

**How does fog affects microclimatic
conditions and leaf functioning in tropical
montane cloud forests?**

**Como a neblina afeta as condições
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em florestas nebulares montanas nos
trópicos?**

**Universidade Estadual de Campinas
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**Universidade Estadual de Campinas
Instituto de Biologia**

Paulo Roberto de Lima Bittencourt

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Biology of the University of Campinas in
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da Dissertação defendida pelo candidato
**PAULO ROBERTO DE LIMA
BITTENCOURT**
e aprovada pela Comissão Julgadora.

Rafael S. Oliveira

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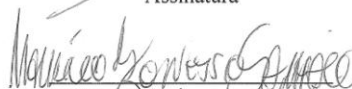
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Abstract

Tropical montane cloud forests (TMCFs) are ecosystems with frequent fog immersion influencing almost all aspects of its functioning. TMCFs are extremely important both due to the ecosystem services it provides, particularly hydrologically, and because of its high biodiversity. With climate and land use changes already happening there is urgency on understanding TMCFs functioning to devise conservation and restoration strategies. The objective of this work is to analyze and quantify fog effects on the microclimate and leaf functioning of TMCFs. We measured fog occurrence, microclimatic variables, photosynthetic parameters and used a new methodology to measure foliar water uptake capacity of five abundant TMCFs tree species in the region of Campos do Jordão, Brazil. We used these data to estimate fog effects on water availability, atmospheric water demand, potential photosynthesis, leaf water uptake and leaf thermal balance of TMCF. Fog had a pronounced effect on increasing soil water availability and reducing atmospheric water demand. Fog had a negligible effect on reducing potential photosynthesis of the studied species. We provide for the first time estimates of fog effects on leaf thermal balance showing it has an important effect on buffering mean daytime leaf temperatures by reducing it 0.5°C for each hour of fog occurrence. We found that foliar uptake of fog water constitutes an important water source for the studied species, with nocturnal fog having the potential to rehydrate leaves of two of the studied species from its driest conditions to fully rehydration more than 50% of the nights. Differences in foliar water uptake capacity in the studied species suggests leaf water uptake is an important resource niche with potential of selecting leaf water uptake related traits in TMCFs species.

Resumo

Matas nebulares montanas tropicais (MNMT) são ecossistemas frequentemente inundados por neblinas, o que influencia quase todos os aspectos de seu funcionamento. MNMTs são extremamente importantes devido aos serviços ecossistêmicos que provêm, principalmente hidrológicos, e devido a sua alta biodiversidade. Com mudanças climáticas e de uso de terra já acontecendo, há urgência em compreender o funcionamento de MNMTs para o desenvolvimento de estratégias de conservação e restauração. O objetivo deste trabalho é analisar e quantificar os efeitos da neblina no microclima e funcionamento foliar de MNMTs. Medimos a ocorrência de neblina, variáveis microclimáticas, parâmetros fotossintéticos e usamos uma nova metodologia para medir a capacidade de absorção foliar de água de cinco espécies abundantes de uma MNMT na região de Campos do Jordão, Brasil. Utilizamos esses dados para estimar os efeitos da neblina na disponibilidade hídrica, na demanda de água da atmosfera, na fotossíntese potencial, na absorção foliar de água e no balanço térmico foliar de MNMTs. A neblina teve um forte efeito no aumento da disponibilidade hídrica do solo e na redução da demanda atmosférica de água. A neblina apresentou um efeito negligível na redução da fotossíntese potencial das espécies estudadas. Nós apresentamos, pela primeira vez, estimativas do efeito da neblina no balanço térmico foliar mostrando que ela possui um importante papel em amenizar as temperaturas foliares médias durante o dia, reduzindo-as em 0.5°C por cada hora de ocorrência de neblina. Nós encontramos que a absorção foliar de água constitui uma fonte importante de água para as espécies estudadas, com a neblina noturna possuindo o potencial de reidratar as folhas de duas das espécies estudadas nas suas condições mais secas até hidratação total em mais de 50% das noites. Diferenças na capacidade de absorção foliar de água das espécies estudadas sugere que a absorção foliar é um nicho importante de recursos com o potencial de selecionar características foliares relacionadas à eficiência de absorção foliar de água em espécies de MNMTs.

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Abbreviations

E_l	Leaf evaporation
INMET	Instituto Nacional de Meteorologia
PAR	Photosynthetic active radiation
G_{tot}	Total incoming solar radiation
RH	Relative humidity
SWC	Soil water content
TMCF	Tropical cloud montane forest
T_{air}	Air temperature
T_l	Leaf temperature
VPD	Vapour pressure deficit
WUE	Water use efficiency

1. Introduction

Tropical montane cloud forests (TMCf) are ecosystems characterized by frequent occurrence of orographic clouds at ground level (Hamilton 1995). Clouds occurring at ground level (i.e. fog, as defined from its relevance to biological processes in contrast to meteorological definitions) can lower atmospheric evaporative demand, provide water inputs and reduce incoming solar radiation, deeply affecting the water, energy and nutrient balances of these ecosystems, with consequences to species composition and functioning (Still *et al.*, 1999). TMCfs are extremely important both due to its hydrology, as important watershed water sources, and to its high biodiversity and endemism (Hamilton 1995; Bruijnzeel 2001). Recent climate-change trends points towards a rise in cloud formation altitudes, which, coupled with higher temperatures, intensification of precipitation regimes and land use change, will strongly affect TMCfs distribution (Still *et al.*, 1999; Lawson *et al.* 2011; Al, 2003; IPCC 2013). To predict the fate of TMCfs and to devise conservation and restoration strategies we need to understand which climatic factors most affect TMCfs functioning.

Although TMCfs are generally moist places, due to their high altitudes, in clear days the radiation input is considerably higher than in lowlands, and, together with short dry spells and rainfall seasonality in some TMCfs, plant water stress can occur (Eller *et al.* 2013). TMCfs are characterized by low statured trees (2-20m of height) with scleromorphic features like small and thick leaves, crooked and gnarled branches and stems; epiphytic moss and lichen cover is extremely high and the occurrence of lianas is generally small; soils are peaty and frequently waterlogged (Bruijnzeel, 2001; Unesco 2000). The scleromorphic features of plants are often associated to the intense transient water stress, particularly of plants direct exposed to sunlight (Leuschner, 2000). TMCfs occur all through over the tropics in mountainous regions where the average temperature falls below 18°C and frequent cloud condensation occurs (1700m on average, but lower heights for island mountains and higher latitudes), with rainfall ranging from 600-4500mm y⁻¹, with or without a dry season, and confined to within 350km of the coast (Bruijnzeel, 2001; Jarvis & Mulligan, 2011).

Mountains worldwide have a disproportional importance in the hydrologic balance, supplying on average 32% of total basin river discharge in the tropics and up to 95% in some regions, while only representing a fraction of land cover (Viviroli *et al.*, 2007). TMCs have a particular role in this balance as they increase ecosystem water inputs by up to 50% of total annual rainfall through plant fog interception and may have an even more pronounced effect during the dry season (Bruijnzeel, 2001; Garcia-Santos *et al.*, 2004). In the coastal mountains of Fray Jorge, Chile, rain forest patches occur in a desert matrix due solely to fog interception, which also provides water for human use (Garreaud *et al.*, 2008). They also have two, almost always ignored, additional roles in increasing water inputs through: (1) stem flow of intercepted fog water and (2) transport of water from the leaves surfaces through the plant directly to the soil (Crockford & Richardson 2000; Eller *et al.*, 2013). Brazilian cloud forests are distributed along the Serra do Mar and Serra da Mantiqueira ranges and, even though mountains contribute little to total Brazilian hydrology, in these regions they are considered important, with a water catchment three times higher than the total catchment of the basin in the lowlands (Viviroli *et al.* 2007).

Most TMCs occur at the center of biodiversity hotspots, resulting in a disproportionately high contribution to biodiversity (about 20% of plant and 16% of vertebrate global biodiversity) while occupying only 0.4% of the terrestrial area (Ray *et al.*, 2006). Although tree species diversity in TMCs are not so high as in other tropical forests, the diversity of herbs, shrubs, lycophytes, epiphytic bryophytes, orchids, bromeliads and ferns is extremely high (Hamilton 1995). The true value of TMC's biodiversity lies in its high endemism, due to its particular environment and to being, many times, the last remnants of plant formations that were lost due to human land use (UNESCO 2000). In South and Southeastern Brazil, TMCs comprise a distinct phytogeographic formation in relation to other montane forests and they represent refuges to formations that had larger distributions during the last glaciation, further increasing their biodiversity value (Behling & Lichte 1997; Bertoncello *et al.*, 2011).

As almost all aspects of TMCs are affected by the cloud regimes and, particularly, cloud immersion, an increase in cloud base heights coupled to greater temperatures and precipitation extremes would greatly affect these ecosystems (Still *et*

al., 1999; IPCC 2013). Predicted consequences include biodiversity loss, community composition changes, altitudinal shifts in species and communities occurrence and even changes in vegetal formation, with additional consequences to ecosystems that depends on their hydrologic function (Foster, 2001). These effects are even more intense if we consider that TMCs occur on narrow bands at mountain tops with small or no room to upwards altitudinal shifts, many times isolated in patches in different “mountain top islands”, reducing the connectivity and potential of recolonization (UNESCO 2000; Foster, 2001).

TMCs are also highly threatened by land use changes including wood cutting for fuel, conversion to crop plantations and conversion to grazing lands (UNESCO 2000). Recent studies in the Monte Verde cloud forests in Costa Rica indicate that TMCs are also subject to influence of land use in lowland forests, with reduction of lowland forests associated to reduced fog, higher clouds formations and upward shifts of anuran and birds populations occurrence (Lawton *et al.* 2001; Nair, 2003; Ray *et al.*, 2006; Nair *et al.*, 2010).

1.1 Fog Effects on Plant Functioning

Fog effects on plant functioning can be divided in four areas that are interconnected at the ecosystem and plant functioning levels: plant water availability, evaporative demand, radiative inputs and thermal buffering.

1.1.1 – Water availability

Arguably the most studied fog effects on plant functioning is its increase in soil water availability. Many studies have quantified total fog contribution to soil water content through fog stripping, the interception of fog droplets that hits leaves and falls to the ground. Studies shows fog stripping can amount up to 50% of total annual rainfall input, with an even greater importance in some particular environments and during the dry season (Bruijnzeel, 2001; Liu, 2004; Barbosa *et al.*, 2010). To our knowledge, the amount of stemflow generated by fog stripping was never quantified. Fog effects like leaf water uptake on plant water status and on soil water content through hydraulic redistribution,

although somewhat studied in a few fog dependent ecosystems like the red wood forests (Dawson 1998), are largely unknown in TMCFs, both qualitatively and quantitatively.

It is known for a long time that leaves can directly absorb water (Slatyer, 1956), but its importance to plant functioning has only recently been demonstrated. It was shown that leaf water uptake (the process of absorbing water through the leaf) occurs in 80% of the most abundant species in the frequently fog inundated Redwood Forests, California, and that leaf water uptake has positive effects on leaf rehydration (Burns *et al.*, 2009). Recently, Eller *et al.* (2013) demonstrated that fog has a key role in the functioning of *Drimys brasiliensis*, the most abundant species from Campos do Jordão's TMCFs. According to their work, fog related leaf wetting is responsible for a great part of the leaf foliar water content of *D. brasiliensis* and has positive effects on its leaf water potential. Moreover, Eller *et al.* (2013) also found that fog affects *D. brasiliensis* overall fitness and can be hydraulic redistributed to the soil, through reversed sap flow, significantly contributing to soil water content. Needless to say that leaf uptake is fundamental to the abundant epiphytic moss and lichen cover present in TMCFs (Villegas *et al.*, 2008).

The fog-related increase in soil water content and leaf water uptake allow plants to maintain a higher water potential, reducing xylem cavitation occurrence, which results in them functioning with a greater hydraulic safety margin (the difference between actual plant water potential and the plant water potential where significant cavitation occurs; Choat *et al.*, 2012). If fog-related increases in plant water potential results in fully rehydration then xylem bubbles can dissolve, removing xylem cavitation from previous drought events and further increasing the hydraulic safety margin (Sperry *et al.*, 2003). Increased water availability coupled to leaf wetting may also have a role in vessel refilling for herbs, shrubs and small trees by favoring positive root pressures (Fisher *et al.* 1997). This greater safety margin further allows them to maintain stomata open for a longer time, as they have less need to control xylem water potential to avoid cavitation, resulting in greater carbon assimilation and overall fitness. Plant fitness is also increased, not only by the increase in carbon assimilation, but also by reduction of hydraulic failure, which leads to disconnection of water and carbon flows in the different plant organs, resulting in dehydration or starvation of these organs and possible plant death (Sala 2010; McDowell, 2011).

1.1.2 – Photosynthesis and Radiation Inputs

Fog, like any other type of cloud, has an important effect in reducing incident solar radiation, which is reflected back to the sky or absorbed, reducing radiative inputs at ground level. This reduces photosynthetically active radiation (PAR) availability to plants and may reduce photosynthesis if it is not already CO₂ limited, that is, stomata are not closed to reduce plant water loss. The few studies that addressed this question found a strong effect of fog on PAR reduction but with no consequences to photosynthesis or even an increase in photosynthesis despite the lower PAR (Johnson & Smith, 2008; Ritter *et al.*, 2009; Berry & Smith, 2013).

