer, E. H., E. A. Gerson, L. Scott Baggett, Benjamin J. Bird, Thomas S. Ruzycki, and Shannon M. Voggesser. 2019b. “Neotropical Cloud Forests and Páramo to Contract and Dry from Declines in Cloud Immersion and Frost.” *PLOS ONE* 14(4): e0213155. doi:10.1371/journal.pone.0213155.
- Holder, Curtis D. 2007. “Leaf Water Repellency of Species in Guatemala and Colorado (USA) and Its Significance to Forest Hydrology Studies.” *Journal of Hydrology* 336(1): 147–54. doi:10.1016/j.jhydrol.2006.12.018.
- Holder, Curtis D. 2011. “The Relationship between Leaf Water Repellency and Leaf Traits in Three Distinct Biogeographical Regions.” *Plant Ecology* 212(11): 1913–26. doi:10.1007/s11258-011-9963-6.
- Intergovernmental Panel on Climate Change (IPCC). 2023. *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press. doi:10.1017/9781009157896.

- Karger, Dirk Nikolaus, Michael Kessler, Marcus Lehnert, and Walter Jetz. 2021. “Limited Protection and Ongoing Loss of Tropical Cloud Forest Biodiversity and Ecosystems Worldwide.” *Nature Ecology & Evolution* 5(6): 854–62. doi:10.1038/s41559-021-01450-y.
- Lawton, R. O., U. S. Nair, R. A. Pielke, and R. M. Welch. 2001. “Climatic Impact of Tropical Lowland Deforestation on Nearby Montane Cloud Forests.” *Science* 294(5542): 584–87.
- Lenz, Anne-Kristin, Ulrike Bauer, and Graeme D Ruxton. 2022. “An Ecological Perspective on Water Shedding from Leaves.” *Journal of Experimental Botany* 73(4): 1176–89. doi:10.1093/jxb/erab479.
- Limm, Emily Burns, Kevin A. Simonin, Aron G. Bothman, and Todd E. Dawson. 2009. “Foliar Water Uptake: A Common Water Acquisition Strategy for Plants of the Redwood Forest.” *Oecologia* 161(3): 449–59. doi:10.1007/s00442-009-1400-3.
- López-Ramírez, Sergio M., Leonardo Sáenz, Alex Mayer, Lyssette E. Muñoz-Villers, Heidi Asbjornsen, Z. Carter Berry, Nathaniel Looker, Robert Manson, and León Rodrigo Gómez-Aguilar. 2020. “Land Use Change Effects on Catchment Streamflow Response in a Humid Tropical Montane Cloud Forest Region, Central Veracruz, Mexico.” *Hydrological Processes* 34(16): 3555–70. doi:10.1002/hyp.13800.
- Los, Sietse O., F. Alayne Street-Perrott, Neil J. Loader, and Cynthia A. Froyd. 2021. “Detection of Signals Linked to Climate Change, Land-Cover Change and Climate Oscillators in Tropical Montane Cloud Forests.” *Remote Sensing of Environment* 260: 112431. doi:10.1016/j.rse.2021.112431.
- Lowman, Lauren E. L., and Luis Dil Godoy. 2020. “Simulating Stomatal Response to Cloud Immersion for Montane Cloud Forests in the Southern Appalachians.” *Agricultural and Forest Meteorology* 295: 108165. doi:10.1016/j.agrformet.2020.108165.
- Metcalf, Daniel B., Darcy F. Galiano Cabrera, Luis Miguel Alvarez Mayorga, Roxana Sacatuma Cruz, Daniela Corrales Alvarez, Blanca Rosa Espinoza Otazu, Walter Huaraca Huasco, et al. 2025. “The Wayqecha Amazon Cloud Curtain Ecosystem Experiment: A New Experimental Method to Manipulate Fog Water Inputs in Terrestrial Systems.” *Methods in Ecology and Evolution* 16(2): 400–413. doi:10.1111/2041-210X.14483.
- Muñoz-Villers, L. E., and J. J. McDonnell. 2013. “Land Use Change Effects on Runoff Generation in a Humid Tropical Montane Cloud Forest Region.” *Hydrology and Earth System Sciences* 17(9): 3543–60. doi:10.5194/hess-17-3543-2013.
- Nadkarni, Nalini M., and Rodrigo Solano. 2002. “Potential Effects of Climate Change on Canopy Communities in a Tropical Cloud Forest: An Experimental Approach.” *Oecologia* 131(4): 580–86. doi:10.1007/s00442-002-0899-3.
- Newell, Felicity L., Ian J. Ausprey, and Scott K. Robinson. 2022. “Spatiotemporal Climate Variability in the Andes of Northern Peru: Evaluation of Gridded Datasets to Describe Cloud Forest Microclimate and Local Rainfall.” *International Journal of Climatology* 42(11): 5892–5915. doi:10.1002/joc.7567.

