Universidade do Estado do Rio de Janeiro
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O papel ecológico de eventos de molhabilidade foliar na resposta de plantas à seca: Respostas funcionais entre ecossistemas e cenários climáticos

Rio de Janeiro
2022

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Tese apresentada, como requisito parcial para obtenção do título de Doutora, ao Programa de Pós-graduação em Ecologia e Evolução da Universidade do Estado do Rio de Janeiro. Área de concentração: Ecologia de Comunidades e Ecossistemas.

Orientador: Prof. Dr. Bruno Henrique Pimentel Rosado

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Rio de Janeiro
2022

DEDICATÓRIA

À minha avó Oreni por compartilhar o seu amor pelas plantas e pelo campo e a me inspirar a entender como a natureza funciona. À minha mãe Léa por ser como a água que chega no deserto permitindo que meus sonhos floresçam.

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Several possible explanations worthy of investigation come to mind. It was decided, however, to consider only one at this time, the possibility that aerial portions of these plants take up water from the atmosphere

Stone 1950

RESUMO

ZORGER, B. B. *O papel ecológico de eventos de molhabilidade foliar na resposta de plantas à seca:* respostas funcionais entre ecossistemas e cenários climáticos. 2022. 136 f. Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2022.

Investigar os mecanismos por trás da vulnerabilidade de organismos à seca permanece como um intrigante e crescente tópico na ecologia. No entanto, o impacto da seca, seja natural ou intensificada pelas mudanças climáticas na vegetação, é ainda focado nas flutuações na precipitação, enquanto o papel ecológico dos eventos de molhabilidade foliar (i.e. recursos complementares de água absorvidos via folha, como neblina e orvalho) é ainda negligenciado. Nesse sentido, o objetivo dessa tese foi avaliar o papel ecológico das fontes complementares de obtenção de água na vulnerabilidade de plantas à seca em diferentes ecossistemas e cenários climáticos. Para alcançar esse objetivo, no primeiro capítulo, nós avaliamos os benefícios e custos dos eventos de molhabilidade foliar em plantas, usando cinco características funcionais ecofisiológicas (i.e. potencial hídrico foliar, fotossíntese, condutância estomática, transpiração foliar e fluxo de seiva). Após a análise de 252 observações pertencentes à 45 estudos ao longo de oito fitofisionomias, identificamos que eventos de molhabilidade foliar elevam a hidratação de plantas, embora não influenciem na fotossíntese e na transpiração foliar. Adicionalmente, verificamos que a hidratação se torna menos eficiente à medida que a altitude aumenta e as chuvas fracas diminuem, sugerindo que estes fatores são importantes mediadores dos efeitos de molhabilidade foliar na vegetação. No segundo capítulo nós investigamos quais espécies de plantas, se em campos de altitude ou floresta tropical chuvosa, são mais vulneráveis à seca. Através de 13 características funcionais morfo-fisiológicas nós identificamos que plantas de floresta são mais vulneráveis à seca em relação as de campos. No entanto, apesar da maior sensibilidade à seca na floresta, ambos ambientes podem se tornar mais vulneráveis à seca nas próximas décadas, uma vez que os campos estarão menos expostos à neblina, o que já pode estar sendo experienciado com base nos poucos eventos de neblina registrados no período de estudo em campos. Por fim, no capítulo 3 se apresenta modelos paleoclimáticos com base em características funcionais de plantas que não só são capazes de reconstruir o clima passado, como podem indicar mudanças futuras na flora. Tais modelos evidenciaram que ecossistemas nebulares de altitude quando sob maior temperatura e precipitação exibiram uma maior proporção de plantas com características conservativas sugerindo que o aumento da precipitação não é capaz de minimizar os efeitos da temperatura e da altitude no modelo de estudo. Além disso, os mecanismos por trás das predições foram melhor compreendidos quando descritos por características fisiológicas. Os resultados dessa tese trouxeram evidências de que eventos de molhabilidade foliar influenciam na vulnerabilidade de plantas à seca entre ambientes e cenários climáticos, de forma que tais eventos já não devem ser negligenciados e sim considerados na avaliação de vulnerabilidade de plantas à seca e na construção de modelos climáticos mais realísticos.

Palavras-chave: Absorção hídrica foliar. Aumento da altitude da neblina. Características funcionais econômicas. Deficit de pressão de vapor. Mata atlântica. Resistência ao Embolismo. Vias de fotossíntese.

ABSTRACT

ZORGER, B. B. *The ecological role of leaf wetting events in plant responses to drought:* functional responses between ecosystems and climate scenarios. 2022. 136 f. Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2022.

Investigating the mechanisms behind organism vulnerability to drought remains one intriguing and increasing topic in ecology. However, the impact of drought, natural or intensified by climate change on vegetation, is still focused on precipitation fluctuations. In this sense, the ecological role of wetting events (i.e. complementary resources of water uptake via leaves, such as fog or dew) in vegetation is still neglected. This thesis aimed to evaluate the ecological role of complementary resources of water in plant vulnerability to drought in different ecosystems and climate change scenarios. To achieve this goal, the first chapter assessed the benefits and costs of leaf wetting events in vegetation using five ecophysiological traits (i.e. leaf water potential, photosynthesis, stomatal conductance, leaf transpiration and sap flow). After analyses of 252 observations from 45 studies across eight vegetation types, we identified that leaf wetting events improved plant water status, even though that phenomenon did not influence photosynthesis and leaf transpiration. In addition, we found a progressive reduction of wetting events on plant water status with an increase of altitude and decrease of light rains, which means they were essential mediators of leaf wetting effects on vegetation. The second chapter investigated which contrasting cloud ecosystems (tropical montane forest or tropical rainforest) would be the most vulnerable vegetation to drought. Using 13 morpho-physiological traits, we found that forest plants are more sensitive to drought than grassland ones. Despite higher drought sensitivity in the forest, both environments can become more vulnerable in the future since grassland would be less exposed to fog in the following decades, based on a few fog events recorded in the study period. Finally, the third chapter showed that paleoclimatic models based on traits not only are able to reconstruct the climate in the past but also can indicate changes in vegetation in the future. Such models showed that cloud ecosystems at high altitudes under higher temperature and precipitation scenarios exhibit a higher proportion of plants with conservative traits, which suggests that an increase in precipitation cannot minimize the temperature and altitude effects in the study model. Also, we verified that the mechanisms behind the patterns found are better explained when described by ecophysiological traits. In conclusion, this thesis showed evidence that leaf wetting events influence the plant vulnerability to drought between environments and climate scenarios. In this sense, such events should not be neglected, but considered in plant vulnerability to drought evaluation and development of more realistic climate models.

Keywords: Atlantic rainforest. Fog-uplift. Foliar water uptake. Leaf economic traits. Photosynthetic pathways. Resistance to embolism. Vapour pressure déficit.

LISTA DE ABREVIATURAS E SIGLAS

Ψ - Potencial hídrico foliar
AB - abaxial
AD - adaxial
AICc - Variante de segunda ordem do critério de informação
ANOVA – Análise de variância
asl – Acima do nível do mar
CAM – Metabolismo ácido das crassuláceas
CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
CI – Intervalo de confiança
CLAMP – Programa de analises multivariadas climático – foliar
DF – Grau de liberdade
ECMWF – Centro europeu para previsões do clima de média amplitude
ERA5 - Quinta geração do “ECMWF *Reanalysis”*
FAPERJ – Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro
FU – Absorção foliar
FWU – Absorção hídrica foliar
FWU rate – Average rate of foliar water uptake
Gs - Condutância estomática
INMET - Instituto Nacional de Meteorologia
L:W-3 -4:1 – Quatro vezes o comprimento de uma folha pela largura
LA – Área foliar
LD – Densidade foliar
LDMC – Conteúdo de matéria seca na folha
LEV – Laboratório de ecologia vegetal
Lth Espessura foliar
LWR – leaf water repellency
LWU - Absorção hídrica foliar
MAP – Média da precipitação em um ano
MAT – Média da temperatura em um ano
MD – Meio dia
p50 – Potencial hídrico em que a planta perde 50% de sua condutividade hidráulica

p88 –	Potencial hídrico em que a planta perde 88% de sua condutividade hidráulica
PD –	Antes do amanhecer
pmin	Potencial mínimo (mais negativo) mensurado
PNI –	Parque Naional do Itatiaia
PNT –	Parque Nacional da Tijuca
RJ –	Rio de Janeiro
SLA –	Área foliar específica
SM –	Margem de segurança
SM50 –	Margem de segurança hidráulica a partir do p50
SM88 -	Margem de segurança hidráulica a partir do p88
SPAC –	Continuum solo – planta – atmosfera
TCMF –	Floresta tropical montana nebular
Three–DRY-	Média de precipitação nos três meses mais secos
TLP –	Potencial hídrico em que ocorre a perda de turgor na folha
UERJ -	Universidade do Estado do Rio de Janeiro
VPD –	Déficit de pressão de vapor
WD –	Densidade da madeira

SUMÁRIO

INTRODUÇÃO GERAL

O aquecimento global decorrente do aumento da emissão de gases estufa e poluentes atmosféricos pelo Homem, tem aumentado a frequência de ondas de calor e flutuações pluviométricas acentuadamente a partir da década de 1980 (IPCC 2021). A aceleração de tais desequilíbrios tem causado eventos climáticos extremos de diferentes intensidades e magnitudes ao redor do mundo (e.g. inundações, aumento de ondas de calor, secas prolongadas, ciclones, Knutson et al. 2010; Dai 2011; Eccles et al. 2019; IPCC 2021). Nesse ritmo são previstos desequilíbrios ainda mais intensos, onde um aumento de 1.5°C é indicado nos próximos 20 anos no cenário climático brando, enquanto um aumento em 3.3 à 5.7°C é esperado até 2100 em um cenário climático extremo (IPCC 2021). Um aumento na temperatura rápido em um curto período tem como um dos desdobramentos a rápida intensificação de secas (i.e hidrológica, agrícola, ecológica e atmosférica, Novick et al. 2016; Konapala et al. 2020; IPCC 2021) com consequências catastróficas para o mundo (e.g. desde a perda de biodiversidade à escassez de alimentos, Allen et al. 2010; Bellard et al. 2012; Tito et al. 2018).

Particularmente, nos trópicos, é esperado um aumento da intensidade de chuvas (Kao and Ganguly 2011; Lyra et al. 2018) porém, mesmo que ocorra o aumento da precipitação em determinadas regiões, esta pode ocorrer de forma sazonal, podendo ocorrer chuvas concentradas em maiores intensidades intercaladas por períodos de seca (Feng et al. 2013; Lyra et al. 2018). O aumento da intensidade e duração da estiagem associada a altas temperaturas pode não apenas aumentar a demanda evaporativa do ar resultando no aumento da transpiração vegetal, mas também estreitar o filtro ambiental associado à disponibilidade hídrica (Novick et al. 2016; Brodribb et al. 2020; Konapala et al. 2020). Tal cenário de redução na disponibilidade hídrica e aumento da transpiração foliar conduz a um aumento da tensão na coluna da água no xilema (McDowell et al. 2008; Brodribb et al. 2020) favorecendo o embolismo (i.e. ruptura na coluna dá água por formação de bolhas de ar) (Tyree e Sperry 1989). Quando essas bolhas de ar são distribuídas entre os vasos do xilema, elas impedem a chegada de água nas folhas limitando a assimilação de carbono, o que pode ocasionar a morte de indivíduos e a extinção de populações (McDowell et al. 2008; Choat et al. 2018). Dentre os desdobramentos da morte de plantas por seca existem evidências de mudanças na distribuição de espécies (Engelbrecht et al. 2007), na estruturação de comunidades (Trugman et al. 2020;

Matos et al. 2020) no ciclo da água e na produtividade primária em vegetações (Boisvenue and Running 2006; Allen et al. 2010; Bruijnzeel et al. 2011).

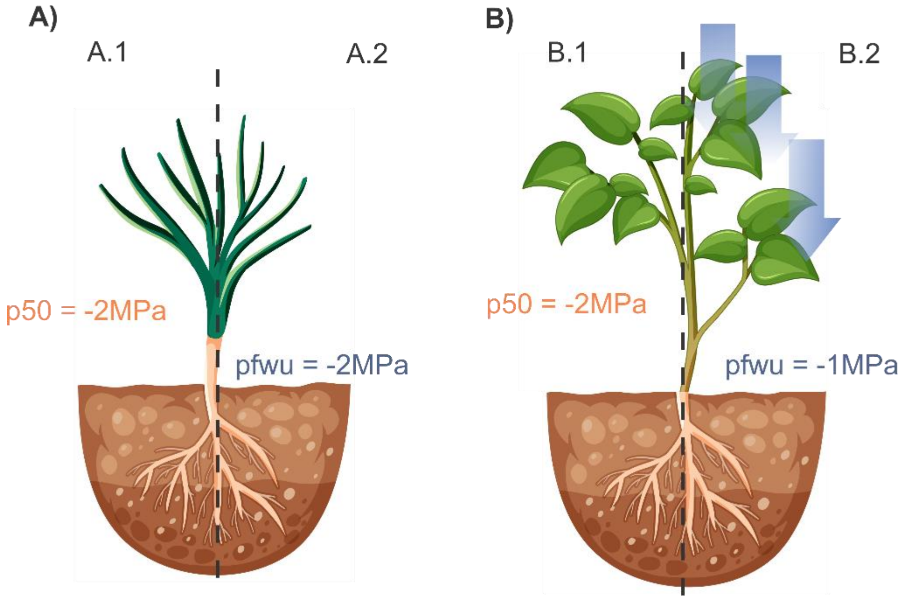
No entanto, mesmo na ausência de precipitação, a água pode continuar entrando no sistema através da água em suspensão na atmosfera, por neblina (água em suspensão na atmosfera em relação a superfície terrestre que possui visibilidade abaixo de 1000 m), névoa (menos densa em relação a neblina, com visibilidade entre 1000 m e 11000 m) (National oceanic and atmospheric administration, 1995) ou orvalho (condensação e deposição do vapor de água em uma superfície mais fria) (Agam e Berliner 2006), além de chuvas fracas (com menos de 5 mm ver Wu et al. 2016). Tais fontes de água quando depositadas na folha ou como vapor de água podem minimizar a perda de água por transpiração através do resfriamento foliar (Monteith 1957; Monteith and Butler 1979) (1) podem umedecer o solo tornando a água disponível para as raízes superficiais através do escoamento de gotículas da folha para o solo (Baguskas et al. 2017) (2) ou podem ser absorvidas passivamente via estômato (Guzmán-Delgado et al. 2021), hidatódio (Martin and von Willert 2000), cutícula (Eller et al. 2013) ou demais estruturas epidérmicas na folha (Tan et al. 2013; Wang et al. 2016; Boanares et al. 2018; Bryant et al. 2021) (3).

A absorção de água em suspensão na atmosfera pelas folhas é mais evidente na estação seca quando os solos estão mais secos devido a menor ocorrência de chuvas (Rundel 1982). Dessa forma, as folhas se tornam menos saturadas o que favorece a entrada de água da atmosfera (mais saturada devido ao evento de molhabilidade foliar) para o mesofilo (menos saturado) devido a diferença de gradiente osmótico (Rundel 1982). Após a absorção de água pela folha (*FWU, foliar water uptake,*), a água pode voltar para a atmosfera por transpiração foliar ou ser redistribuída para os demais órgãos da planta no sentido reverso ao continuum solo – planta – atmosfera (SPAC, *soil-plant-atmosphere continuum*) (Eller et al. 2013; Goldsmith 2013; Berry et al. 2019). Enquanto a água obtida por FWU é redistribuída ela pode elevar o potencial hídrico (Schreel et al. 2019), repreencher vasos cavitados pela seca (Laur and Hacke 2014) , contribuir para manutenção da abertura estomática (Berry et al. 2014) e consequentemente aumentar a assimilação de carbono pela vegetação (Eller et al. 2013; Berry et al. 2014; Binks et al. 2019).

Apesar de parte dos estudos evidenciarem efeitos positivos dos eventos de molhabilidade em plantas, principalmente nos descritores do status hídrico (e.g. potencial hídrico, sap flow) (Gouvra and Grammatikopoulos 2003; Burgess and Dawson 2004; Goldsmith et al. 2013; Schreel et al. 2019), parte deles tem verificado efeitos negativos na fotossíntese (Reinhardt and Smith 2008; Berry and Goldsmith 2020). Por exemplo, estudos na última década evidenciaram uma redução na taxa fotossintética em alguns ecossistemas, uma vez que eventos de neblina de maior densidade podem dificultar a chegada de luz na folha (Berry e Goldsmith 2020). Somado a isso a presença de água sobre a folha pode obstruir os estômatos, reduzindo a difusão de gás carbônico da atmosfera para o mesofilo (Fogg 1947; Ishibashi e Terashima 1995), o que pode comprometer a assimilação de carbono por plantas. Ainda, estudos sugerem que folhas úmidas também são mais propensas a deposição de poluentes (Burkhardt et al. 2012) e proliferação de patógenos (Arnold e Engelbrecht 2007), o que pode contribuir para maiores chances de morte em plantas.

Independente das nuances de benefícios gerados por eventos de molhabilidade, é evidente que tais eventos podem resultar em mudanças no grau de vulnerabilidade de plantas à seca, podendo trazer benefícios ou custos. Por exemplo, se duas espécies possuem o mesmo valor de p50 (potencial hídrico em que a planta perde 50% de sua condutividade hidráulica devido à cavitação por seca) (Figura 1-A, B) e, no entanto, uma delas é capaz de absorver mais água pela folha (Figura 1-B, B.2) que a outra (Figura 1-A, A.2), a planta capaz de absorver mais água pela folha seria menos vulnerável à seca, uma vez que poderia aumentar seu status hídrico (pfwu) sem depender exclusivamente da água retida no solo. Portanto, caso não considerado a performance do FWU nas plantas ambas poderiam ser categorizadas equivocadamente com similares graus de vulnerabilidade à seca (Figura 1).

Figura 1 - Representação da influência da capacidade de absorção hídrica foliar na vulnerabilidade de plantas à seca.



Legenda: Exemplo hipotético de um estudo com duas plantas A e B, onde a planta A possui uma performance insignificante de FWU, enquanto a planta B possui uma maior performance de FWU. No primeiro cenário A.1 e B.1 não foi considerado a influência de eventos de molhabilidade foliar o que resultou em uma similar vulnerabilidade à seca segundo o valor de p50. No segundo cenário foi considerado a influência dos eventos de molhabilidade em ambas as plantas. Como a planta B é capaz de um maior FWU, essa planta foi capaz de minimizar a redução do potencial hídrico impedindo que ele alcançasse o valor de p50, o que sugere que na realidade a planta B é menos vulnerável à seca que a planta A. Setas azuis indicam maior performance de FWU.pfwu significa potencial hídrico pós exposição a evento de molhabilidade foliar.

Fonte: O autor, 2022.

Em uma escala de maior complexidade biológica, a performance do FWU pode estar sujeita a estratégia ecológica predominante em um dado ecossistema. Nesse sentido, estudos recentes tem associado a capacidade de performar FWU ao espectro econômico de plantas (e.g. Matos et al. 2020) proposto por Reich (2014) com base no espectro econômico de folhas de Wright et al. (2004). Nesse espectro é possível identificar, ao longo dos gradientes de recursos (e.g. quantidade de água e nutrientes no solo) qual seria a estratégia ecológica preponderante em um determinado ecossistema (Wright et al. 2004; Reich 2014). Por exemplo, em áreas com alto teor de recursos predominam plantas com estratégias de uso rápido de recursos, o que reflete em um rápido crescimento (*fast-strategy*, Reich 2014). Tais plantas geralmente possuem características relacionadas a aquisição de recursos, como folhas finas e com maior área foliar específica (SLA, *specific leaf area*), com madeira menos densa, maior condutância estomática, investimento em eficiência hidráulica no xilema e aquisição de recursos por folha e raiz (Reich 2014; Pierce et al. 2017; Matos et al. 2020; Oliveira et al. 2021). Por outro lado, plantas que ocupam ambientes com poucos recursos, possuem o uso lento de recursos como estratégia predominante, o que consequentemente reflete em um lento crescimento da planta (*slow-strategy*, Reich 2014) (Figura 2). A maioria dessas plantas possuem uma alta capacidade de conservar recursos em seus órgãos (i.e. folha, caule e raiz) ou mesmo minimizar a perda de recursos para o ambiente (Wright et al. 2004; Reich 2014), uma vez que exibem menor condutância estomática que as plantas de estratégia rápida (Oliveira et al. 2021). Geralmente também possuem folhas grossas e com baixo SLA, madeira densa, maior investimento em segurança hidráulica e lenta aquisição de recursos por folha (FWU) e raiz (Reich 2014; Pierce et al. 2017; Matos et al. 2020; Oliveira et al. 2021) (Figura 2). Portanto de forma geral, com base na estratégia de uso de recursos predominante em cada ecossistema, é sugerido que plantas de rápido uso de recursos sejam aquelas com maior sensibilidade à seca, enquanto as de uso lento aquelas mais resistentes à seca. Apesar dos estudos apontarem nessa direção, aspectos relacionados a influência dos eventos de molhabilidade foliar em ecossistemas permanecem pouco esclarecidos meta-analiticamente e empiricamente.

Figura 2 - Representação do espectro econômico de plantas com inclusão do FWU

Legenda: Espécies de plantas com estratégia de lenta aquisição de recursos (em laranja, descrito por menor SLA, folhas grossas, maior investimento em segurança hidráulica e menor condutância estomática) performam menos FWU. Enquanto plantas com estratégia de rápida aquisição de recursos (em verde, descrita por maior SLA, folhas finas e maior investimento em eficiência hidráulica e condutância estomática) são capazes de performar mais FWU. Setas azuis indicam maior performance de FWU.

Fonte: O autor, 2022.

Além da inclusão de eventos de molhabilidade em estudos entre ecossistemas no presente, tais eventos podem ser propostos para diferentes cenários climáticos. Modelos climáticos atmosféricos apesar de abrangentes, não consideram aspectos como eventos de neblina, muitas vezes ocorrentes em ambientes em maiores altitudes. Além da maior propensão a eventos de neblina, ecossistemas em maior altitude são sujeitos a uma maior aridez devido a maior demanda evaporativa, radiação solar, ar rarefeito e solos rasos, condições e recursos diferentes do entorno (Leuschner 2000; Körner 2007) e que podem não ser abrangidos por modelos atmosféricos. Por outro lado, modelos com base na relação clima x características funcionais são uma alternativa interessante na descrição da flora futura em regiões de elevada altitude, o que pode evitar projeções equivocadas. Um exemplo de modelos com base em clima x características funcionais são aqueles aplicados na reconstrução climática com base em características morfológicas de folhas fósseis. Dessa forma, características como tamanho e espessura da folha tem sido importantes descritoras do clima (Wolfe 1993) em estudos sobre reconstrução climática (Bailey e Sinnott 1915; Wolfe 1993; Peppe et al. 2011). Por exemplo, plantas com folhas simples, estreitas e não denteadas (com menor superfície foliar) têm sido relacionadas a ambientes mais secos ou frios (Bailey e Sinnott 1915), onde existe uma maior necessidade de conservação de agua pelas plantas devido à falta desse recurso no solo, devido à estiagem ou congelamento (Royer et al. 2012). Além disso, através do uso de características funcionais coletadas atualmente e projetadas em cenários futuros, é possível projetar quais plantas seriam mais ou menos resistentes à seca em cenários de mudanças climáticas.

Somado a isso, embora o uso de características funcionais morfológicas na descrição de respostas de plantas a mudanças ambientais no presente e como base para modelos climáticos seja muito presente na literatura, ainda existe uma incerteza se o uso de apenas características morfológicas é suficientemente robusto em previsões da flora. Isso porque características ecofisiológicas (e.g. potencial hídrico foliar, FWU, p50, condutância estomática) possuem maior especificidade em menores escalas de tempo e/ou espaço (Rosado and de Mattos 2017; Volaire 2018; Volaire et al. 2020), uma vez que capturam maiores flutuações ambientais, o que pode abranger áreas sujeitas à rápidas variações climáticas (Volaire et al. 2020), como áreas com variação altitudinal. Inclusive, apesar de dificilmente conseguirmos usar descritores ecofisiológicos para o passado, ainda que alguns autores consigam usar algumas características como proxy de características ecofisiológicas (e.g. densidade e tamanho estomático como proxy de absorção de CO2, como obervado em Roth-Nebelsick e Konrad

2019), nós podemos usar a relação proposta por modelos paleoclimáticos entre clima e características funcionais morfo-fisiológicas coletadas atualmente em projeções. Dessa forma é possível obter respostas mais precisas sobre a vulnerabilidade de plantas, também, futuramente.

Em geral, entender os potenciais efeitos dos eventos de molhabilidade foliar não só no presente, mas também na flora futura pode contribuir para o entendimento a respeito do papel ecológico dos eventos de molhabilidade foliar na vulnerabilidade de plantas à seca a médio e a longo prazo. Tal abordagem é ainda mais relevante quando considerada a predições de redução do orvalho (Tomaszkiewicz et al. 2016; Feng et al. 2021) e do aumento da altitude de nuvens em relação a superfície terrestre (Pounds et al. 1999; Still et al. 1999), o que resulta na redução do contato da neblina com a vegetação. Esse cenário poderá, junto ao aumento da temperatura global nas próximas décadas, maximizar o grau de vulnerabilidade à seca em plantas. Isso, principalmente nas plantas mais dependentes da neblina como fonte de obtenção de água, uma vez que as plantas que mais performam FWU são aquelas mais propensas a perder água para a atmosfera (Matos et al. 2020). Dessa forma, vegetações que usam eventos de molhabilidade foliar como fonte complementar de água, e especialmente as de maior altitude que enfrentam naturalmente uma maior demanda evaporativa e solos mais secos durante o ano, podem ser tornar mais vulneráveis nas próximas décadas.

Levando em consideração que as predições climáticas indicam aumento acelerado da temperatura conduzindo a formação de ondas de calor e secas de maiores duração (através da redução da precipitação, maior demanda evaporativa e aumento da altitude da neblina), essa tese trouxe como objetivo geral avaliar o papel ecológico das fontes complementares de obtenção de água na vulnerabilidade de plantas à seca em diferentes ecossistemas e cenários climáticos. Para alcançar esse objetivo, essa tese foi subdivida em três capítulos.

O primeiro capítulo se intitula "*Elevation and precipitation mediate leaf wetting benefits in plants – a global meta-analysis* e foi desenvolvido a partir da necessidade de buscar um real entendimento sobre benefícios ou prejuízos da exposição de plantas a eventos de molhabilidade foliar (i.e. neblina, névoa, orvalho ou chuvas fracas). Por meio de uma abordagem meta-analítica nós quantificamos o efeito dos eventos de molhabilidade foliar em cinco caraterísticas ecofisiológicas de plantas com base em 252 observações de 45 estudos distribuídos em oito fitofisionomias. Em seguida, nós buscamos entender os efeitos de fatores abióticos e biológicos na resposta ecofisiológica das plantas expostas a eventos de molhabilidade foliar. Finalmente, avaliamos aspectos relacionados a limitações ainda persistentes nesse tópico, bem como propomos direcionamentos relativos a futuras pesquisas sobre o papel de eventos de molhabilidade em plantas.

O segundo capítulo intitulado *“Cloud ecosystems are differently affected by drought: An integrated approach considering plant economic-spectrum, resistance to embolism and foliar water uptake”* objetivou entender como pares filogenéticos de plantas ocorrentes em dois ambientes contrastantes sujeitos a eventos de neblina (uma floresta tropical acima de 700 m do nível do mar e uma área de campos de altitude acima de 2000 m do nível do mar no sudeste brasileiro) respondem à seca. Para isso nós usamos uma combinação de 13 características funcionais morfo-fisiológicas como descritores de vulnerabilidade à seca.

Finalmente o terceiro capítulo *“Paleoclimate models predict the functional profile of vegetations on climate change scenarios”* investigou se modelos climáticos com base em características funcionais de plantas não apenas são capazes de reconstruir o clima no passado, como também podem ser usados na previsão de mudanças climáticas. Adicionalmente, esse capítulo investigou a importância da inserção de características funcionais fisiológicas como mecanismo explicativo para mudanças na flora em cenários climáticos futuros. Nós usamos como modelo uma região de altitude (acima de 2000 m do nível do mar) no sudeste brasileiro sujeita a neblina e com condições e recursos que conferem maior aridez a esse ambiente em relação ao entorno. As características específicas desse ambiente muitas vezes podem conduzir a resultados pouco precisos por modelos atmosféricos tradicionais, e por isso, essa área foi escolhida para o emprego de um modelo com base em clima x característica funcional.

