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TAMIRES SOARES YULE

ESTUDO MORFOFISIOLÓGICO DE FOLHAS E TECIDOS CONDUTORES SECUNDÁRIOS EM ESPÉCIES SOB DIFERENTE DISPONIBILIDADE HÍDRICA NA CAATINGA

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Doutora em Biologia Vegetal.

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Área de concentração: Ecologia e Conservação
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esforços iniciais me permitem hoje trilhar a vida com
tranquilidade, dedico.

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“Eu quase que nada não sei.
Mas desconfio de muita coisa”
Guimarães Rosa,
“Grande Sertão: Veredas”

Resumo

Espécies que ocorrem em ambientes secos podem ajustar seu comportamento morfofisiológico, adotando estratégias mais relacionadas à segurança dos processos de transporte e assimilação, ou relacionadas à eficiência desses processos. Assim, espécies distribuídas em um gradiente de disponibilidade hídrica podem apresentar fenótipos diferentes em função das condições a que são submetidas. Tecidos foliares e vasculares estão fortemente relacionados a essas mudanças e às estratégias de eficiência do uso da água, afetando a aptidão do indivíduo e a distribuição das espécies. Com o objetivo de identificar se e como leguminosas variam com a disponibilidade hídrica na Caatinga, realizamos um estudo anatômico de folhas, caules e raízes de sete espécies, mais ou menos abundantes em áreas mais úmidas ou secas. As folhas de espécies mais abundantes em parcelas mais úmidas apresentam caracteres foliares mais relacionados à segurança de assimilação e condutividade, quando ocorrendo em parcelas mais secas, ao passo que espécies mais abundantes em áreas mais secas, apresentam o mesmo comportamento mesmo quando ocorrem em parcelas com maior disponibilidade hídrica. Nos tecidos vasculares, em áreas de maior disponibilidade hídrica, as espécies menos exigentes investiram em mudanças na casca e na eficiência de transporte, enquanto as espécies mais exigentes investiram em mudanças na madeira e na redução da densidade específica da madeira. A espécie indiferente foi a mais plástica, ajustando tecidos para prover mais capacidade de armazenamento e transporte aos caules. Esses resultados demonstraram a importância da casca e do floema nessas espécies e sugerem que pequenas mudanças no xilema podem aumentar a eficiência sob déficit hídrico. Entretanto, essas mudanças não estão relacionadas à abundância de espécies, o que sugere que populações ou indivíduos já submetidos a condições mais severas são mais vulneráveis a eventos de seca do que aqueles com maior disponibilidade de água, uma vez que mesmo nessas condições, as populações não tendem a aumentar numericamente. Os resultados demonstram alta adaptação das espécies às condições ambientais, sugerem que pequenas mudanças podem fornecer aumento suficiente de eficiência e/ou tolerância ao estresse e salientam a importância de tecidos e órgãos como casca e raiz, comumente negligenciados em estudos morfofisiológicos, no sucesso de espécies em ambientes com recursos limitados. Nossos resultados demonstram o risco de conservação dessas espécies, uma vez que as condições adversas inerentes às florestas tropicais sazonalmente secas devem ser agravadas pelas mudanças climáticas de origem antropogênica.

Palavras-chave: Xilema, Floema, Seca, Floresta tropical sazonalmente seca.

Abstract

Species that occur in dry environments can adjust their morphophysiological behavior by adopting strategies that prioritize either the safety or the efficiency of transport and assimilation processes. Thus, species distributed along a gradient of water availability may exhibit different phenotypes depending on the conditions to which they are subjected. Leaf and vascular tissues play a crucial role in these adaptations and in strategies for water-use efficiency, affecting both individual fitness and species distribution. To determine whether and how legumes vary with water availability in the Caatinga, we conducted an anatomical study of the leaves, stems, and roots of seven species, which vary in abundance between wetter and drier areas. Species that are more abundant in wetter plots exhibit leaf traits associated with greater safety in assimilation and conductivity when occurring in drier plots. Conversely, species more abundant in drier areas maintain the same behaviour even when found in plots with greater water availability. Regarding vascular tissues, in areas with higher water availability, the less water-demanding species invested in modifications to the bark and in transport efficiency, while the more water-demanding species invested in changes to the wood and in reducing wood-specific density. The species classified as indifferent displayed the greatest plasticity, adjusting its tissues to enhance both storage and transport capacity in the stems. These findings highlight the importance of bark and phloem in these species and suggest that small changes in the xylem can improve efficiency under water deficit. However, these changes do not appear to be linked to species abundance, suggesting that populations or individuals already exposed to harsher conditions may be more vulnerable to drought events than those in areas with greater water availability. This is because, even under improved conditions, populations do not show a tendency to increase numerically. Our results demonstrate the high adaptability of these species to environmental conditions and suggest that even minor anatomical adjustments can significantly enhance efficiency and/or stress tolerance. They also underscore the importance of tissues and organs such as bark and roots, which are often overlooked in morphophysiological studies, in determining species success in resource-limited environments. Furthermore, our findings indicate a conservation risk for these species, as the adverse conditions characteristic of seasonally dry tropical forests are expected to be exacerbated by anthropogenic climate change.

Keywords: Xylem, Phloem, Drought, Seasonally dry tropical forest

Sumário

Apresentação

Aumentos na temperatura média global e alterações nos padrões de distribuição de chuva são efeitos previstos como consequência das mudanças climáticas de origem antropogênica pelas quais o planeta vem passando. Essas variações nos padrões climáticos influenciam diretamente o funcionamento da vegetação, alterando o balanço hidráulico e, consequentemente, a assimilação, resultando em mudanças na dinâmica e composição das comunidades e na distribuição das espécies. O entendimento de mecanismos e estratégias, bem como da capacidade de tolerância a maiores temperaturas e menor disponibilidade hídrica auxilia na predição das futuras comunidades, no estabelecimento de medidas de conservação de ecossistemas e controle ou mitigação dos efeitos das mudanças climáticas.

Nesse contexto, baseados na falta de informações anatômicas e fisiológicas de espécies de florestas tropicais sazonalmente secas (FTSS), bem como nas lacunas de conhecimento acerca da dinâmica dos processos de sucessão e regeneração desses ecossistemas, propusemos a avaliação anatômica e fisiológica de espécies lenhosas da Caatinga, uma FTSS de ocorrência restrita ao Brasil. Avaliamos quantitativamente atributos de folha como espessura de cutícula, espessura total da folha e de cada um dos parênquimas, densidade e tamanho de estômatos e tricomas, diâmetro de células condutoras de xilema e floema, além de avaliar o custo de construção foliar. Nos caules e raízes, avaliamos atributos de madeira e casca como diâmetro e comprimento de células condutoras no xilema e floema, densidade específica de madeira, tamanho de pontoação, espessura de casca, percentual de floema condutor e não condutor, além de índices de grupamento de vasos, mesomorfia e vulnerabilidade, e condutividade hidráulica potencial. A análise visou verificar a variação de atributos em espécies distribuídas e submetidas a diferentes níveis de disponibilidade hídrica, a fim de identificar suas respostas e capacidade de tolerar o aumento previsto das condições adversas do ambiente.

Fundamentação teórica

A Caatinga

A Caatinga (do tupi: floresta branca) é um ecossistema semiárido que se distribui inteiramente dentro do território brasileiro, pelo interior da região Nordeste e na região insular de Fernando de Noronha (Prado 2003), caracterizado por sua sazonalidade marcada e baixa precipitação. Distribui-se em depressões inter planálticas e chapadas, em regiões de solo de origem sedimentar e cristalina. Em função de sua origem geológica, bem como dos processos de formação do substrato, a Caatinga apresenta solos rasos e pedregosos, com a rocha-mãe pouco decomposta, exposta ou pouco profunda, e ocorrência de afloramentos de rocha maciça (IBGE 2002). O território é drenado por cursos d'água sazonais intermitentes, que fluem na estação chuvosa, com participação do lençol freático abastecido. Ao final da estação, seu volume é gradualmente reduzido, ocorrendo a retroalimentação do lençol pelos rios, que permanecem secos durante o período de estiagem (Ab'Saber 1974; Andrade *et al.* 2017).

Consequência da influência das massas de ar secas e estáveis, resultantes da descarga de massas úmidas no litoral, constantemente empurradas para o sudeste pelos ventos Alísios, o clima semiárido da Caatinga experimenta condições extremas dentre os parâmetros climáticos registrados no Brasil (Prado 2003). É na Caatinga que se registram a mais alta temperatura média anual e as menores e mais irregulares precipitações do país, normalmente concentradas em um curto período no ano (de 2 a 5 meses), além das mais altas taxas de radiação solar e menor umidade relativa (Prado 2003; Kottek *et al.* 2006; Andrade *et al.* 2017). O período chuvoso se concentra de novembro a janeiro nas porções oeste e sudoeste, com chuvas vindas da Amazônia, e de fevereiro a abril, no norte e nordeste da região, com chuvas formadas a partir do movimento sul da Frente Intertropical no verão (Andrade *et al.* 2017). Em função das dinâmicas climáticas regidas por eventos cíclicos e plurianuais, na região são comuns eventos extremos como grandes secas e cheias, que ao longo do tempo, selecionaram e modularam a biodiversidade local (Prado 2003).

A paisagem das Caatingas do semiárido nordestino é composta por diferentes fitofisionomias, correspondentes às suas sub-regiões, com suas respectivas histórias de formação pedológica e condições ambientais (Silva *et al.* 2003). Ocorrem cerrados nos topos de tabuleiros, florestas úmidas nos topos das serras (brejos de altitude), florestas secas ou caatinga arbórea nas encostas e matas de galeria ou ciliares ao longo dos cursos d'água perenes (Prado 2003). Além disso, a densa e antiga ocupação humana no domínio da Caatinga tem grande influência na estrutura e composição, e mais recentemente reconhecido, em sua conservação (Rito *et al.* 2017; Silva e Barbosa 2017). Em recente avaliação, Silva e Barbosa (2017) concluíram que 63,3% da vegetação da Caatinga foi modificada pelo homem.