- Oliveira, Rafael S., Cleiton B. Eller, Paulo R. L. Bittencourt, and Mark Mulligan. 2014. "The Hydroclimatic and Ecophysiological Basis of Cloud Forest Distributions under Current and Projected Climates." *Annals of Botany* 113(6): 909–20. doi:10.1093/aob/mcu060.
- Ramírez-Barahona, Santiago, Ángela P. Cuervo-Robayo, Kenneth J. Feeley, Andrés Ernesto Ortiz-Rodríguez, Antonio Acini Vásquez-Aguilar, Juan Francisco Ornelas, and Hernando Rodríguez-Correa. 2025. "Upslope Plant Species Shifts in Mesoamerican Cloud Forests Driven by Climate and Land Use Change." *Science* 387(6738): 1058–63. doi:10.1126/science.adn2559.
- Ray, Deepak K., Udaysankar S. Nair, Robert O. Lawton, Ronald M. Welch, and Roger A. Pielke Sr. 2006. "Impact of Land Use on Costa Rican Tropical Montane Cloud Forests: Sensitivity of Orographic Cloud Formation to Deforestation in the Plains." *Journal of Geophysical Research: Atmospheres* 111(D2). doi:10.1029/2005JD006096.
- Reinhardt, Keith, and William K. Smith. 2008. "Impacts of Cloud Immersion on Microclimate, Photosynthesis and Water Relations of *Abies Fraseri* (Pursh.) Poiret in a Temperate Mountain Cloud Forest." *Oecologia* 158(2): 229–38. doi:10.1007/s00442-008-1128-5.
- Schreel, Jeroen D. M., Jonas S. von der Crone, Ott Kangur, and Kathy Steppe. 2019. "Influence of Drought on Foliar Water Uptake Capacity of Temperate Tree Species." *Forests* 10(7): 562. doi:10.3390/f10070562.
- Schreel, Jeroen D. M., and Kathy Steppe. 2020. "Foliar Water Uptake in Trees: Negligible or Necessary?" *Trends in Plant Science* 25(6): 590–603. doi:10.1016/j.tplants.2020.01.003.
- Sunny, Ron, Malavika Venu, Peddiraju Bandaru, Souparna Chakrabarty, and Deepak Barua. 2026. "It's about Time! Leaf Minimum Conductance Determines Time to Reach Critical Thresholds for Leaf Dehydration in a Seasonal Tropical Forest." *Tree Physiology* 46(4): tpag027. doi:10.1093/treephys/tpag027.
- Wang, Yan, Binbin Li, Peipei Bao, Ronghua Wang, Aoyun Min, and Peifeng Xiong. 2023. "A Case Study of Leaf Wettability Variability and the Relations with Leaf Traits and Surface Water Storage for Urban Landscape Plants." *Water* 15(12): 2152. doi:10.3390/w15122152.
- Wittemann, Maria, Myriam Mujawamariya, Bonaventure Ntirugulirwa, Felicien K. Uwizeye, Etienne Zibera, Olivier Jean Leonce Manzi, Donat Nsabimana, Göran Wallin, and Johan Uddling. 2024. "Plasticity and Implications of Water-Use Traits in Contrasting Tropical Tree Species under Climate Change." *Physiologia Plantarum* 176(3): e14326. doi:10.1111/ppl.14326.