Como obervado buscamos avaliar desde a escala global até a local o grau de vulnerabilidade à seca em plantas, considerando o papel dos efeitos de fontes complementares de água na vegetação. Os dados obtidos aqui são valiosos para avançarmos no entendimento teórico sobre as respostas de plantas à seca, assim como podem ser base para modelos climáticos em uma abordagem aplicada.

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1 **ELEVATION AND PRECIPITATION MEDIATE LEAF WETTING BENEFITS IN PLANTS – A GLOBAL META-ANALYSIS**

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Abstract

Wetting events (i.e. fog, mist, dew or light rain) play a key-ecological role in nature since they are a complementary water resource via leaf uptake in plants. However, despite interest in this subject over the last decades, the actual benefits and costs of leaf wetting events in plant functioning are not clear. Our study aims (1) to evaluate the actual benefits/costs of leaf wetting to plants through five ecophysiological traits (leaf water potential, photosynthesis, sap flow, stomatal conductance, and leaf transpiration); and (2) to understand the role of elevation, mean temperature, mean precipitation, duration and type of wetting events and, photosynthetic pathways in the physiological traits exposed to wetting events. From 252 observations of 45 articles, we showed that leaf wetting increases the water status and stomatal conductance while decreasing sap flow of plants. However, contrary to expected, leaf wetting events do not affect photosynthesis and leaf transpiration. Additionally, we assessed that precipitation, elevation and wetting duration are important moderators of responses of plants exposed to wetting events and should be considered in leaf wetting studies. Finally, we suggest more studies in drylands and high environments, investigations about dew events and standardization of foliar water uptake method allowing comparisons between vegetations.

Keywords: cloud ecosystems, cloud-uplift, drought, ECMWF *Reanalysis*, foliar water uptake (FWU), plant vulnerability, refilling.

1.1 **Introduction**

Wetting events from atmosphere (e. g. fog, mist, dew or short rains), also called “occult precipitation” (Nicholson 1930) or horizontal precipitation (Schellekens et al. 1998), occur since desertic ecosystems (Ebner et al. 2011; Li et al. 2014) to temperate forest (Dawson 1998; Burgess and Dawson 2004; Simonin et al. 2009), mangroves (Schreel et al. 2019; Hayes et al. 2020) tropical rainforest (Zhang et al. 2014; Binks et al. 2019) and tropical montane cloud forest (TMCFs) (Goldsmith et al. 2013; Oliveira et al. 2014; Gotsch et al. 2016). Across the different environments, these events may act as complementary water source for plants via (1) indirect absorption by roots, when water droplets on leaf surface runoff and drip to soil (Ingraham and Matthews 1995; Baguskas et al. 2017); (2) leaf direct vapour absorption (Stone et al. 1950; Guzmán-Delgado et al. 2021); (3) leaf direct absorption by water deposition (Dawson 1998; Eller et al. 2013). This water deposited on the foliar surfaces may be absorbed by a variety of leaf structures, such as stomata (Emery 2016; Guzmán-Delgado et al. 2021), trichomes (Boanares et al. 2019), scales (Wang et al. 2016), cuticle (Eller et al. 2013), cork warts (Bryant et al. 2021), hydathodes (Martin and Willert 2000) and salt glands (Tan et al. 2013). After leaf absorption, water from the atmosphere can be redistributed to other organs or returned to the atmosphere by leaf transpiration. Besides leaf epidemical structures, epiphylls (organisms that grow on or into foliar surface, such as bryophytes, fungi, bacteria, liverworts *sensu* Ruinen 1961) may also influence the water flow of between atmosphere plant tissues (Rosado and Almeida 2020), through a higher (Burgess and Dawson 2004) or lower uptake in plants (Shirtcliffe et al. 2006) depending on their hydrophilic potential (Rosado and Almeida 2020).

Although inferences about foliar water uptake have been dated since 1727, when Hales (1727) suggested that sunflower leaves increase their weight due to foliar uptake from dew, only in 1950 Stone showed empirically FWU based on an accurate scientific method (Stone et al. 1950). Despite these findings, studies about leaf wetting events and foliar water uptake started increasing rapidly from 2000s with the development of new methodologies and climate change concerns (Fig. 1). Such efforts have resulted in several reviews publications (Dawson et al. 2018; Berry et al. 2019; Schreel and Steppe 2020) and experimental studies (Gouvra and Grammatikopoulos 2003; Burgess and Dawson 2004; Eller et al. 2013; Cavallaro et al. 2020); which provided evidence of FWU in six biomes, 77 families and 233 species (Berry et al. 2019) so far. However, although the studies about leaf wetting have increased rapidly over the literature and some hypotheses about costs and benefits of FWU to plants have been discussed (Dawson and Goldsmith 2018), there is still an unclear consensus about the actual contribution of leaf wetting on plant responses.

Studies performed in the last decades have shown beneficial effects of leaf wetting, such as an increase in water status (Limm et al. 2009; Schreel et al. 2019), via water drip (also called fog drip) (Baguskas et al. 2017) and via FWU followed by hydraulic redistribution toward other plant organs (Nadezhdina et al. 2010; Eller et al. 2013) colling down and increasing of photosynthesis in species (Berry et al. 2014; Berry et al. 2019) and gross primary productivity in ecosystem level (Binks et al. 2019). Although the leaf wetness effects in plant water status seem clear in the literature, they are still unclear in photosynthesis, where studies have also shown costs (Letts and Mulligan 2005; Reinhardt and Smith 2008; Berry and Goldsmith 2020). Fog/mist/dew decreases light availability for leaves lowering photosynthesis (Parkhurst and Loucks 1972; Berry and Goldsmith 2020). In addition, CO2 assimilation into the leaves is slow due to water film covering the stomata (Parkhurst and Loucks 1972), reducing the photosynthesis rate. Moreover, wetted leaves may be prone to pathogens growth (Arnold and Engelbrecht 2007) and pollute deposition (Burkhardt et al. 2012), which may decrease plant fitness in a given environment (Rosado and Almeida 2020)

Besides the plant responses *per se*, an arrange of factors could mediate the difference among responses of plants to wetting events, such as climate factors (precipitation, temperature), topography (elevation), type (fog, mist, dew, and short rain) and characteristics of wetting events (duration, intensity and frequency) and biological traits (e.g. leaf and root traits, photosynthetic pathways) (Berry et al. 2014; Dawson and Goldsmith 2018; Berry et al. 2019; Boanares et al. 2019; Cavallaro et al. 2020). For example, vegetation under higher solar radiation, temperature and low precipitation might have a higher foliar water uptake by wetting events than others vegetations, mostly in a via regardless of stomata opening control (e.g. cuticle, trichomes, etc.). More restrictive conditions and limited resources make the soils drier and decrease the water potential in the leaves, while the occurrence of wetting events increase air humidity around leaves. These changes in leaf water potential of atmosphere and leaves provide a reverse gradient to the soil-plant-atmosphere (Berry et al. 2019), which means a reverse water flow from the atmosphere (more positive water potential) into leaf (more negative water potential) (Berry et al. 2019). On the other hand, wetting events in rainy environments could result in a low difference between leaf and atmosphere, which decreases the foliar water uptake. The elevation is also a possible factor of FWU mediation since it relates to higher VPD, solar exposure, inclination, runoff, and shallow soils (Körner 2007;

Antonelli et al. 2018) which may cause a higher difference in the leaf-atmosphere gradient and reflect a higher FWU. And, if the wetting events exhibit a higher duration and intensity this effect could be maximized in nature.

Finally, the photosynthetic pathways (C3, C4 and CAM), could mediate FWU effects, through different ways of stomata control with consequences in the water-saving. Plants CAM could perform less FWU by wetting events once these plants save more water and open the stomata to CO2 uptake only during the night when the conditions are more favourable. In contrast, C3 could perform more FWU since these plants need higher CO2 entering the mesophyll to compensate photorespiration effects (a wasteful via based on enzyme rubisco preference in part by oxygen than CO2) (Keeley and Rundel 2003; Taiz & Zeiger 2004) and need to open the stomata, while loss water to atmosphere simultaneously. Differently, C4 could save more water than C3 but less than CAM. C4 have a mechanism of CO2 fixation spatially different, which avoid photorespiration and save more water due to lesser need for CO2 uptake via stomata. However, C4 opens the stomata during the day, such as C3, when needed (Keeley and Rundel 2003; Taiz & Zeiger 2004) losing water. Other biological factors could mediate the foliar water uptake (e.g. leaf traits, deep roots), as have been shown in previous studies (Boanares et al. 2019; Cavallaro et al. 2020), however there is still a small dataset for these types of traits in the literature.

Overall, the main goal of this study was to advance in the topic “how beneficial are wetting events to plants?”. To achieve it, we used a meta-analysis approach, where it is possible to make quantitative comparisons between studies worldwide, considering the heterogeneity between them. Through this approach, we especifically sought (1) to evaluate which are benefits and costs of leaf wetting events (fog, mist, and dew) to plants and their respective magnitudes; (2) to discuss the main factors that mediate plant responses to leaf wetting events; and (3) to discuss methodological limitations and future directions in this topic. Especifically, we used five ecophysiological traits related to water use in plants (i.e. leaf water potential, photosynthesis, stomatal conductance, sap flow and leaf transpiration) as descriptors of cost and benefit of plant responses. Besides, we explored climate, topographical, leaf wetting events and biological factors that could influence the effect of leaf wetting events in plants. This approach becomes more needed when considering the cloud-uplift from Earth, as predicted by climate models which reduce the contact between fog/mist and vegetations in high altitudes (Pounds et al. 1999; Still et al. 1999). It, combined with a decrease in dew events (Tomaszkiewicz et al. 2016; Feng et al. 2021), makes an opportunity to evaluate wetting event ecological role in plants and the possible consequences of their effectiveness in a hotter and drier world (IPCC 2021).

1.2 **Materials and Methods**

1.2.1 Literature search and data extraction

We searched peer reviewed articles published between 1950-2020 (until July 29th) using the classic interface of Web of Science database (https://www.webofknowledge.com). On Web of Science, we used the keyword combinations (fog* OR mist* OR dew* OR wet* OR rain*) AND (lwu OR fu OR fwu OR "leaf water uptake" OR "foliar water uptake" OR "leaf wet*" OR "foliar absorption" OR "leaf absorption") AND (plant* OR tree* OR herb* OR shrub* OR grass* OR epiphyte*). These keywords were searched in abstract, title and in the abstract keyword. Subsequently, we refined the articles by idiom (English) and by document type (Original Article). We chose the year 1950 to start our research due to Stone's article published in this year (Stone et al. 1950), where was evaluated foliar water uptake from water in suspension in atmosphere through an experiment with plants of shrublands in California, USA (Stone 1950). Dew (condensation of water vapour on a colder surface), as well as fog (water in suspension in the atmosphere characterized by visibility below 1000 m) and mist (less dense than fog, characterized by visibility between 1000 m and 11000 m) (National oceanic and atmospheric administration, 1995, Agam and Berliner 2006), all three wetting events are related to saturated air mass that condense on a colder surface forming droplets (Stone 1957; Goldsmith et al. 2013). These wetting events, in addition to short rains (<5mm), are intercepted by leaves but, they do not usually reach root zone in soil (Wu et al. 2016). The droplets on leaf surface may be also uptake by leaf mostly in dry season, when the precipitation is less frequent. Aiming to obtain a higher range in our search, we used all those events in the literature search.

In the first collection, we obtained 579 articles on Web of Science platform. Secondly, we selected studies with (1) native and vascular species (2) with plant ecophysiological responses to leaf wetting events information and (3) mean, standard deviation (SD) and sample number (N) available. When data of criterion 3 was not available in the article, we contacted the author correspondent to complete our database. After used the selection criteria, we obtained a total of 45 articles and 252 observations across eight vegetation types. When we analysed these articles A) In case of treatments with different wetting exposure, duration, and frequency we chose the one with higher duration and/or intensity/frequency and, B) In case of plants measured during many months we chose the month under conditions more restricted, C) Experimental and in-situ studies were selected in this meta-analysis, D) We only used observations that show the actual exposure of plants to leaf wetting events (not in potential or suggested). Regarding sap flow, we measured the difference between begin (about 12 AM) and end (we considered the up of pulse usually in midday) of each sap flow pulse from image available of studies. Pulses in which there were not wetting events were considered control and pulses during wetting events were considered treatment. In this sense, a negative effect in sap flow means smaller water pulses when the plants are exposed to wetting events, which indicates a decrease in sap flow when leaves are wetted. The numbers of pulses in control and treatment corresponded to number sample (N).

Besides wetting events *per se* other factors can influence how plants respond to wetting events, which include the capacity of performer FWU. Because of this, for each study, we chose climate (mean precipitation, mean temperature), topographic (elevation), wetting (type and duration of wetting events) and biologic variables (photosynthetic pathways) as moderators, totalling six moderators. All climate variables, except elevation, were directly downloaded from the ERA5 land reanalysis product (~ 9 km; ECMWF, 2019) from coordinates and moment/period of measurement of a given variable. We extracted elevation from articles and when this variable was not available in the studies, we obtained it through geoplaner (https://www.geoplaner.com/). In addition, the 2 variables linked to wetting events, type of wetting events (fog, mist, dew, or short rain) and leaf wetting duration in minutes and the biological variable correspondent to photosynthetic pathways (C3, C4 or CAM) were extracted from studies.

1.2.2 Effect size and selection models

We calculated the effect size of leaf wetness events in plants through Hedge's d that consider the difference between control and treatment means, standardized by the standard deviation (SD) and the sample size (N). Results of studies that used standard error as a measure of dispersion were transformed in SD before running effect size analysis. Hedge's d is an index that ranges from - ∞ to + ∞. For example, in our study, a Hedge's d (-) means the negative influence of wetting events in ecophysiological responses of plants, while Hedge's d (+) means a positive effect in the traits. When the value is zero, there is no wetting event influence in the trait investigated. As this index consider SD and N, a higher weight is given to more precise studies. When the data were available only on figures, we used the ImageJ software v1.53a for data extraction. When the authors used a sample interval instead of the exact value to each set of species, we chose the intermediated value to effect size calculation. Hedge's d mean effect size was computed using random effects to each trait.

To understand how moderators could mediate the wetting events in plants, we used selection models (Burnhan & Anderson 2002). Firstly we fitted based on the eight moderators investigated (mean temperature, mean precipitation, elevation, duration and type of event and photosynthetic pathways). Secondly, we extracted the most important moderators from all models generated. In this case, more important moderators have a higher weight based on the sum of Akaike weights and appear more times in the set of models built. Moderators that crossed the red line in 0.8 are considered important for our study. We ran these analyses using "Metafor" and "Glmulti" Package on the R software version 4.1.0.

1.2.3 Sensitive analyses

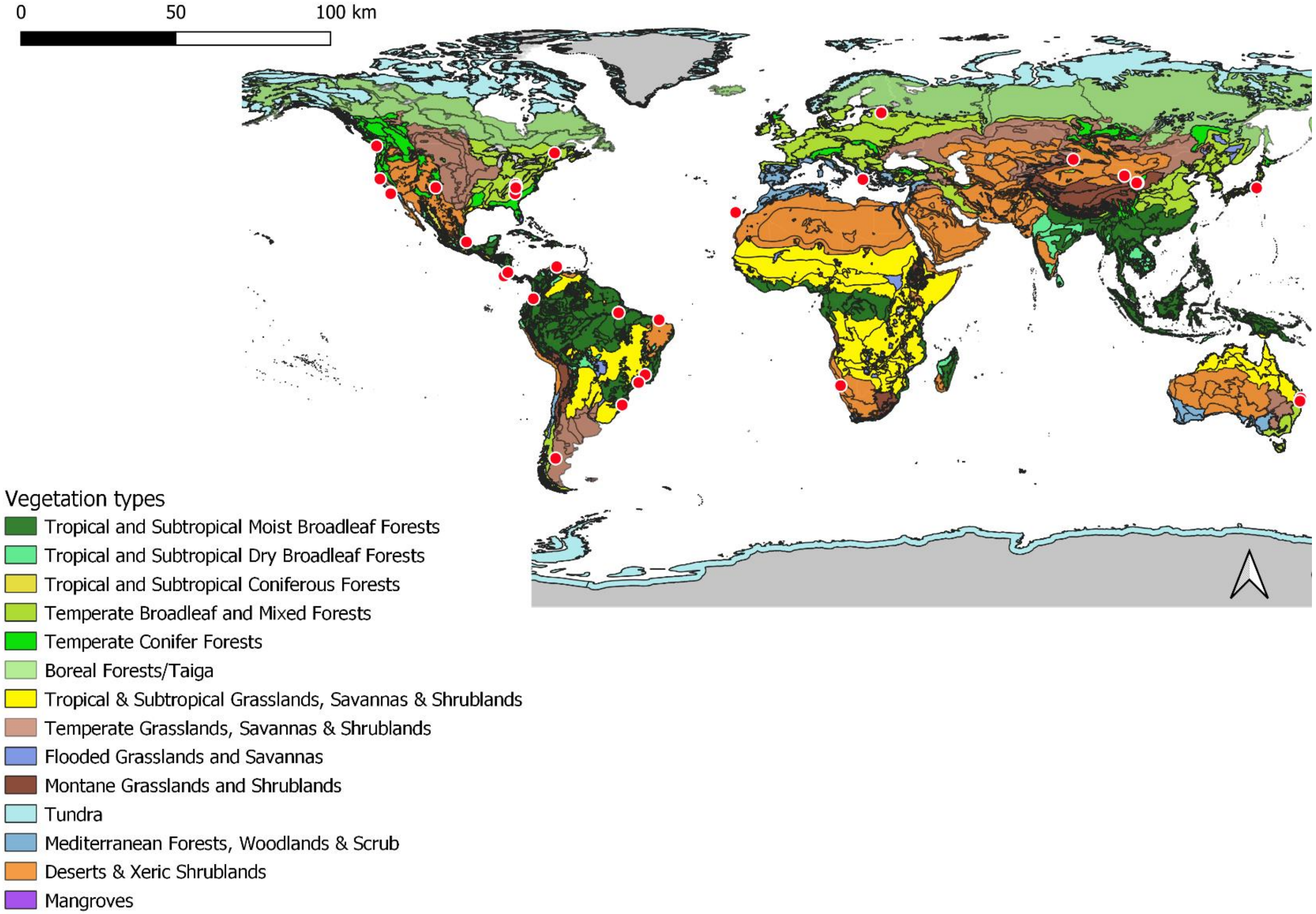
We ran sensitives analyses to assess publication and locality bias e potential outliers in our database to avoid misleading results (see Appendix S2).

1.3 **Results**

1.3.1 Distribution of leaf wetness studies in the world

Most studies were carried out on forests (69% of studies), among Temperate forests (40%, 22 studies) and Tropical and Subtropical forests (29%, 16 studies) (Fig. 1). Desert and shrubland totalling 18%, ten studies. All other ecosystems (Grasslands, Mediterranean and Mangrove) exhibited a percentage of 13% together (Fig. 1). Studies about leaf wetness effects are supported mainly by the USA (46.7%, 21 studies), followed by Brazil (15.5%, seven studies) and China (8.8%, four studies), among a total of 13 countries. Data based on the first author.

Figure 1 – Distribution of leaf wetness studies in the world



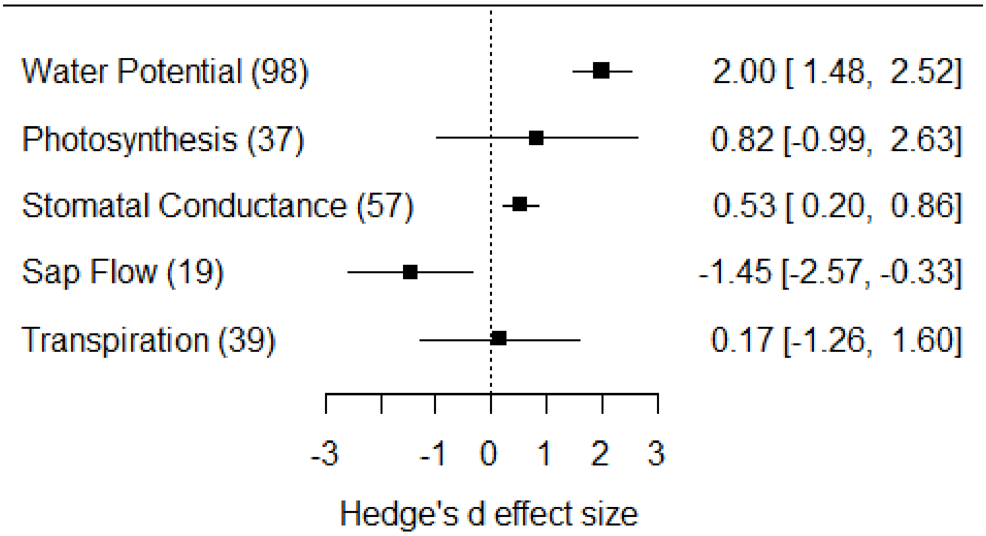
Legend: red dots mean study area locations
Source: The author, 2022.

Despite interest increasing in this subject, we found different methods to measure foliar water uptake and their modifications over the years. The method more used in our database was based on changes in leaf water potential (11 studies), followed by changes in leaf mass (9 studies), sap flow (5 studies) and stable isotopes (3 studies) of a total of 28 studies. As field conditions can show a variety of factors, we did not consider leaf water potential as FWU measuring in our study. Among studies, some of them sought to understand the fog/dew/mist effect via chamber experiment (Berry et al. 2014; Emery 2016), experimental rains (Wu et al. 2016; Binks et al. 2019; Schreel et al. 2019) and the immersion in distilled water (in this case obtaining the maximum capacity of water uptake by leaves). The last one has been applied in the mass and in potential change methods (Limm et al. 2009; Goldsmith et al. 2013; Gotsch et al. 2015; Holanda et al. 2019). However, few studies sought to understand the dew effect, only two studies (a study of Pina et *al.* 2016) in a dry forest in Brazil and another one in a desert in China (Zhuang and Ratcliffe 2012).

1.3.2 Leaf wetness contributes to water status of plants

Leaf wetting events exerted a positive effect in leaf water potential (n = 98, mean = 2.06, CI = 1.55-2.46, p = <.0001, AICc = 479.69) and stomatal conductance (n = 57, mean = 0.53, CI = 0.20 – 0.86, p = 0.001, AICc = 198.62) as our expectations, but surprisingly exerted a negative effect in sap flow (n = 19, mean = -1.45, CI = -2.57 - - 0.33, p = 0.01, AICc =100.02). Besides photosynthesis and leaf transpiration were not affected by leaf wetting events (n = 37, mean = 0.82, CI = -0.99 – 2.63, p = 0.37 =, AICc = 242.31; n = 39, mean = 0.17, CI = -1.26 – 1.60, p = 0.82, AICc = 240.33, respectively) (Fig. 2). Overall, these results indicate a water status improved when plants are exposed to wetting events.

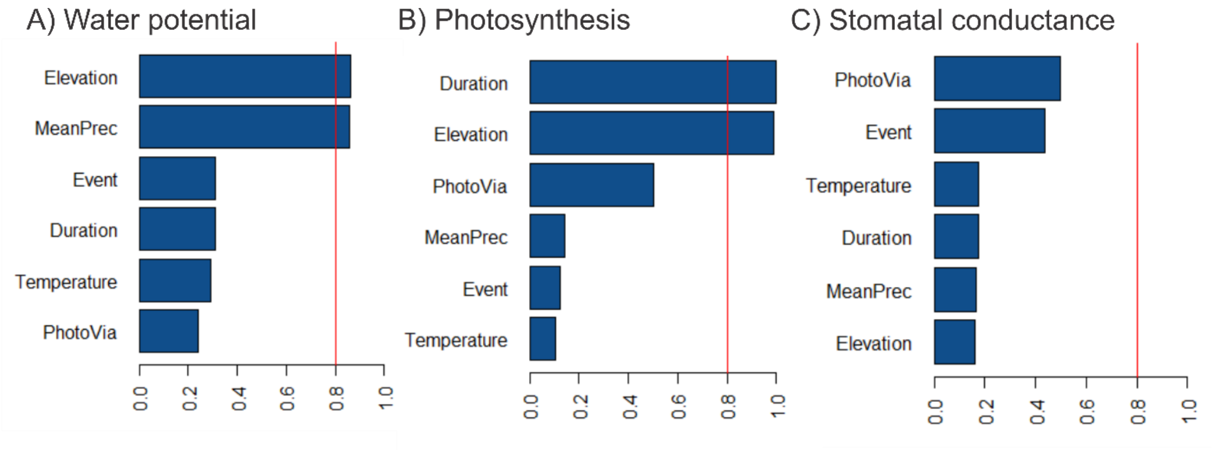
Figure 2 - Effect size of leaf wetting events in the ecophysiological traits of plants



Legend: Hedge’s d effect size of leaf wetting events about leaf water potential, photosynthesis, stomatal conductance, sap flow and transpiration of vascular plants in the world. Variable followed by the number of observations.
Source: The author, 2022.

All variables showed high heterogeneity. Photosynthesis was the most heterogeneous trait (99.33% of heterogeny), followed by leaf transpiration (96.80%), leaf water potential 94.14%, sap flow 86.38% and stomatal conductance 76.33%. The selection model showed that climate, topography, and wetting moderator categories explain heterogeneity observed in the plant ecophysiological traits exposed to wetting events. Among of moderators’ precipitation, elevation and duration were the most important (Fig. 3) to explain the data heterogeneity. While mean precipitation contributed positively to leaf water potential, elevation contributed negatively to leaf water potential and photosynthesis. Besides elevation, leaf wetting duration also affected photosynthesis negatively. Stomatal conductance was not affected by moderators. We did not find moderators' contributions to sap flow and transpiration due to few data available over literature to use moderator analyses.

Figure 3 – Model-averaged of importance of the terms to ecophysiological traits with higher sample size



Legend: Importance of elevation, mean temperature (Temperature), mean precipitation (MeanPrec), duration of leaf wetting event (duration), type of leaf wetting event (Event) and photosynthetic pathways (PhotoVia) in (a) leaf water potential (b) photosynthesis and (c) stomatal conductance in plants exposed to wetting events at a global level assessed through model-averaged of the importance of terms. Highers bars include the factors included in a major number of models and consequently have a higher weight by AICc. Moderators that cross the red line (0.8) are considered important mediators of ecophysiological traits exposed to wetting events. There is no difference between PhotoVia and stomatal conductance samples. Hence the variable was omitted in the photosynthesis and stomatal conductance models.
Source: The author, 2022.

1.4 **Discussion**

Our meta-analysis showed that leaf wetting events increase leaf water potential and stomatal conductance while decreasing the sap flow, which suggests a positive contribution to water status in plants. However, leaf wetting events do not affect photosynthesis and leaf transpiration in plants, different from the positive (Eller et al. 2013; Berry et al. 2014) or negative expectations of some studies (Gotsch et al. 2016; Berry and Goldsmith 2020), but according to Dawson and Goldsmith (2018). Precipitation, elevation, and wetting duration were important mediators of responses of plants and should be considered in studies about this topic. Additionally, we concluded there are few studies in dry ecosystems despite increasing interest in leaf wetting in the last 20 years. Also, few studies use dew as a leaf wetting event. Using different foliar water uptake measuring methodologies is still a challenge to vegetation comparisons.

A higher stomatal conductance in plants exposed to wetting events can be explained by higher water flow from the atmosphere (more saturated due to wetting events) to guard cells (less saturated due to drying soils), which lead to guard cell expanding, causing stomata opening. Hence, the stomata opening allows an increase in water flow, from water deposited on the leaf or as vapour (Berry et al. 2019) into mesophyll, causing an increase in leaf water potential in plants. However, different from our expectations, sap flow decreased during leaf wetting events. This result can be explained by a higher part of water absorbed by leaves being returned to the atmosphere by leaf transpiration (Berry et al. 2019). Another one is distributed to mesophyll and terminal branches, filling the capacitance of plant tissues (Burgess and Dawson 2004). In this way, when the water from FWU achieves the stems, where the sap flow sensors are localized, it is with a low magnitude, as Burgess and Dawson (2004) pointed out in their study with redwoods. Besides that, a low magnitude was found in different ecosystems such as temperate (5-7%, Burgess and Dawson 2004), drylands (10%; Li et al. 2014), subtropical (1-10% Cassana et al. 2016) and tropical rainforest (25%, Eller et al. 2013). It can be common even in different vegetation. Therefore, despite most plants exhibiting water status improved due to FWU in leaves and potentially in terminal branches, a smaller amount of water from FWU seems to be redistributed until stem and hence roots in most species.