A vegetação da Caatinga apresenta componentes xerófitos, micrófilos e espinescentes, além de característica suculência e um estrato herbáceo com predominância de espécies terófitas (Prado 2003). As famílias Fabaceae, Euphorbiaceae, Cactaceae, Bromeliaceae, Anacardiaceae, Apocynaceae, Bignoniaceae, Burseraceae, Arecaceae, Rhamnaceae, Malvaceae e Portulacaceae contém vários dos componentes principais da comunidade vegetal da Caatinga (Prado 1991). Prado (1993) considera a Caatinga a mais rica floresta tropical seca da América do Sul, baseado em sua composição florística e número de gêneros e espécies endêmicas (Silva *et al.* 2003). Ainda assim, a taxa de endemismo é menor do que o esperado, uma vez que a vegetação está estabelecida na província biogeográfica da Caatinga desde o Terciário (Ab'Saber 1974; Prado 2003). Nesse contexto, diversas teorias de formação da flora da Caatinga são postuladas, descrevendo rotas vindas da África (baseada na distribuição de *Commiphora*), do Caribe (baseada em gêneros de Cactaceae e Arecaceae), dos Andes (em função da distribuição de alguns gêneros arbóreos de Fabaceae), através da Amazônia (por conta da distribuição de gêneros de diversas famílias abundantes na Caatinga), ou ainda do conjunto de rotas (teorias do movimento de pinças e arco pleistocênico) e da invasão da vegetação de outros biomas (florestas Amazônica e Atlântica ou Cerrado) durante períodos glaciais e interglaciais passados (Prado 2003). Uma teoria definitiva, porém, ainda carece de estudos taxonômicos mais amplos e que as relações filogenéticas entre seus componentes sejam melhor compreendidas.

A Caatinga e as mudanças climáticas

A delimitação fitogeográfica da Caatinga coincide com as isoietas de 1000mm, o que significa que sua vegetação é naturalmente submetida a precipitações anuais médias inferiores a isso. Sabe-se que 50% da vegetação de Caatinga está submetida a precipitação inferior à 750mm anuais, enquanto existem áreas que recebem menos de 500mm/ano (Prado 2003). Porém, não é a precipitação anual absoluta o fator de maior importância na distribuição das espécies, mas sim a variação das chuvas ao longo do ano e sua amplitude em relação à moda (Prado 2003).

Alterações nos padrões de distribuição de chuva, intensificação de eventos com temperaturas extremas e aumento na temperatura média global são alguns dos efeitos esperados em função das mudanças climáticas de origem antropogênica. Atividades humanas como emissão de gases e partículas, que causam alterações na composição da atmosfera (ex. gases do efeito estufa e aerossóis derivados de queimadas e uso de combustivos fósseis), e modificações severas de uso do solo (ex. desmatamento e substituição de vegetação nativa por monoculturas), impactam os padrões climáticos globais acima do que é esperado baseado na média histórica dos ciclos anuais e plurianuais de variações naturais no clima (Myhre *et al.* 2013; PBMC 2014a; Torres *et al.* 2017). As alterações e suas consequências ocorrem em cascata e se retroalimentam, causando a aceleração das mudanças conforme elas se agravam e levando a danos irreversíveis na escala humana. Diversos mecanismos físico-químicos e biológicos estão envolvidos nos processos de alterações nos padrões climáticos (Ciais *et al.* 2013). Aumentos na temperatura média global, causadas por intensificação do efeito estufa, por exemplo, comprometem a manutenção de grandes áreas permanentemente congeladas como *permafrost* em altas latitudes e calotas polares. O derretimento de solos permanentemente congelados, *permafrost*, torna disponível grandes quantidades de carbono para lançamento na atmosfera, intensificando os efeitos das mudanças climáticas (Vaughan *et al.* 2013). O derretimento de calotas polares é ainda mais danoso, pois tende a aumentar o nível dos oceanos e reduzir a salinidade de suas águas, alterando as correntes marítimas, que formam e regulam padrões de chuva em todo o mundo (Rhein *et al.* 2013). Dessa forma, a pluviosidade tende a ser reduzida em áreas atualmente florestadas, reduzindo alguns ou parte desses biomas, ou ainda convertendo em ecossistemas mais abertos e com menor concentração de carbono. Dessa forma, biomas que funcionam como dreno de C, podem passar a atuar com fonte, intensificando as alterações climáticas (Christensen *et al.* 2013; PBMC 2014b; c).

As previsões de futuros cenários climáticos são feitas com técnicas de modelagem, que levam em conta os parâmetros físicos, químicos e biológicos que regem o clima mundiais (Flato *et al.* 2013). O Painel Intergovernamental de Mudanças Climáticas (The Intergovernmental Panel of Climatic Changes- IPCC) produz estudos interdisciplinares sobre o tema e publica periodicamente relatórios sobre as bases científicas, os impactos e vulnerabilidades sobre a biodiversidade e população humana, além de diretrizes para políticas públicas de mitigação e cenários possíveis para os anos subsequentes. No Brasil, o Painel Brasileiro de Mudanças Climáticas (PBMC 2014c) atua interpretando os dados mundiais especificamente para os ecossistemas e território brasileiro. As estimativas para o Brasil, baseadas nas atividades econômicas impactantes e na postura governamental de conservação preveem alterações nos padrões de distribuição, bem como na frequência e intensidade de chuvas, aumento na temperatura média e dos eventos extremos de temperatura (grandes secas e geadas) e pluviosidade (tempestades) (PBMC 2014c). Tais efeitos levarão à perda de biodiversidade, aceleração de processos de desertificação, mudanças nas vocações de áreas agriculturáveis, eventos extremos de chuvas e inundações, e impactarão diretamente atividades econômicas como produção de alimentos e energia, bem como na disponibilidade de água para populações e processos biogeoquímicos (PBMC 2014d).

Nesse contexto, as mudanças climáticas atuam intensificando o estresse hídrico por falta d'água inerente da Caatinga, uma vez que espera-se aumento de 1,5 a 3,5°C na temperatura média, acompanhado de 20 a 60% de redução da pluviosidade, ainda neste século, para a região Nordeste do Brasil (Rodrigues-Filho *et al.* 2016; Torres *et al.* 2017). Essas mudanças implicam em alterações na dinâmica da vegetação, aumento da insegurança hidráulica, atraso nas respostas de recuperação dos danos e do risco de eventos de mortalidade em massa, relacionados a eventos de seca cada vez mais frequentes e severos (Anderegg *et al.* 2015a; Anderegg *et al.* 2015b). Compreender os mecanismos utilizados pelas plantas e identificar seus limites de tolerância a essas condições é fundamental para o entendimento e previsão de futuros cenários, bem como para a elaboração de planos de mitigação das mudanças climáticas.

Respostas e padrões ao clima

Embora as respostas frente às mudanças e condições ainda mais severas ainda sejam incertas (Anderegg *et al.* 2015a), a capacidade de tolerância à seca e alta assimilação mesmo sob maior restrição hídrica, torna as florestas secas ecossistemas chave para armazenamento de carbono, redução de seus níveis atmosféricos e, consequentemente, das mudanças climáticas mundiais (Santos *et al.* 2014; Silva *et al.* 2017). Em estudo realizado com diversas espécies distribuídas ao longo do gradiente de disponibilidade hídrica do istmo do Panamá, atributos funcionais relacionados à sensibilidade à seca mostraram-se bons preditores da distribuição de espécies em florestas tropicais (Engelbrecht *et al.* 2007). No mesmo estudo não foi observada relação entre sensibilidade à seca e disponibilidade de nutrientes no solo, atestando a importância da disponibilidade de água na composição da comunidade.

Em espécies de ambientes com maior disponibilidade hídrica, a elevação da temperatura leva à redução da abertura estomática e a restrição da captação de CO_2, devido ao maior déficit de pressão de vapor do ar (Sevanto 2014). Por outro lado, estudos sugerem que as espécies de ambientes secos podem otimizar a captação de CO_2, mesmo em baixos níveis de condutância estomática, provocados pela restrição hídrica e alta temperatura (Santos *et al.* 2014). Nessas espécies o aumento da concentração de CO_2 atmosférico representa um acréscimo de recurso para assimilação quando associado às estratégias de uso eficiente da água (Anderegg *et al.* 2015b), conforme observado em espécies da Caatinga (Donohue *et al.* 2013). Os mecanismos associados ao uso eficiente da água são investigados sob diversos aspectos como deciduidade (Wispelaere *et al.* 2017), concentração de CO_2 (Domec *et al.* 2016), além de suscitar questionamentos quanto a características e processos combinados (Brodribb *et al.* 2016; Hacke *et al.* 2016; Sperry *et al.* 2016; Buckley *et al.* 2017). Domec et al. (2016) observaram que as respostas quanto ao uso eficiente da água sob elevadas concentrações de CO_2 são variáveis entre grupos filogenéticos e plantas diferentes fases de desenvolvimento. Relatam ainda que espécies lenhosas, quando comparadas com não-lenhosas, apresentam maior vulnerabilidade a falhas hidráulicas durante eventos de seca. Entretanto, os autores apontam que a vulnerabilidade, bem como suas estratégias, é variável entre os diferentes componentes lenhosos de diferentes comunidades, sendo necessário, portanto, estudos mais amplos, combinados com outros fatores ambientais (ex. temperatura) e biológicos (genéticos e anatômicos) e com florestas maduras, a fim de compreender os riscos e potenciais de cada ecossistema. Em contrapartida, estudo realizado nas florestas semiáridas do Lago Chala, avaliando a partição espacial de água (lago x solo x chuva) em espécies arbóreas e arbustivas, decíduas e semidecíduas (Wispelaere et al. 2017) demonstrou diferentes valores de distância evapotranspirativa (ED) para diferentes tipos de solo e distâncias do lago, ou seja, água sendo adquirida de diferentes profundidades. Árvores tendem a captar água mais superficialmente em solos mais altos e secos e mais profundamente em solos mais baixos e úmidos, comparativamente às espécies arbustivas. Além disso, os autores também observaram maiores valores de enriquecimento de isótopos de deutério do xilema para as folhas, isto é, maior aquisição e transpiração, em espécies decíduas quando comparadas com perenifólias, sugerindo maior eficiência no uso e proteção contra perda de água no segundo grupo.