The net effect of PAR reduction on photosynthesis is complex to determine as it depends on the relationship between the time of PAR reduction and plants already being under stomatal limitation in that time. It also depends on the reduced stomatal limitation due to fog-related decrease of water stress and it must be considered relative to background non-fog PAR reduction. Plant photosynthetic properties also influence this effect as plants may still be light saturated even under reduced PAR. Fog radiative inputs reduction is also associated with an increase in diffuse radiation, which is thought to have a beneficial effect on overall photosynthesis as it reaches shaded areas of the canopy and produces a more uniform canopy irradiation (Mercado *et al.*, 2009). The increase in diffuse radiation is probably very important to understory and epiphytic plants and, possible, favors plant traits that increase diffuse radiation harvesting like non-horizontal leaves.

1.1.3 – Temperature

Fog is associated with a strong reduction in solar energy inputs. Solar energy input is the principal driver of surfaces temperature deviations from air temperature (T_{air}). As TMCs occurs in high altitudes, clear day solar inputs are extremely high and provides an energy to leaves that must be readily dissipated, either through radiative energy transfer, sensible heat exchange or evaporative cooling, to not cause leaf thermal damage or physiological photosynthesis reduction (Leuschner, 2000). Evaporation is responsible for around one third of total leaf thermal energy dissipation and is almost

entirely driven by radiation energy inputs (Ye *et al.*, 2013). Due to the high energy inputs, plant morphology traits associated to reduction of the boundary layer and greater coupling between plant and atmosphere may be important in reducing leaf temperatures (T_l) in TMCFs.

Fog can also trap long wave energy at ground level which is absorbed by fog and reflected back to the ground. This may be important in buffering minimum T_l at night and, in the winter, in reducing frost occurrence (Leuning & Cremer, 1988). On the other hand, it is possible that lower temperatures during fog events may decrease photosynthetic activity by making plants operate in the lower range of their thermal niche.

Fog events may also have a role in mean T_{air} if fog air masses have different thermal characteristics than non-fog air masses, although this effect has not been evaluated. One possibility is that fog clouds air masses may be inherently colder if they are associated with faster winds, leading to a faster vertical rise upon contact with mountain slopes and less time for it to exchange heat after its temperature has been decreased by adiabatic cooling. Alternatively, fog air masses may have higher temperatures as the adiabatic cooling during vertical rise is smaller for moist air masses in relation to dry air masses due to latent heat released by water condensation.

High radiation inputs coupled with lower temperatures associated to mountain climates makes TMCFs experience an enormous daily T_{air} change, with mean amplitudes higher than 10°C though the year (Jarvis & Mulligan, 2011). Direct consequences of fog thermal buffering to plant functioning are increases in photosynthetic rates and reductions in plant thermal damage, which may be directly related to plant mortality due to reduction in temperature extremes.

1.1.4 – Evaporative Demand

Fog events are inherently moist with its air mass filled with many floating small water droplets. Vapour pressure deficit (VPD) and leaf evaporation (E_l) during foggy events and in foggy days are known to be greatly reduced (Johnson & Smith, 2008; Ritter *et al.*, 2009; Eller *et al.*, 2013; Berry & Smith, 2013). This is a compound effect of lower atmospheric VPD, lower T_l due to lower radiation and overall persistence of higher air

humidity as the wet leaves will continue to increase the environment relative humidity even after the fog is gone. To our knowledge, the individual contribution of each effect has not been studied. Direct consequences to plants are (1) higher water use efficiency (WUE; the amount of water lost for each unit of photosynthetic assimilation); (2) increased plant water potentials, which further affects xylem vessel refilling, hydraulic safety margin, photosynthesis and plant mortality; and (3) a reduced latent heat loss. The indirect consequence is increased soil water content in the long term, as less soil water is evaporated to the atmosphere through E_i , which further benefits plant water potential.

Additional fog effects, not addressed in this work, include nutrient inputs to ecosystem in fog intercepted water inputs to soil (Eugster, 2007), possible increases in phytopathologies related to constant leaf wetting (Djurle *et al.*, 1996) and decreased plant CO_2 conductance due to the water film cover of wet leaves and its possible reduction in plant photosynthesis (Ishibashi & Terashima 1995).

1.3 – Objectives and Hypotheses

The objective of this work was to analyze fog effects on microclimatic conditions and leaf functioning in TMCFs. We hypothesize fog significantly affects plant water availability, evaporative demand, radiation inputs and thermal conditions of TMCFs plants. The following questions and expectations were addressed:

- (1) How frequent are fog events? What is the contribution of fog to soil water inputs?
What is the importance of fog to plant rehydration through leaf water uptake?
 - Fog is frequent all through the year and is equally important during periods of soil drought.
 - Fog events contribute as much as rain events to soil water input.
 - Leaf rehydration during night fog events can fully rehydrate plant leaves.
- (2) How much does fog reduces daytime PAR? Does reduced PAR leads to reduced plant photosynthesis? If it does, in which periods of the day these reductions are more important?
 - Fog reduces plants potential photosynthetic rates.

- Fog reductions of PAR and plant potential photosynthesis is different in the morning, mid day and evening.
- (3) How much fog affects VPD and E_l ? Through which mechanisms fog affects VPD and E_l ?
- Fog affects VPD mainly through increased air umidity.
 - Fog affects E_l through increased air umidity and decreased incident solar radiation.
- (4) Does fog has a role in buffering T_{air} and T_l ? If it does, through which mechanisms fog affects T_{air} and T_l ?
- Fog events reduce T_{air} and T_l .
 - The main fog effect on leaf temperatures is through decreased incident solar radiation.
 - Fog reduces minimum night air temperature.

To address these questions and test the hypotheses we measured fog occurrence, microclimatic variables, soil water dynamics and plant functional characteristics in a TMCF. We used these data to directly test for fog effects or to simulate fog effects on plant functioning.

2. Material and Methods

2.1 – Site description

The study was carried out in the edge of a TMCF fragment in the Campos do Jordão Plateau, Mantiqueira Range, in the Céu Estrelado Farm (22°43'09"S 45°27'20"), near the town of Campos do Jordão, São Paulo, Brazil, from February to November of 2013. The forest fragment is situated at 2000m altitude, approximately 120 km from the Atlantic Ocean, at the border of the Campos do Jordão Plateau, where the altitude quickly drops from 2000m to 500m in 5km of horizontal distance, making orographic generated events particularly important in this area.

Mean annual rainfall, as measured for the period of 1961 to 2011 from a nearby weather station in the town of Campos do Jordão (INMET; 1642m a.s.l.) is 1849 mm, with a dry and cold season from June to August and occurrence of small drought spells

during the wet and warm season. Mean annual T_{air} is 14.9°C with the lowest minimum mean T_{air} in July of 10.8°C. Fog frequency is extremely high for the entire region. Frosts occur frequently at night in the coldest months in the grassland but not so frequently in the TMCF (personal observations). To the best of our knowledge, frost effects on TMCFs were never studied. According to the 1961-2011 climatic data, the region climate is considered subtropical highland with dry winter in the Köppen classification. A summary of month T_{air} and month precipitation frequencies and intensities is presented in table 1. T_{air} and air relative humidity (RH) for the study period can be seen in figure 1.

Table 1. Monthly mean (μ) and standard deviation (SD) of mean day temperature, month precipitation frequency (number of days with precipitation events by month) and precipitation event intensity ($\text{mmH}_2\text{O day}^{-1}$) for the period of 1961-2011 in the region of Campos do Jordão, Southeastern Brazil. Data was obtained from Instituto Nacional de Meteorologia – INMET.

Month	Temperature (°C)		Precipitation Frequency (number of days with rainfall)		Precipitation Intensity ($\text{mmH}_2\text{O day}^{-1}$)	
	μ	SD	μ	SD	M	SD
Jan	18.0	1.7	22.9	2.6	13.1	3.3
Feb	18.1	1.4	22.9	4.6	11.8	3.3
Mar	17.3	1.5	19.6	4.2	11.0	3.3
Apr	15.2	2.0	11.7	2.8	9.6	4.3
May	12.7	2.1	9.2	2.1	8.8	3.4
Jun	11.2	2.2	5.7	2.3	7.1	2.9
Jul	10.8	2.2	4.8	1.6	8.8	3.9
Aug	12.2	2.2	4.7	2.2	10.0	8.2
Sep	14.1	2.3	9.3	3.1	10.2	4.7
Oct	15.5	2.1	14.3	3.6	11.7	4.9
Nov	16.4	2.1	17.4	3.5	11.2	3.4
Dec	17.3	1.8	22.3	3.0	12.8	3.7

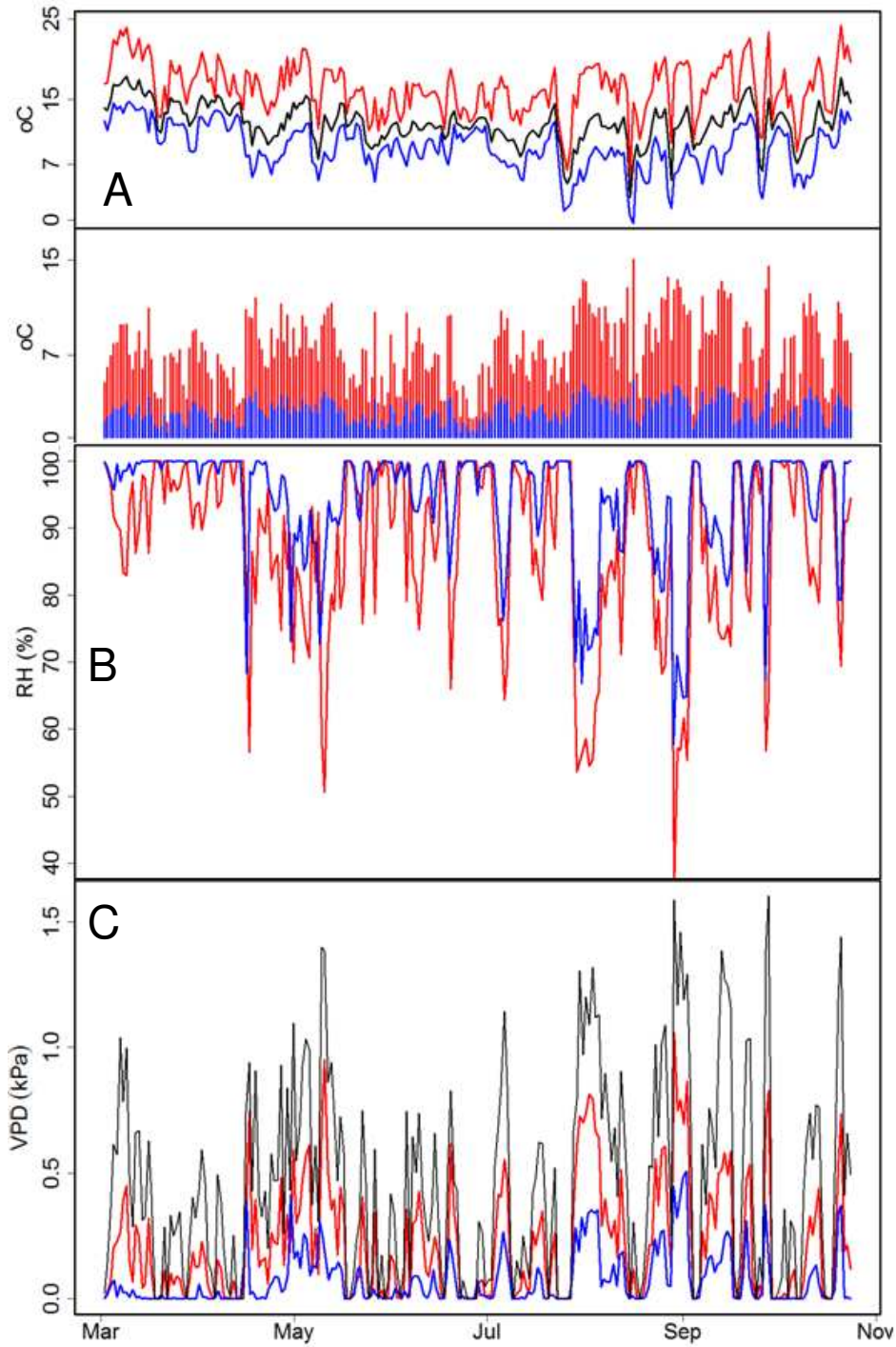


Figure 1. Temperature ($^{\circ}\text{C}$), relative umidity (RH; %) and vapour pressure deficit (VPD; kPa) in the studied TMCF in Campos do Jordão from March to November 2013. (A) Upper panel: Mean day temperature (black), minimum day temperature (blue) and maximum day temperature (red). Lower panel: Daily temperature range (red bars) and daily temperature standard deviation. (B) Day time mean temperature (red) and night time mean temperature (blue). (C) Mean daily air VPD for nighttime (blue), daytime (red) and maximum air VPD.