Despite no influence of moderators in stomatal conductance, the leaf water potential ranged in magnitude when considering precipitation and elevation (Fig. 2). Plants located in high elevations and exposed to few short-rains (e.g. drizzly and slights orography rains) were less positively affected in their leaf water potential (Fig 2). Higher elevations are environments with shallow soils, rain seasonality, VPD and solar exposure, conditions that cause water loss to the atmosphere via cuticle, decreasing the leaf water potential. Besides that, when higher elevations are combined with few short-rains (about 0.003), the plants become less wetted. As a result, they could maintain their stomata close, which contributes to a lesser FWU when considered stomata via minimizing FWU magnitude effect. In this sense, the water absorbed from FWU could not compensate for negative values of leaf water potential in those plants at higher altitudes prone to short and low rains. This condition is more common in plants with thin leaves since they lose and gain water faster than thicker leaves (Boanares et al. 2019). However, there are many species with thicker leaves with wax (Körner et al. 1989). In plants with this characteristic, a lesser performance of FWU is expected due to higher leaf capacitance, which reduces the leaf-atmosphere gradient (Gotsch et al. 2015) and hydrophobic wax on leaves (Körner et al. 1989). Therefore, a higher altitude and few short-rains can reduce the leaf water potential benefit in plants even with different types of leaves in the vegetation.

Elevation also reduced photosynthesis under wetting events scenarios similar to leaf water potential. An explanation is that plants under higher elevations were often prone to fog or mist events in our database, which reduces the light that arrives on the leaf surface of plants, decreasing photosynthesis (Berry and Goldsmith 2020). In addition, the water in suspension is often deposited on the leaf surface, reducing carbon dioxide diffusion into leaves (Brewer and Smith 1997; Smith and Mcclean 2011; Holder 2012), resulting in lower photosynthesis (Letts and Mulligan 2005b; Reinhardt and Smith 2008). This negative effect in photosynthesis is maximized when the leaf wetting event duration is long since plants remain more time with obstructed stomata and lower light arriving on the leaf surface. On the other hand, plants in lower elevations and prone to shorter leaf wetting events can be beneficed once the wetting event waters the vegetation but does not reduce the CO2 entering by stomata or the light arriving on leaves. The influence of a high variety of elevations and leaf wetting duration in our database in photosynthesis can have contributed to a neutral response of wetting events in this variable. For example, we observed in our database plants in low altitudes exposed to long periods of leaf wetting events and plants in high altitudes exposed to short leaf wetting events which could lead to similar responses to wetting events.

Despite few of our data having enough information about moderators, we speculated about the potential effect of mediators in sap flow and leaf transpiration. For example, different duration and frequencies of wetting events in plants can cause different sap flows. Evidence is observed in Cassana et al. (2016), in which on the first day, there was a lower sap flow (only 1% of the maximum sap flow), and after 35 days, a higher sap flow was observed (about 10% of the maximum sap flow). Based on (Burgess and Dawson (2004), we speculated that the first wetting event could be used to refill embolized vessels and increase the capacitance over the days could be used to improve the sap flow. Besides that, this trait could be affected by the high of plants. Most studies with sap flow were done in trees (Burgess and Dawson 2004; Nadezhdina et al. 2010; Moore et al. 2018) with sap flow sensors in the stem. Therefore, it could cause a low magnitude of sap flow recorded. Regarding leaf transpiration, when plants are not exposed to wetting events, they possibly close their stomata to minimize the water loss, reducing the leaf transpiration (Alvarado-Barrientos et al. 2014). Similarly, leaf transpiration can remain low during leaf wetting events since plants do not need to cool down via leaf transpiration because leaf wetting reduces leaf temperature. Therefore, both scenarios can provide similar transpiration rates between plants exposed or not to wetting events, which cause a neutral effect of leaf wetting events in plants.

Although in low magnitude and prone to climate, topography and wetness mediators, the contribution from wetting events via FWU, remains important to whole-plant and vegetation. According to the magnitude of contribution, plants could be benefited at a leaf level through cellular growth (Schreel et al. 2019), stomatal opening (Berry et al. 2014) and vessel refilling (Laur and Hacke 2014), which could be reflected in other levels of biological complexity. In this sense, the contribution to vessel refilling might contribute to avoiding hydraulic failure (one of the main processes behind plant mortality, McDowell et al. 2008), being a process that could impact predictions about the vulnerability of plants to drought with consequences in the biodiversity and ecosystem services (Klein et al. 2018). For example, FWU can contribute to 8% of the productivity of plants (Binks et al. 2019) as well as fog-drip contributes to higher soil moisture in until 40% achieving 15 cm in the soil deep, which can contribute to buffer drought effects in plants, especially during dry seasons (Carbone et al. 2013; Baguskas et al. 2017).

1.4.1 Future paths and gaps in leaf wetting events in plants

Considering FWU importance, we suggest more studies in high elevations (e.g. páramos, punas, tropical montane grasslands, alps) and drylands (dry forest and savannas) and deserts since most studies are concentrated in temperate ecosystems and tropical rainforest. As demonstrated in our study, environments in higher elevations exhibit difficulty coping with drought because of a set of conditions that make these vegetations susceptible to drought. Although many studies have been carried out in higher elevations, most of them were developed in the tropical cloud montane forests (TCMFs) (Eller et al. 2013; Gotsch et al. 2015; Darby et al. 2016; Aparecido et al. 2017; Berry and Goldsmith 2020), while other higher elevations ecosystems are still few explored.

Such environments are endemic spots and provide important resources for society (e.g. water source, carbon allocation, tourism) (Bruijnzeel 1998; Safford 1999; Palomo 2017). Moreover, the contribution of leaf wetting for those plants could provide data to a better understanding of vulnerability to drought and their effects on the vegetation. Similarly, environment extra-forest, such as desert and drylands under low and seasonal precipitation and land use than rainforest, is less studied, although occurring in most tropics (Murphy and Lugo 1986; Pennington et al. 2018). Such ecosystems are valorous to agriculture, and many families depend on them to survive (Murphy and Lugo 1986). Besides that, drylands and highlands are rich in endemic species (Banda-R, Karina et al. 2016), being important environments to society and biodiversity.

Another point is, while fog and short rains have increased researchers' attention, dew is still less explored in literature. Studying dew could give us insights into foliar water uptake in areas with no occurrence of fog and during periods of drought. Besides, dew is a global phenomenon, so all ecosystems are prone to uptake water from dew. Lastly, we reinforce the importance of a standardized method to FWU measure. Our study described four methods used regardless of species, making difficult comparisons between studies. We support the use of a standardized method from now on, being the method of changes in mass a good choice because it allows handling a higher number of samples. Furthermore, it is the cheapest method among all methods reported, which could become FWU measure more popular to labs with few resources. Considering FWU's importance, we suggest more studies in high elevations (e.g. páramos, punas, tropical montane grasslands, alps) and drylands (dry forest and savannas) and deserts since most studies are concentrated in temperate ecosystems and tropical rainforest. As demonstrated in our research, environments in higher elevations exhibit difficulty coping with drought because of conditions that make these vegetations susceptible to drought. Although many studies have been carried out in higher elevations environments, most were developed in the tropical cloud montane forests (TCMFs) (Eller et al. 2013; Gotsch et al. 2015; Aparecido et al. 2017; Berry and Goldsmith 2020), while other higher elevations ecosystems are still few explored.

1.5 **Conclusion**

In 1950 Stone suggested that water in suspension from the atmosphere play an important ecological role across vegetation. However, most studies have been developed only in the last two decades, and so far, many incongruences about plant responses have been observed in the literature. Therefore, we contributed with evidence that FWU is beneficial for plants when improving their water status, as well as this effect is mediated by elevation and precipitation.

These findings show the importance of considering foliar water uptake in studies and predictions about the effect of environmental factors on plants. Such results can make patterns more realistic in future studies about climate change effects in vegetation. Despite leaf water uptake mainly contributing to leaf-level, such contributions (e.g. resistance to cavitation and stomatal control) can cause effects in community structure and ecosystems services. In a world each day hotter and prone to a reduction of water input (by precipitation, dew and cloud-uplift), we hope this article contributes to untangling responses of plants to leaf wetness considering environmental factors mediating these responses. Besides that, we hope this meta-analysis helps other researchers to focus on the gaps, considering standardized methods and ecosystems still few explored.

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Supplementary material

Appendix S1

List with the 45 references of papers used in this article after selection criterion. Details about variables extracted in each article can be found in Excel database.

1 - Aparecido LMT, Miller GR, Cahill AT, Moore GW. 2017. Leaf surface traits and water storage retention a ff ect photosynthetic responses to leaf surface wetness among wet tropical forest and semiarid savanna plants. :1–16. doi:10.1093/treephys/tpx092.

2 - Aparecido LMT, Teodoro GS, Mosquera G, Brum M, Barros FD V, Pompeu PV, Rodas M, Lazo P, Müller CS, Mulligan M, et al. 2018. Ecohydrological drivers of Neotropical vegetation in montane ecosystems. Ecohydrology. 11(3):e1932. doi:10.1002/eco.1932. http://doi.wiley.com/10.1002/eco.1932.

3 - Baguskas SA, King JY, Fischer DT, D’Antonio CM, Still CJ. 2017. Impact of fog drip versus fog immersion on the physiology of Bishop pine saplings. Funct Plant Biol. 44(3):339. doi:10.1071/FP16234. http://www.publish.csiro.au/?paper=FP16234.

4 - Baguskas SA, Still CJ, Fischer DT, D’Antonio CM, King JY. 2016. Coastal fog during summer drought improves the water status of sapling trees more than adult trees in a California pine forest. Oecologia. 181(1):137–148. doi:10.1007/s00442-016-3556-y. http://link.springer.com/10.1007/s00442-016-3556-y.

5- Berry ZC, Emery NC, Gotsch SG, Goldsmith GR. 2019. Foliar water uptake: Processes, pathways, and integration into plant water budgets. Plant Cell Environ. 42(2):410–423. doi:10.1111/pce.13439. http://doi.wiley.com/10.1111/pce.13439.

6 - Berry ZC, Smith WK. 2012. Cloud pattern and water relations in Picea rubens and Abies fraseri, southern Appalachian Mountains, USA. Agric For Meteorol. 162–163:27–34. doi:10.1016/j.agrformet.2012.04.005.

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Appendix S2 Details of sensitive analyses - 1) outliers detection, 2) publication bias, and 3) locality bias

1) Outliers detection

Through function “influence” of Metafor package, we detected an outlier in photosynthesis (observation four on Letts and Mulligan 2005) and another one in Stomatal conductance (Eller et al. 2013). However, when we reran the analysis without outliers, only the outlier of photosynthesis showed a significant influence in the model results after comparisons between estimate, p-value, and percentage total of heterogeneity between studies (I^2) with and without outliers. So we removed the photosynthesis outlier and kept all observations in the stomatal conductance variable.

Variable	Estimate	p-value	I^2
Photosynthesis (all observations)	0.27	0.83	99.65
Photosynthesis (without outlier)	0.82	0.37	99.33
Stomatal conductance (all observations)	0.52	0.01	76.33
Stomatal conductance (without outlier)	0.41	0.02	61.27

Source: The author, 2022.

2) Publication bias

We used Rosenthal's Fail-safe N (1979) to evaluate the publication bias. Rosenthal (1979) suggests that a meta-analysis is robust when N > 5k + 10, where the N=number of studies suggested by Rosenthal that would be necessary to become the p>0.05 (no significant) and K = number of studies in this meta-analysis. This analysis was run in R using the function "fsn" of the metaphor package. Results were robust to leaf water potential, stomatal conductance, sap flow, and marginally robust to photosynthesis (K was not higher than N, but p-value = 0.02). In contrast, our results were not robust to leaf transpiration, as indicated below:

- *Leaf water potential*: N > 5k + 10 → 21960> 5(98) +10 = 500 (p<.0001)
- *Photosynthesis*: N > 5k + 10 → 14 > 5(37) +10= 195 (p = 0.02)
- *Stomatal conductance*: N > 5k + 10 → 914>5 (57) +10=295 (p<.0001)
- *Sap flow*: N > 5k + 10 → 299 > 5 (19) +10=105 (p<.0001)
- *Leaf transpiration*: N > 5k + 10 → 0 > 5(39) +10=205 (p=0.49)

3) Locality bias

To verify locality bias, we ran two models, one independent model without considering the locality and another one regarding the study locality. As both models do not considerably change when compared estimate ± SE, p-value and AICc, we considered that observations are independent.

Effect size	**Independent model**			**Locality model**		
	Estimate ± se	**p-value**	**AICc**	**Estimate ± se**	**p-value**	**AICc**
Leaf water potential	2.05±0.25	<.0001	479.69	2.05±0.25	<.0001	479.69
Photosynthesis	0.82 ±0.92	0.37	242.31	0.82 ±0.95	0.38	237.06
Stomatal conductance	0.52±0.16	0.0015	198.62	0.50±0.16	0.0031	195.86
Sap flow	-1.45±0.57	0.01	100.02	-1.45±0.57	0.01	100.02

Transpiration	0.16±0.72	0.82	240.33	0.16± 0.72	0.82	240.33

Source: The author, 2022.

2 - CLOUD ECOSYSTEMS ARE DIFFERENTLY AFFECTED BY DROUGHT: AN INTEGRATED APPROACH CONSIDERING PLANT ECONOMICS SPECTRUM, RESISTANCE TO EMBOLISM AND FOLIAR WATER UPTAKE

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Abstract

Precipitation reduction and fog-uplift (i. e. a water source to vegetation via leaf) are consequences of climate change which increase the risk of mortality of plants by drought worldwide. However, it is still unclear how co-occurring plants in contrasting fog-ecosystems (e.g. tropical montane grassland and tropical rainforest) respond to drought considering the role of fog in those vegetation. As tropical montane grassland plants grow from shallower soils and are exposed to higher solar radiation and evaporative demand due to higher elevation than forest (~2000 m above sea level in grassland and 700 m above sea level in forest), we hypothesized that (I) species in tropical montane grassland will be more resistant to drought and (II) they will be less dependent on fog by potentially exhibit more conservative traits than forest. We used 13 morpho-physiological traits to investigate the vulnerability to drought of 10 phylogenetic pairs of plants in the Atlantic rainforest and tropical montane grassland in the Brazilian Southeast. We found that plants in the tropical montane grassland exhibited more conservative traits (i.e. slow-strategy) and higher resistance to embolism, but different from expected, they performed more foliar water uptake (FWU) than tropical rainforest. Despite tropical rainforest species being more vulnerable to drought than grassland species, a higher vulnerability to drought in both environments is expected in the future. Even less sensitive to drought than forest, grassland plants might be prone to a low fog exposure in the next decades, which can be already happening based on few numbers of fog events recorded in this study.

Keywords: Campos de altitude, cloud ecosystems, functional trait, FWU, hydraulic failure, resistance to embolism, safety margin, vulnerability to drought.

2.1 **Introduction**

Although changes in precipitation regimes are among the most studied effects of global warming, complementary water sources to vegetation via leaf (e.g. fog, mist and dew) may also be affected due to climate change (Feng et al. 2013; Stilll et al. 1999; IPCC 2021). Climate models have predicted fog uplift in cloud ecosystems due to rises in air temperature, which reduce the contact fog-vegetation resulting in lower access of plants to fog (Pounds et al. 1999; Still et al. 1999). The lower exposure of plants to both water sources (i.e. precipitation and fog) may maximize the plant vulnerability to drought around the world since fog is absorbed by leaves and contribute up 25% to sap flow in plants (Eller et al. 2013). However, it is still unclear if co-occurring plants in distinct ecosystems respond similarly to drought and how variable would be their vulnerability considering the role of fog in vegetation.

Events of wettability are essential for the occurrence of foliar water uptake (FWU), resulting in increases in plant water status (Eller et al. 2013; Schreel et al. 2019) and xylem refilling (Laur and Hacke 2014; Fuenzalida et al. 2019). Moreover, such events can increase the photosynthetic rate and avoid carbon starvation in several species (Berry and Smith 2013; Eller et al. 2013; Berry et al. 2014). In this sense, fog events could play an essential role in minimizing the vulnerability of plants to drought, mainly across cloud environments, such as tropical montane rainforest, páramos, punas and tropical montane grassland (Körner 2007; Uehara et al. 2015; Aparecido et al. 2018) where fog events are commons. Although high FWU from fog is expected in higher altitudes, this process does not depend entirely on the frequency, duration, and intensity of fog events and different plant traits that affect this water uptake. For example, montane ecosystems with acquisitive traits (e.g. higher SLA, thin leaves and higher hydraulic efficiency) (Wright et al. 2004; Reich 2014; Oliveira et al. 2021) predominant in vegetation could exhibit a higher FWU. On the other hand, montane ecosystems with the predominance of species with conservative traits (i.e. lower SLA , thicker leaves and higher investment in xylem safe) (Wright et al. 2004; Reich 2014; Oliveira et al. 2021) tend to exhibit a lower FWU.

In the southeast of Brazil, two vegetation share plant families prone to fog events and can be affected by similar consequences of climate change (i.e. precipitation reduction and fog-uplift) (Still et al. 1999; Scarano 2002; Lyra et al. 2018), tropical rainforest about 700 m.a.s.l and tropical montane grassland above 2000 m.a.s.l, (Scarano 2002). Forest plants occur in an environment historically with higher resources (e.g. water) in soils. In that vegetation, most species can exhibit acquisitive strategies such as higher hydraulic efficiency and lower xylem safety, which reflect fast growth (Sperry 2003; Hacke et al. 2006; Oliveira et al. 2021). On the other hand, grassland plants occur in an environment with higher atmospheric drought due to higher elevation. As a result, grassland species may have evolved more conservative traits and more embolism resistance and hence higher resistance to drought.

In those two environments, we used 13 morpho-physiological traits (Table 1) to investigate the vulnerability to drought in 10 phylogenetic pairs of plants in rainy and dry seasons. Despite both environments being exposed to fog events, we hypothesized that species in the forest will be more vulnerable to drought than in grassland. In contrast, as tropical montane grassland occurs in the poorest environment, it will be more resistant to drought, exhibiting more conservative traits and, hence, performing less foliar uptake from the fog.

Table 1 - Trait (abbreviation, unit), its type, its description, its functional significance linked to water availability, reference.

Trait (Abbr., Unit)	Type	Concept	Functional significance linked to drought	Reference
Leaf area (LA, cm²)	Morphological	One-sided area of an individual leaf	Plants with smaller leaves have smaller surface leaves which minimize the water loss to atmosphere	Perez-Harguindeguy *et al.*, 2013
Specific leaf area (SLA, cm² g-1)	Morphological	One-sided area of a fresh leaf, divided by its oven-dry mass	A low SLA is linked to a strategy conservative of use of resources (i.e. water)	Perez-Harguindeguy *et al.*, 2013; Pierce *et al.*, 2013)
Leaf dry matter content (LDMC, %)	Morphological	oven-dry mass of a leaf (cm²), divided by its water-saturated fresh mass (g) transformed in percentage (%).	A higher LDMC is linked to a strategy conservative of use of resources (i.e. water)	Perez-Harguindeguy *et al.*, 2013; Pierce *et al.*, 2013
Leaf Density (LD, mg mm-3)	Morphological	1/SLA divided by thickness	A higher leaf density is linked to a strategy conservative of use of resources (i.e. water)	Niinemets 2001
Leaf thickness (Lth, mm)	Morphological	Thickness of one leaf	A higher leaf thickness is linked to a strategy conservative of use of resources (i.e. water)	Perez-Harguindeguy *et al.*, 2013
Foliar Water Uptake (MPa)	Physiological	Flux of water uptake via leaf during a given period.	During wetting events plants tend to uptake more water via leaf during periods of drought, when the soils are driest.	Berry *et al.*, 2019
Adaxial leaf water repellency (LHR, °)	Wetting	Angle between a water drop and the adaxial leaf surface	A low adaxial leaf water repellency in some species can contribute to higher leaf water uptake and higher colling down. However, it can contribute to a low CO2 uptake and	Holder 2020

			hence decrease of photosynthesis rate.	
Abaxial leaf water repellency (LHR, °)	Wetting	Angle between a water drop and the abaxial leaf surface	A low abaxial leaf water repellency in some species can contribute to higher leaf water uptake and higher colling down. However, it can contribute to a low CO2 uptake and hence decrease of photosynthesis rate.	Holder 2020
Stem wood Density (WD, cm^3)	Morphological	the oven-dry mass of a section of stem of a plant divided by the volume of the same section, when still fresh	Plants with high wood density are linked to high cavitation resistance by drought and have a slow water conductivity through xylem.	Reich, 2014
p50 (MPa)	Physiological	Leaf water potential at which the plant loss 50% of conductivity of xylem	Plants more vulnerable to drought reach 50% of cavitation in vases in water potential more positive.	Tyree & Ewers, 1991
p88 (MPa)	Physiological	Leaf water potential at which the plant loss 88% of conductivity of xylem	Plants more vulnerable to drought reach 88% of cavitation in vases in water potential more positive.	Urli *et al.*, 2013
SM50 (MPa)	Physiological	Difference between p50 and minimum water potential in a day.	Plants with a large SM50 can support more water fluctuations in environment than plants with a narrow SM50.	Meinzer et al. 2009
SM88 (MPa)	Physiological	Difference between p88 and minimum water potential in a day.	Plants with a large SM88 can support more water fluctuations in environment than plants with a narrow SM88.	Meinzer et al. 2009

Source: The author, 2022.

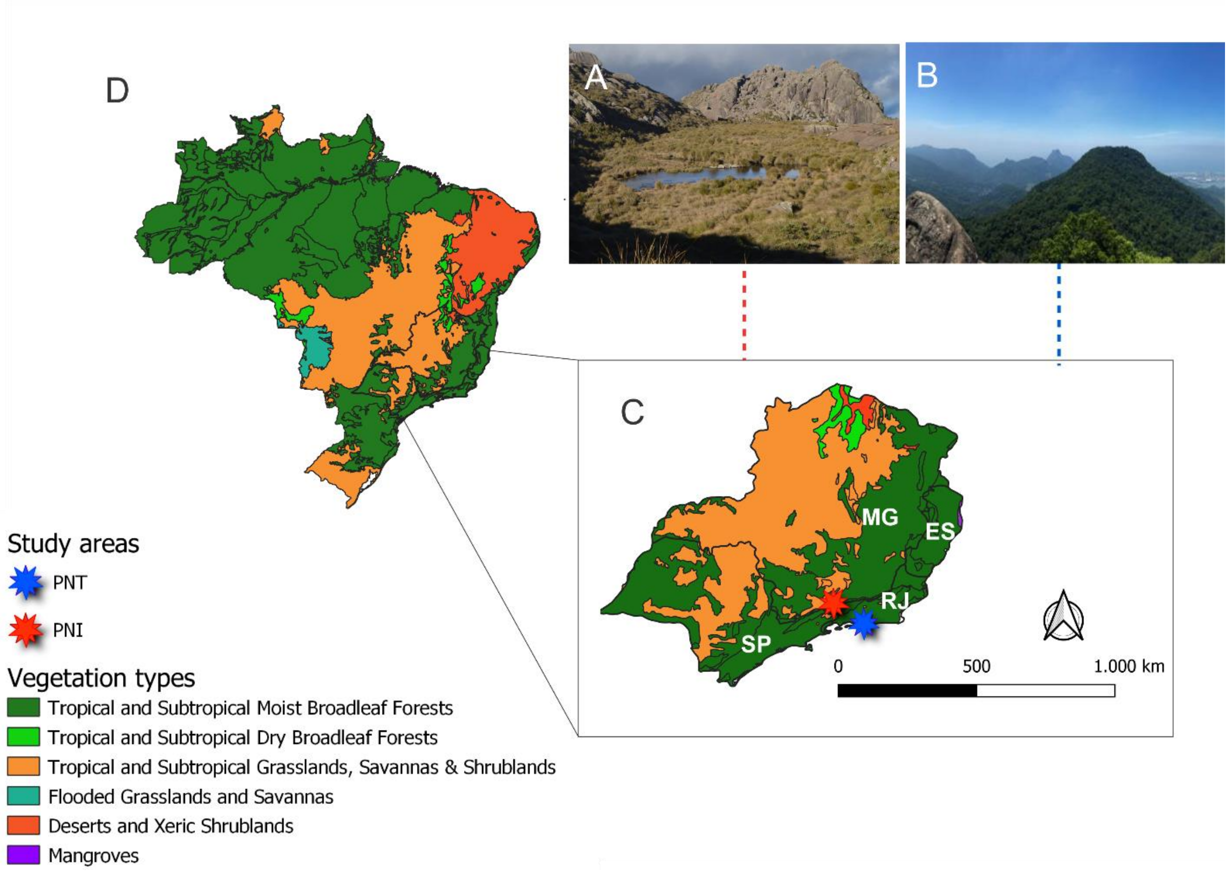
2.2 **Materials and methods**

2.2.1 Study area and species

The study was carried out in two areas prone to fog events from September/2018 to August/2019. One of the areas is a montane tropical rainforest at Tijuca National Park (22°57'S, 43°18'W) and another one is a tropical montane grassland (i.e. campos de altitude) at Itatiaia National Park (22°21'S, 44°40'W), both in Rio de Janeiro, Brazil (Fig. 1). the montane rainforest has about 700 – 1000 m (ICMBio 2008) is a remaining Atlantic tropical rainforest. Climate is wet tropical (Aw, Köppen classification), with rainy summer (December - February) and dry winter (June - August) (ICMBio 2008), mean annual temperature (MAT) between 18°- 26°C and mean annual precipitation (MAP) of 2500 mm (ICMBio 2008). Campos de altitude is an ecosystem associated with the Atlantic tropical rainforest occurring in areas above 2000-2300 m.a.s (Safford 1999; Scarano 2002). The climate is tropical of altitude (Cw, Köppen classification) (Safford 1999), mean annual temperature of 14.4°C and mean annual precipitation 2400 mm (Segadas-Vianna and Dau 1965), with a rainy summer (December - February) and a dry winter (May-September) (Segadas-Vianna and Dau 1965; ICMBio 2014). Frost events are often in this ecosystem with a mean of 56 days a year (Segadas-Vianna and Dau 1965) and natural fires may be common during the dry season (Safford 2001). In this region, besides fog events decreasing according to models to high altitudes (Still et al. 1999), models have also predicted a decrease of 3 – 6 mm in precipitation by day until 2100, with lower precipitation input in high altitudes. When considered an extreme scenario is expected a reduction of 50% in rains, with greater rains in short-time periods followed by periods of drought and heatwaves in this region (Lyra et al. 2018).in vegetation.

To carry out this study, we selected ten phylogenetic pairs of 10 families of eudicotyledons, totalling 19 species of tropical rainforest and tropical montane grassland. The pairs of grass, herbs, shrubs, and small trees encompass the botanical families, Asteraceae, Cyperaceae Fabaceae, Iridaceae, Melastomataceae, Myrtaceae, Poaceae, Primulaceae, Proteaceae and Rubiaceae (Table 2).

Figure 1 – Tijuca National Park and Itatiaia National Park location in Rio de Janeiro, southeast of Brazil.



Legend: Tropical montane grassland identified as tropical and subtropical grasslands, savannas and shrubland based on WWF ecoregions, localized at Itatiaia National Park (A) and tropical rainforest identified as Tropical and subtropical moist broadleaf forest based on WWF ecoregions, located at Tijuca National Park (B) in Rio de Janeiro, southeast (C) of Brazil (D). The blue dot means Tijuca National Park (Parque Nacional da Tijuca, PNT) and the red dot means Itatiaia National Park (Parque Nacional de Itatiaia, PNI).

Source: The author, 2022.

Table 2 - The 19 species used in this study, their botanical family, their life form and site, tropical rainforest (Forest) or tropical montane grassland (Grassland) in Rio de Janeiro, Brazil.