Estresse hídrico, convergência funcional e composição das comunidades

Em função das diversas e mutáveis condições ambientais, ao longo do curso evolutivo das traqueófitas, especialmente gimnospermas e angiospermas, houve o desenvolvimento de mecanismos e arquitetura hidráulica que otimizam a fotossíntese e a condutividade da água, minimizando a vulnerabilidade dos tecidos assimiladores e condutores em espécies submetidas a essas condições (Hacke and Sperry 2001; Chaves *et al.* 2009). Os atributos funcionais relacionados a esses mecanismos refletem na distribuição das espécies em diferentes ecossistemas e ao longo do tempo (Falcão *et al.* 2015; Cosme *et al.* 2017) e suas variações ocorrem em diversos níveis entre os componentes lenhosos de uma comunidade (Woodcock 2000; Fortunel, Paine, *et al.* 2014; Plourde *et al.* 2015). Entretanto, os padrões de alocação de recursos e estratégias apresentam uma ampla gama de possibilidades, reduzidas especialmente em ambientes mais restritivos, uma vez que a priorização de um atributo pode custar a limitação de outro (Bucci *et al.* 2004), o que pode levar à convergência funcional entre espécies e indivíduos submetidos à condições ambientais semelhantes (Hacke and Sperry 2001; Sungpalee *et al.* 2009).

Sabe-se que permutas entre determinados traços ocorrem e explicam a performance de espécies na composição de comunidades, entre diferentes congêneres ao longo da paisagem ou mesmo de populações de uma mesma espécie em diferentes paisagens (Reich 2014). A nível fisiológico, os *trade offs* que determinam a abundância e distribuição dos indivíduos no espaço e no tempo são causados pela alocação de recursos limitados para um propósito versus outro. Ainda, segundo Reich (2014) as escolhas conhecidos para uma espécie em um local são previsivelmente similares em outros locais, em diferentes escalas (local, regional ou mesmo global). Esse efeito já foi observado em espécies da Caatinga por Vieira & Lisi (2019), que demonstrou relação entre características anatômicas e condições ambientais (temperatura e precipitação), distinguindo espécies lenhosas em diferentes grupos funcionais na comunidade.

Xilema e floema

O estudo de atributos a nível celular permite a avaliação em escala funcional e estrutural, colaborando mais apuradamente com o entendimento da dinâmica de condutividade hidráulica em plantas (Fonti and Jansen 2012). No xilema, a ocorrência de vasos estreitos e curtos, densamente agrupados, com pontoações guarnecidas e placas de perfuração simples são amplamente relatados para espécies de ambientes xerófitos (Alves and Angyalossy-Alfonso 2000; Evert and Eichhorn 2006; Sonsin *et al.* 2012). Essas características são relacionadas à segurança hídrica que facilitam a condutividade e evitam a ocorrência de eventos de embolias e cavitações, embora reduzam a capacidade de condução (Hacke and Sperry 2001; Bucci *et al.* 2004). Para atender a demanda de água, as plantas são capazes de ajustar as propriedades do xilema, promovendo modificações baseadas em parâmetros mensuráveis como densidade de vasos por área, composição dos vasos (de muitos estreitos a poucos largos) e área do alburno suprindo uma dada unidade de folha (Zanne *et al.* 2010). Vieira and Lisi (2019) em estudo anatômico da madeira de caule, com quatro espécies, de diferentes grupos funcionais da Caatinga, não observaram variações nos atributos qualitativos em função das condições ambientais. Porém, os autores encontraram forte ligação entre as variações de parâmetros quantitativos do xilema secundário e das condições ambientais permitindo a distinção das espécies dentro dos grupos funcionais (Vieira and Lisi 2019). Os principais fatores ambientais relacionados às variações anatômicas foram temperatura e precipitação, que afetam e geram respostas diferentes entre os grupos funcionais. Temperatura e precipitação foram os fatores mais importantes para *Aspidosperma pyrifolium*, cujo xilema apresenta características mais relacionadas à segurança hidráulica. *Libidibia ferrea* e *Tabebuia aurea*, do grupo funcional caracterizado pelo investimento em estocagem de recursos no xilema, foram influenciadas pela variação sazonal da precipitação e variação da precipitação no período seco, respectivamente (Vieira and Lisi 2019). *Ziziphus joazeiro*, por sua vez, componente do grupo funcional intermediário entre os dois anteriores, não apresentou relação direta com nenhum fator relacionado à precipitação, sugerindo que conta com outras estratégias, fisiológicas ou estruturais, que garantem sua ocorrência no ambiente. Esses resultados demonstram que o estudo de diferentes tecidos e órgãos, sob diferentes aspectos, é necessário para a compreensão das estratégias desenvolvidas pelas espécies de ambientes restritivos.

Alterações anatômicas interferem diretamente na densidade da madeira, atributo relacionado ao crescimento dos indivíduos, arquitetura e mortalidade das espécies, sua performance em gradientes ambientais e estocagem de recursos, e portanto, à estrutura das comunidades (Fortunel, Ruelle, *et al.* 2014). Densidade de madeira é altamente influenciada pela razão espessura de parede x lúmen, e aumenta com a resistência à cavitação (Lens *et al.* 2011), que por sua vez é determinada pela quantidade e densidade de pontoações, qualidade (espessura de membrana, tamanho, estrutura), e, quantidade e tipo de tecido circundando o vaso. Segundo Zanne et al. (2010) densidade específica de madeira é um bom preditor de resistência mecânica, pois nessa medida, os espaços dos lúmens são desconsiderados.

Além de parâmetros macroscópicos e estruturais, a microestrutura de parede no xilema, sobretudo nos elementos de vaso, é intimamente relacionada à segurança no tecido. Estudo realizado com espécies do gênero *Acer* demonstrou que pressão média de cavitação é fortemente relacionada à morfologia da pontoação (espessura de membrana, porosidade e profundidade da câmara), fracamente relacionada ao número de pontoações por vaso e não relacionada ao número de pontoações por área no vaso (Lens *et al.* 2011). Os autores observaram que pontoações respondem a mais de 50% da resistência de fluxo, indicando a importância dessas estruturas na composição de estratégias de tolerância ao estresse hídrico por falta d’água.

Menos frequente nos estudos relacionados às relações hídricas dos vegetais, o floema tem sido observado com mais atenção nos últimos anos. O tecido é a principal via de transporte de foto assimilados a longa distância em vegetais e, segundo a teoria de Münch (1930), seu funcionamento é regulado pela diferença de pressão hidrostática entre órgãos fonte (folhas) e órgãos dreno (caule, raiz). A obtenção de dados experimentais diretos que confrontem a teoria, é um desafio, de forma que os estudos geralmente são realizados através de observações indiretas do funcionamento do tecido (Epron *et al.* 2019). Sabe-se, porém que a demanda e transporte de carboidratos não ocorre apenas no sentido fonte-dreno, mas ao longo de todo o corpo do vegetal (Van Bel 2003). Além disso, acredita-se que de maneira geral, traços funcionais ligados à estrutura e padrões floemáticos são mais estáveis que os xilemáticos, refletindo, comparativamente entre os tecidos mais a história evolutiva do que as variações ambientais atuais (Rosell 2016; Prislan *et al.* 2018).

No floema ainda pouco se sabe sobre as características relacionadas à segurança e eficiência da condutividade (Sevanto 2014). Entretanto, sabemos da dependência mútua dos dois tecidos condutores em termos de estratégias para segurança hidráulica. O floema secundário, que constitui parte da casca do vegetal (Rosell 2016), atua aumentando e fornecendo açúcares para garantir a pressão necessária para manutenção do fluxo no xilema que, por sua vez, fornece água para reduzir a viscosidade da seiva e evitar que o fluxo do floema cesse ou que suas células percam turgor (Sevanto 2014).

A conexão entre os dois tecidos é feita principalmente pelo parênquima radial, contínuo para ambos os lados do câmbio (Pfautsch *et al.* 2015). Dessa forma, reduções na condutância do xilema estão relacionadas a limitações na produtividade e na capacidade de transporte de carboidratos pelo floema (Lens *et al.* 2011; Epron *et al.* 2019). Dannoura et al. (2019) avaliaram *Fagus sylvatica* em condições normais e de estresse hídrico, e observaram redução do potencial osmótico das folhas, bem como redução do raio do floema nas plantas sob estresse. A redução do raio levou à redução da condutividade dos elementos de tubo crivado e da condutância do floema no caule. Os autores concluíram, portanto que secas prolongadas afetam a capacidade de condutividade através de mudanças na anatomia do floema e que a redução do fluxo ocorre para reduzir o efeito da diferença e pressão hidrostática entre os órgãos fonte e dreno. As alterações anatômicas observadas incluem a redução do percentual de floema condutor, causando a redução da capacidade de condutividade do tecido (Dannoura *et al.* 2018). Por outro lado, em *Fraxinus ornus* L., a redução da água disponível causou aumento da porção condutora, bem como do raio dos elementos de vaso, como forma de compensar o aumento da viscosidade da seiva (Kiorapostolou and Petit 2018). A resposta ao aumento da restrição é, portanto, espécie específica, deve refletir a história natural do táxon, mas principalmente pode indicar a capacidade de tolerância aos diferentes cenários de mudanças climáticas.