Appendix 1

Popular Science Summary

Tropical montane trees and clouds: An investigation

Tropical forests are one of the most unique and diverse ecosystem types on the planet, and unfortunately, one of the most threatened by the rapid shifts in temperature and humidity caused by climate change. Among them, tropical montane cloud forests – perpetually covered in dense fog due to their special local weather conditions – are home to species found only there and form unique habitats that are especially vulnerable to climatic change, as stable fog levels are important for their survival. However, research on the exact impact of cloud coverage on the natural ecosystem processes is limited, especially when it comes to plants.

In our study, we examined 25 tropical tree species that are found in the Wayqecha Amazon region of Peru, across 15 different sites characterized by different fog density (High, Medium and Low), testing three of the most key traits related to how trees might be benefited by the fog: their capacity to absorb water droplets through their leaves (a process called foliar water uptake, FWU). Their minimum conductance (g_{min}) which is essentially a measure of how open or closed the little mouth-like cells (stomata) on the surface of their leaves are, since they are responsible for how much moisture comes in and out of the plant during breathing. Lastly, their leaf water retention is measured by the angle at which water slides off the surface of different leaves, which is affected by different leaf features, such as the presence of hair or their texture.

Along with these 15 sites, we sampled two more special plots, which were part of a previously established experiment, the Wayqecha Amazon Cloud Curtain Ecosystem Experiment (WACCCE), where a large net was set up between the control and test site, to reduce the amount of fog the latter would receive and thus, allow us to compare the differences between them. Branches and leaves were collected from all these sites and were brought back to our makeshift lab, where some were submerged into water for two hours to test their FWU capacity, some were air-dried to measure their g_{min} and others used for water retention estimates.

After in-depth analysis of the collected data, apart from differences between the different species, showed that leaf water retention angle appears to have a significant effect on the formation of tree communities in the cloud gradient. There was no effect of cloud immersion into any of the traits, neither in the cloud gradient, nor in the WACCCE fog exclusion treatment. Another interesting observation, however, was that the trees in the sites that were marked with Medium fog levels showed either the highest or lowest values consistently across all species, with few exceptions. This can be attributed to our classification system for each site, as the distinction between High, Medium and Low cloud levels was based on atmospheric models, rather than actual humidity measurements. This opens up interesting possibilities for future experimentation, as installing specialized equipment could give us a clearer picture of how to characterize different sites according to their fogginess more accurately.

Despite the lack of significant results besides the effects of leaf water retention on tree communities, the observed patterns could provide vital information for researchers who aim to expand the topic. It is clear that species react differently to different cloud levels, so refining our approach in future experiments might be the key. Our understanding of how these fragile ecosystems function is so limited that any progress is vital for future conservation efforts, and our efforts are only the beginning.