Family	**Species**	**Life form**	**Site**

Asteraceae	*Critoniopsis stellata* (Spring) H. Rob., DC.,	Shrub	Forest
	Baccharis uncinella DC.,	Shrub	Grassland
Cyperaceae	*Pleurostachys tenuiflora* Brong.,	Grass	Forest
	Machaerina ensifolia (Boeckeler) T. Koyama,	Grass	Grassland
Fabaceae	*Pseudopeptadenia leptostachya* (Benth) Rauschert,	Tree	Forest
	Mimosa monticola Dusén,	Shrub	Grassland
Iridaceae	*Neomarica longifolia* (Link & Otto) Sprague.,	Herb	Forest
	Sisyrinchium palmifolium L. *var. nidulare* Hand.-Mazz.	Herb	Grassland
Melastomataceae	*Leandra variabilis* Raddi.,	Shrub	Forest
	Pleroma hospita (Schrank et Mart. ex DC.) Triana,	shrub	Grassland
Myrtaceae	*Plinia cauliflora* (Mart.) Kauser	Tree	Forest
	Myrceugenia alpigena (DC.) Landrum,	Shrub	Grassland
Poaceae	*Chusquea bambusoides* McClure & L.B.Sm.,	Grass	Forest
	Chusquea pinifolia (Nees) Nees,	Grass	Grassland
Primulaceae	*Myrsine* cf. *gardneriana* A. DC,	Shrub	Forest
	Myrsine cf. *gardneriana* A. DC.	Shrub	Grassland
Proteaceae	*Roupala* cf. *sculpta* Sleumer,	Tree	Forest
	Roupala montana Aubl.,	Shrub	Grassland
Rubiaceae	*Psychotria leiocarpa* Cham. & Schltdl.,	Shrub	Forest
	Galium humile Cham. & Schltdl.,	Shrub	Grassland

Source: The author, 2022.

2.2.2 Meteorological data

To calculate the frequency of fog events in tropical rainforest and tropical montane grassland we used meteorological data from Itatiaia meteorological station (22°22’S, 44°42’W), 300 m near the grassland study area, and we used data from Alto da Boa Vista (22° 47’S, 43°16’W) 5 km near of the forest study area. These data, from September/2018 to December/2019, were available by INMET (www.inmet.gov.br) and Alerta Rio (www.alertario.rio.rj.gov.br), respectively. From these data, we selected air temperature and relative humidity of every hour/month, when available, to vapour pressure deficit (VPD) calculation. We stipulated the fog events from VPD (Rosado et al. 2010) and precipitation events. When VPD was close to zero and the pluviometer did not record precipitation at the moment, we classified this as a fog event (Rosado et al. 2010).

2.2.3 Morphological functional traits

In each area, during the rainy and dry season of 2018 and 2019, we sampled five individuals of each species and one branch of each individual - ~ 1 meter length. At Plant Ecology Laboratory at UERJ, we cut the branches off under water and rehydrated them for 12 hours. We sampled five mature leaves of each branch and obtained the fresh mass using a balance (g). we measured the leaf thickness with a digital calliper (mm), digitalized the leaves using a scanner and put them in the oven for 72h to obtain the leaf dry mass. From these data, we measured the leaf area (LA cm^2) with ImageJ software (version 1.51) and calculated the leaf dry matter content (LDMC %), specific leaf area (SLA cm^2 g-1) and leaf density (LD mg mm-3) (Perez-Harguindeguy et al., (2013). To stem wood density, we sampled a section about 4 cm length and 1 cm of diameter of each branch, we removed the bark and rehydrated it for 30 min. The volume was obtained using the Archimedes Principle using a balance (0,01g). Wood samples were put in the oven for 72 h to obtain the dry mass. From these data (volume and mass) we calculated stem wood density (WD g. cm^3) (Perez-Harguindeguy et al., 2013). In addition, we completed the data with leaf traits and stem wood density of montane tropical grassland from lab database. Such data were sampled during the dry season of 2015 and 2016.

2.2.4 Foliar Water Uptake

During the rainy (February/2019) and dry season (June/2019), we sampled a branch of five individuals of 10 species. In the laboratory, we cut branches off underwater and rehydrated them for 12h. Leaf water potential of one of the leaves of each branch was measured by Scholander Pressure Chamber (model 1505D-EXP, PMS, Albany, OR, USA) to verify if the leaves were saturated (pfwu1). Subsequently, two new leaves from the same branch and individual to each species were detached and bench dried for 3h. After, we measured the leaf water potential of one of the bench dried leaves (Pfwu2) and simultaneously, we submerged another one in distilled water for 3h with the petiole sealed with parafilm and Vaseline, similar to Eller et al. (2016). We maintained the sample covered with black plastic to avoid stomatal opening. In the last, we measured the water potential of rehydrated leaf using the Scholander Pressure Chamber (pfwu3). The difference between the last leaf water potential after rehydration (pfwu3) and leaf water potential after bench dried (pfwu2), resulted in the FWU of each species.

2.2.5 Leaf Water Repellency

In rainy (November-February/2019) and dry season (June/2019), we sampled a branch of each one of five individuals of 10 species. After the the branches rehydrated for 12h, five leaves were detached and placed on a Styrofoam. We added a distilled water droplet (5µL) (P10, Pipetman, Gilson SAS, Villiers-le-Bel) in abaxial and adaxial leaf surfaces. We took photos of each droplet with a digital camera (Nikon D3200, 24.2 mpx, AF-S NIKKOR 18-55mm 1:3.5-5.6G VR II, CMOS) to calculate leaf water repellency (ImageJ software, Version 1.51). Since *Galium humile* (Rubiaceae) present smaller leaves than droplet volume recommended (Matos & Rosado 2016), we removed this species from the analysis.

2.2.6 Susceptibility of xylem to embolism and safety margin

To resistance of xylem to embolism, we sampled a branch of three-five individuals of six species in both environments in dry season (September/2018). At laboratory, we obtained sigmoid vulnerability curves (Fig. S1) following the protocol described by Pereira et al. (2016) and Zhang et al. (2018) and, subsequently, we extracted the p50 and p88 values from them. For safety margin calculation, we collected the samples during rainy season (January, February, and December/2019) in tropical rainforest. In addition, we used the leaf water potential of tropical montane grassland collected in December and January/2019 and in the first week of March/2020 to safety margin (SM) obtained in Moraes et al. in press. In both environments the leaf water potential was obtained between 12-14h using the Scholander pressure chamber, from three leaves of three individuals of six woody species. Safety margins of p50 (SM50) and p88 (SM88) were calculated through the difference between the minimum leaf water potential and p50 (SM50=pmin-p50) and the difference between minimum leaf water potential and p88 (SM88=pmin-p88), respectively.

2.2.7 Data analysis

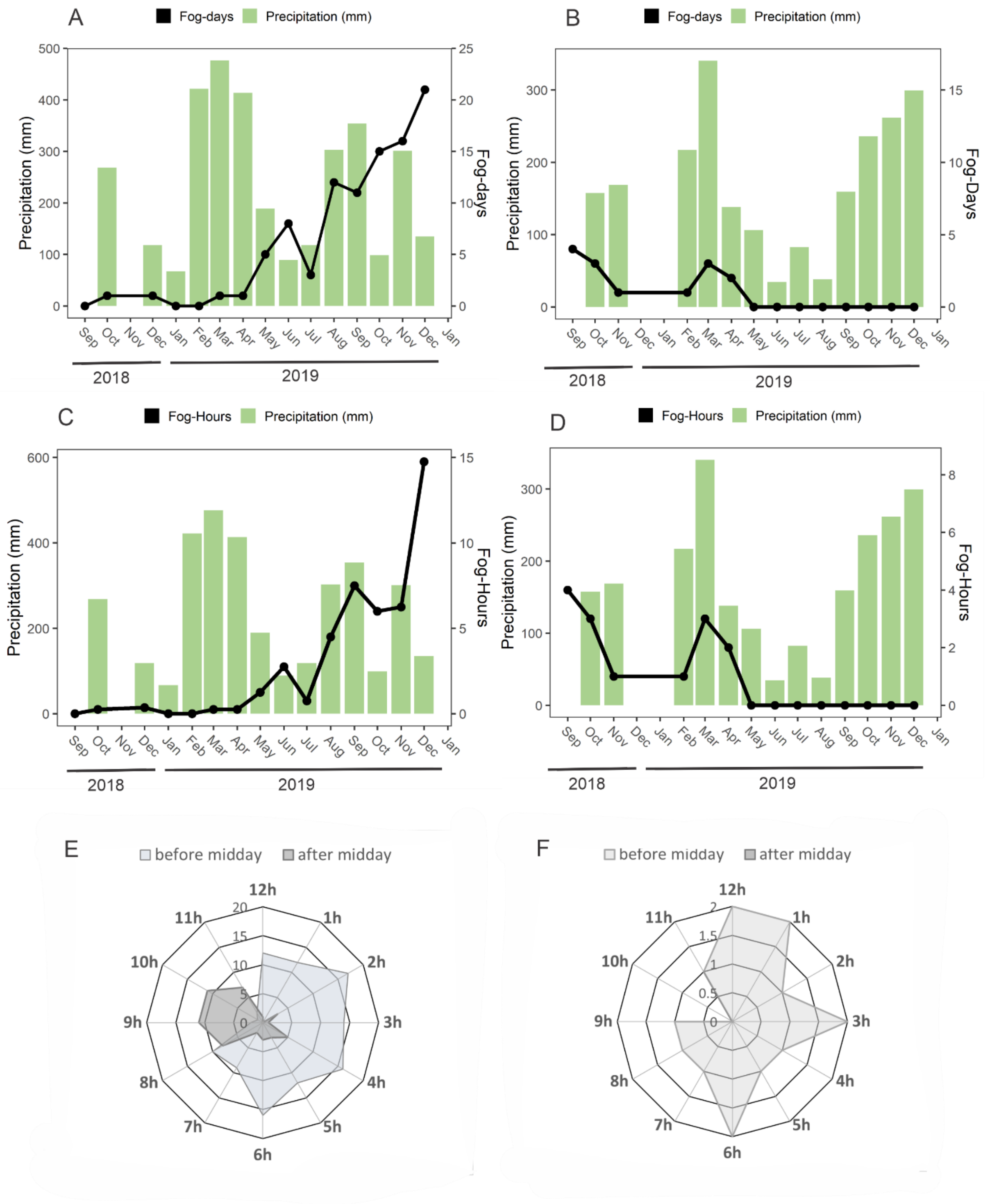
We used paired t-test using phylogenetic independent contrast to evaluate differences in trait responses between environments. For LWR we used a Wilcox-Test. To describe where the resistance to embolism (p50 and p88) and safety margin (SM50 and SM88) of both sites are located among angiosperms global scale, we plotted our data in the global relationship between resistance to drought and MAP (Choat et al. 2012). To assess the conservatism degree of each trait in phylogeny, we built a phylogenetic tree with Phylocom 4.2 (Fig. S2) software, (super tree R20120829) available in Phylomatic v.3 (Webb and Donoghue 2005). We used this phylogeny in Blomberg’ K statistics (Blomberg et al. 2003) to evaluate the phylogenetic conservatism degree (Picante Package in R). When Blomberg’ K was higher for a given trait in phylogeny, this indicates a higher phylogenetic conservatism. When K>1 (high phylogenetic signal), while K<1 means traits with low conservatism in phylogeny. In addition to the K statistics, we ran a Mantel test (phylogenetic distance matrix x traits matrix) to detect phylogenetic signals of traits since for sample sizes below 20 species the metric K might be less robust Sedio et al. (2012). All analyses were running on R software (Version 3.5.3).

2.3 **Results**

2.3.1 Meteorological data

As expected, precipitation was higher in the tropical rainforest than grassland (3430 mm from September/2018 to December/2019), with 396 mm during the driest three months (May – July/2019). In tropical montane grassland the precipitation was 2387 mm for the same period and of 155 mm during the driest three months (June – August/2019). However, different of expected, fog frequency was higher in forest, mainly from October to December/2018 (45 hours along 95 days). In the grassland, fog events were reduced and concentrated between September and November/2018 (16 hours along 5 days). Temperature in forest was higher than grassland 18°C (dry season) and 27°C (rainy season), while in grassland the lower temperature was 7°C (dry season) and the higher one 12°C (rainy season) in 2019. Regarding daytime, fog events occurred mainly between 12 AM and 6 AM in both sites (Fig. 2).

Figure 2 – Rains and fog event distribution during the study period



Legend: Sum of fog days and sum precipitation per month in tropical rainforest (A) and in tropical montane grassland (B), Sum of fog days and sum precipitation in tropical rainforest (C) and in tropical montane grassland (D), hours long the day in which plants are exposed to fog events in tropical rainforest (E) and in tropical montane grassland (F) during study period (September 2018 – December 2019).

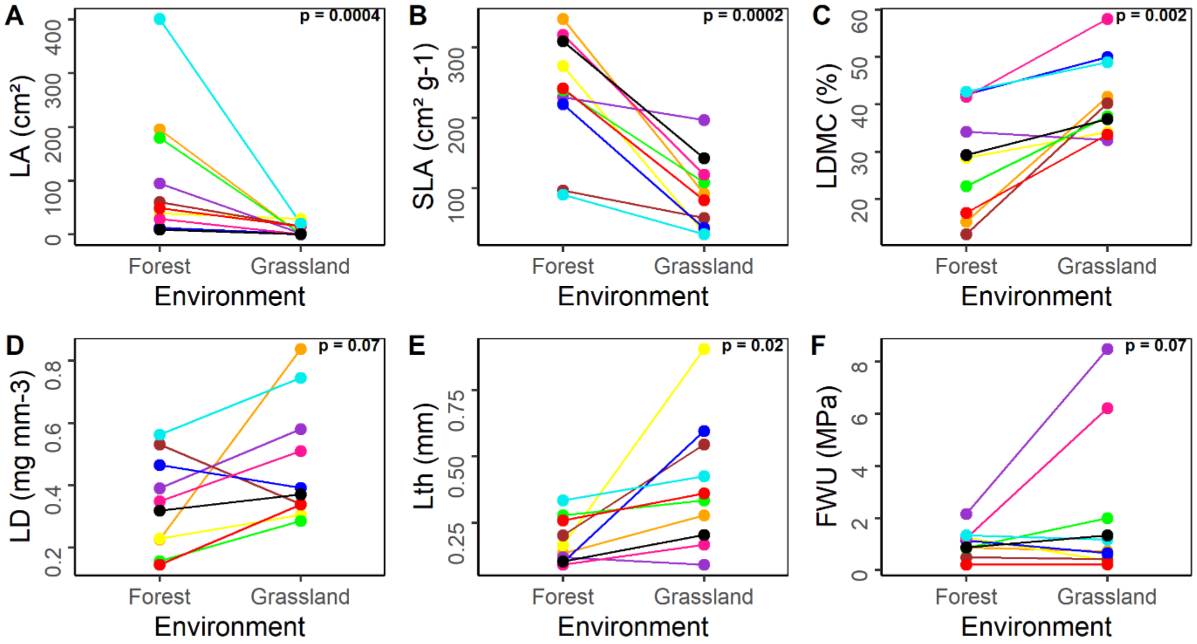
Source: The author, 2022.

VPD was lower in the forest in May/2019 (0.33 KPa) and higher in January/2019 (1.66 KPa), while in grassland the VPD was lower in November/2018 (0.09 KPa) and higher in July/2019 (0.47 KPa). We also observed a decrease of VPD in tropical rainforest, while fog events increase in the same area during the study. Air relative humidity was higher and more constant in forest, where exhibited a lower percentage in January/2019 (70%) and a higher in May/2019 (89%). In contrast, grassland exhibited a higher VPD range, with lower air relative humidity in July/2019 (57%) and a higher in November/2018 (94%). Despite we have accessed data to major part of study period, two months (September/2019 and November/2019) were not computed in forest and three months (September/2019, December/2018 and January/2019) in grassland due to sensors failures.

2.3.2 Morphological functional traits and foliar water uptake

Most traits differed between ecosystems, where tropical montane grassland plants had lower LA, SLA and higher LDMC and Lth than tropical rainforest during rainy season (LA, t = 2.58, df = 9, t = 0.02; SLA, t = 5.82, df = 9, p = 0.0002; LDMC t = - 4.27, df = 9 p = 0.002, Lth t = -2.78, df = 9 p = 0.02) and dry season (LA, t = 5.45, df = 9, t=0.0004; SLA, t = 0.65, df= 9, p =0.0001; LDMC, t = - 3.86, df = 9, p = 0.003; Lth, t = - 3.60, df = 9, p = 0.005) (Fig. 3, 4). Although LD and FWU did not differ between ecosystems in the rainy season (LD, t = -2.00, df = 9, p = 0.07. FWU t = -2.05, df = 9, p = 0.07) (Fig. 3), both traits were higher in grassland in the dry season (t = - 3.69, df= 9, p = 0.004; FWU= t= - 2.28, df = 9, p = 0.04) (Fig. 4). We did not find differences for LWR and WD in both seasons (Fig. S3; S4, respectively). For more details about paired t-teste see Table S1; means of each functional trait are in Table S3 of supplementary material.

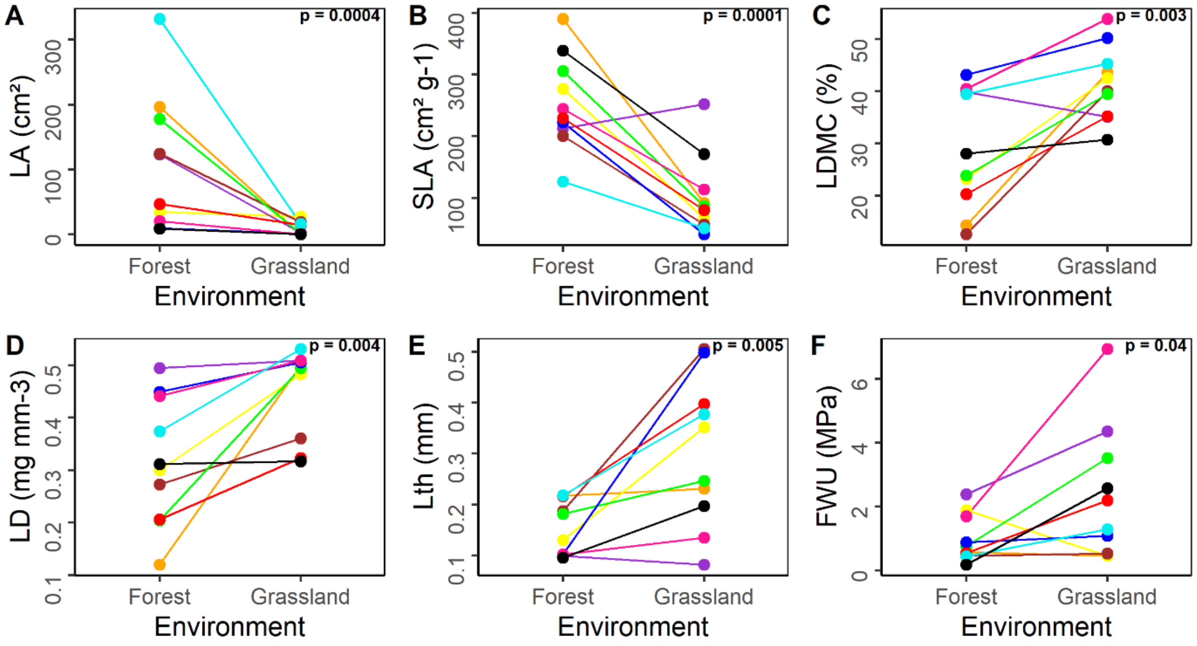
Figure 3 - Phylogenetically comparison of leaf traits during rainy season between plants of tropical rainforest (Forest) and tropical montane grassland (Grassland), in Rio de Janeiro, Brazil.



Legend: Phylogenetically independent contrast comparison of leaf area (LA) (A), specific leaf area (SLA) (B), leaf dry matter content (LDMC) (C), leaf density (LD) (D), leaf thickness (Lth) (E), foliar water uptake (FWU) (F) of 10 pairs phylogenetic of plants of each environment, tropical rainforest and tropical montane grassland in rainy season, in Rio de Janeiro, Brazil. Asteraceae = orange, Cyperaceae = yellow, Fabaceae = violet, Iridaceae = brown, Melastomataceae = green, Myrtaceae = Dark blue, Poaceae = pink, Primulaceae = red, Proteaceae = light blue, Rubiaceae = black).

Source: The author, 2022.

Figure 4 - Phylogenetically comparison of leaf traits during dry season between plants of tropical rainforest (Forest) and tropical montane grassland (Grassland), in Rio de Janeiro, Brazil.



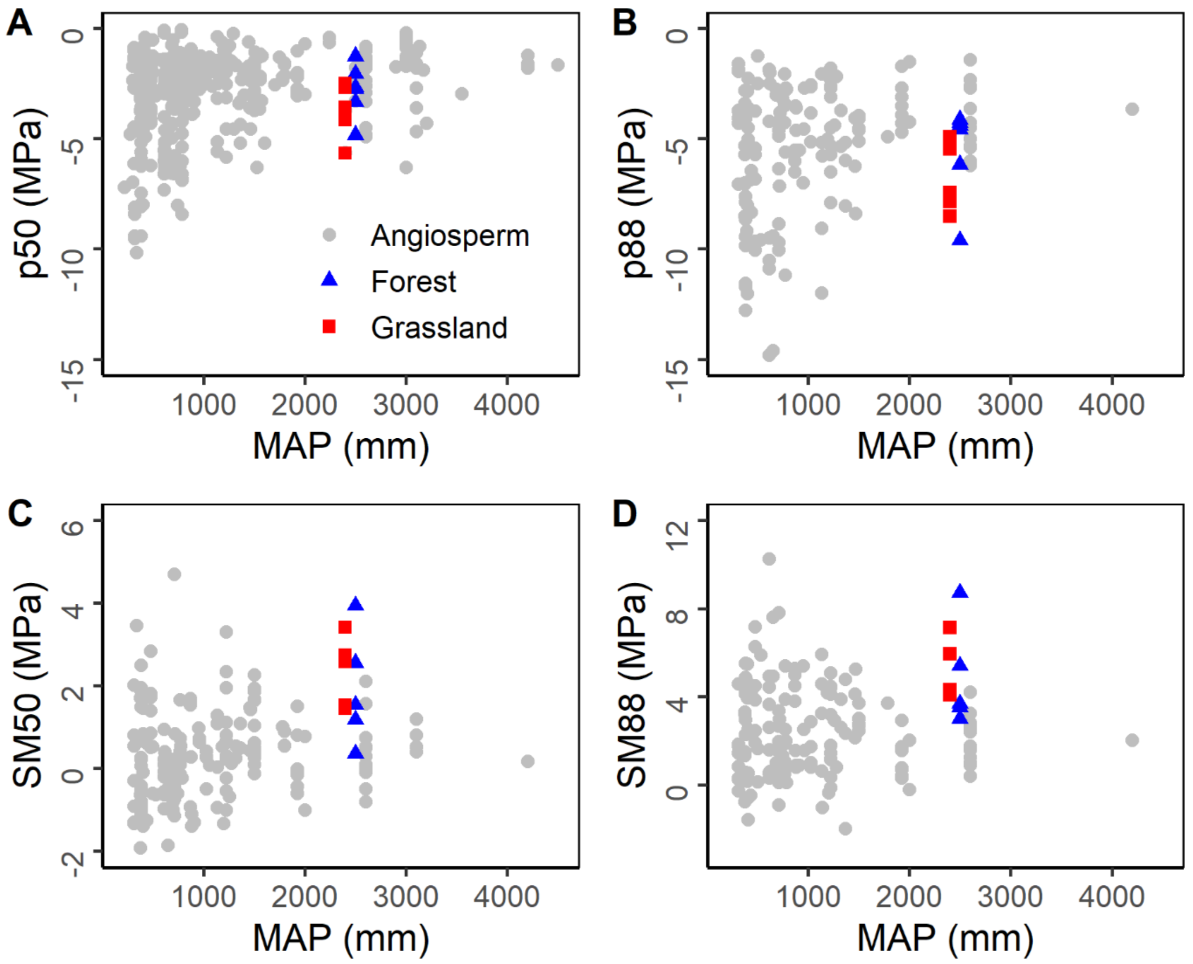
Legend: Phylogenetically independent contrast comparison of leaf area (LA) (A), specific leaf area (SLA) (B), leaf dry matter content (LDMC) (C), leaf density (LD) (D), leaf thickness (Lth) (E), foliar water uptake (FWU) (F) of 10 pairs phylogenetic of plants of each environment, tropical rainforest and tropical montane grassland in dry season, in Rio de Janeiro, Brazil. Asteraceae = orange, Cyperaceae = yellow, Fabaceae = violet, Iridaceae = brown, Melastomataceae = green, Myrtaceae = Dark blue, Poaceae = pink, Primulaceae = red, Proteaceae = light blue, Rubiaceae = black).

Source: The author, 2022.

2.3.3 Susceptibility of xylem to embolism

Plants studied here covered 43% (-4.37 MPa) of amplitude of p50 and 57% (-5.48 MPa) of amplitude of p88 of angiosperms of global database (-10.11MPa; -13.57 MPa, respectively) (Fig. 5 A-B). Similarly, SM50 covered 40% (3.58 MPa) and SM88 38% (5.71 MPa) of amplitude of angiosperms database (9.01 MPa, 15.12 MPa, respectively) (Fig. 5 C-D) that encompass about half of variability of embolism resistance in the global database. p88 values were more negative and SM88 were wider than plants of ecosystems with similar MAP (2000-3000 mm/year) at global level (Fig. 5 B, D). For example. the higher value achieved in global database to p88 and SM88 were -6.2 MPa and 4.2 MPa respectively, while our plants achieved higher values, with p88 and SM88 of - 9.6 MPa and 8.1 MPa respectively.

Figure 5 – Distribution of the percentage of loss of conductance in the xylem and margin safety of forest and grassland plants studied here and angiosperms from global database.

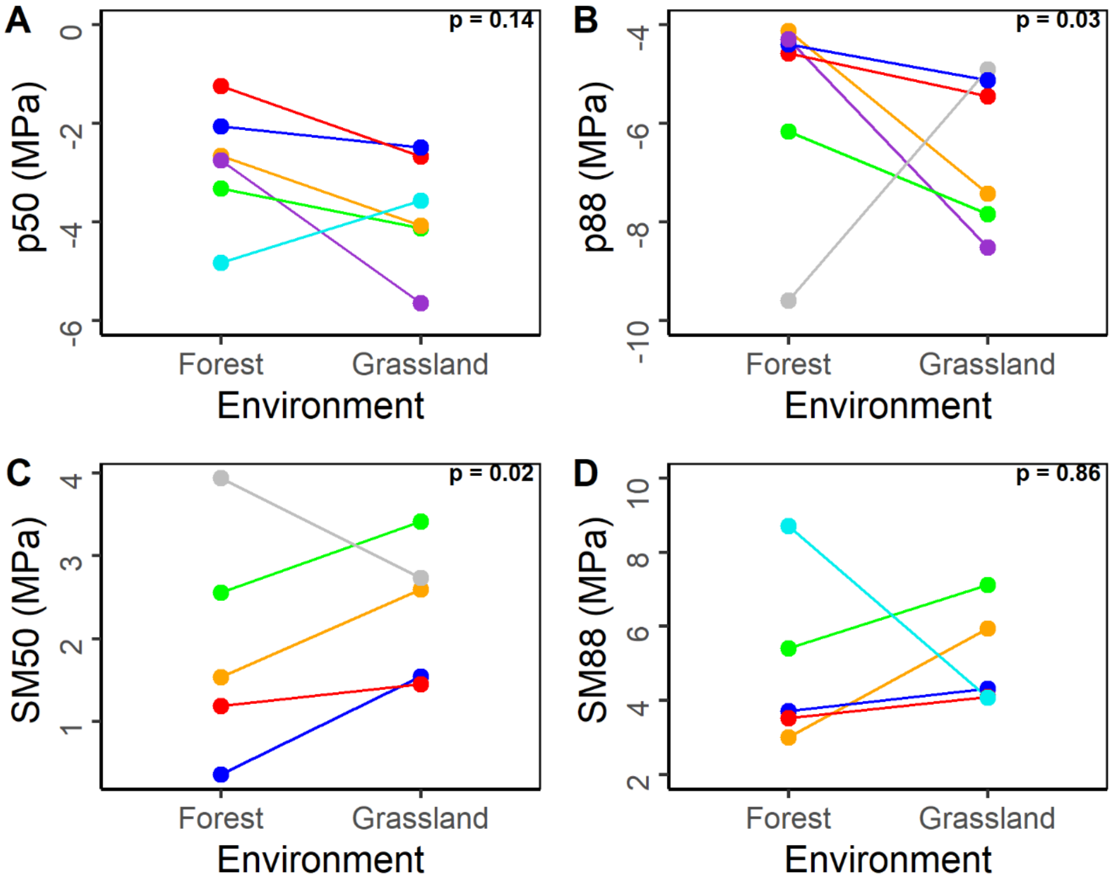


Legend: Distribution of leaf water potential at which 50% hydraulic conductivity is lost (p50) (A) leaf water potential at which 88% hydraulic conductivity is lost (p88), (B), safety margin from p50 (SM50) (C) and safety margin from p88 (SM88) (D) and mean annual precipitation (MAP) of plants studied here, and the angiosperms species at global level. Blue triangles mean tropical rainforest and red squares mean tropical montane grassland, localized in Rio de Janeiro, Brazil. Grey dots are angiosperms from database of Choat et al. (2012).
Source: The author, 2022.