Além do transporte de carboidratos dos órgãos fonte aos órgãos dreno, o floema secundário cumpre a função de armazenamento através do parênquima que circunda os elementos de tubo crivado. Nessas células são acumulados carboidratos não-estruturais, proteínas e água (Epron *et al.* 2019). A produção de células de parênquima axial pelo câmbio concentra-se no fim da estação de crescimento de espécies de clima temperado (Prislan *et al.* 2018), nas quais a sazonalidade tem papel importante na atividade cambial. Padrões de distribuição do parênquima axial são, portanto, indicativos da variação anual e interanual da atividade cambial, que por sua vez, é reflexo das taxas de assimilação desempenhadas pela planta. A formação dessas células marca o fim da estação favorável, período em que as condições ambientais permitem que demandas energéticas básicas sejam atendidas e a produtividade excedente seja armazenada.

O armazenamento de água na casca tem demonstrado ser essencial para a manutenção do equilíbrio osmótico do vegetal, e para a manutenção da assimilação. A água acumulada no parênquima da casca e do alburno é demandada conforme a temperatura ambiente aumenta, causando aumento na taxa de transpiração. A variação diária de espessura da casca, diretamente relacionada a variação da transpiração ao longo do dia observada em *Pinus silvestres* L. exemplifica o funcionamento desse mecanismo e demonstra a importância desse tecido para o equilíbrio osmótico da planta e para a manutenção da assimilação (Lazzarin *et al.* 2018). Avaliando comparativamente o floema secundário de caules e raízes de *Cytharexylum myrianthum* Cham. (Verbenaceae), Vergílio et al. (2017) observaram maior capacidade de transporte, sustentação e armazenamento nos órgãos aéreos, diferente do que era recorrente na literatura (MacDaniels 1918; Machado *et al.* 2005). Essa diferença foi evidenciada através de células maiores no parênquima e esclerênquima em caules, e elementos de tubo crivado mais calibrosos, embora todos os tecidos ocorressem em número de células semelhante ao das raízes. Segundo os autores, o maior diâmetro do caule permite a ocorrência de células maiores e tecidos mais amplos, corroborando o observado para xilema e sugerido por Olson e Rosell (2013), e casca por Rosell (2016). Dessa forma, caules apresentariam maior área disponível para armazenamento, facilitando a mobilização de carboidratos para rebrota e contribuindo para a manutenção dos indivíduos na comunidade (Vergílio *et al.* 2017).

Considerações finais

Embora um grande volume de informações sobre anatomia da madeira de espécies de todo o mundo esteja disponível em bancos de dados, o conhecimento sobre floema ainda é incipiente (Epron *et al.* 2019). Mais escasso ainda é o conhecimento sobre o funcionamento desses dois tecidos (xilema e floema), bem como sua vulnerabilidade frente às mudanças climáticas e seu papel na distribuição das espécies nas comunidades vegetais. Além disso, grande parte dos estudos experimentais são realizados com espécies de clima temperado, que respondem de maneira diferente das espécies tropicais e de ambientes sazonais ou com restrição hídrica severa.

Desde o início da década passada a comunidade científica alerta para a importância de se integrar análises anatômicas, fisiológicas e de modelagem, a fim de elucidar essas questões (Fonti and Jansen 2012). Para espécies tropicais o estudo é particularmente deficiente uma vez que falta estrutura para análises mais refinadas, utilizando técnicas de marcação molecular, tomografia computadorizada e raio-x em plantas vivas.

O estudo integrado de xilema e floema, bem como entre caules e raízes, promove um melhor entendimento das estratégias adotadas pelas espécies que ocorrem em ambientes restritivos (Poorter *et al.* 2018). Conforme exposto previamente, a literatura relata conservação na variação de atributos de xilema em raízes, enquanto o mesmo é descrito para floema em caules. Dessa forma, os resultados obtidos para espécies da Caatinga são importantes para a compreensão da dinâmica das comunidades desse ambiente, colaborando para elaboração de estratégias efetivas para sua conservação.

Bibliografia

Ab'Saber AN. 1974. O domínio morfoclimático semi-árido das caatingas brasileiras. *Geomorfologia* **43**: 1–39.

Albert S, Sharma B. 2013. Comparative foliar micromorphological studies of some Bauhinia (Leguminosae) species. *Turkish Journal of Botany* **37**: 276–281.

Alves ES, Angyalossy-Alfonso V. 2000. Ecological trends in the wood anatomy of some Brazilian species. 1. Growth rings and vessels. *IAWA JOURNAL* **21**: 3–30.

Anderegg William R.L., Flint A, Huang CY, *et al.* 2015. Tree mortality predicted from drought-induced vascular damage. *Nature Geoscience* **8**: 367–371.

Anderegg W. R.L., Schwalm C, Biondi F, *et al.* 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* **349**: 528–532.

Andrade EM de, Aquino D do N, Chaves LCG, Lopes FB. **2017**. Water as Capital and Its Uses in the Caatinga In: Silva JMC da, Leal IR, Tabarelli M, eds. *Caatinga*. Cham: Springer International Publishing, 281–302.

Van Bel AJE. **2003**. Transport Phloem : Low Profile , High Impact. *Plant Physiology* **131**: 1509–1510.

Bento JPSP, Scremin-Dias E, Alves FM, Mansano VDF, Sartori ÂLB. **2020**. Phylogenetic implications of the anatomical study of the Amburaneae clade (Fabaceae: Faboideae). *Botanical Journal of the Linnean Society*: 1–15.

Bertolino LT, Caine RS, Gray JE. **2019**. Impact of Stomatal Density and Morphology on Water-Use Efficiency in a Changing World. *Frontiers in Plant Science* **10**.

Bosabalidis AM, Kofidis G. **2002**. Comparative effects of drought stress on leaf anatomy of two olive cultivars. *Plant Science* **163**: 375–379.

Brodribb TJ, Mcadam SA, Carins Murphy MR. **2016**. Xylem and stomata, coordinated through time and space. *Plant Cell and Environment*: 872–880.

Bucci SJ, Goldstein G, Meinzer FC, Scholz FG, Franco AC, Bustamante M. **2004**. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology* **24**: 891–899.

Buckley TN, Sack L, Farquhar GD. **2017**. Optimal plant water economy. *Plant, Cell & Environment* **40**: 881–896.

Buckley TN, Sack L, Gilbert ME. **2011**. The role of bundle sheath extensions and life form in stomatal responses to leaf water status. *Plant Physiology* **156**: 962–973.

Camarero JJ, Gazol A, Sangüesa-Barreda G, *et al.* **2018**. Forest growth responses to drought at short- and long-term scales in Spain: Squeezing the stress memory from tree rings. *Frontiers in Ecology and Evolution* **6**: 1–11.

Cavalcanti LC de S, Corrêa AC de B. **2014**. Pluviosidade no parque nacional do Catimbau (Pernambuco): seus condicionantes e seus efeitos sobre a paisagem. *Geografia* **23**: 133–156.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. **2009**. Towards a worldwide wood economics spectrum. *Ecology Letters* **12**: 351–366.

Chaves MM, Flexas J, Pinheiro C. **2009**. Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. *Annals of Botany* **103**: 551–560.

Christensen JH, Kumar KK, Aldrian E, *et al.* **2013**. Climate Phenomena and their Relevance for Future Regional Climate Change In: Stocker TF, D. Qin, Plattner G-K, et al., eds. *Climate Change 2013 - The Physical Science Basis. Contribution of Working Group I to* *the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, 1217–1308.

Ciais P, Sabine C, Bala G, *et al.* 2013. Carbon and Other Biogeochemical Cycles In: Stocker TF, Qin D, Plattner G-K, et al., eds. *Climate Change 2013 - The Physical Science BasisClimate Change 2013 - The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, 465–570.

Cosme LHM, Schietti J, Costa FRC, Oliveira RS. **2017**. The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytologist*: 113–125.

Dannoura M, Epron D, Desalme D, *et al.* 2018. The impact of prolonged drought on phloem anatomy and phloem transport in young beech trees. *Tree Physiology* **39**: 201–210.

Díaz S, Kattge J, Cornelissen JHC, *et al.* 2016. The global spectrum of plant form and function. *Nature* **529**: 167–171.

Domec J-C, Smith DD, McCulloh KA. **2016**. A synthesis of the effects of atmospheric carbon dioxide enrichment on plant hydraulics: implications for whole-plant water use efficiency and resistance to drought. *Plant, Cell & Environment*: 921–937.

Donohue RJ, Roderick ML, McVicar TR, Farquhar GD. **2013**. CO2 fertilisation has increased maximum foliage cover across the globe's warm, arid environments. *Geophysical Research Letters* **40**: 3031–3035.

DRYFLOR. **2016**. Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* **353**: 1383–1387.

Eamus D. **1999**. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology and Evolution* **14**: 11–16.

Engelbrecht BMJJ, Comita LS, Condit R, *et al.* 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* **447**: 80–82.

Ennajeh M, Vadel AM, Cochard H, Khemira H. **2010**. Comparative impacts of water stress on the leaf anatomy of a drought-resistant and a drought-sensitive olive cultivar. *Journal of Horticultural Science and Biotechnology* **85**: 289–294.