Appendix 2

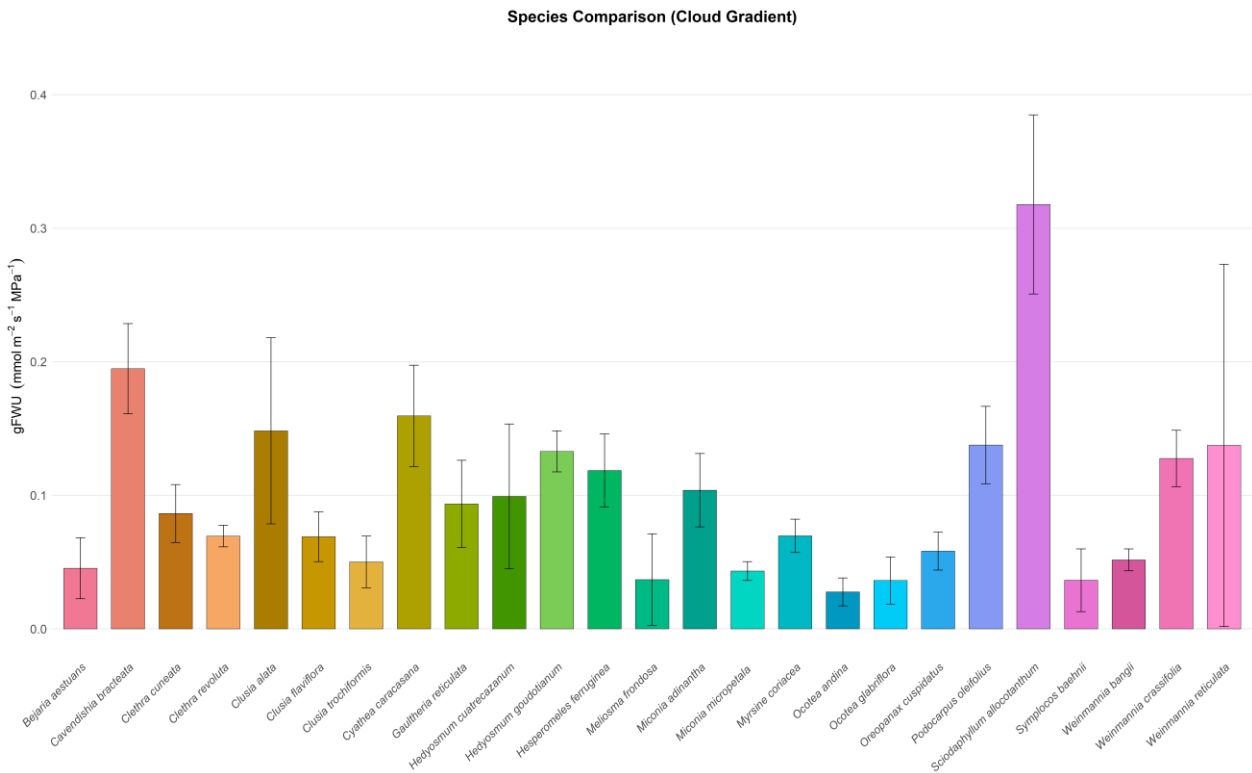


Figure A 1. Species comparison for foliar water uptake conductance (gFWU, $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) in the cloud gradient shown with standard errors (SE).