Regarding all plants of our study, we did not find difference of p50 (t= 1.70, df = 5, p = 0.14) and p88 (t = 0.88, df = 5, p = 0.41) between grassland and forest (Fig. 6). However, to p88, we observed that only *Roupala sculpta* exhibited opposite direction reflected by a great difference of p88 between environments (-9.6 - - 4.90 MPa from forest to grassland species). When we ran the t-test again without *Roupala sculpta*, we found more negative p88 in grassland than forest (t = 3.13, df = 4, p = 0.03) (Fig. 6). Similarly, firstly, there was no difference of SM50 (t= 0.54, df = 4, p = 0.61) and SM88 (t= -0.18, df = 4, p = 0.86) between environments. When we ran the test without *Roupala sculpta*, we verified a higher SM50 in grassland (t= -4.1, df = 3, p = 0.02) than in forests (Fig. 6).

Among species studied *Mimosa montana* (p50 = -5.65 MPa; p88 = -8.52 MPa), *Pleroma hospita* (p50 = -4.13 MPa; p88 = - 7.83 MPa) and *Baccharis uncinella* in tropical montane grassland (p50 = - 4.07 MPa; p88 = - 7.42 MPa) and *Roupala* cf. *sculpta* (p50 = - 4.82 MPa; p88 = 9.6 MPa) in tropical rainforest were the species more resistance to drought. *Plinia cauliflora,* in the forest, was the most vulnerable plant to embolism (p50 = - 1.25; p88 = - 4.59) (For more details about paired t-teste see Table S1, means of each functional trait are in Table S4 of supplementary material).

Figure 6 - Phylogenetically comparison of percentage of loss of conductance and safety margin during dry season between plants of tropical rainforest (Forest) and tropical montane grassland (Grassland), in Rio de Janeiro, Brazil.



Legend: Phylogenetically independent contrast comparison of leaf water potential at which 50% hydraulic conductivity is lost p50 (A), leaf water potential at which 88% hydraulic conductivity is lost, p88 (B), safety margin from p50, SM50 (C) and, safety margin from p88, SM88 (D), evaluated by paired t -test, of six phylogenetic pair of plants occurrents between tropical rainforest (Forest) and tropical montane grassland (Grassland), in Rio de Janeiro, Brazil. Asteraceae = Orange, Fabaceae = violet, Melastomataceae = green, Myrtaceae = Dark blue, Primulaceae = red, Proteaceae = light blue, outlier = grey.

Source: The author, 2022.

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2.3.4 Relationships between p50/p88, stem wood density and foliar water uptake

We observed a negative relationship between p50 and FWU in tropical montane grassland in the rainy season ($R^2 = 0.76$ $p = 0.02$, Fig. S5 A) but not in forest (Table S5, Fig. S5). There was not a significant relationship between p50 and FWU in dry season in both environments. We found relationship between p88 or WD and FWU in both seasons (Table S5, Fig. S5).

2.3.5 Conservation degree of functional traits in phylogeny

Traits of species used in this study were not conserved in the phylogeny, as evaluated ($p>0.05$) through Blomberg's K and Mantel's test ($p>0.05$) (Table S2).

2.4 **Discussion**

We found a significant difference between grassland and forest (Fig. 3,4). As expected, the most traits values in tropical montane grassland were associated with slow strategy (higher LDMC, LD, p88, SM50, Lth, and lower SLA and LA), suggesting that a strategy more conservative (Grime 1977; Pierce et al. 2013; Reich 2014; Oliveira et al. 2021) than the tropical rainforest. Different morphological traits sets between ecosystems (more conservative in grasslands and more acquisitive in the forest) explain a higher resistance to drought in grassland than in the forest. At the global level, we observed that plants in our study are more resistant to drought than other angiosperms under similar MAP.

The higher vulnerability in forests is maximized when considered the higher capacity of foliar water uptake of grassland than forest in the dry season. The higher FWU in grassland plants could compensate for a lesser water input from precipitation during the dry season. Boanares et al. (2019) showed that terrestrial plants with thinner leaves and smaller water storage space in mesophyll have a higher velocity of FWU, which allows a rapid increase of water potential. That characteristic also explains a higher water quantity absorbed by FWU in thin leaves in epiphytical plants (Gotsch et al. 2015). However, as grassland plants had thicker leaves than the tropical rainforest and did not exhibit changes in leaf water repellency, the higher FWU in grassland in dry season can be explained by three main mechanisms: 1) changes in cuticle in response to higher aridity: plants deposit more hydrophilic substances in the leaf cuticle, increasing FWU performance during driest seasons (Goldsmith et al. 2013; Fernández et al. 2017); 2) stomata partially opened: In natural environment, plants can maintain stomata partially opened allowing gas conductance after few minutes under wetting events, which increase the water input from atmosphere (Merilo et al. 2014; Eller et al. 2016); 3) a strong reverse gradient atmosphere-plant due to altitude: Since these plants are exposed to higher evaporative demand and drying soils during this season than forest, such conditions not only can increase cuticle permeability and cause higher stomatal conductance, but also increase leaf transpiration becoming leaves less saturated (Rundel 1982; Fernández et al. 2017).

From this scenario, a reverse gradient is established when the atmosphere is saturated due to wetting event. As a result, the water deposited on the leaf from wetting events (higher saturation) flows into mesophyll (lower saturation) more easily (Rundel 1982; Cassana et al. 2016; Eller et al. 2016; Berry et al. 2019), buffering the water loss through leaf transpiration. On the other hand, as forest plants occur in an environment with lesser water limitation in dry season, the leaves maintain themselves more saturated, decreasing the gradient atmosphere–plant-soil, minimizing the FWU performance. These results also suggest that a strong difference between leaf-atmosphere osmotic gradient, stomatal opening and cuticle are more important than slow-fast strategies to FWU comparisons between ecosystems, once, even grassland exhibiting conservative traits it can perform more FWU than forest plants.

Despite FWU in grassland being higher than forest in the dry season, different from our expectations, the relationship between higher FWU and more negative p50 in this area was observed during rainy instead of dry season. Such results can be related to higher short-rains episodes (unable to achieve rootzone) during the rainy season, which contributes to guarding cell saturation, leads to stomatal opening and hence water absorption by leaves. This relationship was more evident in some species than other ones. Mimosa montana, a Fabaceae, was able to absorb 8MPa in the wet season with the most negative p50 (-5.65MPa). Plants as

Mimosa montana not only live in an environment that provides a strong leaf atmospheric osmotic gradient but also have thin leaves characterized by gain and loss of water easily by FWU, as discussed before. As such plants exhibit a more negative p50, they have a higher embolism resistance even during a drought without fog, when the water-loss is high due to their leaf transpiration. In a different way of FWU x embolism relationship, we did not find the influence of stem woody density in resistance to cavitation in plants. Some studies (Meinzer et al. 2009; Liang et al. 2021) have evaluated the relationship between the WD and resistance to embolism. However, our results are according to studies in local and regional scales (Blackman et al. 2010; Larter et al. 2017; Santiago et al. 2018) in which no relationship was found regardless of the set of plants or ecosystem type. In this case, the resistance to cavitation could be linked to xylem diameter and not necessarily to stem wood density (Larter et al. 2017). Therefore, other traits, such as lignin ornamentation around the xylem vessel, pit membrane thickness among vessels, and vessel length, can contribute to p88 difference between environments (Tyree & Zymmerman, 2013) on smaller one's scales.

Finally, despite grassland exhibiting a higher resistance to drought than forest, we must consider that grassland plants had a low fog exposure during the study period, which can already be a result of global warming. As vulnerability is a concept based on three components, sensitivity, exposure, and adaptation (Adger 2006; Dawson et al. 2011), and as the temperature increases, both environments could be more vulnerable in the next years. On the one hand, rainforest would be more vulnerable because it is more sensitive to drought as described by acquisitive traits values, however, this vegetation has been more exposed to fog regimes so far. On the other hand, grassland even more resistant to drought as described by conservative traits has been exposed to few fog events during study period, which can decrease according to predictions of warming global effects. The fast decrease of fog exposure in grassland may increase the drought vulnerability in these environments, especially because grassland plants evolved under fog exposure (Safford 1999). A similar result was observed in (Aguirre-Gutiérrez et al. 2020) in a comparative study between a dry and a rainforest under dry scenarios in Africa. In this study, dry forest plants with more conservative traits were less exposed to water resources than rainforest and hence had a lower taxonomic and functional diversity (i.e. fewer species and higher functional similarity) when exposed to drought. It indicates mortality of individuals and species by drought in arid vegetation, despite their conservative traits as we suggested here to grassland.

In conclusion, even that 1) both ecosystems being more resistant to drought than other angiosperms under similar MAP (Fig. 5), which is related to those plants have developed strategies to cope with drought along with evolution due to high altitude and; 2) such plants being prone to similar exposure to climate change effects (i.e. similar changes in MAP, MAT and cloud-uplift) according to atmospheric models proposed. Our study showed that the vulnerability is differential between ecosystems with tropical rainforest species more vulnerable (p88 more positive, SM50 narrower and lesser FWU) to drought than grassland plants. However, we supported that a higher vulnerability to drought is expected in both environments when considering climate change scenarios. Even being more resistant than forest and exhibiting conservative traits, grassland might be prone to a lesser fog exposure in the next decades. Finally, our study showed the importance of considering FWU performance since it is a process that increases the resistance to drought in plants in general, and its contribution occurs regardless of the type of plant economics strategy.

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Supplementary material

Table S1 - Summary of paired t – test

	Rainy season			Dry season		
trait	**t**	**df**	**p**	**t**	**df**	**p**
LA	2.582	9	**0.02***	5.4599	9	**0.0004***
SLA	5.8212	9	**0.0002**	0.65	9	**0.0001***
LDMC	-4.2767	9	**0.002**	-3.8679	9	**0.003**
LD	-2.0053	9	0.07	-3.6963	9	**0.004***
LTH	-2.7861	9	**0.02**	-3.6064	9	**0.005***
FWU	-2.0522	9	0.07*	-2.2889	9	**0.047**
Abaxial LWR			0.25			0.49
Adaxial LWR			0.16			0.49
WD	-0.712	5	0.50	-0.902	5	0.40
p50				1.70	5	0.14
p88				3.13	4	**0.03**
SM50	-4.10	3	**0.02**			
SM88	-0.18	4	0.86			

Legend: Leaf area (LA, cm²), specific leaf area (SLA, cm g-1), leaf dry matter content (LDMC, %), leaf thickness (Lth, mm), leaf density (LD, mg. mm3), foliar water uptake (FWU, MPa) and stem wood density (WD, g cm-3), value at which 50% of hydraulic conductivity is lost (p50 MPa), value at which 88% of hydraulic conductivity is lost, (p88, MPa), safety margin from p50, (SM50, MPa) and safety margin from p88, (SM 88, MPa), as well as Wilcoxon-test to abaxial leaf water repellency (ab LWR, °), adaxial leaf water repellency (ab LWR, °) in each environment, tropical rainforest or tropical montane rainforest in a rainy and dry season, in Rio de Janeiro, Brazil. t means t value, df means degrees of freedom, p means p-value. p-value in bold means p<0.05. Values with * were transformated with log to run analyses, except by LD which was transformed with exponential.

Source: The author, 2022.

Table S2 - Summary of Blomberg's K statistics and Mantel test

	Rainy season				**Dry season**			
Trait	**K**	**p**	**R**	**p**	**K**	**p**	**R**	**p**
LA	0.47	0.37	0.01	0.38	0.42	0.46	0.001	0.44
SLA	0.34	0.86	-0.01	0.45	0.30	0.95	-0.12	0.97
LDMC	0.44	0.37	0.03	0.33	0.40	0.56	0.008	0.37
LD	0.40	0.56	-0.04	0.66	0.40	0.54	-0.07	0.85
Lth	0.39	0.64	0.08	0.18	0.33	0.84	0.022	0.40
FWU	0.50	0.26	-0.01	0.49	0.45	0.36	0.02	0.47
Abaxial LWR	0.49	0.33	0.01	0.30	0.54	0.20	0.009	0.42
Adaxial LWR	0.47	0.41	-0.02	0.56	0.62	0.13	0.005	0.31
WD	0.41	0.66	-0.31	1.00	0.51	0.41	-0.23	0.99
p50					0.52	0.44	0.14	0.14
p88					0.44	0.57	0.08	0.26
SM50	0.76	0.13	-0.20	0.87				
SM88	0.55	0.31	-0.22	0.95				

Legend: Blomberg's K statistics K and p-value and Mantel test R and p-value of leaf area (LA, cm²), specific leaf area (SLA, cm g-1), leaf dry matter content (LDMC, %), leaf thickness (Lth, mm), leaf density (LD, mg. mm3), FWU (foliar water uptake, MPa), abaxial leaf water repellency (ab LWR, °), adaxial leaf water repellency (ab LWR, °) stem wood density (WD, g cm-3), value at which 50% hydraulic conductivity is lost, (p50, MPa), value at which 88% hydraulic conductivity is lost p88 (MPa), safety margin from p50, (SM50,MPa) and safety margin from p88, (SM88,MPa) of 19 species, of 6 familes between tropical rainforest and tropical montane grassland in rainy and dry season, in Rio de Janeiro, Brazil. p-value in bold means p<0.05.

Source: The author, 2022.

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Table S3 - Mean of leaf traits and stem woody density

season	**environment**	**family**	**species**	**LA (cm2)**	**SLA (cm2 g-1)**	**LDMC (%)**	**Lth (mm)**	**LD (mg.mm3)**	**WD (gcm-3)**	**Ab LWR (°)**	**ad LWR (°)**	**FWU (MPa)**
rainy	Forest	Asteraceae	*Critoniopsis stellata*	195.16	340.37	15.25	0.13	0.22	0.22	62.79	5.68	0.86
rainy	Forest	Cyperaceae	*Pleurostachys tenuiflora*	39.07	273.11	28.67	0.16	0.22	NA	49.24	3.34	1.23
rainy	Forest	Fabaceae	*Pseudopiptadenia leptostachya*	94.36	229.13	34.17	0.11	0.39	0.58	53.08	10.53	2.14
rainy	Forest	Iridaceae	*Neomarica longifolia*	60.20	97.02	12.54	0.20	0.53	NA	50.52	7.35	0.49
rainy	Forest	Melastomataceae	*Leandra variabilis*	179.52	239.33	22.66	0.27	0.15	0.41	58.71	8.09	0.85
rainy	Forest	Myrtaceae	*Plinia cauliflora*	12.24	219.32	42.09	0.09	0.46	0.69	54.12	2.65	1.13
rainy	Forest	Poaceae	*Chusquea bambusoides*	29.07	317.55	41.55	0.09	0.34	NA	52.80	7.48	1.21
rainy	Forest	Primulaceae	*Mysine gardneriana*	48.40	242.03	17.08	0.25	0.14	0.42	50.11	2.64	0.20
rainy	Forest	Proteaceae	*Roupala sculpta*	401.09	91.37	42.63	0.33	0.56	0.58	43.93	4.93	1.33
rainy	Forest	Rubiaceae	*Psychotria leiocarpa*	9.10	308.17	29.23	0.10	0.31	0.43	NA	NA	0.85
rainy	Grassland	Asteraceae	*Baccharis uncinella*	0.39	92.43	41.53	0.27	0.83	0.58	53.66	5.76	0.72
rainy	Grassland	Cyperaceae	*Machaerina ensifolia*	29.05	36.73	34.07	0.90	0.30	NA	57.84	3.14	0.35
rainy	Grassland	Fabaceae	*Mimosa montana*	1.84	196.85	32.41	0.09	0.57	0.47	103.50	10.38	8.48
rainy	Grassland	Iridaceae	*Sisyrinchium palmifolium*	15.04	57.81	40.18	0.54	0.33	NA	96.60	8.14	0.41
rainy	Grassland	Melastomataceae	*Pleroma hospita*	0.88	108.05	37.47	0.33	0.28	0.45	56.20	7.10	1.98
rainy	Grassland	Myrtaceae	*Myrceugenia alpigena*	0.88	43.50	49.94	0.59	0.39	0.56	48.04	10.91	0.65
rainy	Grassland	Poaceae	*Chusquea pinifolia*	0.38	119.14	58.038	0.16	0.50	NA	60.84	10.66	6.20

rainy	Grassland	Primulaceae	*Mysine gardneriana*	14.89	83.18	33.63	0.36	0.33	0.55	58.35	3.65	0.22
rainy	Grassland	Proteaceae	*Roupala montana*	20.07	34.74	48.85	0.42	0.74	0.61	45.64	4.41	1.17
rainy	Grassland	Rubiaceae	*Galium humile*	0.06	142.65	36.83	0.20	0.37	NA	NA	NA	1.32
dry	Forest	Asteraceae	*Critoniopsis stellata*	196.41	390.25	14.30	0.21	0.11	0.29	60.99	75.10	0.55
dry	Forest	Cyperaceae	*Pleurostachys tenuiflora*	35.00	276.33	23.21	0.13	0.29	NA	41.98	46.92	1.88
dry	Forest	Fabaceae	*Pseudopiptadenia leptostachya*	122.72	212.47	39.81	0.09	0.49	0.54	41.33	47.94	2.37
dry	Forest	Iridaceae	*Neomarica longifolia*	124.61	200.46	12.55	0.18	0.27	NA	63.17	60.78	0.44
dry	Forest	Melastomataceae	*Leandra variabilis*	177.32	305.60	23.86	0.18	0.20	0.43	41.30	45.10	0.75
dry	Forest	Myrtaceae	*Plinia cauliflora*	9.910	222.04	43.11	0.10	0.44	0.73	47.01	46.71	0.86
dry	Forest	Poaceae	*Chusquea bambusoides*	20.13	244.47	40.47	0.10	0.44	NA	37.06	37.07	1.69
dry	Forest	Primulaceae	*Mysine gardneriana*	47.08	228.86	20.22	0.21	0.20	0.39	38.18	41.19	0.52
dry	Forest	Proteaceae	*Roupala sculpta*	331.87	126.09	39.42	0.21	0.37	0.72	42.84	37.93	0.42
dry	Forest	Rubiaceae	*Psychotria leiocarpa*	8.83	338.75	27.99	0.09	0.31	NA	NA	NA	0.17
dry	Grassland	Asteraceae	*Baccharis uncinella*	0.39	91.53	43.58	0.23	0.49	0.55	34.76	76.57	0.44
dry	Grassland	Cyperaceae	*Machaerina ensifolia*	27.28	66.53	42.49	0.35	0.48	NA	43.87	44.16	0.44
dry	Grassland	Fabaceae	*Mimosa montana*	2.10	251.92	35.05	0.08	0.50	0.70	104.94	104.26	4.34
dry	Grassland	Iridaceae	*Sisyrinchium palmifolium*	18.96	57.034	39.98	0.50	0.36	NA	107.41	103.07	0.51
dry	Grassland	Melastomataceae	*Pleroma hospita*	1.25	86.36	39.46	0.24	0.49	0.50	54.62	65.54	3.50
dry	Grassland	Myrtaceae	*Myrceugenia alpigena*	1.31	40.68	50.21	0.49	0.50	0.56	31.09	26.19	1.07
dry	Grassland	Poaceae	*Chusquea pinifolia*	0.39	113.18	53.87	0.13	0.50	NA	40.93	34.65	6.93
dry	Grassland	Primulaceae	*Mysine*	14.62	79.85	35.22	0.39	0.32	0.55	46.13	44.75	2.18

			gardneriana									
dry	Grassland	Proteaceae	*Roupala montana*	15.88	50.46	45.26	0.37	0.53	0.61	37.95	34.47	1.28
dry	Grassland	Rubiaceae	*Galium humile*	0.13	171.10	30.70	0.19	0.31	NA	NA	NA	2.56

Legend: Mean of leaf area (LA, cm²), specific leaf area (SLA, cm2 g-1), leaf dry matter content (LDMC, %), leaf thickness (Lth, mm), leaf density (LD, mg. mm3), stem wood density (WD, g cm-3), abaxial leaf water repellency (ab LWR, °), adaxial leaf water repellency (ad LWR, °) and FWU (foliar water uptake, MPa) of each species of each family studied in each environment, tropical rainforest or tropical montane grassland, in rainy and dry season, in Rio de Janeiro, Brazil.

Source: The author, 2022.

Table S4 – Mean of resistance to embolism traits

Environment	**Family**	**Species**	**p50**	**p88**	**sm50**	**sm88**
Forest	Asteraceae	*Critoniopsis stellata*	-2.66	-4.12	1.53	3.00
Forest	Fabaceae	*Pseudopiptadenia leptostachya*	-2.75	-4.29	NA	NA
Forest	Melastomataceae	*Leandra variabilis*	-3.32	-6.16	2.55	5.39
Forest	Myrtaceae	*Plinia cauliflora*	-1.25	-4.59	0.35	3.69
Forest	Primulaceae	*Mysine gardneriana*	-2.06	-4.40	1.18	3.52
Forest	Proteaceae	*Roupala sculpta*	-4.82	-9.60	3.93	8.71
Grassland	Asteraceae	*Baccharis uncinella*	-4.07	-7.42	2.58	5.94
Grassland	Fabaceae	*Mimosa montana*	-5.65	-8.52	NA	NA
Grassland	Melastomataceae	*Pleroma hospita*	-4.13	-7.83	3.41	7.12
Grassland	Myrtaceae	*Myrceugenia alpigena*	-2.67	-5.46	1.53	4.31
Grassland	Primulaceae	*Mysine gardneriana*	-2.49	-5.13	1.44	4.08
Grassland	Proteaceae	*Roupala montana*	-3.57	-4.90	2.73	4.06

Legend: Mean of leaf water potential in which 50% hydraulic conductivity is lost (p50), the leaf water potential in which 88% hydraulic conductivity is lost (p88), safety margin from p50 (SM50), and safety margin from p88 of 11 species of plants belonging to 6 botanical families between tropical rainforest and tropical montane grassland, in Rio de Janeiro, Brazil.

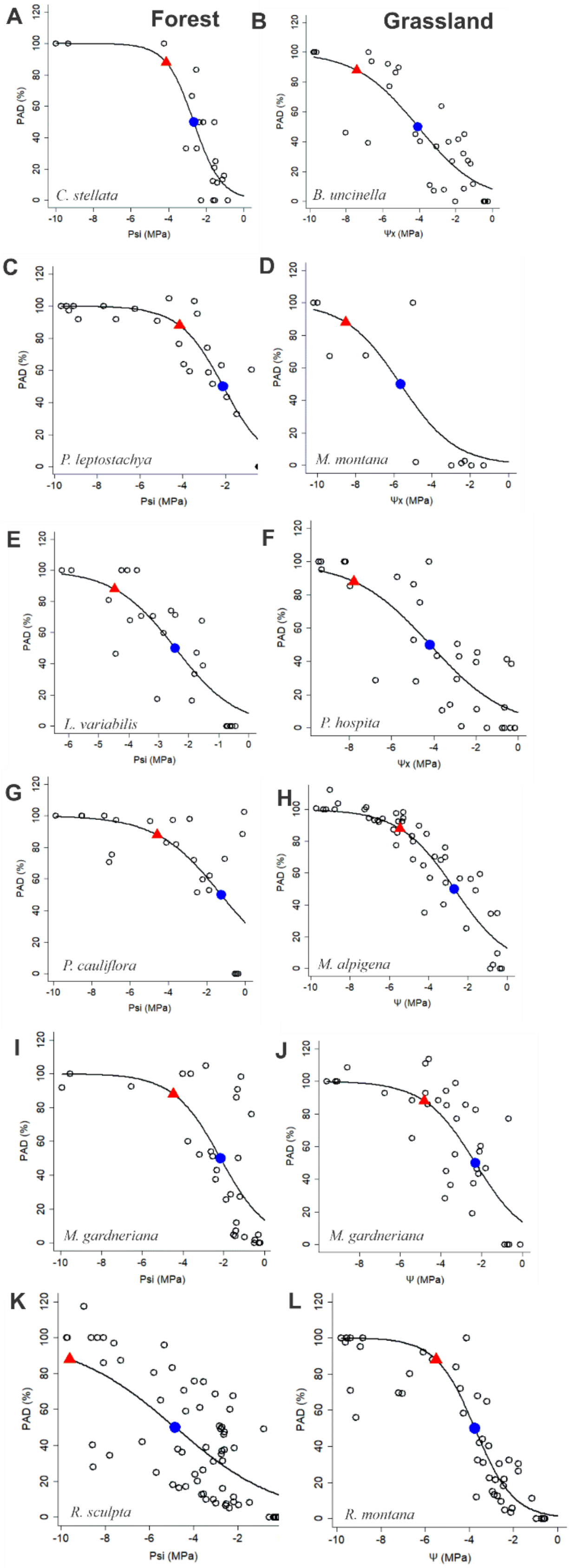
Source: The author, 2022.

Table S5 – Summary of simple regressions between FWU/WD and p50/p88

Environment	**Season**	**Predictor variable**	**Responsive variable**	**Estimate**	**R^2**	**p-value**
Forest	Rainy	FWU	p50	-0.12	0.05	0.64
			p88	-0.57	0.00003	0.99
	Dry		p50	-0.1	0.02	0.75
			p88	34.25	0.13	0.47
	Rainy	WD	p50	0.01	0.006	0.87
			p88	-8.33	0.1	0.52
	Dry		p50	-0.02	0.01	0.79
			p88	-13.70	0.24	0.32
Grassland	Rainy	FWU	p50	-2.37	0.76	**0.02**
			p88	-1.39	0.48	0.12
	Dry		p50	-0.48	0.21	0.12
			p88	-0.18	0.11	0.51
	Rainy	WD	p50	0.03	0.30	0.25
			p88	0.03	0.54	0.09
	Dry		p50	-0.03	0.37	0.19
			p88	-0.009	0.05	0.66

Legend: R means the coefficient of determination; p-value in bold means $p<0.05$.
Source: The author, 2022.

Figure S1 - Vulnerability curves of 11 species belonging to six plant families of woody species

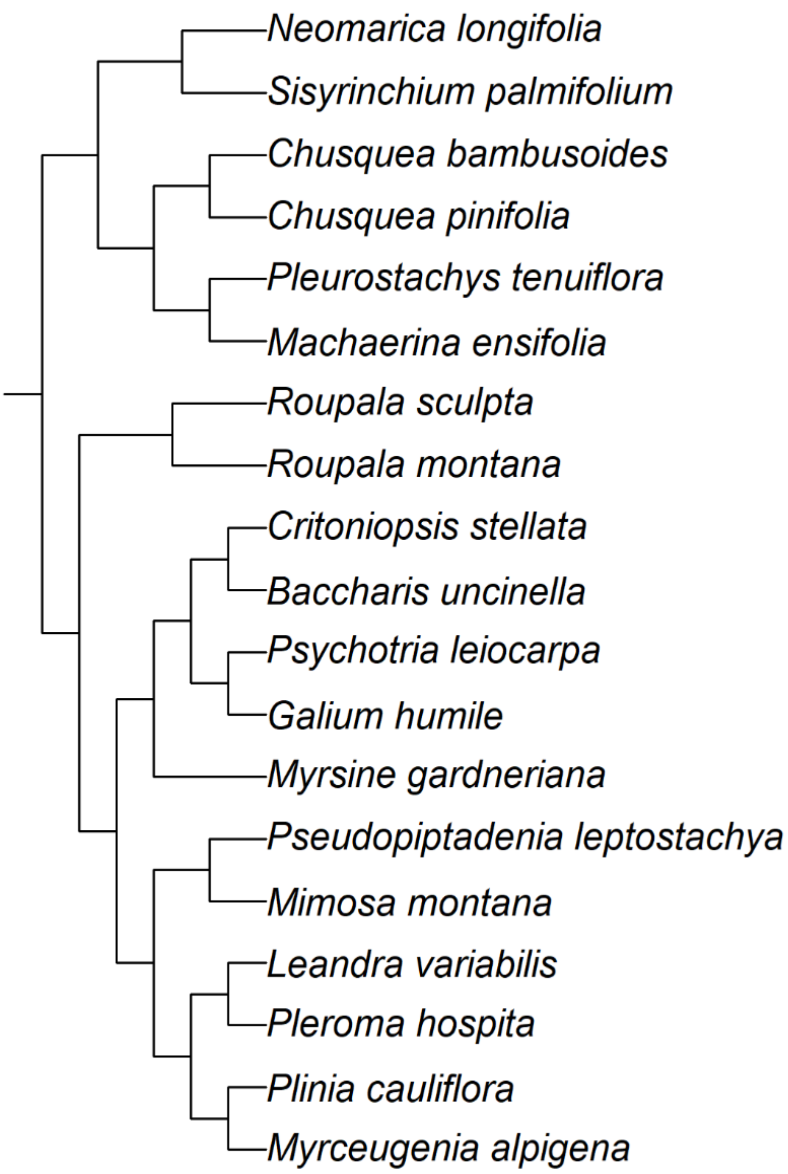


Legend: Plots (A, C, E, G, I, K) show occurring species in tropical rainforest (B, D, F, H, J, L) in tropical montane grassland in Rio de Janeiro, Brazil. Pairs (A, B) = Asteraceae, (C, D) = Fabaceae, (E, F) =

Melastomataceae,(G, H) = Myrtaceae, (I, J) = Primulaceae, (K, L) = Proteaceae. Blue circles mean the leaf water potential at which 50% of hydraulic conductivity is lost (P50), and triangle circles mean the leaf water potential at which 88% of hydraulic conductivity is lost (p88) in xylem vessels.