Epron D, Dannoura M, Hölttä T. **2019**. Introduction to the invited issue on phloem function and dysfunction. *Tree Physiology* **39**: 167–172.

Esquivel-Muelbert A, Baker TR, Dexter KG, *et al.* 2017. Seasonal drought limits tree species across the Neotropics. *Ecography* **40**: 618–629.

Evert RF, Eichhorn SE. **2006**. *Esau's Plant Anatomy: Meristems, Cells, and Tissues of* *the Plant Body: Their Structure, Function, and Development, 3rd Edition*.

Falcão HM, Medeiros CD, Almeida-Cortez J, Santos MG. **2017**. Leaf construction cost is related to water availability in three species of different growth forms in a Brazilian tropical dry forest. *Theoretical and Experimental Plant Physiology* **29**: 95–108.

Falcão HM, Medeiros CD, Silva BLR, Sampaio EVSB, Almeida-Cortez JS, Santos MG. **2015**. Phenotypic plasticity and ecophysiological strategies in a tropical dry forest chronosequence: A study case with Poincianella pyramidalis. *Forest Ecology and Management* **340**: 62–69.

Fernandes MF, Cardoso D, de Queiroz LP. **2019**. An updated plant checklist of the Brazilian Caatinga seasonally dry forests and woodlands reveals high species richness and endemism. *Journal of Arid Environments*: 104079.

Fick SE, Hijmans RJ. **2017**. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**: 4302–4315.

Figueiredo K V, Oliveira MT, Oliveira AFM, Silva GC. **2012**. Epicuticular-wax removal influences gas exchange and water relations in the leaves of an exotic and native species from a Brazilian semiarid region under induced drought stress. : 685–692.

Flato G, Marotzke J, Abiodun B, *et al.* **2013**. Evaluation of Climate Models In: Stocker TF, Qin D, Plattner G-K, et al., eds. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA. 741: Cambridge University Press, 741–866.

Fleta-Soriano E, Munné-Bosch S. **2016**. Stress memory and the inevitable effects of drought: A physiological perspective. *Frontiers in Plant Science* **7**: 1–6.

Fonti P, Jansen S. **2012**. Xylem plasticity in response to climate. *New Phytologist* **195**: 734–736.

Fortunel C, Paine CET, Fine PVA, Kraft NJB, Baraloto C. **2014**. Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology* **102**: 145–155.

Fortunel C, Ruelle J, Beauchêne J, Fine PVA, Baraloto C. **2014**. Wood specific gravity and anatomy of branches and roots in 113\rAmazonian rainforest tree species across environmental\rgradients. *New Phytologist* **202**: 79–94.

Franklin GL. **1945**. Preparation of Thin Sections of Synthetic Resins and Wood-Resin Composites, and a New Macerating Method for Wood. *Nature* **155**: 51–51.

Grime JP. **1977**. Evidence for the Existence of Three Primary Strategies in Plants and

Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**: 1169–1194.

Hacke UG, Sperry JS. **2001**. Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics* **4**: 97–115.

Hacke UG, Spicer R, Schreiber SG, Plavcov?? L. **2016**. An ecophysiological and developmental perspective on variation in vessel diameter. *Plant, Cell and Environment*: 831–845.

IBGE. **2002**. Mapa de Solos Brasileiros - IBGE .pdf.

IBGE. **2012**. *Manual Técnico da Vegetação Brasileira*.

Johansen DA. **1940**. *Plant Microtechnique*. New York.

Kevekordes KG, McCully ME, Canny MJ. **1988**. The occurrence of an extended bundle sheath system (paraveinal mesophyll) in the legumes. *Canadian Journal of Botany* **66**: 94–100.

Kiorapostolou N, Camarero JJ, Carrer M, *et al.* **2020**. Scots pine trees react to drought by increasing xylem and phloem conductivities. *Tree physiology* **40**: 774–781.

Kiorapostolou N, Petit G. **2018**. Similarities and differences in the balances between leaf, xylem and phloem structures in Fraxinus ornus along an environmental gradient. *Tree Physiology* **39**: 234–242.

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. **2006**. World Map of Köppen − Geiger Climate Classification. *Meteorol. Z.* **15**: 259–263.

Kraus JE, De Sousa HC, Rezende MH, Castro NM, Vecchi C, Luque R. **1998**. Astra blue and basic fuchsin double staining of plant materials. *Biotechnic and Histochemistry* **73**: 235–243.

Lazzarin M, Zweifel R, Anten N, Sterck FJ. **2018**. Does phloem osmolality affect diurnal diameter changes of twigs but not of stems in Scots pine? *Tree Physiology* **39**: 275–283.

Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S. **2011**. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer. *New Phytologist* **190**: 709–723.

Li X, Liu F. **2016**. Drought Stress Memory and Drought Stress Tolerance in Plants: Biochemical and Molecular Basis In: *Drought Stress Tolerance in Plants, Vol 1*. Cham: Springer International Publishing, 17–44.

de Lima ALA, de Sá Barretto Sampaio EV, de Castro CC, Rodal MJN, Antonino ACD, de Melo AL. **2012**. Do the phenology and functional stem attributes of woody species allow for the identification of functional groups in the semiarid region of Brazil? *Trees - Structure and Function* **26**: 1605–1616.

MacDaniels LHH. 1918. The Histology of the Phloem in Certain Woody Angiosperms. *American Journal of Botany* **5**: 347–378.

Machado SR, Marcati CR, Morretes BL de, Angyalossy V. **2005**. Comparative bark anatomy of root and stem in Styrax camporum (Styracaceae). *IAWA JOURNAL* **26**: 477.

Maiti R, Rodríguez HG, Balboa PCR, *et al.* 2016. Leaf surface anatomy in some woody plants from northeastern Mexico. *Pakistan Journal of Botany* **48**: 1825–1831.

Marinho CR, Oliveira RB, Teixeira SP. **2016**. The uncommon cavitated secretory trichomes in Bauhinia s.s. (Fabaceae): The same roles in different organs. *Botanical Journal of the Linnean Society* **180**: 104–122.

McClendon JH. **1992**. Photographic Survey of the Occurrence of Bundle-Sheath Extensions in Deciduous Dicots. *Plant Physiology* **99**: 1677–1679.

Myhre G, Shindell D, Bréon F-M, *et al.* 2013. Anthropogenic and natural radiative forcing (TF Stocker, D Qin, G-K Plattner, et al., Eds.). *Climate Change 2013 the Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* **9781107057**: 659–740.

Oliveira FMP, Câmara T, Durval JIF, *et al.* 2021. *Plant protection services mediated by extrafloral nectaries decline with aridity but are not influenced by chronic anthropogenic disturbance in Brazilian Caatinga*.

Olson ME, Rosell JA. **2013**. Vessel diameter-stem diameter scaling across woody angiosperms and the ecological causes of xylem vessel diameter variation. *New Phytologist* **197**: 1204–1213.

PBMC. **2014a**. OBSERVAÇÕES AMBIENTAIS ATMOSFÉRICAS E DE PROPRIEDADES DA SUPERFÍCIE In: *Base científica das mudanças climáticas*.25–63.

PBMC. **2014b**. Mudanças Ambientais de Curto e Longo prazo: Projeções, Reversibilidade e Atribuição. In: *Base científica das mudanças climáticas*.30.

PBMC. **2014c**. MUDANÇAS CLIMÁTICAS NA ESFERA NACIONAL In: *IMPACTOS, VULNERABILIDADES E ADAPTAÇÃO*.22–40.

PBMC. **2014d**. RECURSOS NATURAIS, MANEJO E USO DE ECOSSISTEMAS In: *IMPACTOS, VULNERABILIDADES E ADAPTAÇÃO*.41–195.

PBMC. **2014e**. Avaliação de modelos globais e regionais climáticos In: *Base científica das mudanças climáticas*.278–319.

Pereira S, Leal IR, Tabarelli M, Santos MG. **2020**. Intense mycorrhizal root colonization in a human-modified landscape of the Caatinga dry forest. *Forest Ecology and Management* **462**: 117970.

Pfautsch S, Renard J, Tjoelker MG, Salih A. **2015**. Phloem as Capacitor: Radial Transfer of Water into Xylem of Tree Stems Occurs via Symplastic Transport in Ray Parenchyma. *Plant Physiology* **167**: 963–971.

Pierce S, Brusa G, Vagge I, Cerabolini BEL. **2013**. Allocating CSR plant functional types: The use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology* **27**: 1002–1010.

Pivovaroff AL, Cook VMW, Santiago LS. **2018**. Stomatal behavior and stem xylem traits are coordinated for woody plant species under exceptional drought conditions. *Plant, Cell & Environment*.

Plourde BT, Boukili VK, Chazdon RL. **2015**. Radial changes in wood specific gravity of tropical trees: Inter- and intraspecific variation during secondary succession. *Functional Ecology* **29**: 111–120.

Poorter L, Castilho C V., Schietti J, Oliveira RS, Costa FRC. **2018**. Can traits predict individual growth performance? A test in a hyperdiverse tropical forest. *New Phytologist* **219**: 109–121.

Prado DE. **1991**. A critical evaluation of the floristic links between Chaco and Caatingas vegetation in South America. : 283.

Prado D. **1993**. What is the Gran Chaco vegetation in South America? I: A review. Contribution to the study of flora and vegetaion of the Chaco. V. *Candollea* **48**: 145–172.

Prado DE. **2003**. As Caatingas da América do Sul In: *Ecologia e conservacão da Caatinga*.3–73.

Prislan P, Mrak P, Žnidaršič N, *et al.* **2018**. Intra-annual dynamics of phloem formation and ultrastructural changes in sieve tubes in Fagus sylvatica. *Tree Physiology* **39**: 262–274.