2.2 – Microclimatic variables and soil water content

Microclimatic variables were measured every 30 minutes from February to November of 2013. T_{air} and RH in the forest edge were measure using air temperature and humidity sensors (model U23-001, Onset Computer Corporation, Bourne, MA, USA) and further used to calculate VPD. Leaf wetness, precipitation and incident PAR were measured at the forest edge with sensors models S-LWA-M003, RG3-M and S-LIA-M003 (Onset Computer Corporation) connected to data loggers (H21-002 or H22-001, Onset Computer Coporation). Care was taken to place the sensors in places were they would not be shaded.

Soil water content (SWC) was measured with four water content reflectometers (model S-SMC-005, Onset Computer Corporation), connected to the above described data loggers. Two sensors were placed in the forest edge and two in the campo de altitude (high altitude grassland) next to the forest edge, one at depths of 5cm and one at 25cm in each place. Due to technical problems in the pluviometer and a wild fire in the grassland on September which burned some sensors, SWC in the grassland is available from 3/1/2013 to 09/23/2013 and precipitation from 09/23/2013 onwards. For some data a small gap from 09/23/2013 to 9/28/2013, when we replaced the sensors, is present. The wild fire did not reached the forest border and we believe its effects were negligible for this experiment.

To reduce noise resulting from seasonal differences in T_{air} , RH, VPD, and incident PAR, we used the deviation of variables from the month means in the analysis, according to the formula:

$$X_{\text{dev}} = X_{\text{day}} - X_{\text{month}}$$

Where X_{dev} is the variable deviation from the month mean, X_{day} is the daily mean, and X_{month} is the month mean. When the summarizing function for daily data aggregation was different, the month mean represent the mean of the days aggregated according to the same function (ex.: minimum day temperature deviation is equal to minimum day temperature subtracted from the means of minimum day temperatures of the month)

2.3 – Water Availability

2.3.1 – Fog frequency and leaf wetting

To verify fog effects on plant water availability we quantified fog occurrence during the study period. We considered leaves were wet during fog events and compared the amount of time leaves remained wet due to fog and due to rainfall. We also verified if fog frequency was different during periods of soil drought.

We inferred fog events from climate, precipitation and soil water content data. For daytime, a fog event was assumed to be happening when VPD was below 0.01kPa and rain was not falling. At an RH of 99%, VPD only reaches 0.01kPa when T_{air} falls below 7°C, so we consider VPD lower than 0.01kPa when there is no rain a good criterion for fog occurrence. For nighttime data, as night VPD is smaller than daytime VPD, we added the criterion of leaf wetness higher than 95% in the sensor. Leaf wetness sensors were not used to infer daytime fog events because our observations showed that they do not get wetted in daytime fog, probably due to its low fog interception coupled with incoming solar radiation evaporative forcing. Fog events associated with rains events were indistinguishable and were not considered. Day time was considered as the hours when PAR was higher than $25\mu\text{mol m}^{-2} \text{s}^{-1}$.

In the above procedure, for periods where no precipitation data was available, we used SWC data from the top 5cm layer of the grassland to infer rainfall. We assumed that fog events did not cause changes in the SWC of grasslands due to its very small fog interception caused by low wind speed at the vegetation surface and low vegetation interception area. This assumption was validated correlating data from the SWC sensors in the forest border and in the grassland. A rainfall event was occurring if SWC was increased from time $t+1$ to t . If SWC was draining (that is, SWC_{t+1} minus SWC_t was more negative than the maximum decrease due to evapotranspiration during clear days) we assumed a rain was also potentially occurring. Drainage time until SWC returned to saturated values were usually fast, with values much higher than evapotranspiration values, and did not span more than 2 hours. Very small positive fluctuations in the sensor measurements did occur, but care was taken so the algorithm used did not consider them as rain events.

For the comparisons of fog frequency during soil drought periods and non-soil drought periods and other drought/non-drought comparisons, we considered periods with soil drought when the mean of SWC at 5cm and at 25cm, which integrates both soil layers, in the forest stand were lower than 30% of the value of the wetter months (Mars and April; horizontal line in figure 6).

2.3.2 – Soil water recharge due to fog and to rain

To verify fog contributions to SWC at the border we quantified the contribution of fog and rain to soil water recharge. Fog and rain events recharged the soil, when SWC after fog or rain event increased in relation to the SWC before the event. We iteratively scanned the fog/rain event occurrence data to determine each event start and end. SWC recharge (SWC_r) was calculated as:

$$SWC_r = SWC_{end+1} - SWC_{start-1}$$

That is, the difference between SWC right after the fog/rain event ended (SWC_{end+1}) and the SWC right before the fog/rain event started ($SWC_{start-1}$). If the difference was negative it was assumed that SWC before the fog/rain event was already saturated and the difference was due to soil water drainage. SWC_r was considered 0 in these situations. Individual SWC_r was aggregated into total day SWC_r by summing SWC_r of each event along a day.

2.3.3 – Potential leaf rehydration through leaf water uptake

To evaluate potential leaf rehydration due to water uptake and rehydration due to nocturnal fog we calculated leaf lamina conductivity to water and verified the rehydration effect as a function of nocturnal fog duration. The following approach was used:

We used the leaf relaxation kinetics of the leaf water potential (Brodribb & Holbrook, 2003), normally used to measure leaf xylem conductivity to water, to calculate the hydraulic conductivity of foliar surface to the leaf cellular spaces. This method assumes the detached leaf act as a capacitor, taking water through the petiole to recharge. We used the same principle but we supplied water to the leaf through the leaf lamina and not the petiole. As the driving force for water movement is still the same, the only

difference is that we measured conductivity from leaf lamina to leaf cells. The equation used was the same as in Broodribb & Holbrook (2003):

$$K_{\text{lam}} = C \cdot \ln(\Psi_0/\Psi_f)/t$$

Where K_{lam} is the leaf lamina – leaf cells conductivity ($\text{mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$), Ψ_0 and Ψ_f are the leaf water potential before the water was supplied to the leaf lamina and after the process (MPa), C is the leaf absolute capacitance on a per area basis ($\text{mol m}^{-2} \text{ MPa}^{-1}$) and t is the amount of time water was supplied. For the K_{lam} measurement procedure we let branches of the analyzed species dry for some time, we putted them in plastic bags during 1 hour for the leaf and branch water potential to equalize and measured Ψ_0 of two leaves. We then cut a third leaf of the same branch with a razor blade and covered its petiole with plastic film, immersed its lamina in ultrapure water for 2 hours and then measured Ψ_f . All water potential measures were made with a pressure chamber (Model 1000, PMS, USA).

Leaf capacitance was calculated from the slope of the non linear part of the pressure-volume relationship ($\delta\text{RWC}/\delta\Psi$; MPa^{-1} ; Schulte, 1985). Leaf capacitance was then multiplied by the leaf mass by area ratio (LMA) and by the relative water content of the leaf at saturation ($W_{\text{sat}}/W_{\text{dry}}$, where W_{sat} is saturated leaf weight and W_{dry} is dry leaf weight) and divided by the molar mass of water (M) to obtain C (Brodrribb & Holbrook, 2003).

K_{lam} and C were determined for 5 samples, each of different individuals, of 5 abundant tree species in the TMCFs of the region according to a recent survey we did (unpublished data): *Croton piptocalyx* (Euphorbiaceae), *Drimys brasiliensis* (Winteraceae), *Myrsine ferruginea* (Myrsinaceae), *Siphoneugenea* sp. (Myrtaceae) and *Solanum* sp. (Solanaceae). Having K_{lam} and C we calculated potential leaf rehydration due to night fog for each day reorganizing the equation for K_{lam} as:

$$\Psi_0 = \exp(K_{\text{lam}} \cdot t/C) \cdot \Psi_f$$

Where t is the duration of nighttime fog immersion in each day (s), Ψ_f is equal to -0.1MPa, a value for which we considered plants fully hydrated (the mathematical properties of the rehydration kinetics only reaches zero when t equals infinity). Ψ_0 is, then, the lowest leaf potential that the nocturnal fog of the given day could restore to -0.1MPa in a detached leaf. Actual rehydration will depend on the contributions of soil

water supply to the leaves and on the contribution of leaf uptake to recharge of non-leaf capacitances and the soil.

We considered plants were fully rehydrated in days where the potential leaf rehydration was higher than the minimum mid day leaf water potential of the year for each species. We then divided the number of days that plants were fully rehydrated by the total number of days in the study period to obtain the daily probability of full rehydration due to leaf water uptake. We also verified if the probability of full rehydration in soil drought periods were different from non soil drought periods. Minimum mid day leaf water potential for each species in 2013 was obtained from monthly field measurements with a pressure chamber (Model 1000, PMS, USA).

2.4 – Light availability and plant photosynthesis

To verify if fog reduces available light energy to plants we used incident PAR data and verified if it was different during fog and non fog events. We further associated these data to photosynthesis using plants photosynthetic light response curves to verify if fog reduced plant potential photosynthesis.

We calculated incident PAR reduction as the per cent reduction in available PAR in relation to clear sky incident PAR. As the mechanism of fog or non fog events that reduces available energy light is almost entirely cloud cover (Liepert, 2002), we termed this reduction Cloudiness (%) and calculated as:

$$\text{Cloudiness} = 100 - 100(\text{PAR}_t / \text{PAR}_{\text{max}})$$

Where PAR_t is the mean incident PAR in the interval t (day or hour) and PAR_{max} is the mean incident PAR if there were no clouds in the same interval. To calculate PAR_{max} we took, for each month, the maximum PAR value that each hour of the day had in the month and considered a fully clear day as a day with the PAR composed of these maximums.

We measured photosynthetic rate response to irradiance ($P(I)$ – photosynthetic light response curves) using an infrared gas analyzer (Ciras 2, PPSsystem, USA) for the same species we measured K_{lam} . Quantum irradiance range used was 0 to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and temperature was kept constant at 20°C. Measurements were made early in the

morning in the wet season to ensure plants were not limited by stomatal closure. P(I) was fitted using a Michaelis-Menten equation (Lachapelle & Shipley, 2012):

$$A_n = Q \cdot P_{\max} / (K_I + Q)$$

Where A_n is net photosynthesis rate ($\mu\text{molC m}^{-2} \text{ s}^{-1}$), P_{\max} is the maximum photosynthesis ($\mu\text{molC m}^{-2} \text{ s}^{-1}$), K_I is the half saturation constant and Q is the quantum irradiance ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). Potential photosynthetic rate under no CO_2 limitation was calculated for each hour setting Q in the above equation equal to measured incident PAR.

2.5 – Thermal buffering

We used the temperature deviations from month mean approach, as explained above, to verify if there were relationships between fog and daytime mean and maximum T_{air} , minimum night T_{air} and mean daytime T_l . To calculate T_l we solved the leaf thermal budget for T_l at equilibrium, following Leuschner (2000):

$$(11) (G_{\text{tot}} - \alpha G_{\text{tot}}) + (Q_{\text{ri}} - Q_{\text{re}}) - Q_{\text{conv}} - Q_{\text{evap}} = 0$$

Where G_{tot} is total incoming solar radiation at plant level, α is the albedo (considered 0.13 here; Milly & Shmakin, 2002), Q_{ri} is incident long wave radiation on the leaf, Q_{re} is long wave radiation emitted by the leaf, Q_{conv} is the convective heat transfer between the leaf and the air and Q_{evap} is the leaf latent heat flux. Equation (11) states that the sum of thermal energies coming and leaving a leaf must equal 0, else the leaf is heating or colling in a transient status and will reach an equilibrium with a different T_l .

G_{tot} was inferred from incident PAR measurements (Szeicz 1974) as follow:

$$(12) G_{\text{tot}} = (\text{PAR}/4.6) \cdot 2 \cdot f$$

Where 4.6 is the factor to convert PAR from photon flux units to energy units; 2 is the proportion of all spectrum solar radiation to PAR spectrum radiation; and f is a function of altitude to account for non measured diffuse radiation (see Appendix 1 for calculation of parameters not presented here and their units).

Q_{ri} is the sum of longwave radiation reaching the leaf from the soil and from the sky. Considering thermal equilibrium between the leaf and the soil, Q_{ri} can be simplified as sky-to-leaf longwave radiation only and can be calculated as a function of T_{air} and air water vapour pressure (e_a) according to Leuschner, 2000:

$$(13) Q_{\text{ri}} = 1.24(e_a/(100 \cdot T_{\text{air}}))^{1/7} \cdot \sigma \cdot T_{\text{air}}^4$$

Where σ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$).

Q_{re} can be calculated with the Stefan-Boltzmann law for black body radiation emission multiplied by leaf emissivity (ϵ), considered as 0.97 (Ye *et al.*, 2013):

$$(14) Q_{re} = \epsilon * \sigma * T_l^4$$

Where T_l is leaf temperature.