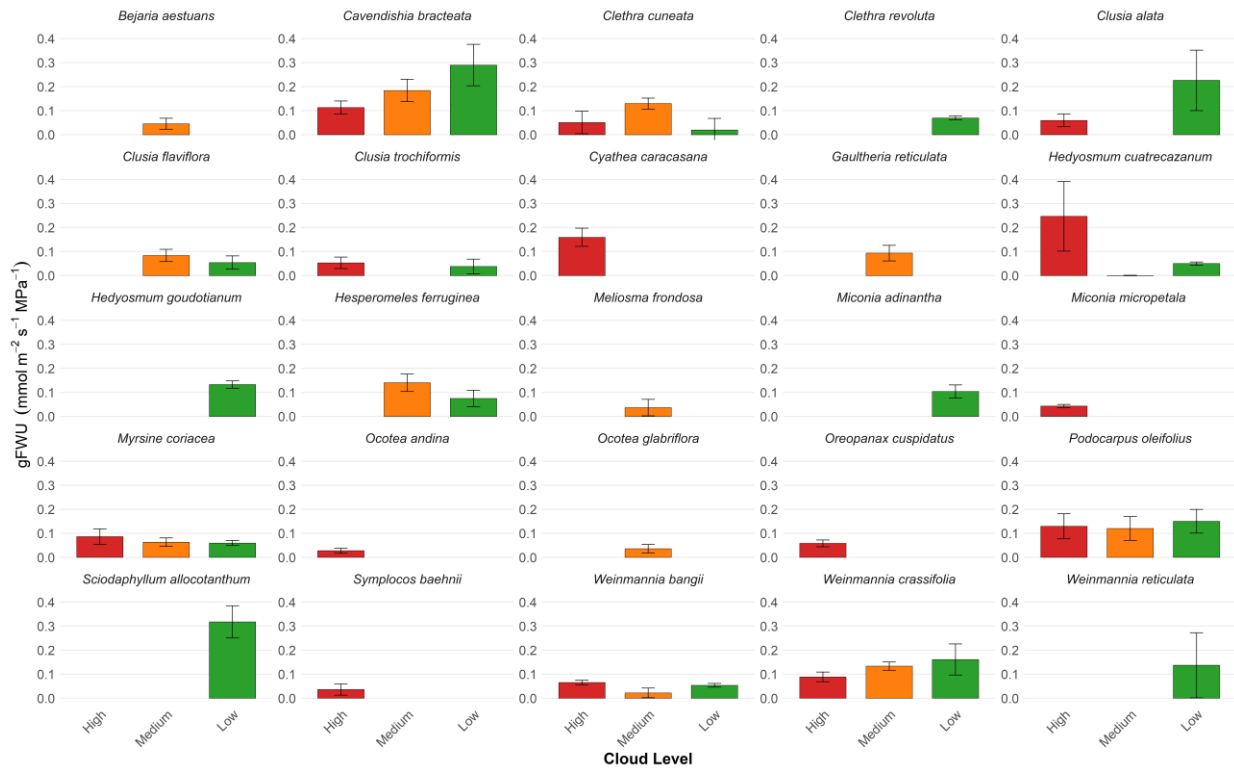


Figure A 2. Cloud cover level plot comparison within each of the 25 species sampled along the cloud gradient for foliar water uptake conductance (gFWU, $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) shown with standard errors (SE). The three cloud levels are (in order of appearance): High (red), Medium (green) and Low (blue). It is important to note that not all species are present across all plots, hence the lack of data for some cloud levels in some species.

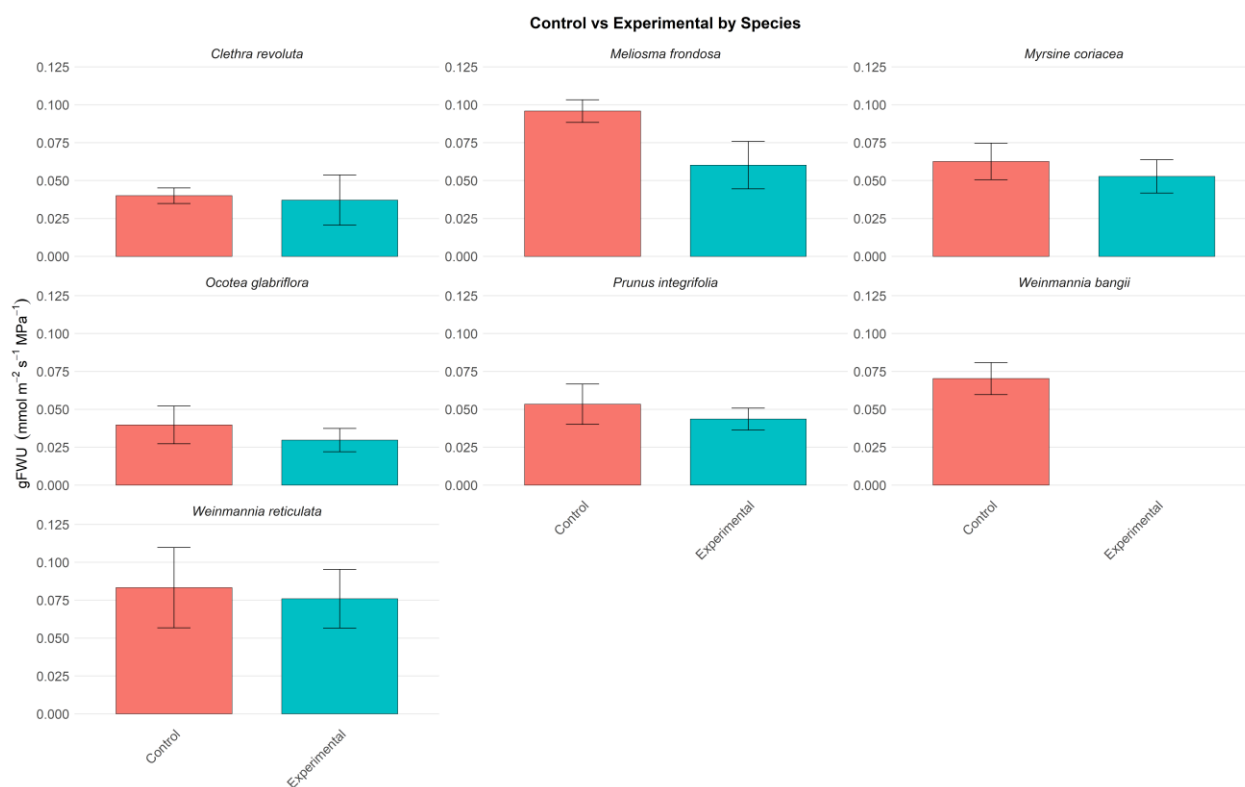


Figure A 3. Comparison foliar water uptake conductance (gFWU, $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) between the control (red) and experimental (blue) plots of the WACCEE for each of the species measured shown with standard errors (SE). The species *Weinmannia bangii* was present only on the control plot.