R Core Team. **2018**. R: A language and environment for statistical computing. R Foundation for Statistical Computing. : Vienna, Austria. URL https://www.R-project.org/.

Rasband W. **2018**. ImageJ. : U. S. National Institutes of Health, Bethesda, Mar.

Reich PB. **2014**. The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology* **102**: 275–301.

Rhein M, Rintoul SR, Aoki S, *et al.* **2013**. Observations: Ocean Pages In: Intergovernmental Panel on Climate Change, ed. *Climate Change 2013 - The Physical Science Basis*. Cambridge: Cambridge University Press, 255–316.

Ribeiro EMS, Santos BA, Arroyo-Rodríguez V, Tabarelli M, Souza G, Leal IR.

2016. Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. *Ecology* **97**: 1583–1592.

Rito KF, Arroyo-Rodríguez V, Queiroz RT, Leal IR, Tabarelli M. **2017**. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. *Journal of Ecology* **105**: 828–838.

Rodrigues-Filho S, Junior DSR, Martins E, Rodrigues SP, Pilau FG, Ferrer JTV. **2016**. *Implicações Para a Sustentabilidade Regional No Brasil*.

Rodrigues TM, Esteves Amaro AC, Fernandes Boaro CS, *et al.* **2017**. Four distinct leaf types in the Brazilian cerrado, based on bundle sheath extension morphology. *Botany* **95**: 1171–1178.

Roeser K. **1972**. Die Nadel der Schwarzkiefer - Massenprodukt und Kunstwerk der Natur. *Mikrokosmos* **61**: 33–36.

Rosell JA. **2016**. Bark thickness across the angiosperms: More than just fire. *New Phytologist* **211**: 90–102.

Roth I. **1990**. Peculiar Surface Structures of Tropical Leaves for Gas Exchange, Guttation, and Light Capture. : 185–238.

Rutten T, Krüger C, Melzer M, Stephan UW, Hell R. **2003**. Discovery of an extended bundle sheath in Ricinus communis L. and its role as a temporal storage compartment for the iron chelator nicotianamine. *Planta* **217**: 400–406.

Santos MG, Oliveira MT, Figueiredo K V., *et al.* **2014**. Caatinga, the Brazilian dry tropical forest: Can it tolerate climate changes? *Theoretical and Experimental Plant Physiology* **26**: 83–99.

Seddon AWR, Macias-Fauria M, Long PR, Benz D, Willis KJ. **2016**. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* **531**: 229–232.

Sevanto S. **2014**. Phloem transport and drought. *Journal of Experimental Botany* **65**: 1751–1759.

Sfair JC, De Bello F, De Frana TQ, Baldauf C, Tabarelli M. **2018**. Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest. *Environmental Research Letters* **13**.

Silva JMC da, Barbosa LCF. **2017**. Impact of Human Activities on the Caatinga In: Silva JMC da, Leal IR, Tabarelli M, eds. *Caatinga*. Cham: Springer International Publishing, 359–368.

Silva PF da, Lima JR de S, Antonino ACD, *et al.* **2017**. Seasonal patterns of carbon dioxide, water and energy fluxes over the Caatinga and grassland in the semi-arid region of

Brazil. *Journal of Arid Environments*.

Silva RA da, Santos AMM, Tabarelli M. **2003**. Riqueza e diversidade de plantas lenhosas em cinco unidades de paisagem da Caatinga In: *As Caatingas Da América Do Sul*.337–366.

Sonsin JO, Gasson PE, Barros CF, Marcati CR. **2012**. A comparison of the wood anatomy of 11 species from two cerrado habitats (cerrado s.s. and adjacent gallery forest). *Botanical Journal of the Linnean Society* **170**: 257–276.

Souden S, Ennajeh M, Ouledali S, Massoudi N, Cochard H, Khemira H. **2020**. Water relations, photosynthesis, xylem embolism and accumulation of carbohydrates and cyclitols in two Eucalyptus species (E. camaldulensis and E. torquata) subjected to dehydration–rehydration cycle. *Trees - Structure and Function* **34**: 1439–1452.

Specht MJ, Pinto SRR, Albuqueque UP, Tabarelli M, Melo FPL. **2015**. Burning biodiversity: Fuelwood harvesting causes forest degradation in human-dominated tropical landscapes. *Global Ecology and Conservation* **3**: 200–209.

Sperry JS, Venturas MD, Anderegg WRL, *et al.* 2016. Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost. *Plant, Cell & Environment*: 816–830.

Sungpalee W, Itoh A, Kanzaki M, *et al.* 2009. Intra- and interspecific variation in wood density and fine-scale spatial distribution of stand-level wood density in a northern Thai tropical montane forest. *Journal of Tropical Ecology* **25**: 359–370.

Tholen D, Boom C, Zhu XG. **2012**. Opinion: Prospects for improving photosynthesis by altering leaf anatomy. *Plant Science* **197**: 92–101.

Tomás M, Flexas J, Copolovici L, *et al.* 2013. Importance of leaf anatomy in determining mesophyll diffusion conductance to CO2 across species: Quantitative limitations and scaling up by models. *Journal of Experimental Botany* **64**: 2269–2281.

Tombesi S, Frioni T, Poni S, Palliotti A. **2018**. Effect of water stress “memory” on plant behavior during subsequent drought stress. *Environmental and Experimental Botany* **150**: 106–114.

Torres RR, Lapola DM, Gamarra NLR. **2017**. Future Climate Change in the Caatinga In: Silva JMC da, Leal IR, Tabarelli M, eds. *Caatinga*. Cham: Springer International Publishing, 383–410.

Vaughan DG, Comiso JC, Allison I, *et al.* 2013. Observations: Cryosphere In: Stocker TF, Qin D, Plattner G-K, et al., eds. *Climate Change 2013: The Physical Sci- ence Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel* *on Climate Change*. Cambridge: Cambridge University Press, 317–382.

Vergílio PCB, da Silva JR, Blagitz M, Longo LR, Marcati CR. **2017**. Structural differences in the secondary phloem suggest higher support and storage potential in stems than roots of Cytharexylum myrianthum Cham. (Verbenaceae). *Botany* **95**: 953–960.

Vieira AJR, Lisi CS. **2019**. Caatinga Tree Wood Anatomy: Perspectives on Use and Conservation. *Floresta e Ambiente* **26**.

Walter J, Nagy L, Hein R, *et al.* **2011**. Do plants remember drought? Hints towards a drought-memory in grasses. *Environmental and Experimental Botany* **71**: 34–40.

Weston GD, Cass DD. **1973**. Observations on the Development of the Paraveinal Mesophyll of Soybean Leaves. *Botanical Gazette* **134**: 232–235.

Wispelaere L De, Bodé S, Hervé-Fernández P, Hemp A, Verschuren D, Boeckx P. **2017**. Plant water resource partitioning and isotopic fractionation during transpiration in a seasonally dry tropical climate. *Biogeosciences* **14**: 73–88.

Woodcock DW. **2000**. Wood Specific Gravity of Trees and Forest Types in. *Acta Amazonica* **30**: 589–599.

Wright SJ. **2010**. The future of tropical forests. *Annals of the New York Academy of Sciences* **1195**: 1–27.

Wylie RB. **1952**. The bundle sheath extension on leaves of dicotyledons. *American Journal of Botany* **39**: 645–651.

Zanne AE, Westoby M, Falster DS, *et al.* **2010**. Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany* **97**: 207–215.

Zorger BB, Tabarelli M, de Queiroz RT, Rosado BHP, Pinho BX. **2019**. Functional organization of woody plant assemblages along precipitation and human disturbance gradients in a seasonally dry tropical forest. *Biotropica*: 1–13.

Zsögön A, Alves Negrini AC, Peres LEP, Nguyen HT, Ball MC. **2015**. A mutation that eliminates bundle sheath extensions reduces leaf hydraulic conductance, stomatal conductance and assimilation rates in tomato (Solanum lycopersicum). *New Phytologist* **205**: 618–626.

Capítulo I

Original article

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Drought-adapted leaves are produced even when more water is available in dry tropical forest

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Abstract

Species in dry environments may adjust their anatomical and physiological behaviors by adopting safer or more efficient strategies. Thus, species distributed across a water availability gradient may possess different phenotypes depending on the specific environmental conditions to which they are subjected. Leaf and vascular tissues are plastic and may vary strongly in response to environmental changes affecting an individual's survival and species distribution. To identify whether and how legumes leaves vary across a water availability gradient in a seasonally dry tropical forest, we quantified leaf construction costs and performed an anatomical study on the leaves of seven legume species. We evaluated seven species, which were divided into three categories of rainfall preference: wet species, which are more abundant in wetter areas; indifferent species, which are more abundant and occur indistinctly under both rainfall conditions; and dry species, which are more abundant in dryer areas. We observed two different patterns based on rainfall preference categories. Contrary to our expectations, wet and indifferent species changed traits in the sense of security when occupying lower rainfall areas, whereas dry species changed some traits when more water was available, such as increasing cuticle and spongy parenchyma thickness, or producing smaller and more numerous stomata. *Trischidium molle*, the most plastic and wet species, exhibited similar strategy to the dry species. Our results corroborate the risks to vegetation under future climate change scenarios as stressed species and populations may not endure even more severe conditions.

Keywords: Water use efficiency, leaf anatomy, heterobaric leaves, paraveinal mesophyll, extended bundle sheath, leaf construction cost.

Introduction

Leaves are plastic organs that adjust their structure and behavior according to environmental conditions and recent events (Tomás et al. 2013), particularly in deciduous species. Therefore, anatomical changes related to water use efficiency (WUE) and assimilation in leaves may be associated with the gradient of environmental resources, such as water and nutrients, and may help us understand the functioning and distribution of species in restrictive environments (Yin et al. 2021).