Source: The author, 2022.

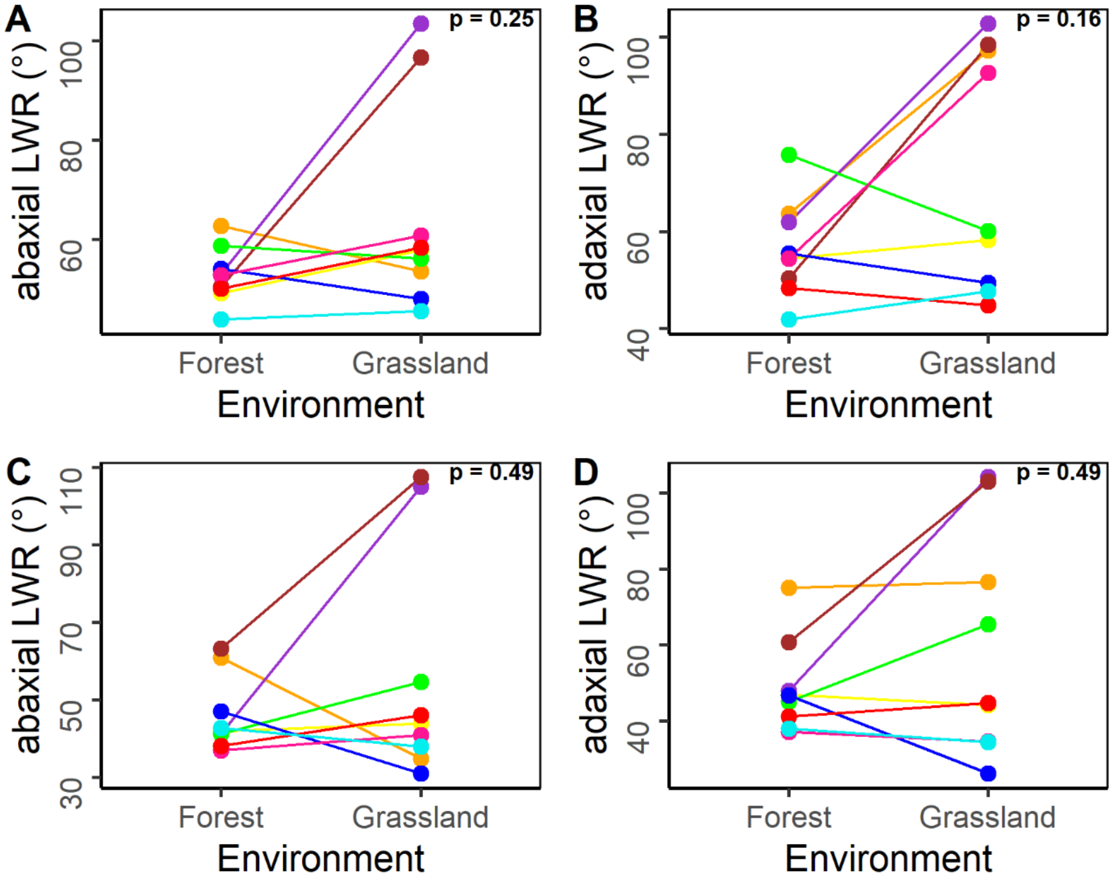
Figure S2 - Phylogenetic tree with pairs of plants used in this study



Legend: The first species of each pair occur in Tropical Rainforest, while the second species correspond to tropical montane grassland in Rio de Janeiro, Brazil. The species Myrsine gardneriana occurs in both environments.

Source: The author, 2022.

Figure S3 - Phylogenetically comparison of leaf water repellency during rainy and dry season between plants of tropical rainforest (Forest) and tropical montane grassland (Grassland), in Rio de Janeiro, Brazil.



Legend: Phylogenetically independent contrast comparison of leaf water repellency during the rainy season on abaxial surface (A) and adaxial surface (B) and during dry season on abaxial surface (C) and adaxial surface (D) evaluated through Wilcoxon-test (P<0,05), of nine phylogenetic pairs of plants between a tropical rainforest (Forest) and a tropical montane grassland (Grassland) in Rio de Janeiro, Brazil. Asteraceae = Orange, Cyperaceae = yellow, Fabaceae = violet, Iridaceae = brown, Melastomataceae = green , Myrtaceae = dark blue, Poaceae = pink, Primulaceae = red, Proteaceae = light blue.

Source: The author, 2022.

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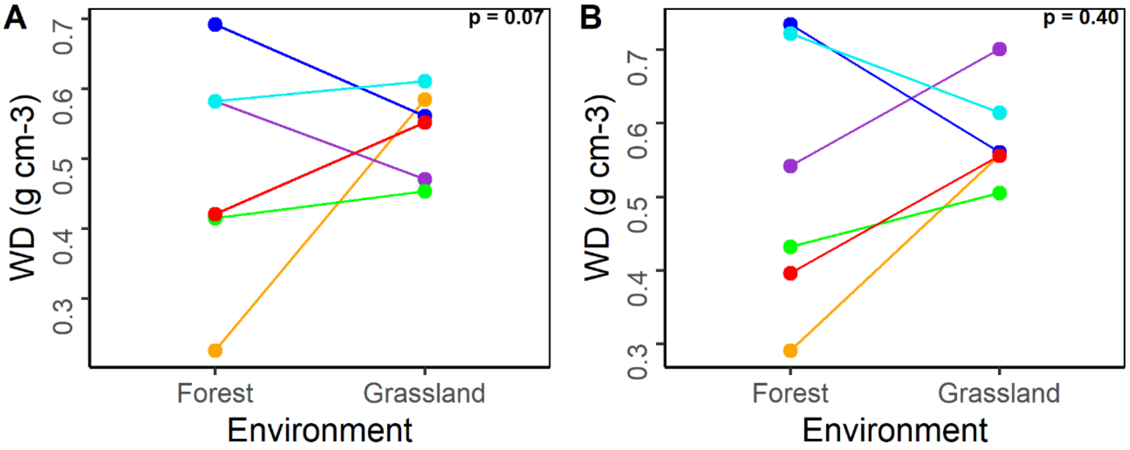
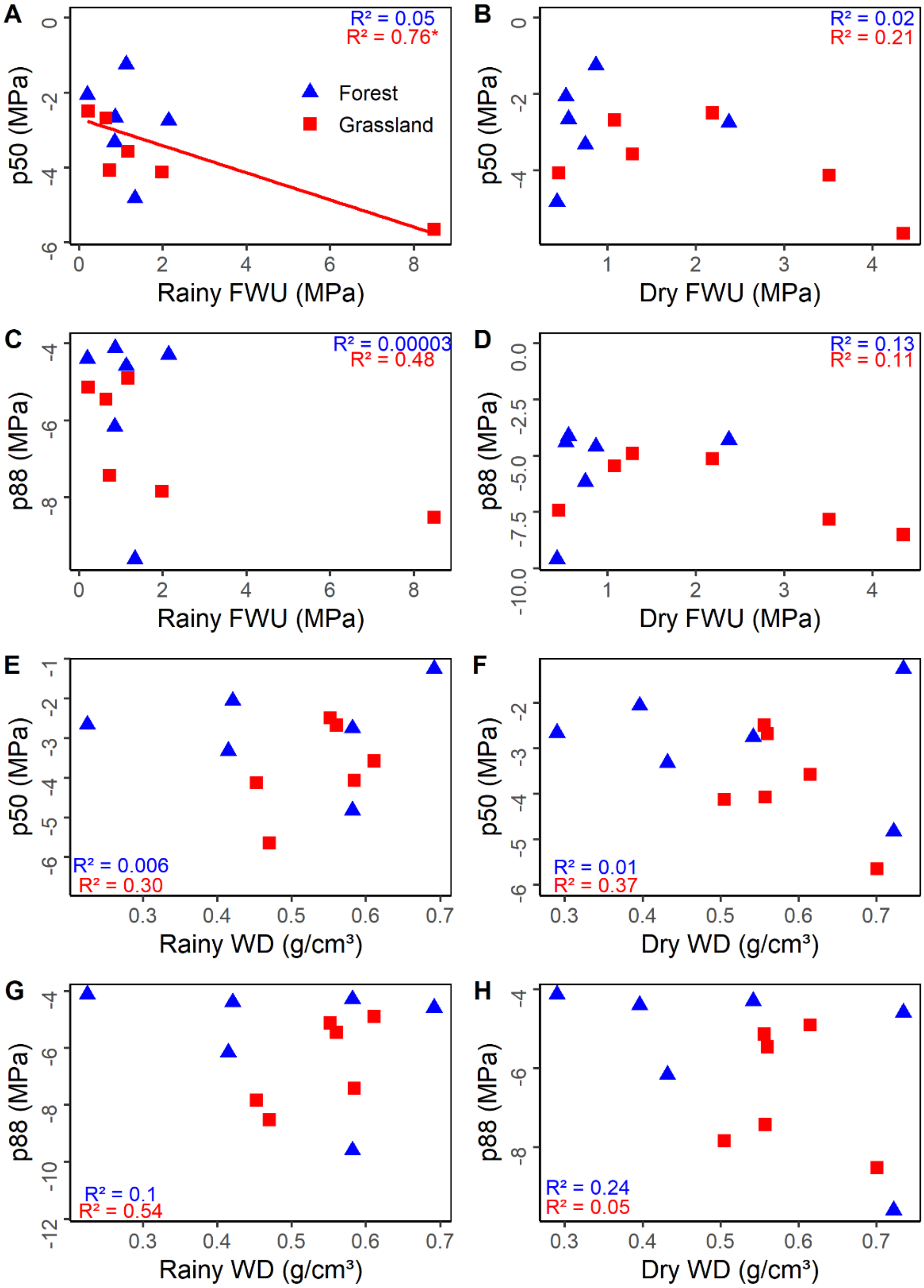
Figure S4 - Phylogenetically comparison of stem woody density during rainy and dry season between plants of tropical rainforest (Forest) and tropical montane grassland (Grassland), in Rio de Janeiro, Brazil.



Legend: Phylogenetically independent contrast of stem wood density (WD) in rainy season (A) and dry season (B), evaluated through paired t-test (P<0,05), between six phylogenetic pairs of plants in regard to occurrence environment, tropical rainforest (Forest) and tropical montane grassland (Grassland) in Rio de Janeiro, Brazil. Asteraceae = Orange, Fabaceae = violet, Melastomataceae = green, Myrtaceae = dark blue, Primulaceae = red, Proteaceae = light blue, outlier = grey.

Source: The author, 2022.

Figure S5 - Correlations between p50 (MPa) and p88 (MPa) and foliar water uptake (FWU) and stem wood density (WD) of plants in tropical rainforest and tropical montane grassland in Rio de Janeiro, Brazil.



Legend: Blue triangles mean the tropical rainforest plants and red squares mean the tropical montane grassland. R squared followed by (*) means $p<0.05$.

Source: The author, 2022.

3 PALEOCLIMATE MODELS PREDICT THE FUNCTIONAL PROFILE OF VEGETATIONS ON CLIMATE CHANGE SCENARIOS

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Running title: Paleoclimate models predict vegetation on scenarios of climate change

Abstract

Atmospheric models have predicted an increase in temperature and precipitation in different regions around the world. However, such models do not consider environmental changes due to altitude. In this case, paleoclimate models based on morphological traits x climate can be an alternative to understanding the effects of climate change in high altitude ecosystems. Here, (1) we evaluated if species with higher resistance to drought (e.g. small and leaves with entire margins) will increase their proportion in function of increase of temperature (3°C) even with a slight increase in precipitation (in 15 mm) in the driest months – as proposed by PBMC (2013); (2) subsequently, we investigated if physiological traits explain changes in the proportion of species on current scenario, using a tropical montane grassland in the southeast of Brazil as a model, We correlated morphological traits (leaf size and leaf teeth) from localities of Southern Hemisphere, including the tropical montane grassland, with temperature and precipitation data. We evaluated if physiological traits (i.e. leaf water potential, stomatal conductance, foliar water uptake and turgor loss point) change in association with presence of teeth in leaves. In tropical montane grassland, an increase of temperature in 3°C associated with an increase in 15 mm in precipitation in 2100, increase the proportion of species with entire leaves from 38% to 75%, hence decreasing the proportion of species with leaf teeth margin from 62% to 25%, which indicate an increase of conservative strategy in that vegetation. In addition, although plants with leaf teeth have a higher leaf water potential, they also have a higher stomatal conductance than plants with entire leaves, which make these plants more vulnerable to drought in the future. In the future, an increase in the proportion of plants with conservative traits (more resistance to drought) and a decrease of acquisitive traits indicate a change in the turnover of species in tropical montane grassland. Therefore, climate models based on traits can be used not only in paleoclimate reconstruction but also to predict changes in flora.

Keywords: Campos de altitude, CLAMP, climate models, drought vulnerability, integrative traits, leaf teeth, foliar water uptake.

3.1 **Introduction**

Climate models based on atmospheric circulation predict an increase of temperature from 1.4 to 4.4°C until 2100 (IPCC 2021). One of the consequences is concentrated heavy rains followed by prolonged droughts (Feng et al. 2013; Lyra et al. 2018). However, such models do not explicitly estimate how climate change affects higher altitude areas, mainly due to the need for high resolution to capture fast variations in altitude. Altitude vegetation is usually exposed to low atmospheric pressure and higher solar radiation (Still et al. 1999; Leuschner 2000; Körner 2007; Assis and Mattos 2016). Those conditions result in a higher vapour pressure deficit (VPD), which promotes water loss via leaf transpiration and consequently increases plants' vulnerability to drought by hydraulic failure (see McDowell et al. 2008; Choat et al. 2018). Among the approaches able to predict how species will respond to climate change, paleoclimate models can be good tools to obtain more accurate predictions at altitude vegetations, such as highlands, páramos, punas, alps, tropical montane cloud vegetation. It because such models are based on detecting specific correspondence between plant functional traits and current climates, so they allow not only climate reconstruction but also detect which are the responsive traits to environment changes (Wolf 1990; Greenwood 1992; Wolfe 1993; Little et al. 2010; Peppe et al. 2018).

Such paleoclimatic approach has been used over the last 100 years (Royer and Wilf 2006; Royer et al. 2008). In this model type, fossil leaves are used as a proxy to climate description for a given period (Wolfe 1993; Little et al. 2010). For example, plant turnover toward the increase of leaf size and cuticle changes can suggest an increase in global temperature, followed by a cooling down, as observed in the cretaceous – tertiary period (Wolfe and Upchurch 1986; Wolf 1990). However, could leaf traits x climate relationship also describe changes in the vegetation in climate change scenarios?

There is evidence that leaf traits are good predictors of climate, regardless of the time of interest, since they are highly responsive to environmental variations (Givnish 1979; Nicotra et al. 2011; Peppe et al. 2011). In dry and warm environments, plants with smaller, narrow, and entire leaves (i.e., entire leaves refer to leaves without teeth in their margins sensu Kennedy et al. (2014) are predominant. Such traits minimize water loss due to smaller leaf transpiration surfaces (Givnish 1979; Givnish 1984) and reduce embolism risks due to higher leaf venation (Scoffoni et al. 2011)). Besides, the leaf morphological traits can describe changes in plant ecological strategies and species distribution over time, resulting in the identification of plants more vulnerable to environmental changes. For example, leaf teeth and larger leaves are traits associated with the fast strategy of leaf economics spectrum, characterized by fast growth (Wright et al. 2004; Royer et al. 2009; Nicotra et al. 2011), higher photosynthesis and leaf transpiration (Wright et al. 2004) and lower leaf mass per area (LMA) (Press 2008, Pierce et al. 2017) and lower resistance to drought (Royer et al. 2008; Peppe et al. 2011; Oliveira et al. 2021). Such traits are predominant in resource-rich sites and/or in seasonal ecosystems (e.g. temperate forests), where the plants exhibit high stomatal conductance and photosynthesis (maximized by leaf teeth) during fast growth phase after winter (Royer and Wilf 2006). On the other hand, plants with entire leaves are associated with conservative resource use, lower photosynthesis and leaf transpiration rates, higher LMA and higher resistance to drought (Wright et al. 2004; Pierce et al. 2017; Peppe et al. 2018). Typical traits of plants from resource-poor environments (Wright et al. 2004).

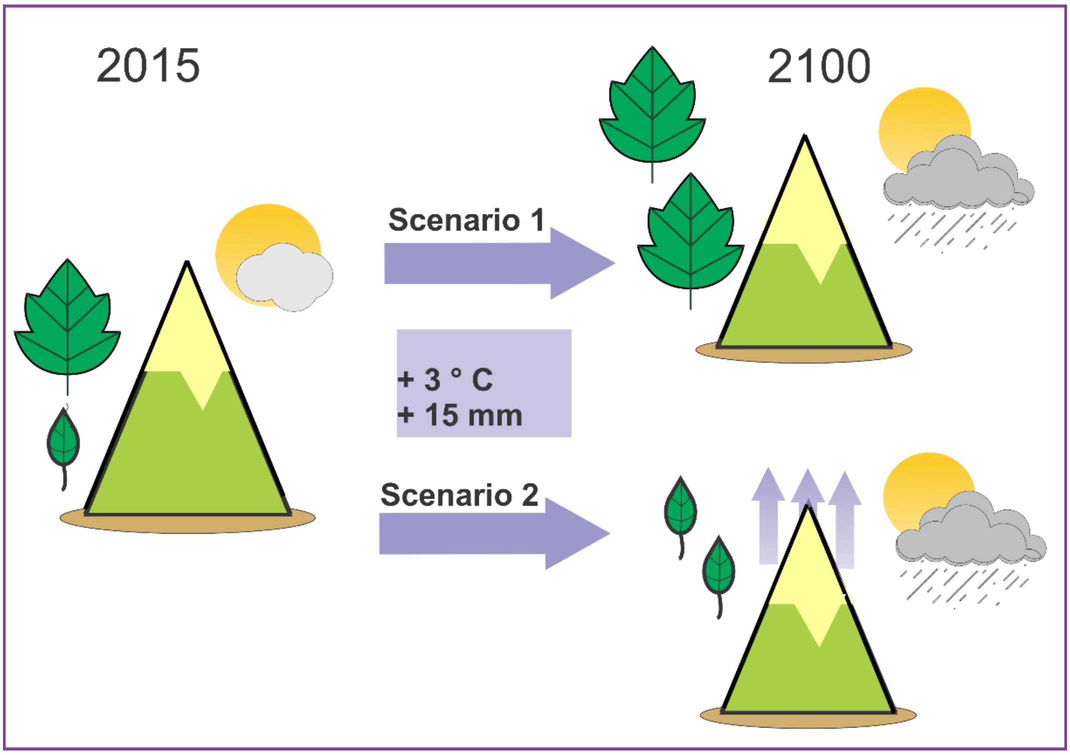
Morphological leaf traits are widely used in literature and considered good predictors of resistance to drought (Nicotra et al. 2011; Pierce et al. 2017). However, they can respond to multiple environmental factors (Rosado and Mattos 2017; Paine et al. 2018; Volaire 2018) (Rosado and de Mattos 2017; Paine et al. 2018; Volaire 2018). In this sense, traits such as LMA or leaf size can be influenced by different factors simultaneously (e.g. soil nutrients, solar radiation, water available), which hamper the understanding of each response (Moles 2018). On the other hand, physiological traits (e.g. leaf water potential) are more integrative, i.e. "traits that are the result of a set of morphological traits" (Rosado and de Mattos 2017) and able to provide a plant response to drought more accurate (Volaire 2018). It means that physiological traits capture more environment fluctuations and access other mechanisms of dealing with drought, sometimes neither achieved by morphological traits (Rosado and de Mattos 2017) nor smaller scales (Volaire et al. 2020).

Unlike paleoclimate studies, in which the use of physiological traits in paleoclimate predictions is not possible, we can use physiological traits collected currently and explore their implications to the future. In this sense, the use of physiological traits may provide insights into the performance of plants, complementing results from models based on morphological traits.

Aiming to investigate the profile functional of plants based on functional x climate models, we chose a tropical montane grassland named "campos de altitude" located to 2300 m.a.s in the southeast of Brazil as a model. This ecosystem with low vegetation has a set of species with different ecological strategies (Safford 1999; Matos et al. 2020) and many rare and endemic species (Safford 1999). Moreover this vegetation is exposed to high solar radiation, wind velocity and VPD (Leuschner 2000), conditions that contribute to water loss by leaf transpiration and make plants more vulnerable to atmospheric drought (McDowell et al. 2008; Méndez-Toribio et al. 2020). Regarding the southeast of Brazil, where the tropical montane grassland is located, climate models have indicated an increase of precipitation in 15 mm in 2100 (PBMC 2013) associated with an increase in temperature in 3°C. Such predictions, according to Lyra et al. (2018) in which is predicted an increase of rains in the driest months to 2100 in the southeast of Brazil. Moreover, Assis and Mattos (2016) also indicated a rise of rains to 2050 during the same season in tropical montane grassland. On the other hand, that increase of rains is small and could not compensate for the higher leaf transpiration in tropical montane grassland vegetation due to warming climate, mainly during the driest months when the mean precipitation is about 50 mm (ICMBio 2014). Simultaneously, atmospheric climate models have predicted a potential cloud-uplift, resulting in a lower fog-vegetation contact in mountainous areas. As fog is a complementary source of water via leaf in plants (Eller et al. 2013; Goldsmith et al. 2013; Berry et al. 2019), the tropical montane grassland may be affected by a lower water input due to cloud-uplift. In addition, higher evaporative demand can affect that vegetation simultaneously in the future, which could overlap the benefits from small rains forecast.

Here, we assessed the functional profile of tropical montane grassland in the current and future climate through predictions based on leaf size and leaf teeth and climate change previsions (we used an increase in 3°C in temperature and 15 mm in precipitation) from PBMC (2013). We chose the Climate leaf analyses multivariate program (CLAMP) as a paleoclimate model from an online platform developed (clamp.ibcas.ac.cn) based on the physiognomy of leaves of woody plants and climate variables (Wolfe 1993; Yang et al. 2015). Such models have high accuracy and a strong correlation between leaves and climate (Royer et al. 2005). Through this tool, we tested the hypothesis that species with higher resistance to drought (i.e. small and entire leaves, Scenario 2 - Fig. 1) will not be the species with morphology compatible with the prediction of precipitation increase (i.e. big and tooth leaves, Scenario 1 - Fig. 1), proposed by PBMC (2013). From this study case, we showed that paleoclimate models can be used to predict climate change impacts on vegetation. Subsequently, we investigated if physiological traits (e.g. leaf water potential, stomatal conductance, turgor loss point) in association with the presence of leaf teeth can explain changes in the proportion of mountainous plants from the current scenario.

Figure 1 - Representation of hypothesis of plant response to climate changes proposed by PBMC (2013).



Legend: Representation of hypothesis in which species with higher resistance to drought, predicted in the function of fog reduction, higher evaporative demand and increase of temperature (scenario 2), will not be the species with morphology compatible with the prediction of precipitation increase (leaves with teeth and bigger) (scenario 1), proposed by PBMC (2013) to 2100, from current scenario (2015). In scenario 1 the increase in precipitation can compensate for the increase in temperature resulting in acquisitive traits (higher leaves with teeth). In comparison, in scenario 2 the increase in temperature does not compensate for the increase in precipitation resulting in conservative traits (smaller leaves and entire leaves).

Source: The author, 2022.

3.2 **Materials and methods**

3.2.1 Data collection

We used leaf morphological traits (leaf size and leaf teeth, see Table 1) of 42 woody species (except monocots) in the CLAMP models, 63 species (42 shrubs and 21 herbs) in the

FWU traits and nine species (four shrubs and five herbs), in the physiological traits (leaf water potential, stomatal conductance and turgor loss point, see Table 1) of tropical montane grassland (all 63 species used in this study are in Table S1).

Table 1 - List of morphological and physiological traits used in this study and their functional significance.

Trait	Type	Functional significance	Functional significance in drought situation	Reference
Percentage of species with entire leaves *(leaves without projections of leaf surface)*	Morphological	Represents a slower cooling down by convection than species with leaf teeth	Plants may have different strategies: Reduce the water-losing through a smaller leaf surface (no teeth) or, cooling down by heat convection through (leaf teeth)	Wolfe 1993
Leaf area (cm^2) Microphyll III *(Leaf area = 14.0-36.0 cm^2)*	Morphological	Represents the leaf size of surface available for water loss.	Plants with smaller leaves tend to conserve more water	Wolfe 1993
L:W-3 -4:1 (cm) *(leaf size - 4 times the length of a leaf by 1 width)*	Morphological	Describes the leaf size of surface available to water loss.	Plants with narrow leaves conserve more water.	Wolfe 1993
Leaf water potential (MPa)	Physiological	Describes the water status of plant	The water potential becomes more negative, increasing the water uptake capacity from the soil.	Scholander et al. 1965
Stomatal conductance (Gs) (Mmol m-2-s-1)	Physiological	Describes the gas exchanges (CO2 uptake) and transpiration in	A lower stomatal conductance decreases the leaf water loss.	Damour et al. 2010

		plants		
leaf water potential at turgor loss point (TLP)	Physiological	Water potential at which plants start closing the stomata.	In the situation of drought, plants could reach the TLP faster than in favourable conditions.	Bartlett et al. 2012
Foliar water uptake FWU (%)	Physiological	Percentage of water uptake via leaf during a given period.	In the situation of drought plants can uptake more water via leaf	Limm et al. 2009
Average rate of foliar water uptake (FWU rate) (Mmol m-2-s-1)	Physiological	Velocity of water uptake via leaf during a given period	plants uptake faster water via leaf than favourable conditions.	Limm et al. 2009

Source: The author, 2022.

The leaf morphological traits were sampled from 2015 to 2016 at Itatiaia National Park (22°21’S, 44°40’W, 2400 a.s.l), Rio de Janeiro, Brazil and are available in a database at Plant Ecology laboratory at Universidade do Estado do Rio de Janeiro (UERJ). The climate is subtropical of altitude (Cwb, Köppen classification), mean temperature of 14.4°C per year and mean precipitation of 2400 mm per year (Segadas-Vianna and Dau 1965) with low precipitation during the three driest months (until 50 mm per month) (ICMBio 2014). The soils are shallow, compound mainly by litolicos neosols and wet cambisols (ICMBio 2014), where the herbs and shrubs of tropical montane grassland occur (Safford 1999) among the rocky substrate and grasses (ICMBio 2014). During the dry season (from May to August)frost events are common (about 56 days/year), as well as fires in this vegetation (Segadas-Vianna and Dau 1965; Safford 2001).

To models buiding, we selected woody dicotyledons species (lianas, shrubs, and trees), because the CLAMP database uses only woody dicotyledons species. We classified the leaves following the online CLAMP platform (Wolfe 1993; Yang et al. 2015). We chose the category of the proportion of species with entire leaves, as a descriptor of drought resistance, a trait used in many models and sensitive to climate variations (Royer et al. 2005; Kennedy et al. 2014; Yang et al. 2015). Moreover, we chose the category of leaf size that characterizes one of the highest plant proportions of tropical montane grassland currently, Microphyll III (14.0-36.0 cm²). We selected this category because it contemplates the most abundant plants in tropical montane grassland and one of the biggest leaves in that type of vegetation. As a higher leaf causes a higher water loss, species with these leaves could become more vulnerable to drought. In addition, we chose the narrow leaf category with a high proportion of plants among other leaf width categories, in which the length is four times the leaf width (L:W-3-4:1), as a drought resistance descriptor. For example, a narrower leaf avoids water loss and contributes to cooling down in leaves by convection due to a lower boundary layer resistance (Vogel 1970). Finally, we calculated the proportion of each leaf trait in tropical montane grassland and added it to CLAMP database.