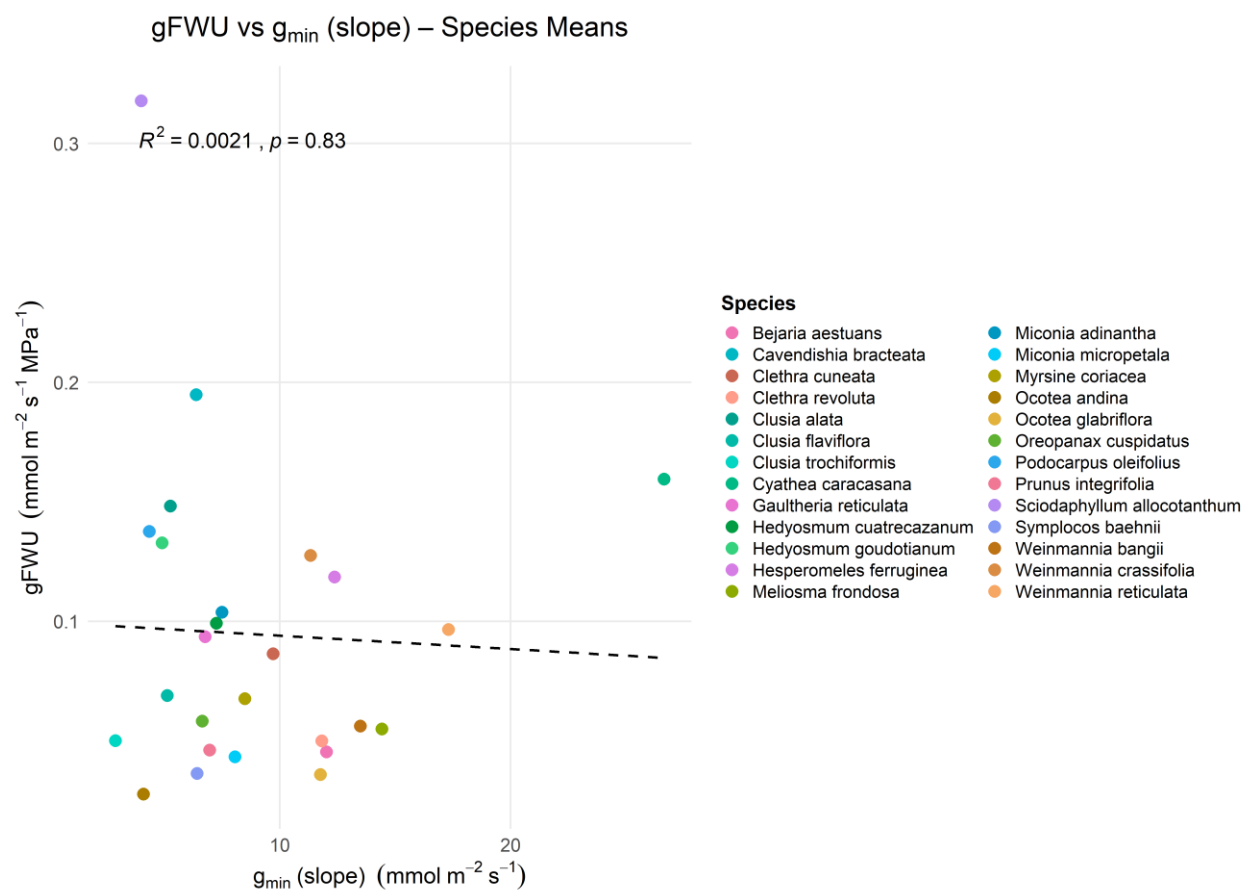


Figure A 4 Scatterplot showing the relationship between minimum conductance ($g_{\min}$, $\text{mmol m}^{-2} \text{s}^{-1}$) and foliar water uptake conductance (gFWU, $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) across species, including data from the cloud gradient as well as the WACCEE plots. No significant relationship was observed ($p = 0.83$).