Q_{con} can be calculated as a function of the leaf boundary layer resistance (r_a) and the Lewis number (Le), which is the ratio of air thermal diffusivity to water vapour mass diffusivity in air (Ye *et al.*, 2013):

$$(15) Q_{con} = 2 * \rho * c_p (T_{air} - T_l) / r_a * Le$$

Where ρ is the density of air, c_p is the specific heat of air at constant pressure and the multiplication by 2 means we are considering the sensible heat transfer at both leaf sides. r_a , for wind speed greater than 0.1 m s^{-1} can be calculated as (Boulard & Wang, 2002):

$$(16) r_a = 220 * (L^{0.2}) / (u^{0.8})$$

Where L is leaf length in the direction of the wind and u is mean wind speed. As wind speed data was not available for the region in 2013, we used the mean month wind speeds of 2012, measured in a weather station approximately 500m from the study field. Mean wind speed for the period from March to November in 2012 was 2.99 m s^{-1} .

Q_{evap} equals the latent heat of vaporization (λ) multiplied by E_l . E_l equals the difference in water vapour concentration inside the leaf (C_l) and in the air (C_a) divided by the sum of the boundary layer resistance (r_a) and the stomatal resistance (r_s). Water vapour concentration was calculated following McRae (1980), with C_l leaved as a function of T_l to further solving in the final form of equation (11). r_s was calculated as a function of leaf and stomata morphological dimensions (Leuschner, 2000). The final form of Q_{evap} is:

$$(17) Q_{evap} = \lambda * E_l = \lambda (C_l - C_a) / (r_a + r_s)$$

Where λ is the latent heat of vaporization. Mean daytime T_l for each day of the study period was calculated substituting equations (12), (13), (14) and (17) in equation (11) and solving it. We used an iterative procedure to solve the equation and find out T_l to the nearest 0.1°C . For all calculations we used the same values for leaf length, stomatal morphology and stomatal density as Leuschner (2000), which allows for easy comparison

and consideration of leaf properties on the overall thermal budget. Although this approach lacks realism at the species level it allows for quantification of general fog effects on leaf functioning.

2.6 – Evaporative demand reduction

We tested if fog was associated with reduced air evaporative demand by verifying if daytime fog occurrence decreased T_{air} , RH, VPD, cloudiness and E_l . E_l was calculated using equation (17) for leaf latent heat flux after calculating leaf temperature as described above.

2.7 – Fog-removal projection

We then made a fog-removal projection of T_l and E_l by calculating fog effects on climate variables, removing the effect from data and using the resulting data to calculate T_l and E_l . We subtracted the slope of the regression of fog effects on T_{air} , RH and incident G_{tot} from monthly means and multiplied by the amount of fog occurrence of each day. The resulting T_l and E_l difference from the projections were then removed from the values calculated using the actual climate data. The slope of the regression was considered as fog effects on T_l and E_l on a per hour of fog occurrence by day basis. This procedure allowed us to calculate the effect of each individual climatic variable affected by fog on the response variables.

2.8 - Statistical Analysis

We performed the Mann-Whitney U test to analyze the difference between medians of different groups. We performed simple linear regression analysis to correlate fog occurrence to different variables. We tested for homoscedasticity in the residuals of linear regression analysis using the Breusch-Pagan test and when homoscedasticity criterion was not met we applied a weighted least square regression. All data processing and statistical analyses were made in R environment and statistical applications (version 2.15.1; R Core Team 2012).

3 - Results

3.1 – Water availability

Fog occurred during the entire study period except for some short periods, which coincides with periods of low soil water content, with a frequency of 21 ± 4.8 (mean \pm SD) days with fog occurrence by month (fig. 2). Fog occurred more frequently (Mann-Whitney $U = 4585$, $p = 0.017$) during wet periods ($12.72 \pm 7.21 \text{ h day}^{-1}$) than drought periods ($9.88 \pm 7.68 \text{ h day}^{-1}$; fig. 3). Daily fog duration varied for each month of the studied period and was more frequently during night hours, with lower values coinciding with the dry season and the drought spell of late May (figures 2B and 3). Total daily leaf wetting events had a longer duration (Mann-Whitney $U = 43682$, $p < 0.0001$; fig. 2A) for fog events ($9.66 \pm 7.66 \text{ h day}^{-1}$) than rain events ($2.19 \pm 3.18 \text{ h day}^{-1}$).

Daily soil water recharge was less contributed (Mann-Whitney $U = 4094$; $p = 0.0047$; fig. 6) by fog ($0.0057 \pm 0.015 \text{ m}^3 \text{ m}^{-3}$) than by rain ($0.015 \pm 0.036 \text{ m}^3 \text{ m}^{-3}$) with total fog soil recharge equaling 36% of total rain recharge. Rain events were the main responsible for soil water recharge after soil drought events (fig. 5).

Potential leaf rehydration due to night fog was lower during drought periods than in wet periods (fig. 6). *D. brasiliensis* showed the highest values, followed by *M. ferruginea*. *Siphoneugenea* sp. showed potential leaf rehydration values much smaller than to the other species. The probability of full rehydration followed this trend, with *D. brasiliensis* being fully rehydrated 67% of the nights of the wet periods and 27.5% of nights of dry periods (fig. 7).

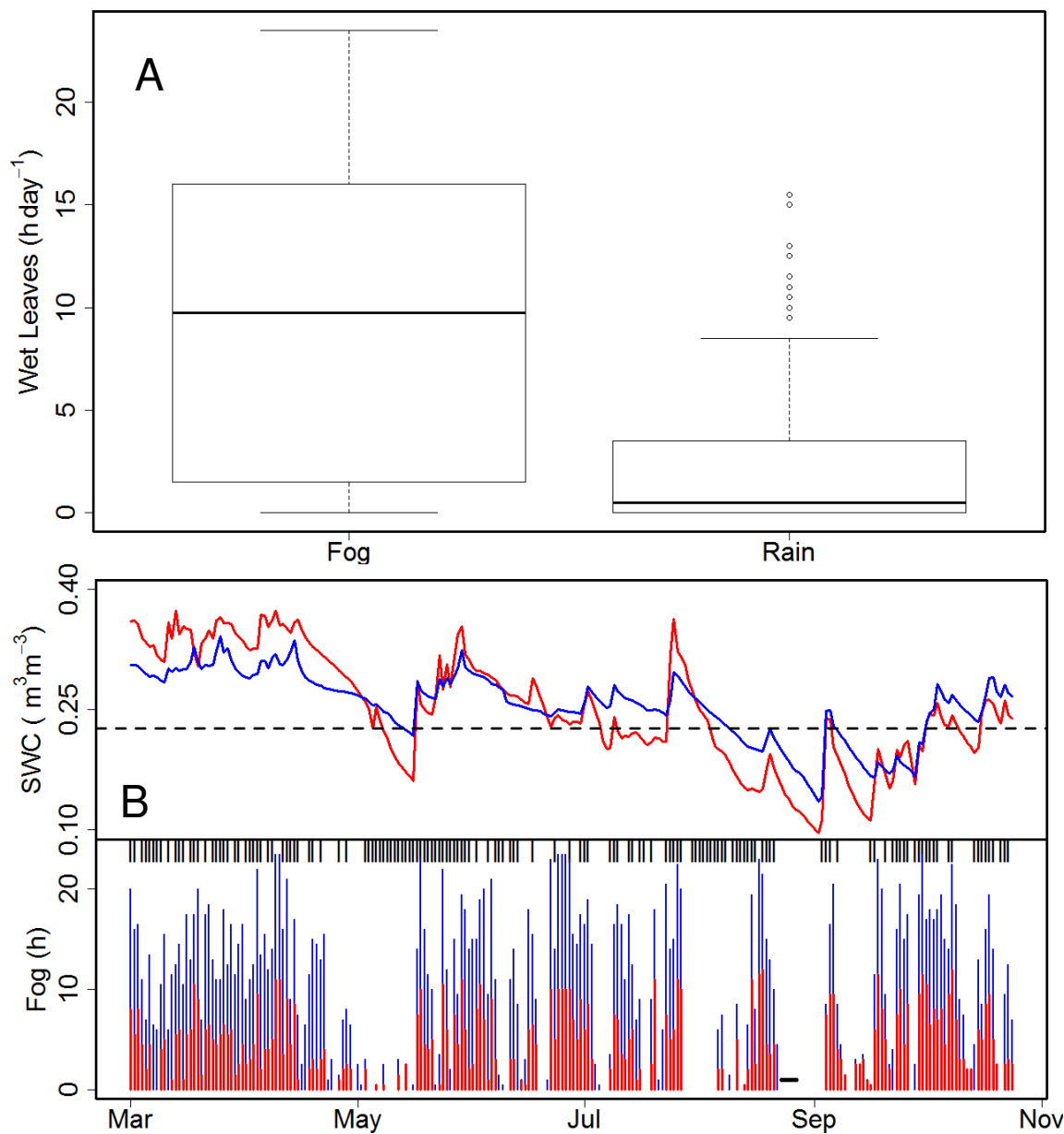


Figure 2. (A) Total hours leaf remains wet by day. (B) Upper panel: Mean daily soil water content (SWC) at 5cm (red) and 25cm (blue) soil deep. When the mean of the two layers were below the dashed line we considered a period of soil drought. Lower panel: Total hours of fog in each day (blue bars) and total hours of fog during daytime period (red bars). Vertical black lines represent days were rain events happened. The horizontal black line is a period were no data was available.

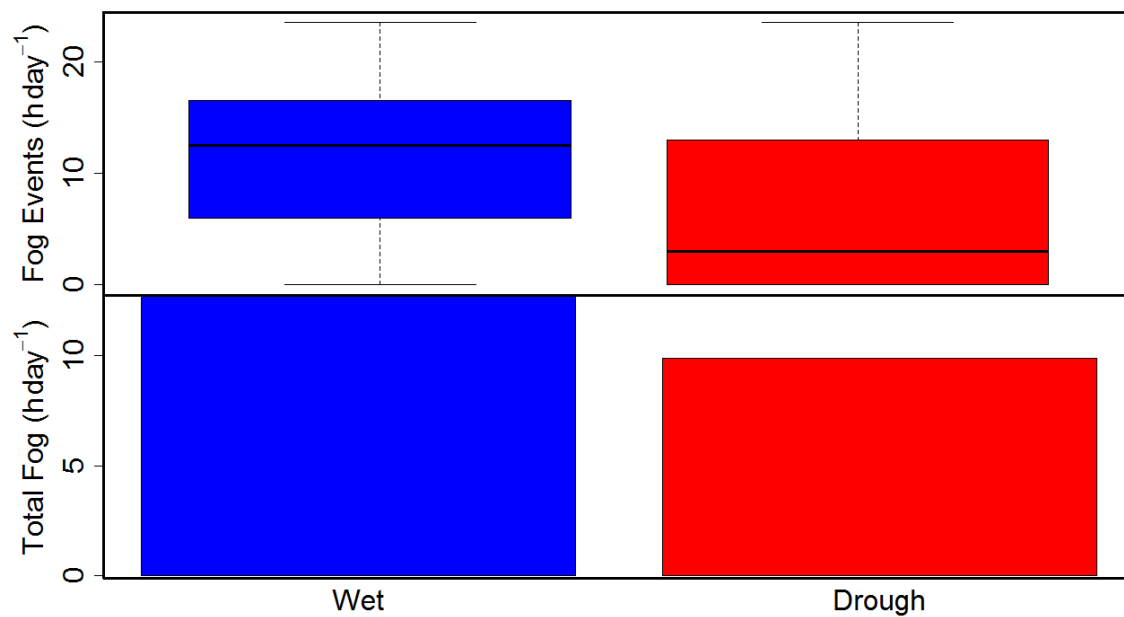


Figure 3. Upper panel: total hours of daily fog occurrence during drought and non-drought periods (wet periods). Lower panel: daily frequency of fog occurrence for the soil drought and non soil drought periods.