3.2.2 Data analyses

We accessed CLAMP database and related the morphological traits of 90 localities of Southern hemisphere flora (Table S2) with the climate variables: MAT (mean temperature per year) and Three – DRY (mean precipitation in the three driest months). So, firstly, we obtained the linear equation (interest trait = slope a * (environmental variable a) + slope b * (environmental variable b) + intercept), from linear regression of each morphological trait selected. Then, we added the temperature and precipitation increased, as proposed by PBMC 2013 to the southeast region of Brazil with the year of greater potential climate change – 2100 (i.e. temperature increase in up 3°C and precipitation increase in up 30% as shown in a more extreme scenario). Finally, we ran the models to verify possible changes in the leaf traits proportion of tropical montane grassland in the future scenario. The equations used in this study are available in Table 2.

Table 2 - Equations of models used to verification of proportion of tropical montane grassland plants

Trait (%)	**Linear model**
Entire margin	a = 1.78 *MAT + 0.1*PREC+ 37.22
Microphyll III	a= 1.03*MAT + 0.07*PREC+ 1.07
L:W-3-4:1	a = 0.75*MAT-0.06*PREC+7.33

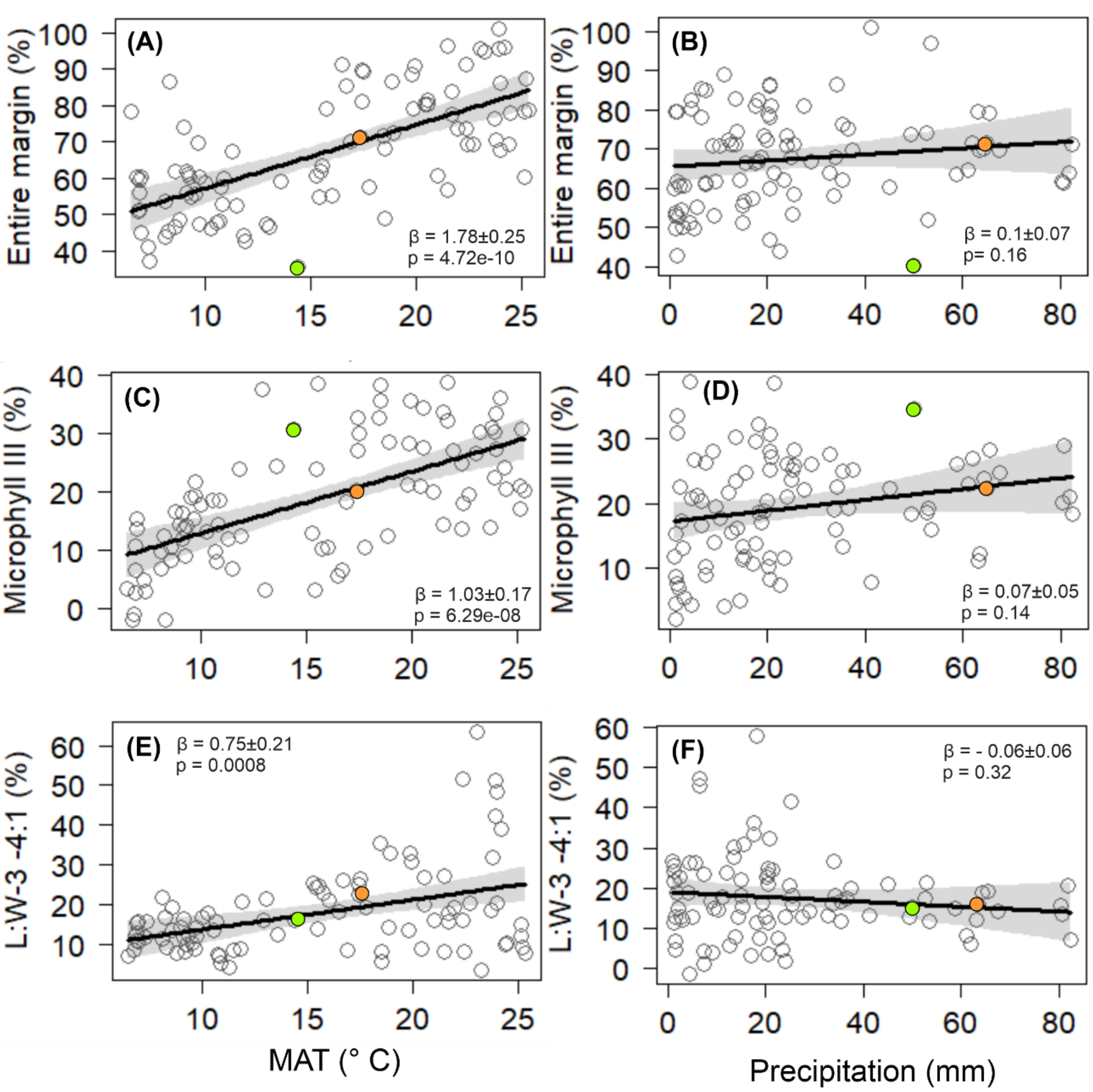
Source: The author, 2022.

Subsequently, we ran a t-test to evaluate if plants of tropical montane grassland with leaf teeth and without leaf teeth (i.e. entire margin) have different values of physiological traits. In this analysis, we used only presence and absence of leaf teeth, because this trait is widely used in paleoclimate studies, as well as is strongly considered responsive to climate. Besides that, all plants of database could be used in this category (toothed leaves x entire leaves), with an N enough to runs the analysis. In addition to t-test, we ran a two-way ANOVA with post hocs Tukey's test to evaluate potentials interactions between presence of teeth in leaves and life form (shrubs or herbs) in response of physiological traits.

3.3 **Results**

The current flora of tropical montane grassland had 38.1% of plants with an entire margin in their leaves, 33.33% of plants microphylas III and 14.29% of plants with narrow leaves with four length times higher than the width of leaf surface (L: W-3 -4:1). In the scenario for 2100, the proportion of plants with entire leaves increased with the increasing temperature and precipitation reaching 74.6 % considering all localities ($R^2 = 0.41$, $p = 6.362e-11$) (Fig. 2 A-B). Similarly, we found a decreasing proportion of plants with big leaves in the vegetation (Microphyll III) with the increase of temperature and precipitation (Fig. 2 C-D) (23.54%, $R^2 = 0.32$, $p = 3.408e-08$). We also found that the proportion of narrow leaves in the tropical montane grassland increases in 2100 ($R^2=0.23$, $p = 8.761e-06$), reaching 16.48% (Fig. 2 E-F) in tropical montane grassland. Such results indicate more plants with small, narrow, entire leaves until 2100 in the tropical montane grassland.

Figure 2 - Relationships between the mean temperature per year (MAT, °C) and precipitation during the three driest months (precipitation, mm) and proportion of species of each leaf trait analysed in 2015 and 2100.

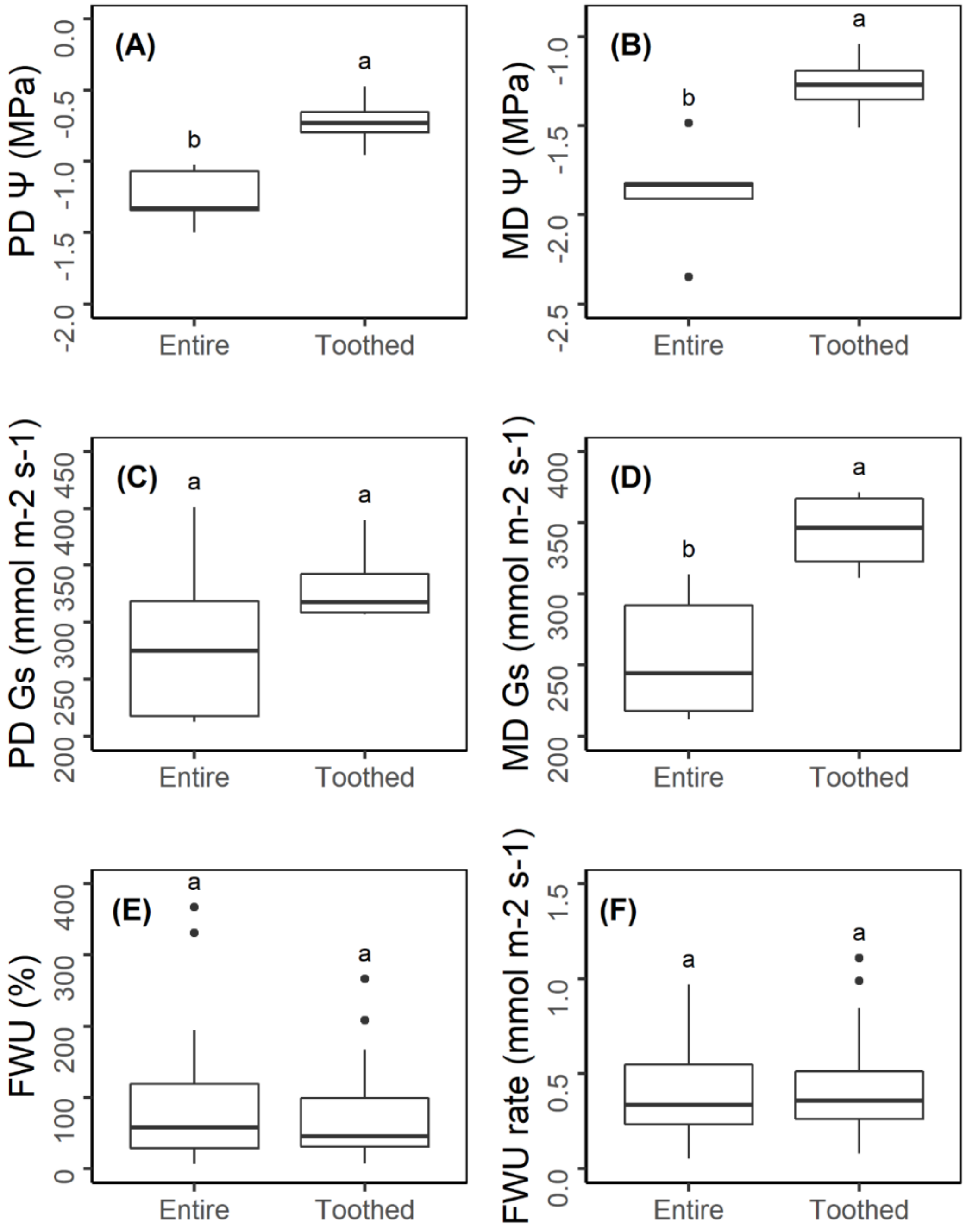


Legend: Relationships between the mean annual temperature (°C) and precipitation of three months driest (precipitation mm)) and proportion of species with leaf entire margins in the leaves (A, B), Microphyll III (C,D) and L:W-3 -4:1 (E.F) on scenarios of 2015 and 2100 in localities of Southern hemisphere (grey circles), including a tropical montane grassland in 2015 and (green circle) and 2100 (orange circle) located in Itatiaia, Rio de Janeiro, Brazil. β = Partial coefficient estimate and p = p-value.

Source: The author, 2022.

Different from expected plants with toothed leaves were those with more positive leaf water potential in predawn and midday (t = -3.96, df = 7, p = 0.005; t = -3.39, df = 7, p = 0.011, Fig. 3 A-B), as well as higher stomatal conductance in the midday (t = 3.33, df = 7, p = 0.012, Fig. 3 D). However, stomatal conductance in the predawn, percentage of foliar water uptake and rate of leaf water uptake were similar between plants with entire and toothed margin in the leaves (t = -1.11, df = 7, p = 0.30; t = 0.52, df = 63, p = 0.60; -0.36, df = 63, p = 0.71, Fig. 3 C,E-F). When considered the life form of plants, we observed that predawn and midday leaf water potential, as well as predawn and midday stomatal conductance are similar between herbs and shrubs (t = -0.45, df = 7, p = 0.66; t = -0.24, df = 7, p = 0.81; df = 1.02, df = 7 , p = 0.34; t= 0.89, df = 7, p= 0.40, Fig. 4 A-D), while the percentage of foliar water uptake and the rate of foliar water uptake are higher in herbs than shrubs (t = 3.10, df = 63, p=002; t = 0.0028; t = 3.47, df = 63, p = 0.0009, Fig. 4 E-F) (more details about t-test in Table 3). There was no difference between TLP (t = 0.03, df = 7, p = 0.97) and leaf teeth and, TLP and life form (t= -0.18, df = 7, p = 0.85) (Fig. S1, Table 3).

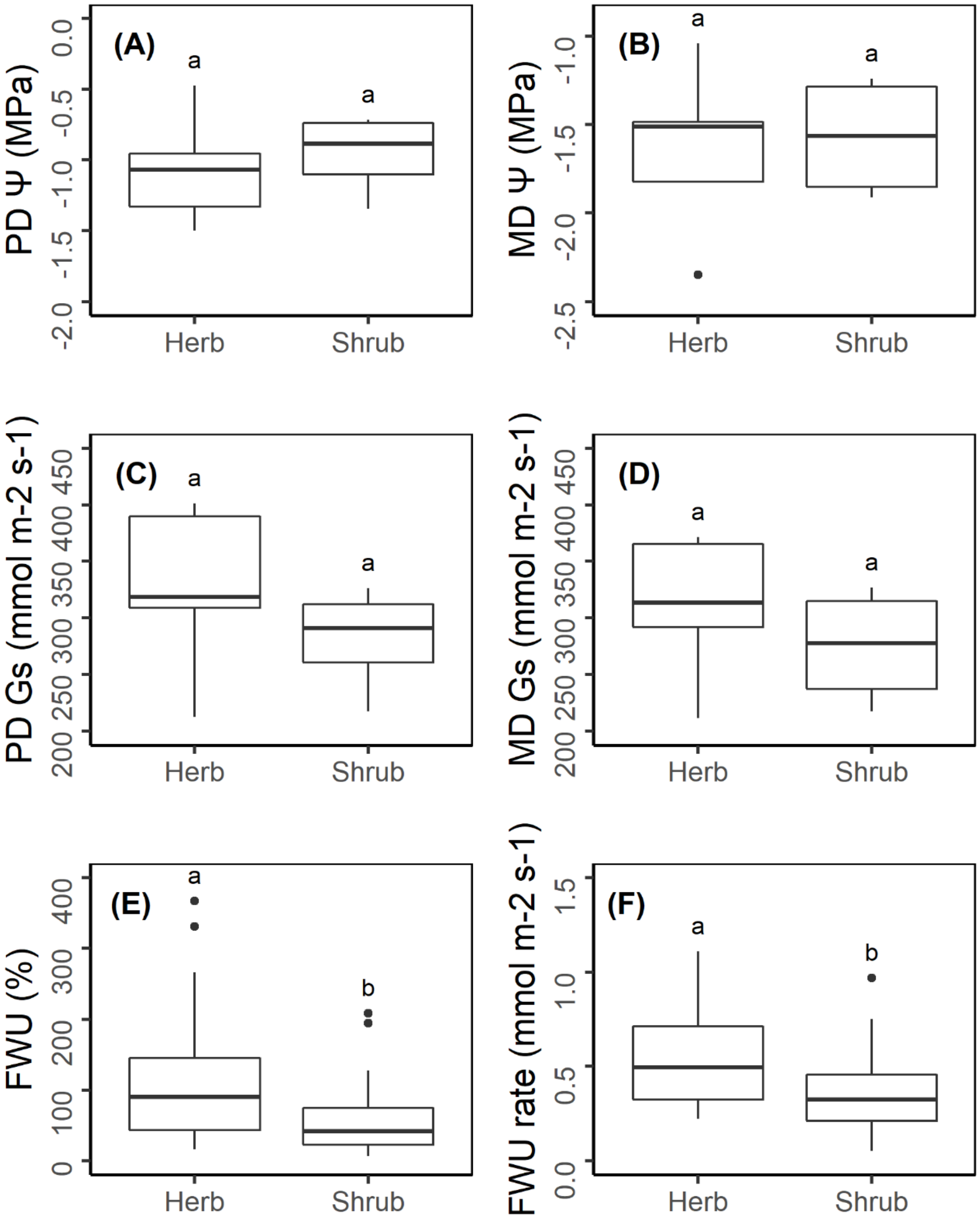
Figure 3 - Difference of ecophysiological traits between plants with entire margin and toothed margin in the tropical montane grassland in Itatiaia, Rio de Janeiro, Brazil.



Legend: Difference of predawn water potential (PD Ψ) (A), midday water potential (MD Ψ) (B), predawn stomatal conductance (PD Gs) (C) midday stomatal conductance (MD Gs) (D) proportion of foliar water uptake (FWU%), (E) and the rate of foliar water uptake (FWU rate) (F) in plants with entire margin and toothed margin in the tropical montane grassland, located in the Itatiaia, Rio de Janeiro, Brazil. Different letters mean $p<0.05$.

Source: The author, 2022.

Figure 4 - Difference of ecophysiological traits between herbs and shrubs in the tropical montane grassland, localized in Itatiaia, Rio de Janeiro, Brazil.



Legend: Difference of predawn water potential (PD Ψ) (A), midday water potential (MD Ψ) (B), predawn stomatal conductance (PD Gs) (C) midday stomatal conductance (MD Gs) (D) proportion of foliar water uptake (FWU%), (E) and the rate of foliar water uptake (FWU rate) (F) between herbs and shrubs in the tropical montane grassland, located in the Itatiaia, Rio de Janeiro, Brazil. Different letters mean $p<0.05$.

Source: The author, 2022.

Table 3 - Summary of t-test between physiological traits and leaf teeth and physiological traits and life form.

Predictor variable	**Response variable**	**t value**	**DF**	**P value**
Leaf teeth	PD Ψ	-3.96	7	**0.005**
	MD Ψ	-3.397	7	**0.011**
	PD Gs	-1.114	7	0.301
	MD Gs	-3.339	7	**0.012**
	FWU	0.52089	63	0.6041
	FWU rate	-0.36975	63	0.7128
	TLP	0.0343	7	0.9735
Life form	PD Ψ	-0.4534	7	0.6639
	MD Ψ	-0.2482	7	0.8110
	PD Gs	1.0223	7	0.3406
	MD Gs	0.8943	7	0.4008
	FWU	3.1037	63	**0.0028**
	FWU rate	3.4709	63	**0.0009**
	TLP	-0.1833	7	0.8597

Legend: PD Ψ = leaf water potential in the predawn, MD Ψ = leaf water potential in midday, PD Gs = stomatal conductance in the predawn, MD Gs = stomatal conductance in midday, FWU = percentage of foliar water uptake and FWU rate = average rate of foliar water uptake and TLP = leaf water potential at turgor loss point. t = t value, df = degree of freedom, p = p-value; p-value in bold means significance ($p<0.05$). FWU was transformed in log and FWU rate in sqrt to run analyses.
Source: The author, 2022.

Two-way ANOVA confirmed that toothed plants have higher midday stomatal conductance (F = 13.714, p = 0.01) and higher predawn and midday leaf water potential (F = 11.94, p = 0.01, Fig. S1 a; F = 8.25, p = 0.03) than species with entire leaves. Predawn stomatal conductance and TLP did not differ between toothed and entire leaves in the plants (Table S3). These physiological traits did not change regarding life forms (shrubs or herbs) (Table S3). We observed that species with teeth and entire leaves have similar FWU and FWU rate (Table 3). However, these traits are responsive to life form, with herbs showing higher FWU than shrubs in tropical montane grassland (FWU, F=9.168, p=0.0036; FWU rate, F = 13.168, p=0.0005). After Tukey-test, we found a higher stomatal conductance in midday in herbs with teeth and lower in shrubs with entire leaves (p=0.04, Fig. S2 D). All other ecophysiological traits were similar for other groups (Fig. S2, S3, S4). There was no interaction among the presence of teeth and life form with influence in physiological traits (All details of Two-way ANOVA are in Table S3).

3.4 **Discussion**

Our results suggest an increase of conservative strategy in tropical montane grassland in response to the projected increased precipitation and temperature by 2100 - described by an increase in the proportion of species with entire and narrow leaves and a decrease in microphyll III (one of the biggest leaves in this vegetation) proportion. Our results corroborated the hypothesis that species with higher resistance to drought (i.e. small and entire leaves, Scenario 2- Fig. 1), predicted by temperature increasing will not be the species with morphology compatible with precipitation increasing prediction, as proposed by PBMC (2013) (big leaves with teeth, Scenario 1 - Fig.1). Besides, from plant physiological traits, we found mechanisms that explain how plants of tropical montane grassland change their proportion due to climate change effects.

According to literature, plants with large and toothed leaves often occur in a wet environment and exhibit an acquisitive strategy (Royer et al. 2009). In contrast, plants with entire and small leaves predominate in arid environments and save more water (Bailey and Sinnott 1915; Wolfe 1993). However, although we found a predominance of plants with small leaves in the current climate, we also found a higher proportion of plants with teeth in montane tropical grassland. This high proportion of toothed leaves plants can be explained by a positive leaf water potential at predawn and midday, even with higher stomatal conductance at midday than plants with entire leaves. As TLP and FWU were similar between entire and tooth leaves, one possible explanation is those plants with teeth have higher efficiency in heat transfer by convection (Vogel 1970; Gottschlich and Smith 1982). This process contributes to leaf cooling down and decreases leaf water loss through leaf transpiration and minimizes water loss in midday (Vogel 1970; Gottschlich and Smith 1982). Then, the lower water loss by leaf transpiration can minimize leaf water potential in plants with leaf teeth and hence to their higher proportion in the tropical montane grassland currently. Also, the stomatal conductance is often associated with plant water status (Martínez-Vilalta et al. 2014). Then, an additional explanation is that plants with leaf teeth only start closing stomata when leaf water potential gradually becomes more negative, which is slow because of the leaf cooling down. In the current scenario, it could explain a higher stomatal conductance simultaneously to more positive leaf water potential in plants with teeth in the leaves.

In the global warming scenario, we found that plants with entire leaves increased the proportion, while plants with toothed leaves decreased it. Similarly, plants with entire leaves increased in tropical montane grassland, even with a tendency to decrease teeth species in other localizations with an increase of rains in the Southern hemisphere. But, if currently, plants with teeth maintain leaf water potential slightly more positive than plants with entire leaves, how species with leaf teeth could decrease their proportion? Although currently, plants with teeth maintain a leaf water potential more positive, in a scenario of severe drought, these plants might lose water easily to the environment due to higher temperature and higher VPD (Grossiord et al. 2020). It is because plants with teeth often have higher leaf surface, hydathodes, stomatal conductance rate, photosynthesis, and growth rate (Canny 1990; Royer and Wilf 2006). Such traits result in higher water loss compensating the water-saving by cooling down and the water input by rains.

In contrast, plants with entire leaves could save more water in the future scenario, because they have smaller leaf surfaces, lesser stomatal conductance and rarely hydathodes (Royer and Wilf 2006). In this case, plants with teeth and bigger leaves, such as *Leptostelma maximun* D. Don (Asteraceae) may be more prone to extinction than plants with conservative traits (smaller and entire leaves), as *Baccharis uncinella* DC. (Asteraceae) (Matos et al. 2020) in this vegetation. Besides, suppose plants with big-toothed leaves are herbs and hence are more dependent on water uptake from fog via leaf (Fig 4, E-F). In that case, such plants can become more threatened in the future, since fog-uplift from vegetation is expected in high altitudes ecosystems due to warming global (Still et al. 1999). In this case, *Leptostelma maximum* would be under more mortality risk in the future for higher leaf transpiration and foliar water uptake reduction. The death of some species and permanence of other ones can cause plant turnover, which might cause changes in community structure, ecosystem services (i.e. water cycle) and the regime of fires in the environment (Nolan et al. 2020; Matos et al. 2020).

In synthesis, climate models can be used not only for paleoclimate reconstruction but also to predict future flora changes. As we showed here, an increase in the proportion of plants with conservative traits (more resistance to drought) and a decrease of acquisitive traits indicate changes in the turnover of species in tropical montane grassland. However, only morphological traits cannot provide mechanisms that explain plant community changes under drought, being needed physiological traits (i. e., more integrative traits) inclusion to understand plant vulnerability in the system better.

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Supplementary material

Table S1 - Species of plants from flora of Itatiaia (except monocots) and their life form and leaf margin type in Rio de Janeiro, Brazil.

Family	**Species**	**Life-form**	**Leaf margin**
Apiaceae	***Eryngium glaziovianum* Urb.**	**Herb**	**Entire**
Apocynaceae	*Oxypetalum glaziovii* (E.Fourn.) Fontella & Marquete	Shrub	Toothed
Asteracaee	***Baccharis uncinella* DC.**	**Shrub**	**Entire**
Asteraceae	***Achyrocline satureioides* (Lam.) DC.**	**Herb**	**Entire**
Asteraceae	*Baccharis altimontana* G.Heiden et al.	Shrub	Entire
Asteraceae	*Baccharis brevifolia* DC.	Shrub	Toothed
Asteraceae	*Baccharis glaziovii* Baker	Shrub	Entire
Asteraceae	*Baccharis grandimucronata* Malag.	Shrub	Entire
Asteraceae	*Baccharis itatiaiae* Wawra	Shrub	Toothed
Asteraceae	*Baccharis parvidentata* Malag.	Shrub	Toothed
Asteraceae	*Baccharis pseudomyriochepala* Malag	Shrub	Toothed
Asteraceae	*Baccharis retusa* DC.	Shrub	Toothed
Asteraceae	*Baccharis stylosa* Gardner	Shrub	Toothed
Asteraceae	*Baccharis tarchonanthoides* DC.	Shrub	Toothed
Asteraceae	*Chaptalia runcinata* Kunth	Shrub	Entire
Asteraceae	***Chionolaena capitata* (Baker) Freire**	**Shrub**	**Entire**
Asteraceae	***Gamochaeta purpurea* (L.) Cabrera**	**Herb**	**Entire**

Asteraceae	*Graphistylis itatiaiae* (Dusén) B. Nord.	Shrub	Toothed
Asteraceae	*Grazielia gaudichaudiana* (DC) R.M. King & H. Rob	Shrub	Toothed
Asteraceae	*Hieracium commersonii* Monnier	Herb	Entire
Asteraceae	***Hypochaeris lutea* (Vell.) Britton**	**Herb**	**Toothed**
Asteraceae	***Leptostelma maximum* D.Don**	**Herb**	**Toothed**
Asteraceae	*Leptostelma tweediei* (Hook & Arn) DJN Hind & GL Nesom	Herb	Toothed
Asteraceae	*Mikania camporum* B.L. Rob.	Shrub	Entire
Asteraceae	***Mikania glaziovii* Baker**	**Shrub**	**Toothed**
Asteraceae	*Senecio adamantinus* Bong	Shrub	Toothed
Asteraceae	*Senecio nemoralis* Dusén	Shrub	Entire
Asteraceae	*Senecio oleosus* Vell.	Shrub	Toothed
Asteraceae	*Stevia camporum* Baker	Shrub	Toothed
Asteraceae	*Trixis glaziovii* Baker	Shrub	Toothed
Asteraceae	*Symphyopappus reitzii* (Cabrera) R.M.King & H.Rob.	Shrub	Toothed
Campanulaceae	*Lobelia camporum* Pohl	Herb	Toothed
Caryophyllaceae	*Cerastium dicrotrichum* Fenzl ex Rohrb.	Herb	Entire
Ericaceae	*Agarista hispidula* (DC.) Hook. ex. Nied.	Shrub	Entire
Ericaceae	*Gaultheria serrata* (Vell.) Sleumer ex. Kin.-Gouv.	Shrub	Toothed
Ericaceae	*Gaylussacia amoena* Cham.	Shrub	Entire
Ericaceae	*Gaylussacia chamissonis* Meisn.	Shrub	Entire
Ericaceae	*Gaylussacia fasciculata* Gardner	Shrub	Toothed
Escalloniaceae	*Escallonia laevis* (Vell.) Sleumer	Shrub	Toothed
Fabaceae	*Lupinus gilbertianus* C.P.Sm	Herb	Entire
Fabaceae	*Mimosa itatiaiensis* Dusén	Shrub	Toothed
Fabaceae	*Mimosa monticola Dusén*	Shrub	Entire
Geraniaceae	*Geranium brasiliense* Progel	Herb	Toothed
Lamiaceae	*Lepechinia speciosa* (A.St.Hil.ex Benth.) Epling	Shrub	Toothed

Letribulariaceae	*Utricularia reniformis* A St.-Hill	Herb	Entire
Melastomataceae	Leandra quinquedentata (DC.) Cogn.	Shrub	Entire
Melastomataceae	***Pleroma hospita* (Schrank et Mart. ex DC.) Triana**	**Shrub**	**Toothed**
Melastomataceae	*Tibouchina sebastianopolitana* Cogn.	Shrub	Toothed
Myrtaceae	*Myrceugenia alpigena* (DC.) Landrum	Shrub	Entire
Onagraceae	*Fuchsia campos-portoi* Pilg. & Schulze-Menz	Shrub	Toothed
Orobanchaceae	*Esterhazya splendida* J.C.Mikan	Shrub	Entire
Oxalidaceae	*Oxalis confertissima* A.St.-Hil.	Shrub	Entire
Plantaginaceae	*Plantago australis* Lam.	Herb	Entire
Plantaginaceae	*Plantago guilleminiana* Decne	Herb	Toothed
Polygonaceae	*Polygala brasiliensis* L.	Herb	Entire
Polygonaceae	*Polygala campestres* Gardner	Herb	Entire
Primulaceae	*Myrsine gardneriana* A. DC.	Shrub	Entire
Proteaceae	*Roupala montana* Aubl.	Shrub	Toothed
Rosaceae	*Fragaria vesca* L.	Herb	Toothed
Rubiaceae	*Coccocypselum cordifolium* Nees. & Mart.	Herb	Entire
Rubiaceae	*Galium humile* Cham. & Schltdl.	Herb	Entire
Rubiaceae	*Coccocypselum condalia* Pers.	Herb	Entire
Symplocaceae	*Symplocos itatiaiae* Wawra	Shrub	Toothed

Legend: The species also used in analyses about physiological traits are in bold.
Source: The author, 2022.