Different aspects of WUE mechanisms have been investigated, such as deciduousness (Wispelaere et al. 2017) and CO_2 concentration (Domec et al. 2016), in addition to raising questions about anatomical traits and combined physiological processes (Hacke et al. 2016; Sperry et al. 2016; Brodribb et al. 2017; Buckley et al. 2017). In this context, the capacity for drought tolerance and high CO_2 assimilation, even under greater water restrictions, makes dry forests key ecosystems for carbon storage (Santos et al. 2014; Silva et al. 2017). Moreover, Dry Tropical Forests (DTF) have high biodiversity, are subjected to severe anthropogenic pressures (Silva and Souza 2018), and are biomes strongly threatened by global climate change (Torres et al. 2017). In a recent evaluation, Silva and Barbosa (2017) concluded that 63% of the Caatinga vegetation, the biggest and exclusive Brazilian DTF, was modified by human action.

Adopting conservative strategies is expected and has been reported for species subjected to restrictive environmental conditions (Engelbrecht et al. 2007; Wispelaere et al. 2017). In environments with greater water availability, a rise in temperature leads to a reduction in stomatal opening and restriction of CO_2 uptake due to a greater deficit in air vapor pressure (Sevanto 2014). However, studies have suggested that species from dry environments can optimize CO_2 uptake, even at low levels of stomatal conductance caused by water restriction and high temperatures (Santos *et al.* 2014; Rivas and Santos 2022). In these species, an increase in atmospheric CO_2 represents an increased assimilation resource when associated with strategies for efficient water use (Anderegg et al. 2015a), while a scenario of an increasingly irregular rainy season and long periods of drought is becoming more frequent.

The traits related to WUE mechanisms, such as stomatal size and density and leaf, cuticle, and assimilation tissue thickness, reflect the distribution of species in different ecosystems and over time (Falcão et al. 2015) and their variations occur at different levels between the woody components of a community, such as anatomical, physiological, and phenological levels (Cosme et al. 2017). However, resource allocation patterns and strategies present many possibilities, which are reduced in more restrictive environments because prioritizing one attribute can limit another (Bucci et al. 2004). This can lead to functional convergence between species and individuals subjected to similar environmental conditions (Hacke and Sperry 2001). Carmona et al. (2016) discussed functional diversity as a multifaceted concept, which encompasses a wide variety of components.

This study described and quantified the anatomical traits and construction costs of leaves of species belonging to the Leguminosae family distributed along a rainfall gradient in the Caatinga domain. The amount of carbon used in the construction of a leaf can be influenced by several factors, mainly in a TDF (Falcão et al. 2017),reflecting how much glucose was used to form the tissue (Williams et al. 1987). Therefore, this trait can be important in the strategy of different species under the variation of water availability. Our main goals were to (1) identify changes in leaf anatomy and function of populations of the same species growing in low- and high-rainfall areas and (2) test whether trait responses vary among species that are typically associated with more mesic areas, significantly more abundant in wetter plots, or more xeric areas, significantly more abundant in drier plots. We hypothesized that (1) species would present trait values that are more associated with conservative water use in drier areas, such as thicker leaves and cuticles, denser trichomes, smaller stomata, and narrower vessels and sieve tubes. Additionally, considering that the differential distribution of species across a climatic gradient might reflect their physiological preferences and limits, we hypothesized that (2) species that are more abundant in the drier plots would present traits associated with adaptation to drought, such as thick leaves, thick cuticles, trichome abundance, and small stomata, and species that are more abundant in the wetter plots would present traits associated with fast growth in the short growing season, such as thick spongy parenchyma, thin cuticle, and low leaf construction costs.

Methods

Study area

The study was conducted in Catimbau National Park, located in Pernambuco State, Brazil (-08.4924745, -37.3617198), an area in the Caatinga domain, a Brazilian tropical dry forest (Fig. 1). The climate is a semi-arid *BSh* type, with a transition to a tropical rainy type *As*' in this area (Kottek et al. 2006). The soils are sandy, well-drained, depauperated, Natric Planosols and Chromic Luvisols, characterized by high sodium saturation and great susceptibility to erosion and high base saturation in the subsurface horizons, easily weathered primary minerals (nutritional reserve), and a large number of stones in the surface horizon, respectively (IBGE 2002). The mean annual rainfall ranges from 400 to 940 mm, and the mean annual temperature ranges from 15 °C to 29 °C, with an average of 23 °C (Cavalcanti and Corrêa 2014). Twenty plots were randomly established throughout the rainfall gradient of the park for PELD Catimbau studies, and the complete design can be consulted in Rito et al. (2017). In this study, we sampled individuals around nine plots: five located at the drier end and four at the wetter end of the gradient (Fig 1). We conducted the study during the rainy season, on March 2018.

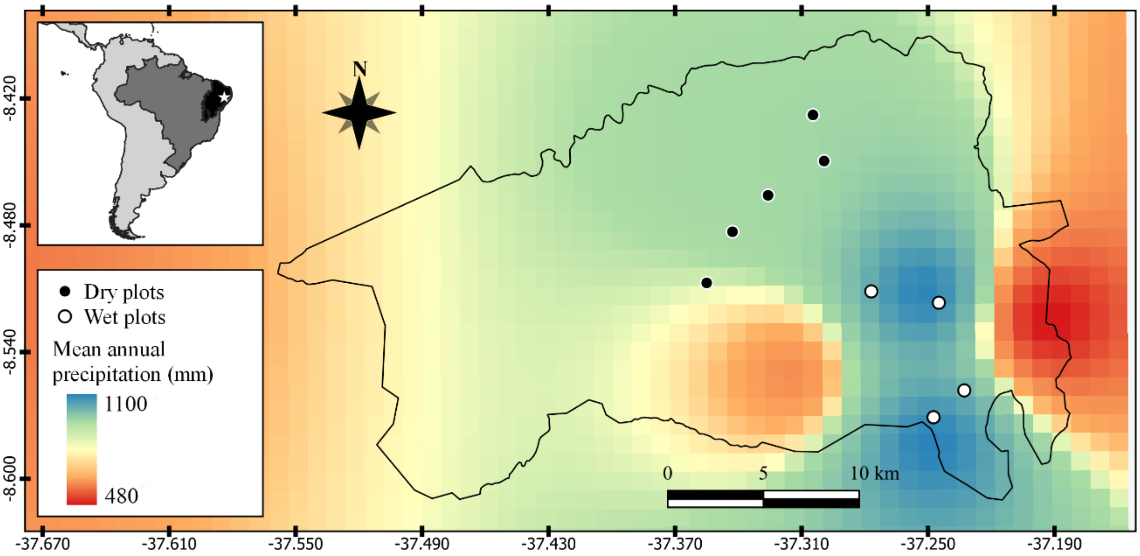

Fig. 1 Study region in Brazil, the mean annual precipitation distribution, and the borders of Catimbau National Park with the 9 (nine) sampled plots represented by dots (dry-black, wet-white)

Studied species and sampling

Based on previous community census data, we sampled seven deciduous Leguminosae tree and shrub species that occurred with different abundances in wet versus dry plots across the rainfall gradient of the park based on previous community census data (Rito et al. 2017). *Cenostigma microphyllum* (Mart. Ex G. Don) E. Gagnon & G.P. Lewis, *Peltogyne pauciflora* Benth., and *Bauhinia acuruana* Moric. were more abundant and evenly distributed in plots with lower rainfall averages (below 762 mm) and were referred to as “dry species” (DS). *Pityrocarpa moniliformis* (Benth.) Luckow & R. W. Jobson was widely distributed and had similar abundance in wet and dry plots and was referred to as “indifferent species” (IS). *Trischidium molle* (Benth.) H.E. Ireland, *Senegalia piauhiensis* (Benth.) Seigler & Ebinger, and *Senegalia bahiensis* (Benth.) Seigler & Ebinger were more abundant in plots with high average rainfall (> 762 mm) (Rito et al. 2017). These species were collectively referred to as “wet species” (WS).

The species, subfamilies, habits, abundance, rainfall preference categories, and rainfall categories of the sampled plots are available in Table 1 and Data S1.

Table 1 Legumes species sampled, classification, habit, rainfall preference category, rainfall category, abundance, and sampled plots/rainfall annual average (according to Rito *et al.* 2017) in Catimbau National Park

Species	**Subfamily**	**Habit**	**Rainfall preference category**	**Rainfall category**	**Abundance (individuals/ category)**	**Sampled plots/ rainfall**
Senegalia piauhiensis	Caesalpinioideae-Mimosoid clade	Tree	WS	low high	160 27	P22/ 552 P08/ 578 P04/ 591 P27/ 903 P30/ 913
Senegalia bahiensis	Caesalpinioideae-Mimosoid clade	Tree	WS	low high	157 55	P29/ 762 P17/ 940 P27/ 903
Trischidium molle	Papilionoideae	Shrub	WS	low high	58 47	P14/ 540 P22/ 552 P04/ 591

						P29/762 P27/903 P30/913
Pityrocarpa moniliformis	Caesalpinioideae-Mimosoid clade	Tree	IS	low high	365 260	P22/552 P04/591 P29/762 P27/903 P17/940
Bauhinia acuruana	Cercidoideae	Shrub	DS	low high	59 40	P14/540 P22/552 P04/591 P20/653 P30/913 P17/940
Peltogyne pauciflora	Detarioideae	Tree	DS	low high	130 44	P22/552 P04/591

						P29/762 P30/913 P17/940
Cenostigma microphyllum	Caesalpinioideae	Tree	DS	low high	369 72	P22/552 P04/591 P29/762 P27/903

For the anatomical study, mature leaves of healthy adult individuals were collected from two or three plots per rainfall category (dry and wet plots), totaling a minimum of six and a maximum of nine individuals per category. To standardize the age of the leaves, we sampled a third pair of leaves from the apex. Leaf samples were transported to the laboratory in plastic bags, fixed in FAA_{50} for 48 h, rinsed in water, and stored in 70% ethanol for anatomical studies. To determine the cost of leaf construction, we collected five individuals of each species per plot. It was placed in a forced ventilation oven at 40ºC for 4 h and stored in organizer boxes containing silica to prevent fungal attack. The samples were oven dried at 60 °C for 72 to dry biomass in the laboratory.