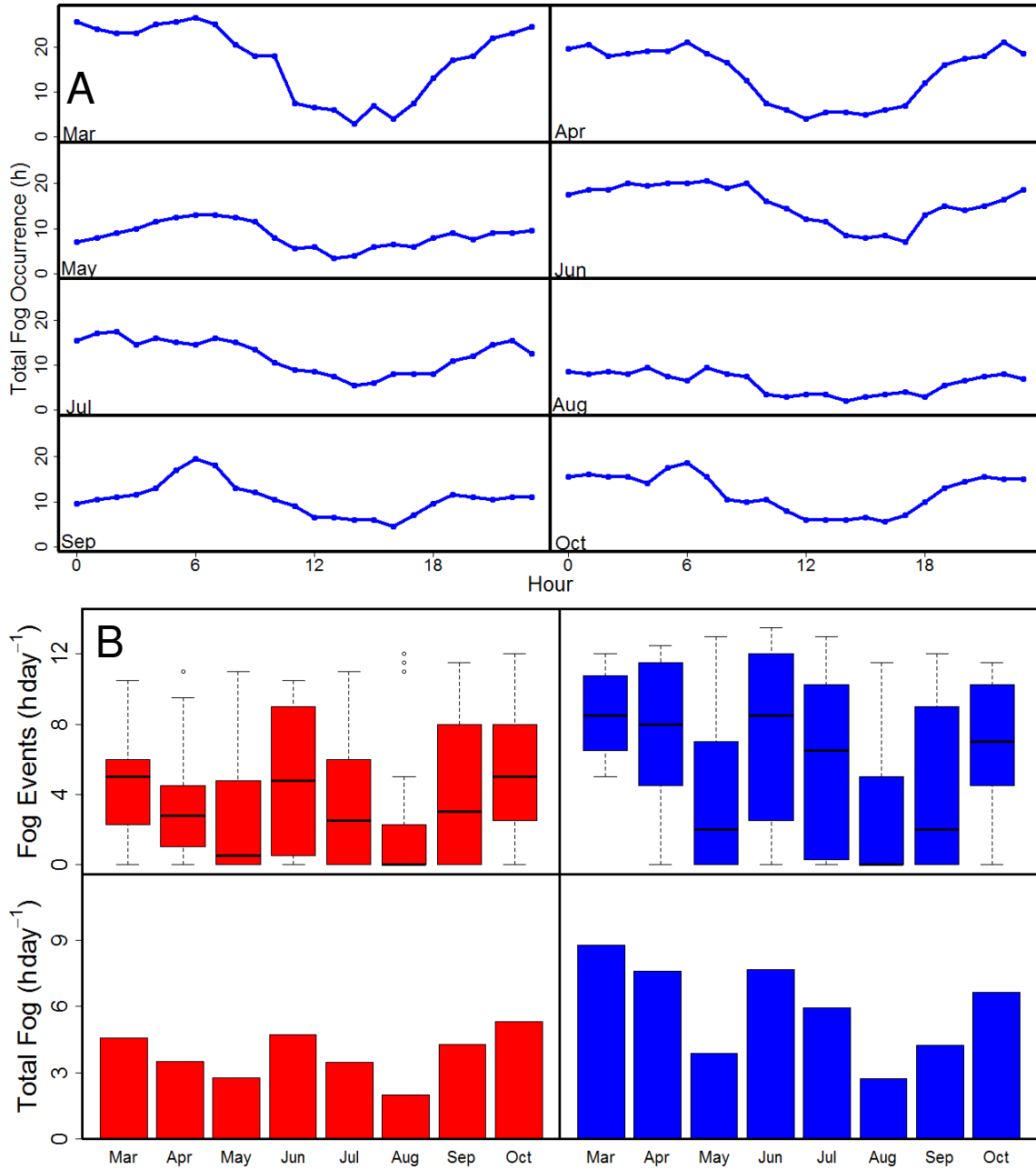


Figure 4. (A) Total hours of fog occurrence in each hour of the day for each month. (B) Upper panel: hours of daily fog occurrence for each month. Lower: frequency of daily fog occurrence in each month. Red bars are for daytime fog and blue bars for night time fog.

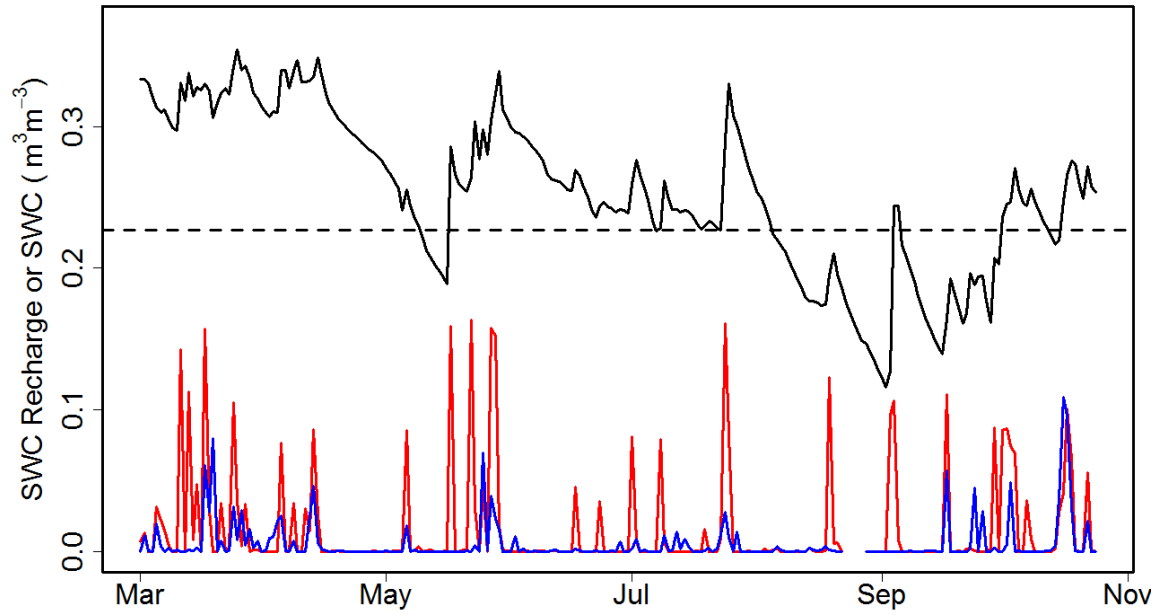


Figure 5. Mean of daily soil water content at 5cm and 25cm soil deep (SWC; $\text{m}^3 \text{m}^{-3}$, black line) and total daily soil water recharge ($\text{m}^3 \text{m}^{-3}$) due to fog events (blue) and rain events (red). Dashed line is the soil water content below which we considered drought periods.

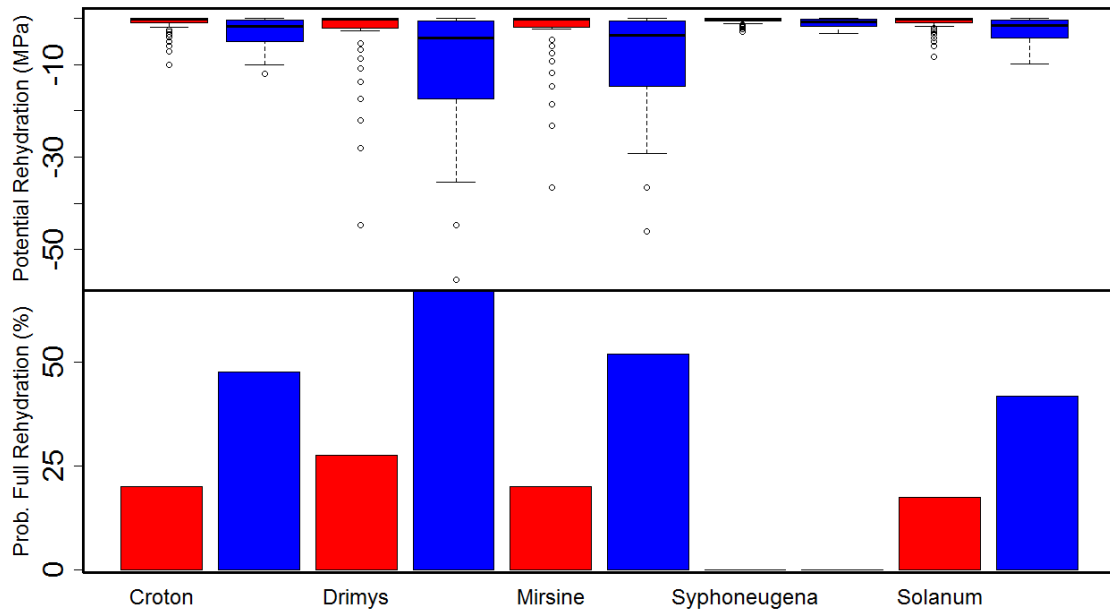


Figure 6. Upper panel: potential night rehydration (MPa) due to fog events for each species. Lower panel: probability that each species will be fully rehydrated (%). Red is for soil drought periods and blue for non soil drought periods.

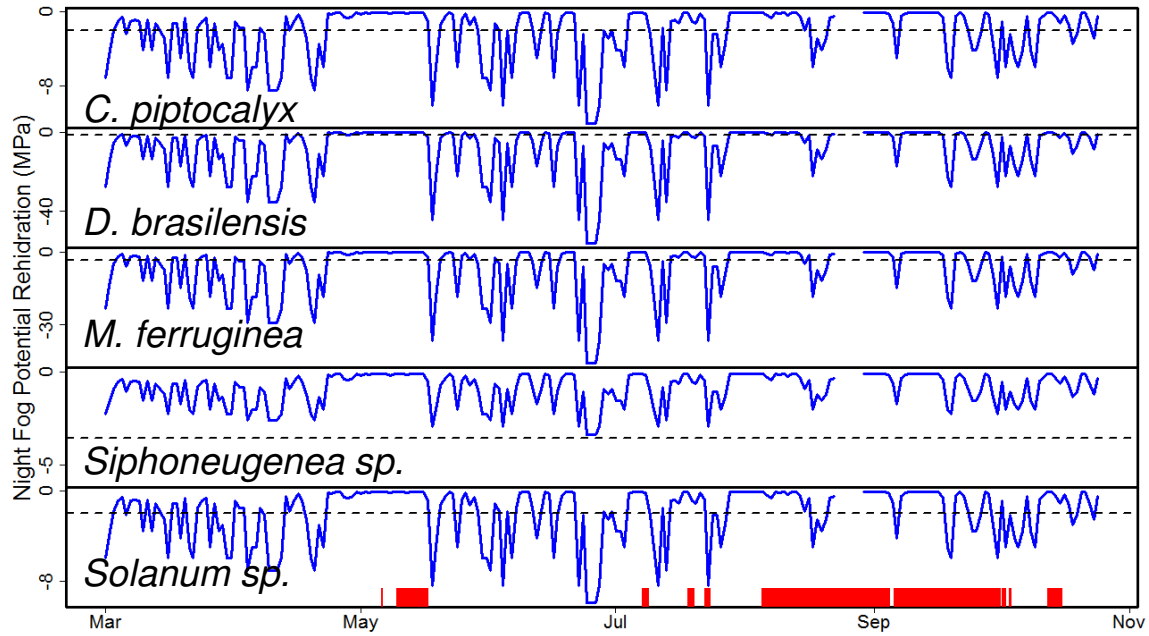


Figure 7. Night fog potential rehydration (MPa) of leaves of the different species analyzed. Dashed line represents the minimum mid day leaf water potential achieved by each species in the year. Red bars marks drought periods. Notice the overall trend is the same, but the scales are different.

3.2 – PAR availability, photosynthesis and fog

Fog decreased mean PAR by $49.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ for each hour of daytime fog (fig. 8; table 2). Fog explained very little of morning and afternoon PAR variation ($R^2 < 0.1$) while it explained some of midday PAR variation ($R^2 = 0.4$). Fog associated PAR reduction (cloudiness) was approximately equal along the day (fig. 9 upper panel). Photosynthesis reduction for each species followed the same trend for morning and afternoon, but showed a percentage of reduction by hour of fog occurrence (slope divided by intercept expressed in percent, with intercept being mean values for days without fog) smaller than the PAR reduction (-5.6% for all species mean against -11.3% for PAR; see Slope (%) in table 2), meaning species were relatively light saturated during midday fog events. Fog contributed little to cumulative hourly total PAR availability during the period except for the morning hours (fig. 9 lower panel).

Table 2. Simple regression analysis statistics of incident PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and photosynthesis rate ($\mu\text{molC m}^{-2} \text{s}^{-1}$) of the analyzed species predicted by fog duration (h) for different times of the day. Slope (%) is the regression slope divided by the intercept multiplied by 100. Morning is considered from dawn to 10h, midday from 10h to 15h and afternoon from 15h until night.