Table S2 - Local of data extraction, country of data extraction, mean temperature per year (MAT) and precipitation in the three months driest (Three DRY) of species from Southern Hemisphere flora.

Samples	Country	MAT	Three_DRY
Alex Knob 5	New Zealand	9.372	67.463
Apies Bay	South Africa	16.725	4.422
Argentina 1	Argentina	7.414	14.797
Argentina 2	Argentina	7.353	14.852
Baie d'Magenta	New Caledonia	22.489	16.849
Banks Peninsula	New Zealand	11.325	13.74
Bellbird Walk	New Zealand	8.161	33.693
Bilburin National Park	Australia	20.589	11.895
Binna Burra Basalt Burned	Australia	17.472	20.543
Binna Burra Basalt	Australia	17.469	20.543
Binna Burra Rhyolite	Australia	17.503	20.566
Blue Duck	New Zealand	9.126	19.437
Bowling Green Bay NP	Australia	23.289	4.431
Brunner Peninsula	New Zealand	8.123	33.897
Buffelsnek	South Africa	15.799	20.273
Camiri	Bolivia	22.419	2.911
Cape Vidal	South Africa	21.741	18.207
Clump Mountain NP	Australia	24.2	20.893
Cochabamba	Bolivia	15.288	1.008
Concepcion	Bolivia	24.404	8.959
Conondale NP	Australia	18.444	17.583
D'Aguilar NP	Australia	18.912	15.467
Daintree NP	Australia	23.972	6.538
Ella Bay NP	Australia	24.032	25.102
Eungella NP	Australia	20.551	8.706
Forest Burn	New Zealand	8.796	35.225
Giants Castle	South Africa	11.828	4.91
Girringun NP	Australia	22.394	6.466

Goukamma	South Africa	16.948	18.733
Hollyford Valley	New Zealand	6.984	58.799
Hull River NP	Australia	23.936	17.426
Kaituna Track	New Zealand	11.888	53.03
Karee Kranz 1	South Africa	18.515	1.598
Karee Kranz 3	South Africa	19.811	1.187
Karee Kranz 4	South Africa	18.543	1.585
Keka	Fiji	25.198	24.12
Kuranda NP	Australia	24.044	10.231
Lady Lake	New Zealand	10.7	80.21
Lake Colenso	New Zealand	9.043	34.114
Lake Mary	New Zealand	10.795	82.402
Lake Wilkie	New Zealand	9.782	25.458
Le Chateau	New Zealand	6.54	53.615
Link Track 4	New Zealand	10.032	37.278
Long Hilly Track	New Zealand	9.172	24.707
Marloth	South Africa	16.546	11.105
Monteagudo	Bolivia	21.06	2.537
Mount Archer NP	Australia	21.959	9.458
Mount Bauple NP	Australia	19.874	13.319
Mount Fyffe	New Zealand	11.481	20.513
Mount Koghis	Fiji	22.759	15.348
Natua	Fiji	25.135	23.405
Otira Gorge 1	New Zealand	6.806	63.226
Otira Gorge 2	New Zealand	6.862	63.491
Otira Gorge 3	New Zealand	6.942	64.224
Otira Gorge 4	New Zealand	7.017	65.341
Otira Gorge 5	New Zealand	8.592	81.694
Otira Gorge 6	New Zealand	10.585	80.72
Padilla	Bolivia	17.776	1.753
Paluma Range NP	Australia	21.507	7.366
Puhipuhi	New Zealand	9.213	19.895
Punakaiki A	New Zealand	10.939	61.949

Punakaiki B	New Zealand	10.806	61.072
Rainbow Gorge	South Africa	12.927	4.038
Riv. Bleue	New Caledonia	21.526	20.554
San Ignacio	Bolivia	24.509	7.378
San Jose	Bolivia	25.365	7.234
Santa Cruz	Bolivia	23.729	14.29
Seqaqa	Fiji	25.188	22.549
Shallow Bay	New Zealand	8.634	36.466
Sheoak Ridge	Australia	23.801	5.511
Sluicebox Footbridge	New Zealand	8.286	44.871
Smithy Creek	New Zealand	6.953	52.494
Sorata	Bolivia	10.296	2.461
South Mavora Lake	New Zealand	6.892	35.407
St Lucia	South Africa	21.708	24.023
Storms River	South Africa	15.565	21.488
Sucre	Bolivia	15.401	1.152
Tarabuco	Bolivia	13.066	1.123
Tautuku Coastal	New Zealand	9.785	25.406
Te Anau Downs	New Zealand	9.303	49.528
Tongariro 1	New Zealand	8.318	41.254
Tongariro 4	New Zealand	9.585	28.871
Tonteldoos	South Africa	15.513	2.194
Tronson	New Zealand	13.625	32.882
Ulva Island	New Zealand	9.723	27.513
Wonderkrater	South Africa	18.865	1.399
Wongi NP	Australia	19.955	13.401
Wooroonoran NP	Australia	23.085	18.277
Woowoonga NP	Australia	20.398	12.659
Zudanez	Bolivia	16.032	1.122
Itatiaia RJ	Brazil	14.400	50.000

Source: The author, 2022.

Table S3 **-** Summary of results of Two-way ANOVA between physiological traits of herbs and shrubs plants with leaf teeth and entire leaves in a tropical montane grassland, Itatiaia, Rio de Janeiro, Brazil.

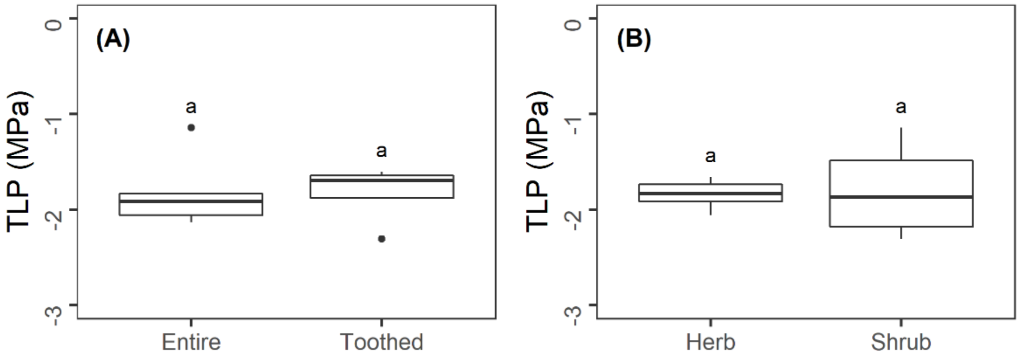
Responsive variable	**Predictor variable**	**Sum sq**	**Mean sq**	**F value**	**DF**	**P value**
Pd Ψ	teeth	0.6244	0.6244	11.948	1	**0.01**
	Life form	0.0067	0.0067	0.128	1	0.73
	Teeth:life form	0.0097	0.0097	0.185	1	0.68
	Residuals	0.2613	0.0523		5	
Md Ψ	teeth	0.8165	0.8165	8.252	1	**0.03**
	Life form	0.0003	0.0003	0.0003	1	0.95
	Teeth:life form	0	0	0	1	0.98
	Residuals	0.4947	0.0989		5	
Pd Gs	teeth	5137	5137	1.121	1	0.338
	Life form	5491	5491	1.198	1	0.324
	Teeth:life form	554	554	0.121	1	0.742
	Residuals	22920	4584		5	
Md Gs	teeth	17115	17115	13.714	1	**0.014**
	Life form	4471	4471	3.583	1	0.117
	Teeth:life form	33	33	0.027	1	0.876
	Residuals	6240	1248		5	
FWU (log)	teeth	0.25	0.255	0.306	1	0.5819
	Life form	7.63	7.627	9.168	1	**0.0036**
	Teeth:life form	0.80	0.803	0.965	1	0.3298
	Residuals	46.22	0.811		61	
FWUrate (sqrt)	teeth	0.0050	0.0050	0.165	1	0.6859
	Life form	0.3951	0.3951	13.168	1	**0.0005**
	Teeth:life form	0.0612	0.0612	2.039	1	0.1584
	Residuals	1.6157	0.0283		61	
TLP	teeth	0.0002	0.00016	0.001	1	0.976

Life form	0.0047	0.00472	0.031	1	0.868
Teeth:life form	0.168	0.16707	1.091	5	0.344
Residuals	0.7702	0.15404			

Legend: PD Ψ = leaf water potential in predawn, MD Ψ = leaf water potential in midday, PD Gs = stomatal conductance in predawn, MD Gs = stomatal conductance in midday, FWU = percentage of foliar water uptake and FWU rate = average rate of foliar water uptake and TLP = leaf water potential at turgor loss point. Sum sq means sum of squares, Mean sq means the mean square value and, DF degree of freddon. Values with $p<0.05$ are in bold and means significance.

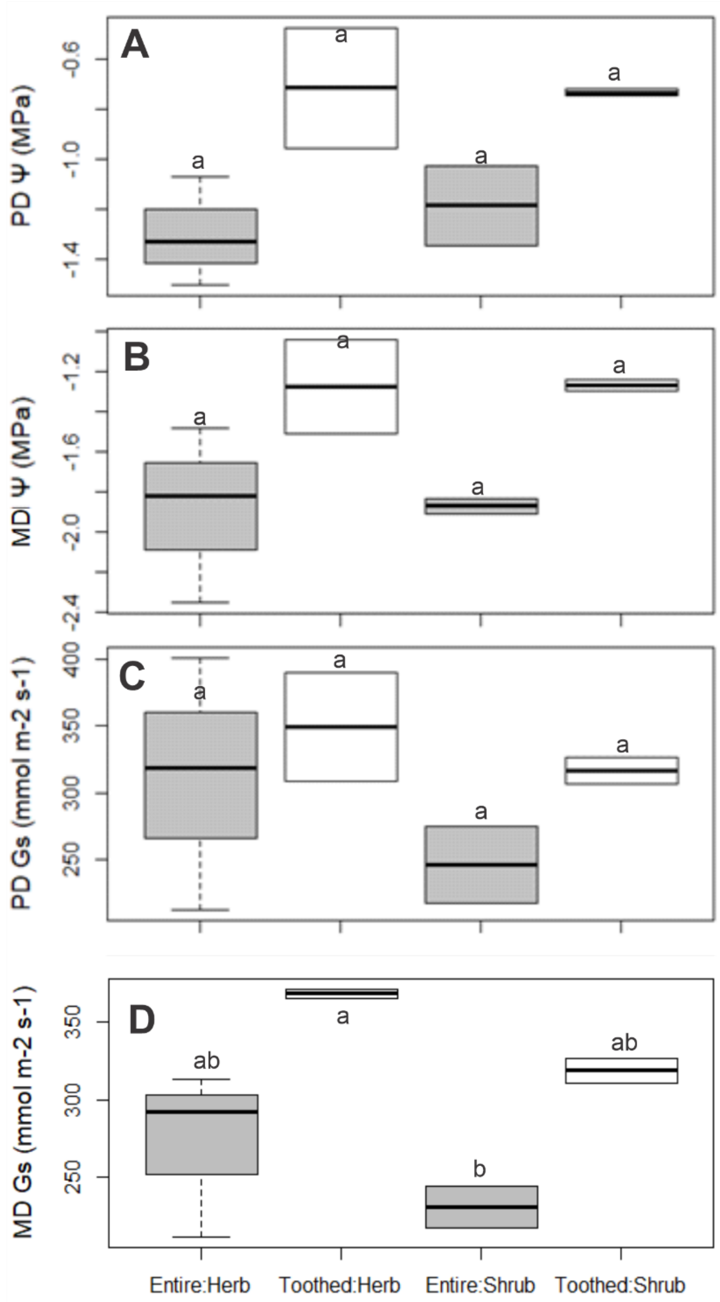
Source: The author, 2022.

Figure S1 - Difference between leaf water potential at turgor loss point (TLP) and plants with entire or toothed leaf margin (A) and TLP and herbs and shrubs of woody angiosperms (except monocots) (B) in a tropical montane grassland, localized in the Itatiaia, Rio de Janeiro, Brazil.



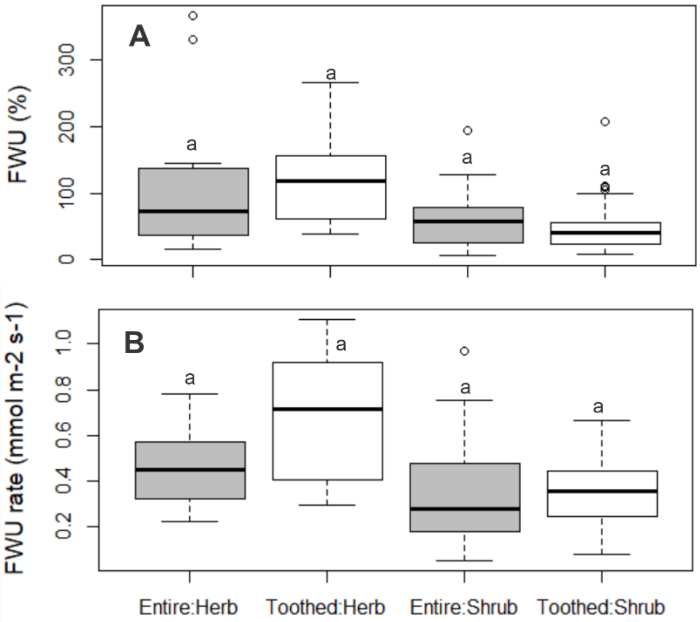
Source: The author, 2022.

Figure S2 - Boxplots with interactions between ecophysiological traits (except foliar water uptake) and life form/presence of teeth in leaves



Legend: Boxplots with interactions between predawn water potential (PD Ψ) (A), midday water potential (MD Ψ) (B), predawn stomatal conductance (PD Gs) (C), midday stomatal conductance (MD Gs) and plants with entire margin and toothed margin in the tropical montane grassland (D), located in the Itatiaia, Rio de Janeiro, Brazil. Different letters mean $p<0.05$.

Figure S3 - Boxplots with interactions between leaf wetting traits and life form/presence of teeth in leaves



Legend: Boxplots with interactions between proportion of foliar water uptake (FWU%), (A) and the rate of foliar water uptake (FWU rate) (B)and plants with entire margin and toothed margin in the tropical montane grassland, localized in the Itatiaia, Rio de Janeiro, Brazil. Different letters mean $p<0.05$.

Source: The author, 2022.

Figure S4 - Integration between leaf water potential at turgor loss point (TLP) in entire and toothed leaves of herbs and shrubs of tropical montane grassland, in Itatiaia, Rio de Janeiro, Brazil.

Source: The author, 2022.

CONCLUSÃO GERAL

> “Penso que não cegámos, penso que estamos cegos, Cegos que veem, Cegos que, vendo, não veem”
>
> *Trecho de Ensaio sobre a cegueira, José Saramago*

Embora haja um crescente interesse a respeito dos mecanismos fisiológicos por trás do que determina a vulnerabilidade de plantas à seca predita por modelos climáticos, muitos aspectos ainda permanecem não claros na literatura. Essa tese contribuiu com esse tópico através do emprego de uma abordagem que avaliou o papel dos eventos de molhabilidade foliar na vulnerabilidade de plantas à seca entre ecossistemas e cenários climáticos contrastantes, na qual usamos características funcionais morfo-fisiológicas permitindo capturar mais flutuações no ambiente quando necessário. O ponto-chave que permeou esse estudo foi: embora a literatura sobre efeitos da seca em plantas esteja em rápido crescimento, muitas vezes essa literatura investe sua atenção na água obtida por precipitação e negligencia os efeitos que os eventos de molhabilidade foliar possam exercer no funcionamento das plantas. Dessa forma, essa tese avançou no sentido de mostrar evidências de que a molhabilidade foliar em plantas deve ser inserida no contexto de vulnerabilidade à seca de uma dada vegetação, bem como, propôs direcionamentos a respeito das principais limitações e lacunas a serem exploradas no tema.

Através de uma abordagem meta-analítica no capítulo 1, acessamos os reais benefícios dos eventos de molhabilidade em plantas, uma questão até então com respostas incongruentes na literatura. Nossos resultados mostram que esse fenômeno não deve ser negligenciado, uma vez que contribui para o melhoramento do status hídrico, como refletido pelo aumento do potencial hídrico, embora tenha efeitos nulos na fotossíntese e transpiração foliar. Também identificamos que parâmetros como a precipitação acumulada/média, a altitude são importantes mediadores de respostas ecofisiológicas em plantas sob eventos de molhabilidade e, portanto, devem ser considerados em discussões sobre esse tópico. Em seguida, evidenciamos algumas limitações e maiores lacunas a serem investigadas a partir de nossa base de dados. A maior limitação diz respeito à necessidade de padronização entre métodos, o que dificulta a comparação entre estudos mesmo numa abordagem meta-analítica. Quanto as lacunas, uma maior necessidade de estudos justamente em áreas com maiores limitações hídricas (por baixa precipitação e/ou elevada demanda evaporativa), como florestas tropicais secas e desertos, assim como em ecossistemas com mais de 2000 m de altitude acima do nível do mar (e.g. parámos, punas e campos de altitude). Adicionalmente, sugerimos também um maior foco em estudos que buscam investigar o efeito do orvalho na vegetação (um evento de molhabilidade foliar global, mas negligenciado em relação aos demais).

Saindo de uma escala global e entrando em uma escala local, especificamente na floresta atlântica e nos campos de altitude no sudeste brasileiro, o capítulo 2 comparou respostas de plantas filogeneticamente próximas à seca ocorrentes nesses dois ambientes considerando o papel dos eventos de molhabilidade foliar em ambas as vegetações. A partir dessa proposta identificamos que mesmo que ambas as vegetações possuam maior resistência à seca quando comparadas sob similar média de precipitação por ano, elas são contrastantes entre si, uma vez que plantas de campos de altitude são mais resistentes à seca como refletido por predominância de características funcionais conservativas, além de exibir maior absorção de água pelas folhas, o que indica que FWU nem sempre é relacionado a estratégia de uso de recursos predominante entre vegetações. No entanto se considerarmos cenários de mudança climática onde é previsto uma redução do contato neblina-vegetação em elevadas altitudes, uma maior vulnerabilidade à seca é esperada em ambos os ambientes. Isso porque mesmo que as espécies da floresta tropical sejam mais sensíveis à seca atualmente, as plantas de campos serão aquelas com menor exposição a neblina nas próximas décadas, como indicado nessa tese pelos baixos números de eventos de neblina registrados durante o período de estudo. De forma geral, esse capítulo mostrou que se não incluíssemos o papel da neblina na comparação entre áreas não seriamos capazes de identificar também a potencial vulnerabilidade à seca de campos de altitude devido aos efeitos do aquecimento global na formação da neblina.

Levando em consideração que os modelos climáticos atmosféricos, apesar de abrangentes, podem ser menos precisos quanto à resposta de vegetações montanhosas e frequentemente nebulares à seca, no capítulo 3 acessamos modelos paleoclimáticos com base em características foliares x clima e o usamos para projetar o perfil funcional de uma vegetação de altitude no cenário climático de 2100. Através desse modelo identificamos que mesmo que haja aumento da precipitação até 2100, esse aumento não será capaz de compensar os efeitos do aumento de temperatura global no ambiente, como refletido pelo aumento na proporção de características foliares conservativas (e.g. plantas com folhas com margem inteira e menores). Além da redução na proporção de plantas denteadas no futuro indicar uma forma de economizar água em plantas (i.e. uma menor superfície foliar possui uma menor perda de água para o ambiente), um entendimento mais profundo sobre os mecanismos por trás da mudança na composição da flora da vegetação foi possível através de características ecofisiológicas. Dessa forma, identificamos que embora plantas denteadas mantenham o potencial hídrico mais positivo que plantas com folhas inteiras atualmente, elas tendem a perder mais água para atmosfera por condutância estomática em situação de seca. Em um futuro no qual a demanda evaporativa é maior e os intervalos entre chuvas maiores, possuir maior superfície foliar e maior condutância estomática reflete em uma maior perda de água via folha o que pode explicar a redução na proporção de espécies com folhas maiores e/ou denteadas até 2100.

Em síntese, as mudanças climáticas são um fenômeno mundial e desdobramentos em secas (seja atmosférica ou do solo) já veem afetando ecossistemas ao redor do mundo. O aumento da velocidade com que ocorrem as mudanças climáticas podem tornar os eventos de seca ainda mais frequentes e intensos de forma acelerada, tornando difícil uma resposta no mesmo ritmo dos organismos. Esse cenário já não permite que continuemos sendo “Cegos que veem”, de modo que precisamos enxergar os efeitos das mudanças climáticas para desacelerá-las. Como evidenciado aqui, mesmo que a seca afete de forma diferente comunidades vegetais de plantas, ambas estão propensas a serem afetadas negativamente e correm maiores riscos de mortalidade diante da restrição hídrica em curto ou longo prazo. Tais achados podem causar reflexos em maiores níveis de organização biológica, com desdobramentos em perda de biodiversidade e redução de recursos disponíveis para a sociedade. Por exemplo, uma maior mortalidade em plantas de floresta montanas pode desencadear a perda de produtividade e redução de água potável, já que montanhas são áreas onde se originam nascentes e riachos podendo gerar colapsos no ambiente e na sociedade.

A partir desse trabalho novas perguntas podem ser originadas para o melhor entendimento sobre como plantas lidam com a seca, como por exemplo identificar a capacidade plástica de plantas à mudanças, os efeitos da mortalidade de plantas para o ecossistema, além da capacidade de resiliência das plantas através de “refilling” por eventos de molhabilidade foliar para que assim vejamos além da resistência o quanto a vegetação poderia ser resiliente à seca. No entanto, reforçamos que as novas perguntas já não devem negligenciar os eventos de molhabilidade foliar, os quais, conforme mostramos nessa tese são capazes de contribuir para o melhoramento do status hídrico das plantas, e portanto, quando não considerados podem gerar resultados diferentes sobre quão vulneráveis as plantas realmente são à seca. Dessa forma, consideramos indispensáveis tal processo na avaliação de vulnerabilidade de plantas à seca e na construção de modelos realísticos sobre esse tópico.

GLOSSÁRIO

Conceito	**Definição**
Absorção hídrica foliar	Processo em que ocorre o fluxo de água na forma de vapor ou água deposita na superfície foliar (mais saturada) para o interior do mesofilo da folha (menos saturado) num fluxo osmótico reverso ao sentido solo-planta-atmosfera (Berry et al. 2019).
Cavitação	Processo em que ocorre a formação de bolhas no interior do xilema (Tyree e Sperry 1989)
CLAMP (Climate Leaf Analysis Multivariate Programe)	Método analítico que utiliza a relação fisionomia de folha de plantas x clima, como base para reconstrução do clima passado com base na fisionomia de folhas fósseis. Clamp utiliza um banco de dados global atual formado a partir da proporção de fisionomias de folhas por localidade e um banco de dados de características climáticas (Wolfe 1993). Também se refere a plataforma online de mesmo nome onde estão disponíveis databases globais e demais informações sobre essa ferramenta (Yang et al. 2011)
Condição	Fatores abióticos que influenciam no funcionamento dos seres vivos (Begon et al. 2007)
Embolismo	Processo em que ocorre a ruptura do fluxo hídrico no xilema devido a formação de bolhas de ar (Tyree e Sperry 1989)
Estratégia	Um conjunto de características funcionais ou características genéticas similares recorrentes dentre espécies ou populações resultando em uma similar resposta ecológica (Grime 2001)
Estratégia aquisitiva de uso de recursos	Estratégia predominante em áreas com recursos abundantes caracterizada pela aquisição de recursos o que reflete em um rápido crescimento. Em plantas usualmente essa estratégia é caracterizada por folhas grandes, menor densidade da madeira e maior taxa fotossintética (Wright et al. 2004, Reich 2014)

Estratégia conservativa de uso de recursos	Estratégia predominante em áreas com recursos limitados, caracterizada pela conservação de recursos o que reflete em um lento crescimento. Em plantas usualmente essa estratégia é caracterizada por folhas pequenas, maior densidade da madeira e menor taxa fotossintética (Wright et al. 2004, Reich 2014)
Evento climático extremo	Sucessão de eventos climáticos que exibem maior intensidade e/ou magnitude do que é registrado em média numa sequência histórica de eventos (e.g. seca, inundações, ciclones em maiores frequências, intensidades ou magnitudes) (Trenberth et al. 2015).
Evento de molhabilidade/ Precipitação oculta/ Precipitação horizontal	Eventos atmosféricos que compreendem agua em suspensão (neblina névoa ou orvalho) ou chuvas fracas (Nicholson 1930; Burgess e Dawson 2004) inferiores a 5 mm (Wu et al. 2016).
Evento de Molhabilidade foliar	É caracterizado pela interceptação dos eventos de molhabilidade por folhas de plantas (Dawson and Goldsmith 2018).
Filtro ambiental	Processo em que o ambiente exerce uma pressão sobre os organismos de modo que aqueles que possuem características funcionais que os permitam lidar melhor com a alteração do ambiente permanecem no ambiente, enquanto aqueles que não as tem ficam retidos (Weiher e Keddy 2004).
Gotejamento da neblina (Fog-drip)	Água da neblina que é depositada sobre a superfície foliar e escorre em direção ao solo, o umedendo. (Baguskas et al. 2017).
Modelo de reconstrução paleoclimática	Modelos estatísticos construídos com base na morfologia de fósseis, dendrocronologia, taxa de deposição de neve ou outro tipo de dado que possa ser usado em série como proxy para reconstruir as características climáticas de um dado período (Cane et al. 2005).
Recursos	Tudo que é consumido de alguma forma por algum organismo (e.g. água, nutrientes, espaço) (Tilman 1982)
“Refilling”	Repreenchimento dos vasos condutores embolizados na planta

	(Choat et al. 2018)
Seca	Fenômeno em que ocorre uma redução na entrada de água no sistema em relação a períodos anteriores na mesma localidade. A seca pode ser de quatro tipos. A) Seca meteorológica resulta de meses de estiagem acompanhadas de temperaturas acima da média registrada; B) seca agrícola onde existe redução de água no solo por baixa precipitação ou elevada evapotranspiração; C) seca hidrológica: quando estoque de águas se tornam abaixo do normal, e D) atmosférica que se refere a alta demanda evaporativa na atmosfera (Dai 2011; Novick et al. 2016).
Vulnerabilidade	É o estágio em que uma espécie está ameaçada refletido por declinío em indivíduos. A vulnerabilidade é composta por três componentes: exposição, sensibilidade e adaptabilidade. Assim uma espécie dita vulnerável poderia ter sido exposta a um dado fator, responder a esse fator com maior sensibilidade (e.g. ecofisiologia e história de vida) e/ou possuir menor capacidade adaptativa (e.g. plasticidade adaptativa, taxas adaptativas, genética) (Dawson et al. 2011).