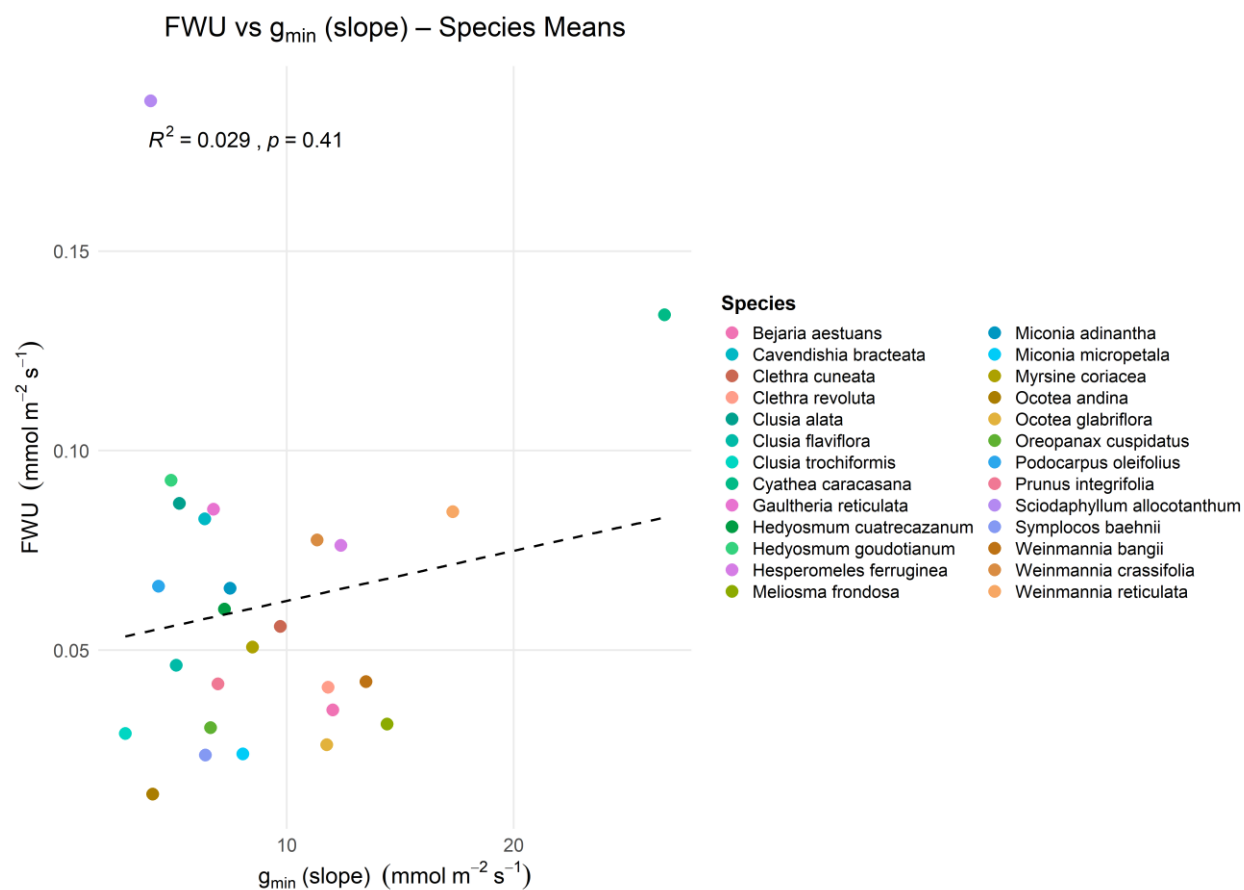


Figure A 5 Scatterplot showing the relationship between minimum conductance ($g_{\min}$, $\text{mmol m}^{-2} \text{s}^{-1}$) and foliar water uptake (FWU, $\text{mmol m}^{-2} \text{s}^{-1}$) across species, including data from the cloud gradient as well as the WACCEE plots. No significant relationship was observed ($p = 0.41$).