Daytime	Dependent \ Variable	Intercept	Slope	Slope (%)	R ²	P
All day	PAR	865.5±21.6	-49.3±4.1	-5.7	0.38	<0.001
Morning	PAR	545.2±27.9	-30.9±10.57	-5.7	0.03	0.0037
	<i>C. piptocalyx</i>	10.53±0.33	-0.34±0.12	-3.2	0.03	0.0060
	<i>D. brasiliensis</i>	6.81±0.18	-0.16±0.07	-2.3	0.02	0.0215
	<i>M. ferruginea</i>	8.82±0.28	-0.29±0.10	-3.3	0.03	0.0055
	<i>Siphoneugena</i> sp.	2.22±0.08	-0.10±0.03	-4.5	0.04	0.0019
	<i>Solanum</i> sp.	8.25±0.25	-0.25±0.09	-3.1	0.03	0.0070
Midday	PAR	1115.8±25.2	-126.1±10.1	-11.3	0.40	<0.0001
	<i>C. piptocalyx</i>	16.02±0.25	-0.86±0.07	-5.4	0.39	<0.0001
	<i>D. brasiliensis</i>	9.78±0.09	-0.43±0.04	-4.4	0.32	<0.0001
	<i>M. ferruginea</i>	13.49±0.22	-0.74±0.06	-5.5	0.39	<0.0001
	<i>Siphoneugena</i> sp.	3.73±0.08	-0.27±0.02	-7.4	0.43	<0.0001
	<i>Solanum</i> sp.	12.45±0.19	-0.65±0.05	-5.2	0.38	<0.0001
Afternoon	PAR	197.8±8.8	-50.3±11.7	-25.4	0.07	0.0002
	<i>C. piptocalyx</i>	6.28±0.20	-1.11±0.27	-17.7	0.07	0.0001
	<i>D. brasiliensis</i>	4.56±0.13	-0.69±0.17	-15.0	0.06	0.0001
	<i>M. ferruginea</i>	5.19±0.17	-0.93±0.23	-18.0	0.07	0.0001
	<i>Siphoneugena</i> sp.	1.10±0.04	-0.23±0.05	-21.3	0.07	<0.0001
	<i>Solanum</i> sp.	5.00±0.16	-0.87±0.21	-17.4	0.07	0.0001

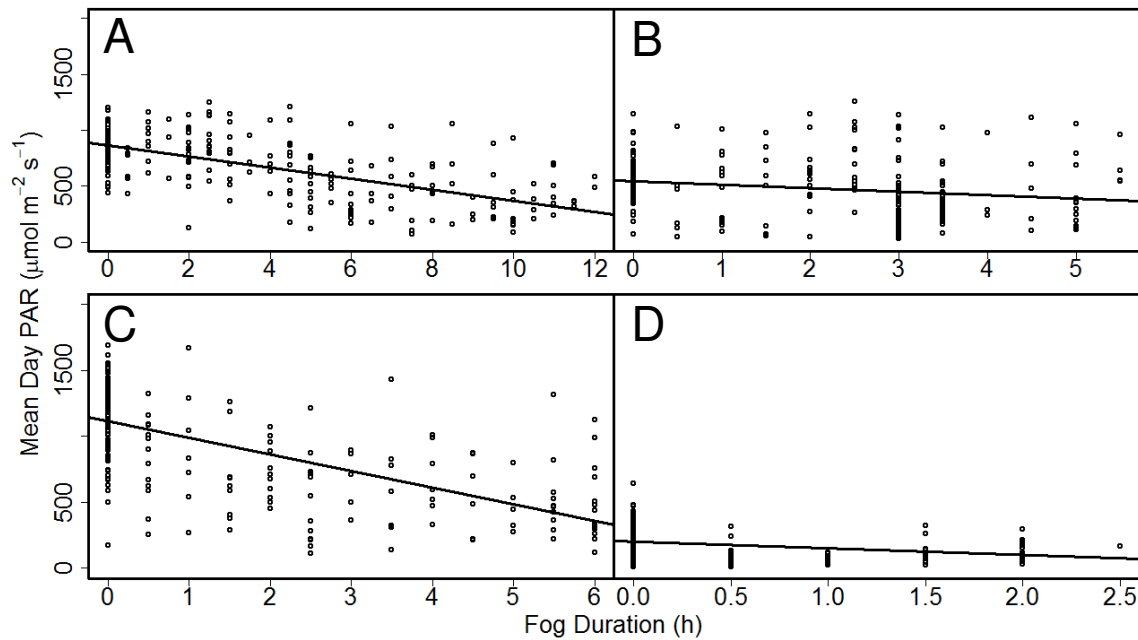


Figure 8. Incident PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) as a function of daytime fog duration (h) for the entire day (A); morning (B); midday (C); and afternoon (D). Black lines are the regression fit. Morning is considered from dawn to 10h, midday from 10h to 15h and afternoon from 15h until night.

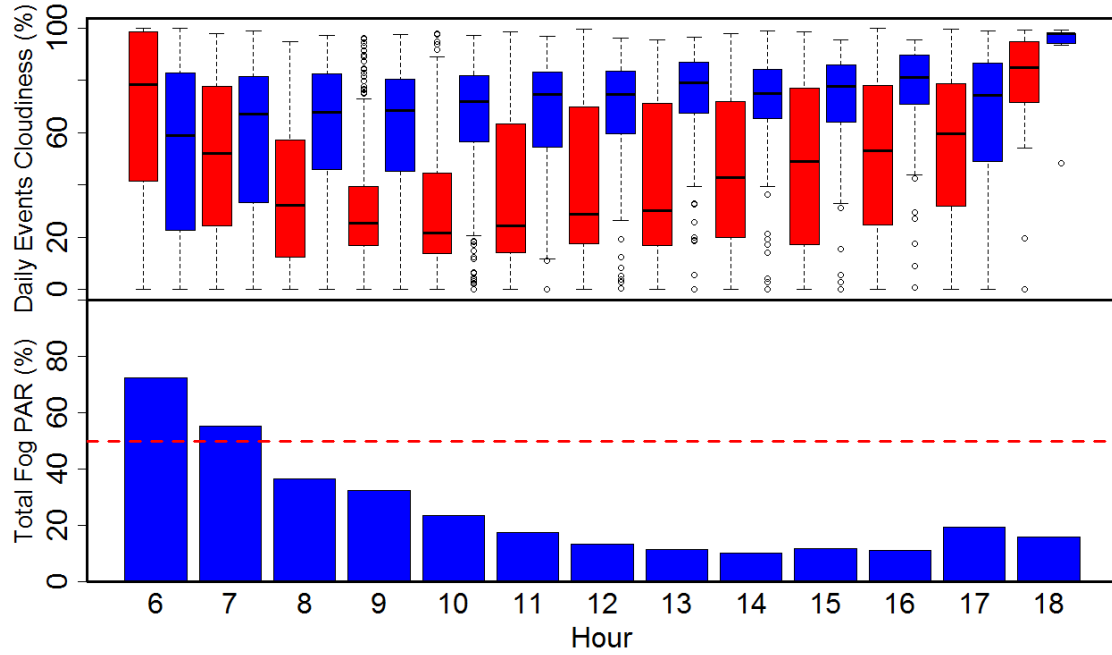


Figure 9. Upper panel: cloudiness (%) distribution along the day for the entire period. Blue boxplots represents cloudiness during fog events and red boxplots represents cloudiness during non-fog events. Lower panel: contribution of PAR during fog events to cumulative hourly PAR during the entire study period (%). Dashed red line marks 50% contribution, values higher than the line means fog contributed more than 50% of that hour cumulative fog for the study period.

3.3 – Evaporative demand reduction

Fog had a significant relationship with all daytime climatic variables, decreasing daytime T_{air} and VPD by 0.34°C and 0.039kPa , respectively, for each hour of daytime fog (fig. 10; summaries are presented in table 3). Daytime RH and cloudiness increased respectively 2.13% and 3.71% for each hour of daytime fog. We tested for incident G_{tot} effects on daytime T_{air} and found a weak relationship (intercept = -1.52 ± 0.38 , slope = 0.0023 ± 0.0005 , $R^2 = 0.07$, $F = 18.77$, $\text{df.} = 231$, $p = 0.0005$). We removed the effects of fog on incident PAR using the regression presented in section 3.2 and tested again for this relationship and found no trend ($R^2 = 0$, $F = 0.75$, $\text{df.} = 231$, $p = 0.39$), implying that fog has an effect on daytime T_{air} independent on the reduced incident G_{tot} . Fog effects on VPD, T_{air} and RH were slightly stronger for soil drought periods than wet periods (table 3).

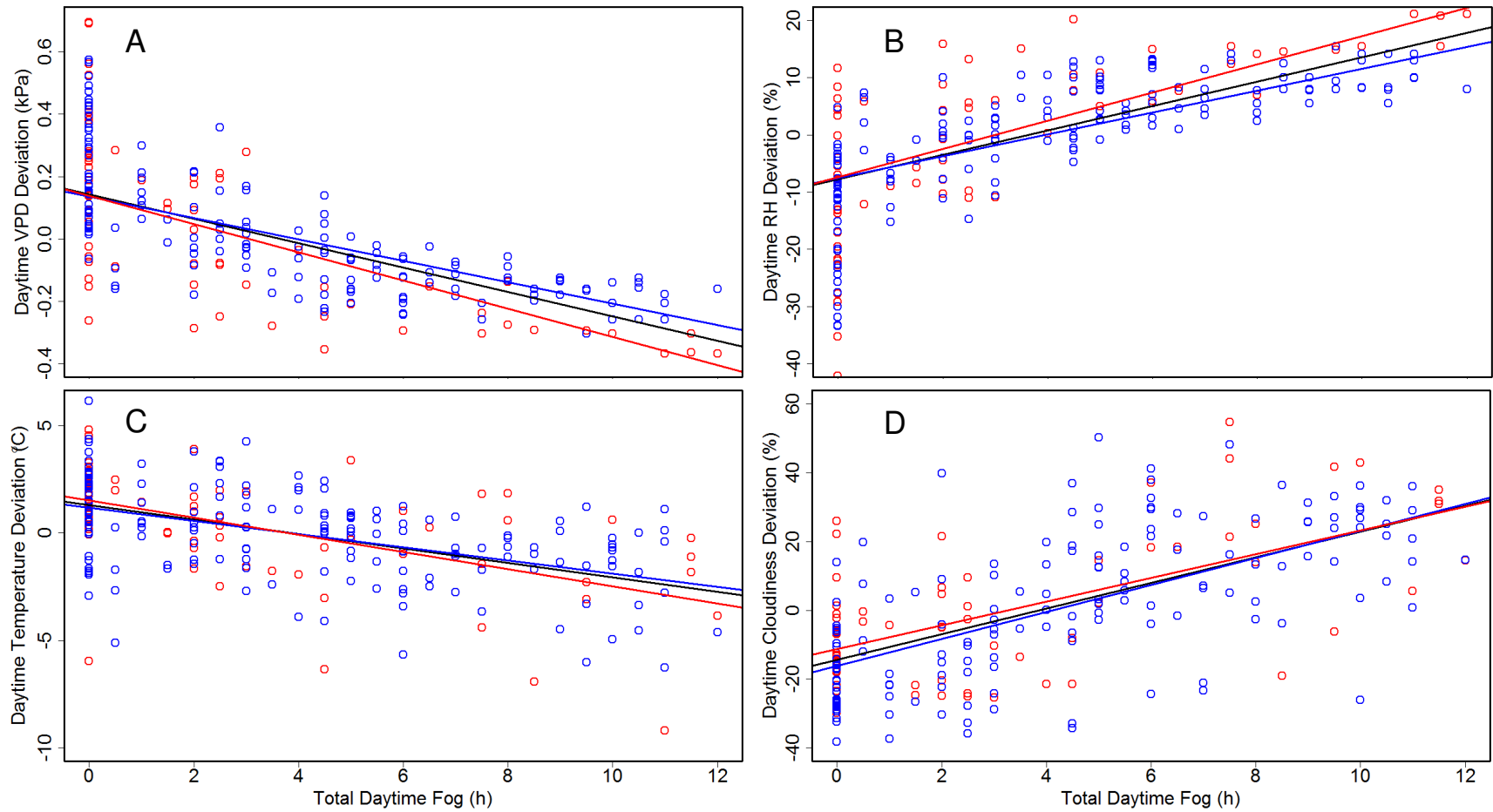


Figure 10. Daytime climatic variables deviation from daytime month means as a function of total daytime fog occurrence (h): (A) daytime vapour pressure deficit deviation (VPD;kPa); (B) daytime air relative humidity (RH; %) deviation; (C) daytime temperature deviation (°C); and (D) daytime cloudiness deviation (%). Lines are the fit from the regression for soil drought period (red), non soil drought period (blue) and all data together (black).

Table 3. Simple regression analysis statistics of climatic variables deviation from month means predicted by fog duration (h). VPD is air vapour pressure deficit (kPa); RH is air relative humidity (%); T_{air} is air temperature ($^{\circ}\text{C}$); max, min and amp subscripts indicates the T_{air} data analyzed is the daily maximum, minimum or amplitude. Wet means the data subset is for the non-drought period and Drought for the drought period; Winter means the data subset is from June to October. All climatic variables, except for T_{min} , are daytime values tested against daytime fog totals.

Test	Intercept	Slope	R^2	F	df	P
VPD x Fog	0.140 \pm 0.0150	-0.039 \pm 0.002	0.53	263.5	236	<0.0001
VPD-Wet x Fog	0.135 \pm 0.0165	-0.034 \pm 0.002	0.56	204	161	<0.0001
VPD-Drought x Fog	0.133 \pm 0.029	-0.045 \pm 0.004	0.63	128.5	73	<0.0001
T_{air} x Fog	1.26 \pm 0.19	-0.34 \pm 0.04	0.26	84.42	236	<0.0001
T_{air} -Wet x Fog	1.14 \pm 0.23	-0.30 \pm 0.04	0.23	50.31	161	<0.0001
T_{air} -Drought x Fog	1.44 \pm 0.33	-0.41 \pm 0.07	0.29	31.94	73	<0.0001
RH x Fog	-7.72 \pm 0.81	2.13 \pm 0.13	0.53	267.4	231	<0.0001
RH-Wet x Fog	-7.54 \pm 0.90	1.91 \pm 0.13	0.56	205.3	161	<0.0001
RH-Drought x Fog	-7.39 \pm 1.61	2.46 \pm 0.23	0.61	110.6	68	<0.0001
Cloudiness x Fog	-14.33 \pm 1.57	3.71 \pm 0.30	0.4	156.8	231	<0.0001
Cloudiness-Wet x Fog	-16.15 \pm 1.96	3.91 \pm 0.36	0.42	118.9	161	<0.0001
Cloudiness-Drought x Fog	-11.2 \pm 2.60	3.44 \pm 0.54	0.37	40.9	68	<0.0001
T_{max} x Fog	18.29 \pm 0.26	-0.49 \pm 0.05	0.28	96.09	236	<0.0001
$T_{amplitude}$ x Fog	8.96 \pm 0.20	-0.58 \pm 0.04	0.48	216.6	236	<0.0001
T_{min} x Nightfog	-0.047 \pm 0.25	0.008 \pm 0.033	0	0.56	236	0.81
T_{min} -Winter x Nightfog	0.274 \pm 0.421	-0.062 \pm 0.068	0	0.85	83	0.36

E_l decreased linearly with daily fog occurrence (intercept = 0.94 \pm 0.09, slope = -0.25 \pm 0.02, R^2 = 0.49, F = 232.4, df. = 236, p < 0.0001; fig.11). Fog removal projections lead to the same trend with E_l decreasing for each hour of fog on each day (intercept = -2.14 \pm 0.04, slope = -0.25, R^2 = 0.82, F = 1112, df. = 236, p < 0.001). Fog effects on E_l , according to our fog-removal projection, were higher for RH and G_{tot} , with T_{air} having only a small effect (table 4).

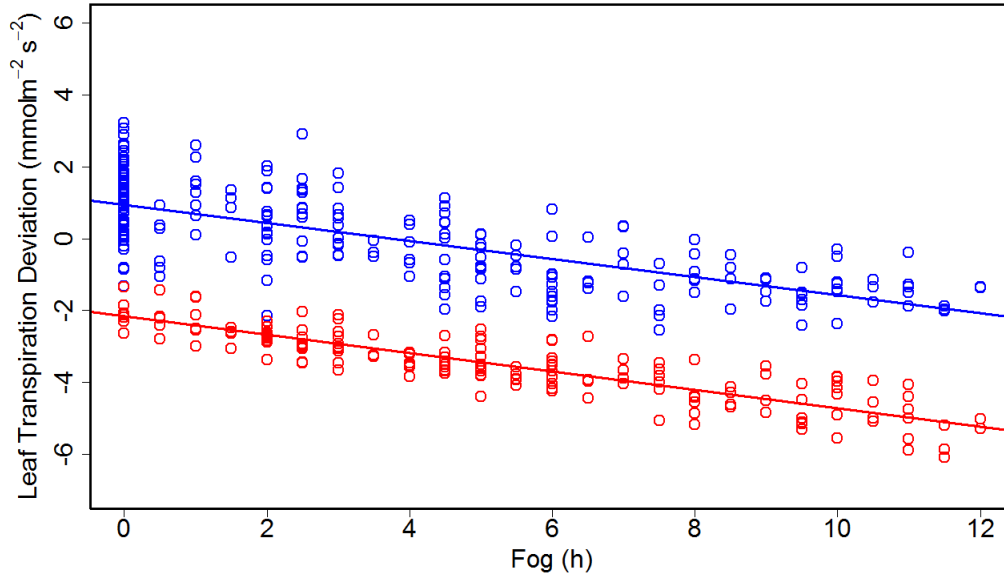


Figure 11. Mean daytime leaf transpiration deviation from monthly mean ($\text{mmol m}^{-2} \text{s}^{-1}$; blue; blue line is the regression fit) as a function of fog occurrence (h) and difference between leaf transpiration and projected leaf transpiration after removing fog effects on climate variables proportionally to the number of fog hours that happened in each day ($\text{mmol m}^{-2} \text{s}^{-1}$; red; red line is the regression fit).

3.4 – Thermal buffering

Additionally to the fog effects of reducing T_{air} described above, fog had a pronounced effect in reducing 0.49°C of maximum day T_{air} and 0.58°C of T_{air} amplitude for each hour of daytime fog (table 3). We found no relationship between minimum T_{air} and night time fog during all the study duration and for the winter period.

Table 4. Fog-removal projections of leaf temperature (T_l ; $^{\circ}\text{C}$) and leaf transpiration (E_l ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) against daily fog occurrence (h) after removing fog effects on climatic variables individually or in group: air humidity (RH; %); air temperature (T_{air} ; $^{\circ}\text{C}$); and solar radiation (G_{tot} ; $\text{J m}^{-2} \text{s}^{-1}$).

Fog Effect Removed	Response	Intercept	Slope	R2	F	DF	P
RH	T_l	-0.02 ± 0.01	-0.09 ± 0.002	0.92	3028	231	<0.0001
T_{air}		-0.04 ± 0.01	0.34 ± 0.01	0.93	78830	231	<0.0001
G_{tot}		-0.02 ± 0.01	0.28 ± 0.01	0.97	17300	231	<0.0001
		-					
RH and T_{air}	E_l	0.03 ± 0.009	0.25 ± 0.01	0.99	22480	231	<0.0001
RH, T and G_{tot}		-0.04 ± 0.02	0.50 ± 0.01	0.99	26960	231	<0.0001
RH		2.11 ± 0.03	0.07 ± 0.01	0.32	114.8	231	<0.0001
T_{air}		2.13 ± 0.03	0.01 ± 0.01	0.01	3.895	231	0.049
G_{tot}		2.13 ± 0.03	0.13 ± 0.01	0.59	348.9	231	<0.0001
RH and T_{air}		2.05 ± 0.04	0.11 ± 0.01	0.43	180.4	231	<0.0001
RH, T_{air} and G_{tot}		2.15 ± 0.04	0.26 ± 0.01	0.82	1112	231	<0.0001

T_l decreased linearly with daily fog occurrence (intercept = 1.88 ± 0.19 , slope = -0.49 ± 0.03 , $R^2 = 0.42$, $F = 168$, $df. = 231$, $p < 0.0001$; fig. 12). In the fog-removal projection T_l increased proportionally to day time fog occurrence after fog effects were removed from G_{tot} and from daytime T_{air} and decreased after removal of fog effects on RH (table 4). The cumulative effect of all climatic variables together on T_l was higher than any individual effect. Fog-removal projections resulted in the same negative relationship as T_l against fog occurrence calculated from actual values, albeit with a different intercept (intercept = 0.04 ± 0.01 , slope = -0.50 ± 0.01 , $R^2 = 0.99$, $F = 26960$, $df. = 231$, $p < 0.0001$; fig. 13), suggesting our fog-removal procedure was quite realistic.

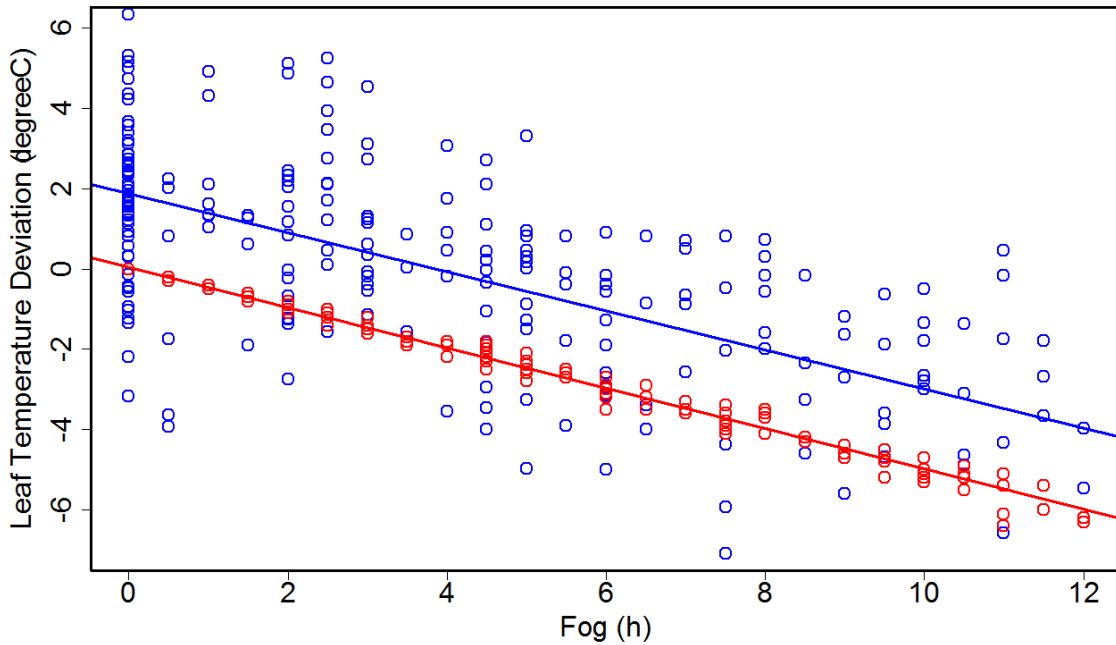


Figure 12. Mean daytime leaf temperature deviation from monthly mean ($^{\circ}\text{C}$; blue; blue line is the regression fit) as a function of fog occurrence (h) and difference between leaf temperature and projected leaf temperature after removing fog effects on climate variables proportionally to the number of fog hours that happened in each day ($^{\circ}\text{C}$; red; red line is the regression fit).

4 – Discussion

4.1 – Water availability

Fog occurred frequently and persistently during the entire year mostly at night and morning. Fog was also frequent, although somewhat less, during soil drought periods.

Leaves were wet due to fog events much more frequently than due to rain events and fog also wetted leaves in times it did not had any effect on soil water through fog drip. Illustratively, if we consider that for some days leaf remained wet half a day or more, we could compare their conditions to the ones of plants living in the intertidal zones of a shore!

Fog had a profound effect on soil water recharge, being responsible for 36% of total recharge for the period. This value is even more considerable if we consider fog inputs also occur during rain events and they were not quantified. Although we could not access the fog importance to the water balance of the region because fog inputs to soil during periods when soil was already saturated could not be accessed, the value of soil water recharge parallels the findings for other cloud forests (Bruijnzeel, 2001).

Considering the recent findings of fog hydraulic redistribution to soil and to recharging plant capacitances (Burns *et al.*, 2009; Eller *et al.*, 2013) and our current findings of fog's effects on plant rehydration, fog related leaf wetting has a pronounced effect on plant and soil water balance that is frequently not considered. Few studies have addressed the importance of foliar water uptake to plant water status, but they found a general trend in leaf wetting events recharging leaf water content and leaf water potential also associated to dew and rain events, suggesting foliar water uptake can be much more widespread (Martin & von Willert, 2000; Breshears *et al.*, 2008; Liu *et al.*, 2011). Even though leaves can absorb water direct from saturated air, evidence suggests the water uptake is much higher when leaves are in direct contact with water (Slatyer, 1956; Yates & Hutley, 1995). The mechanisms of leaf water uptake are still unknown, but hydathodes are known to be important in some species and direct water diffusion through the cuticle was found for *D. brasiliensis* (Martin & von Willert, 2000; Eller *et al.*, 2013). Leaf surface water repellency may also play an important role in foliar water uptake, as less repellent leaves may remain wet for more time and be more conductive to water (Oliveira *et al.*, in press). Up until now the importance of stomata and, consequently, plant control on leaf water absorption has never been addressed.

Studies on leaf absorption dynamics found that leaf usually absorbs water fast then slows down and reaches a plateau (Liu *et al.*, 2011), which is the expected behavior if plants act as capacitors. Studies that quantified the leaf water uptake effects on

rehydration found values ranging from -0.4 to -2MPa and up to fully plant rehydration (Yates & Hutley, 1995; Breshears *et al.*, 2008; Eller *et al.*, 2013). Considering the exponential rehydration dynamics of leaves the results obtained with our potential leaf rehydration approach is in accord with the few literature data.

The current finding of night fog associated leaf wetting events being able to fully rehydrate a -50MPa water stress for leaves of *D. brasiliensis* and a similar value to *M. ferruginea* highlights that leaf uptake can constitute an important water source to these plants. It is possible that leaf water uptake is a resource niche for which plants have evolved adaptations to exploit and species with less capacity to benefit from leaf wetting events may have other adaptations to deal with water stress, like more resistance to cavitation, more stomatal control or deeper roots.

Night fog could fully restore *D. brasiliensis* and *M. ferruginea* from its highest water stress possible more than half of the days in the wet periods and almost one in each four days during drought periods. If we consider plants usually finish daytime with a water potential much lower than the lowest midday potentials, fully rehydration due to leaf uptake becomes even more important, even for *Siphoneugena* sp., which had the lowest potential rehydration values. Being able to fully rehydrate during night events, with the additional possibility of cavitation removal, means plants can operate with narrower, or even negative, cavitation safety margins. This suggests we should reevaluate plant functioning in all ecosystems where fog, dew or rain events that wet leaves but do not reach the ground are frequent..

4.2 – PAR availability and potential photosynthesis

Fog events were associated with high cloudiness during their occurrence but their effects on reducing incident PAR was only relevant for midday hours ($R^2 = 0.4$), which dominates the daily trend. This is due to the already high non-fog cloud cover during morning and afternoon. Potential photosynthesis reduction followed this trend, indicating fog only reduces available PAR during midday hours. The total photosynthetic reduction was somewhat less than the total light reduction during midday hours, indicating plants were already light saturated even during midday fog events. The actual photosynthetic

reduction in midday hours is even lower if we consider that plants are usually CO₂ limited during this period due to some stomatal closure, even in the wet periods.

Solar radiation input is correlated to incident PAR and is the principal driver of E_l and, thus, of reducing xylem water tensions and causing cavitation (Ye *et al.*, 2013; see section 4.4). Decreased PAR during midday hours, with its consequent decrease in solar radiation input have an important effect in reducing plant transpiration. This results in plants being able to keep their stomata more open and reducing CO₂ limitations during this period which can increase actual photosynthetic activity and allow plants to fully utilize available light energy. Diffuse radiation was not considered here but is supposed to increase with increasing cloudiness, compensating the actual light and potential photosynthetic rates reduction caused by fog (Mercado *et al.*, 2009).

4.3 – Evaporative demand

Fog had a pronounced impact on all climatic variables evaluated in a general trend towards reducing water evaporative demand. This is consistent with the current literature (Garcia-Santos *et al.*, 2004; Berry & Smith, 2012, 2013; Carbone *et al.*, 2013). Even though fog events were defined by us as events of low VPD, its effect was consistent and could be statistically detected on daily means among the noise from not-evaluated process. The finding that fog reduction on daytime T_{air} is independent on solar radiation inputs highlights a new aspect of fog events. Fog events air masses in this region are probably associated with colder air masses and air inversion effects. Although this effect can be considered independent of cloud formation at ground level, the coupled importance of both effects must be considered. Fog reduction of T_{air} and RH were more pronounced during drought periods. This is probably related to a more contrasting effect as during drought air is drier and cloud cover is smaller than during wet periods.

Calculated daytime leaf transpiration decreased proportionally to fog occurrence. Our fog-removal projections showed the principal drivers of leaf transpiration reduction were decreases in RH and G_{tot} (table 4). T_{air} had little effect on E_l although it showed a synergistic effect with RH when both were considered together. This implies that the principal driver of VPD differences between leaf and air is RH and, probably, the energy input coming from G_{tot} .

By reducing evaporative demand fog also reduces plant xylem water tension, increasing its safety margin, stomatal opening and carbon assimilation (Eller *et al.*, 2013; Berry & Smith, 2013), which means fog reduction of evaporative demand is directly linked to plant fitness.

4.4 – Thermal buffering

Fog had a pronounced effect on reducing mean and maximum T_{air} , indicating it has important role in buffering temperature changes and preventing leaf thermal damage and photosynthetic reductions associated to non optimal temperatures. The effect may be particularly important during periods when plants are water stressed and can not lose water to evaporative cooling.

Frost in this region is almost always related to nighttime long wave radiation loss by surfaces as night T_{air} rarely go below 5°C. As fog traps longwave radiation at ground level surfaces temperatures are expected to increase with fog occurrence and we expected night T_{air} to reflect some of this increase. We did not find this relationship, suggesting that either the effect does not exist or it is not strong enough to be felt in T_{air} . Another possibility is that T_{air} is particularly decoupled from surface temperatures in this region due to constant fast winds (mean annual wind speed for 2012 was 3m s⁻¹) and air masses carries the characteristics of the place it came from before arriving at the cloud belt.

Daytime T_l of our hypothetic leaf, as calculated from the thermal budget approach, decreased proportionally to fog duration and the decrease was the same as the one estimated with the fog-removal projections, suggesting our fog-removal projections accurately removed the fog climatic drivers of leaf thermal budget. Fogs effects on reducing T_l were strong for increased T_{air} and increased solar radiation. This is associated to high values of sensible heat transfer due to high winds. T_l was also more coupled to radiation energy than was found by Ye *et al* (2013), this is probably due to the low evaporative demands of TMCFs, which leaves small room for evaporative cooling unless leaf temperatures increases relatively to air temperature. The small decrease in T_l due to decreased RH was due to higher latent heat exchange.

Increases in T_l are related to stomatal control (Schulze *et al.*, 1974) as stomatal opening can reduce T_l at the cost of higher xylem tension and lower safety margins.

Higher T_l also lead to increased plant respiration, consequently reducing net photosynthesis and increasing the risk of carbon starvation (King *et al.*, 2006). Additionally to enzymatic optimums, optimal conditions of T_l on a water use efficiency basis require that T_l is equal to T_{air} , resulting in the only driver of E_l being the difference in water pressure between the leaf and the air (Ball *et al.*, 1988).

Our results suggests fog has an extremely important role in reducing leaf temperatures, with a mean decrease of 0.5°C for each hour of fog occurrence. This has a profound effect on leaf physiology as the effect is even bigger if we consider maximum temperatures, which could potentially be highly detrimental to leaf functioning. These effects would be even more pronounced if we had incorporated increases in stomatal resistance during drought periods, which would reduce leaf evaporation and evaporative cooling, increasing leaf temperatures even more in the absence of fog.

Conclusions

As noted by Jarvis & Mulligan (2011), almost all aspects of TMCFs are related to fog occurrence. We presented a complex picture of fog effects and their relationships on TMCFs and its plants. Fog had pronounced effects on water availability, water demand, light availability and thermal regulation resulting in an overall decrease in water and thermal stresses. A schematic summary of this work conclusions is presented in figure 14 (red arrows), together with main hypotheses and expectations about fog and plant functioning as presented in the introduction.

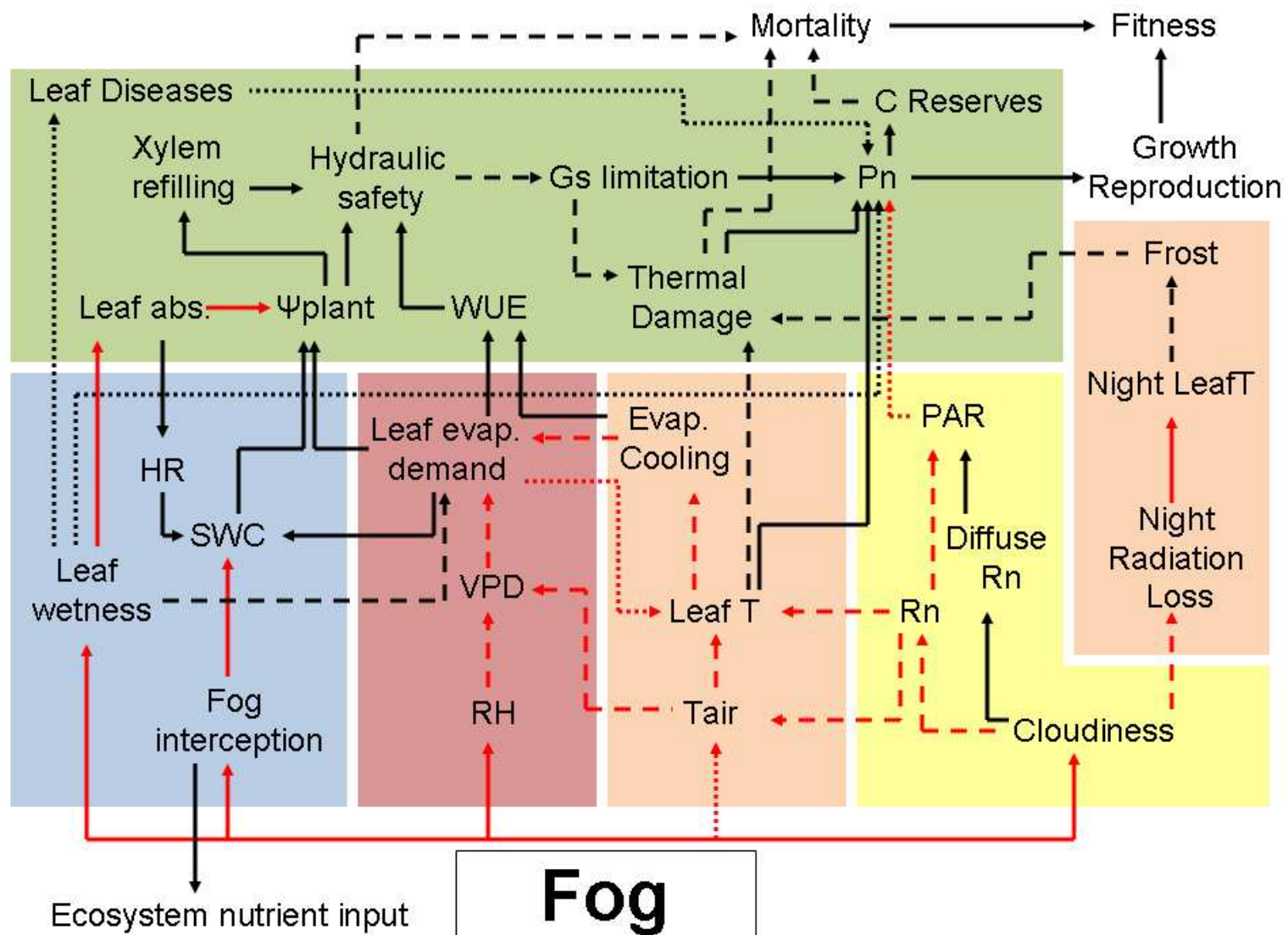
We found fog reduces incident light energy available to plants differentially through the day but this reduction is not significant in reducing the analyzed species photosynthesis. Moreover, it can even be positive with increases in diffuse light energy. We also estimated fog effects on foliar thermal balance for the first time in the literature finding that fog greatly reduces leaf thermal amplitude and quantified the mechanisms by which fog buffers daytime leaf temperature.

We proposed a methodology to estimate nocturnal fog effects on plant rehydration and found that leaf water uptake of fog water constitutes an important water source to TMCFs plants. The species analyzed had different capacities to utilize water from leaf

wetting events. This finding suggests that leaf wetting events can be a water resource important to plant fitness in TMCFs and can thus result in the selection of plants with leaf traits related to harvesting of water in leaf surfaces and interception of fog water. If selection for leaf traits associated to fog harvesting and leaf water uptake do exists an entire new horizon opens for studies of plant evolution, functioning and community structure of TMCFs.

Our study suggests land use and climate change associated changes in fog regimes will profoundly and differentially affect plant species functioning in TMCFs and points to the urgent need of studies to address the functioning of this peculiar type of ecosystem. We highlight the need of further coupling the fog effects addressed here to complete plant functioning models, paired with experimental validation of those models, so we can understand TMCFs species mortality, growth and reproduction relationships to fog and better predict community changes and its consequences on ecosystem functioning.

Figure 13. Fog effects on plant functioning, plant fitness and their interrelations. Continuous arrows imply a positive effect; dashed lines imply negative effects; dotted lines are for unknown or variable effects; red arrows represent the pathways being tested in this work. Blue box are the effects on water availability; red box are evaporative demand effects; orange box are temperature changes effects; yellow boxes are radiation input effects; and green box are the plant functioning components. SWC is soil water content; HR is hydraulic redistribution; RH is air relative humidity; VPD is air vapor pressure demand; Tair is air temperature; LeafT is leaf temperature; R_n is net radiation input; PAR is photosynthetically active radiation; Night LeafT is night leaf temperature; Leaf abs. is leaf water absorption (or leaf water uptake); Ψ_{plant} is plant water potential; WUE is plant water use efficiency; G_s limitation is stomatal conductance bellow the necessary to fully utilize light available or to evaporative cool the leaf; Rd is dark respiration; Pn is net photosynthesis; C reserves are plant carbohydrates energy reserves.



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Appendix 1 – Equations used in leaf thermal budget calculation

To calculate the leaf thermal budget we used the same approach as used by Leuschner (2000), with the exception of the calculation of boundary layer resistance and

sensible heat exchange, which followed Ye *et al.* (2013) and some climatic variables we measured, as described in the section 2.6.

To calculate non measured diffuse radiation we used a correction factor, f:

$$f = 1.1733 * \exp[(-2.997 * 10^{-5}) * z]$$

Where z is the altitude (m).

Latent heat of vaporization (λ) as a function of T_{air} was calculates according to Fritschen & Gay (1979):

$$\lambda = (2500.25 - (2.365(T_{air} - 273))) * 18$$

Lewis number (Le) is the ratio of air thermal diffusivity (D_h) to water vapour mass diffusivity in air (D_{wv}). D_h was corrected for temperature and pressure using the equation (Fuller *et al.* 1966, Campbell 1977):

$$D_h = 2.15 * 10^{-5} * (T_{air}/293)^{1.75} * (100000/P)$$

Where P is air pressure at the location. P was measured in a nearby weather station in 2012 and the mean value for the year was used. D_{wv} was calculated as (Fuller *et al.* 1966):

$$D_{wv} = 2.42 * 10^{-5} * (T_{air}/293)^{1.75} * (100000/P)$$

Stomatal resistance (r_s) was calculated as a function of leaf morphology and stomata dimensions (Leuschner, 2000):

$$r_s = X / (D_{wv} * N * \pi * s^2)$$

Where X is leaf length in the direction of the wind, s is the stomatal pore radius and N is the number of stomata pores by unit leaf area. We used the same values in the calculation of leaf temperature as Leuschner (2000): 0.04m for X, $3 * 10^{-6}$ m for s and $1 * 10^{-8} m^{-2}$ for N.