Analyses

To obtain histological sections, midrib samples of large leaflets (> 1 cm wide) and whole medium leaflets of compound leaves with small leaflets (less than 1 cm wide) were selected. Those samples were dehydrated in ethanol (70%–100%), embedded in paraffin (Johansen 1940), and transversally sectioned on a rotary microtome (Leica RM2145) at 8–13 µm thickness. The sections were deparaffinized in n-butyl acetate solution, rehydrated in ethanol (100%–50%), and subjected to double staining in 1% ethanolic Astra blue and 1% ethanolic safranin (Roeser 1972). The completely dehydrated sections were mounted on permanent slides with an anhydrous mounting medium (Entellan®).

We selected mesophyll samples to obtain an isolated epidermis and analyzed the cells, trichomes, and stomata following the same sampling standard described above, focusing on the intercostal region. We dissociated these tissues by placing the samples in acetic acid and hydrogen peroxide (1:1) solution and keeping them in a drying oven at 60 °C (Franklin 1945). The epidermis was stained with a 5% basic fuchsin aqueous solution and mounted on 50% glycerin semi-permanent slides (Kraus et al. 1998).

Images of the epidermis and cross-sections of the leaves were then taken under a light microscope coupled with a camera (Nikon Eclipse Ci light microscope coupled to a Motic MoticamPro 252 B camera with a Motic Images Advanced 3.2 capture system). In addition to light microscope images, leaf samples were oven-dried at 60 °C for 48 h and sputtered with gold (using Denton Vacuum Desk III, Moorestown, New Jersey, USA) for Scanning Electron Microscopy imaging (SEM; JEOL microscope Model: JSM-6380LV, Tokyo, Japan). Cell counts and measurements were performed using ImageJ software (Rasband 2018).

We measured 14 anatomical traits, including the epidermal, mesophyll, and conductive traits. In the epidermis, we measured the cuticle thickness (Ct), adaxial and abaxial epidermal thicknesses (Etad and Etab, respectively), trichome density (Td), stomatal pore size (SPs), stomatal density (Sd), epidermal cell density (Ecd), stomatal index (Si), and stomatal frequency (Sf). Stomatal index values were obtained from stomatal and epidermal cell densities using the following formula: $Si=[Sn/(Sn+Ecn)]x100$, where Sn= stomatal N per mm^2 and Ecn=epidermal cell N per mm^2 (Salisbury 1928). Stomatal frequency corresponds to the ratio of stomata to epidermal cell density: $Sf=Sn/Ecn$ (Speckmann et al. 1965). In the mesophyll (or overall leaf structure), we measured the leaf thickness (Lt), palisade parenchyma thickness (PPt), and spongy parenchyma thickness (SPt). In the conductive tissue, we measured the vessel diameter (VD) and sieve tube diameter (STD) of leaflet midrib sections.

For the density and thickness measurements, we used five fields of 1 mm^2. For the size measurements, we used ten cells or structures per individual. We calculated descriptive statistics for all measured traits for each species and, owing to the differences between the sample sizes of the measures, performed analyses at the individual level.

We collected healthy leaves from five individuals per category (wet and dry) and obtained an ash content (g kg^{-1}) of 100 mg of dry matter using a muffle furnace at 500 ºC for 6 h. The ash content was calculated as the ratio between the pre-and post-muffle masses (Li et al. 2015). We obtained the calorific value (ΔHC; kJ g^{-1}) by burning 150 mg of dry matter in a calorimeter

(C200, IKA, Heiters-Heim, DE, USA) using the formula: ΔHC = calories/(1-Ash), where ash is the ash content (g: g^{-1} leaf dry mass) (Villar and Merino 2001). We determined the leaf construction cost (LCC) per unit mass (Ccmass) (g glucose g^{-1} DW) from the results of ash, nitrogen concentration, and ΔHC, where Ccmass = [(0.06968 ΔHC – 0.065) × (1 – Ash) + 7.5 (k × NM/14.0067) × 0.89 (Williams et al. 1987). We considered ΔHC as the combustion heat without ash (kJ g^{-1}), k as the oxidation state of the nitrogen source (−3 for ammonium and+5 for nitrate), and NM as the total nitrogen concentration (g^{-1} dry mass) (Williams et al. 1987). As the main source of soil nitrogen was ammonium, we used k = −3 (De Vries et al., 1974). Finally, we calculated the leaf construction cost (CC) per unit area (Ccarea) (g glucose m^{-2}) as the ratio of Ccmass and specific leaf area (SLA). This parameter is obtained from the division of the leaf area by the dry weight of the same leaf.

We did a Permutation Multivariate Analysis of Variance using Distance Matrices, using the function “adonis2” in the “vegan” package (Oksanen *et al.*, 2022), to infer the influence of rainfall over the anatomical traits, or its relationship with abundance.. We also included species in the analysis to verify if there were differences in anatomical attributes between the evaluated species. We considered traits as dependent variables, and rainfall, abundance, and species as independent variables.We performed a linear model (LM) test for each analyzed trait. As the number of generated models was high, we chose to present only the significant slopes in the results, that is, those with $p<0.05$. All the analyses were performed using R Studio [Version 4.2.2] (R Core Team, 2023).

Results

In the present study, we observed the anatomical leaf responses of seven legume species distributed along a rainfall gradient in the Caatinga domain to verify how vegetation reacts to its conditions. Six of the 14 anatomical traits analyzed showed variations in rainfall. Leaf construction costs varied with rainfall only in *Senegalia bahiensis*. The seven analyzed species presented leaves with dorsiventral leaflets, bi-collateral bundles in *Peltogyne pauciflora* and *Pityrocarpa moniliformis*, and collateral bundles in the others. Paraveinal mesophyll was present in both *Senegalia* species. An extended bundle sheath was present in *Bauhinia acuruana*, *P. moniliformis,* and *Trischidium molle*, dividing the mesophyll into sub-areas. Epidermal, mesophyll, and conductive traits, the categories due which we split anatomical traits, varied due to rainfall but not due to abundance, for each species, particularly for those with larger distributions (Fig. 2).

Fig. 2 General behavior of legumes due to rainfall and abundance in Catimbau National Park. The rainfall varies from lowest to highest from left to right, and the species are distributed due to abundance: *Cenostigma microphyllum* Mart. Ex G. Don) E. Gagnon & G.P. Lewis, *Peltogyne pauciflora* Benth., and *Bauhinia acuruana* Moric. are more abundant in low rainfall average plots. *Pityrocarpa moniliformis* (Benth.) Luckow & R. W. Jobson is widely distributed and similarly abundant under both conditions. *Trischidium molle* (Benth.) H.E. Ireland, *Senegalia bahiensis* (Benth.) Seigler & Ebinger, and *Senegalia piauhiensis* (Benth.) Seigler & Ebinger are more abundant in higher rainfall average plots

The distribution of attribute values showed differences between rainfall (df=1, R^2=0.0077, p=0.04419) and species (df= 6, R^2=0.65746, p=0.0002), interactions between rainfall and species (df=6, R^2=0.03494, p= 0.0104), rainfall and abundance (df=1, R^2=0.01018, p=0.0114), and species and abundance (df=6, R^2=0.02907, p=0.04339). The interaction between rainfall and species indicates that traits vary differently in each species depending on rainfall and abundance.

The studied species showed traits related to security against dehydration but in response to different situations, except *Senegalia piauhiensis,* which did not respond to rainfall with any of the sampled variables. Dry species (DS), which were more abundant in lower rainfall plots, were the most plastic group and changed some traits in the sense of security when more water was available, contrary to our expectations (Fig 3-5). *Bauhinia acuruana* showed increased stomatal pore size (0.02921±0.01234) and reduced vessel diameter (-0.04645±0.01783), thus investing in acquisition and security. *Peltogyne pauciflora* increased the epidermal cell density (Ecd) (0.011168±0.004371) and Ct (0.03529±0.01261), creating a safer epidermis against desiccation. Similarly, *Cenostigma microphyllum* also increased Ecd (0.0157±0.00654) but reduced SPs (-0.08088±0.03278) and Ct (-0.04559±0.02036), prioritizing the reduction of stomatal loss. In contrast, the indifferent species (IS) and wet species (WS) *Senegalia bahiensis* changed their traits in the sense of security when occupying lower rainfall areas, that is, when less water was available (Fig 4-6). In wetter areas, *Pityrocarpa moniliformis* increased spongy parenchyma thickness (0.4963±0.2306), investing in assimilation. Similarly, *Senegalia bahiensis* was the only species that changed its leaf construction cost because of an increase in rainfall. This species increases this trait, increasing the cost and, thus, the efficiency of leaves when more water is available (0.0005281±0.0001168). *Trischidium molle* was the most plastic species, varying in four traits: it adopted a dry species similar behavior, reducing the stomata pore size (-0.04486±0.01681), increasing the stomatal density (0.00334±0.0009), epidermis cells (0.036759±0.008188) and the cuticle thickness (0.10178±0.03635, when more water was available (Fig. 3-5). Descriptive statistics were verified using Data S2.

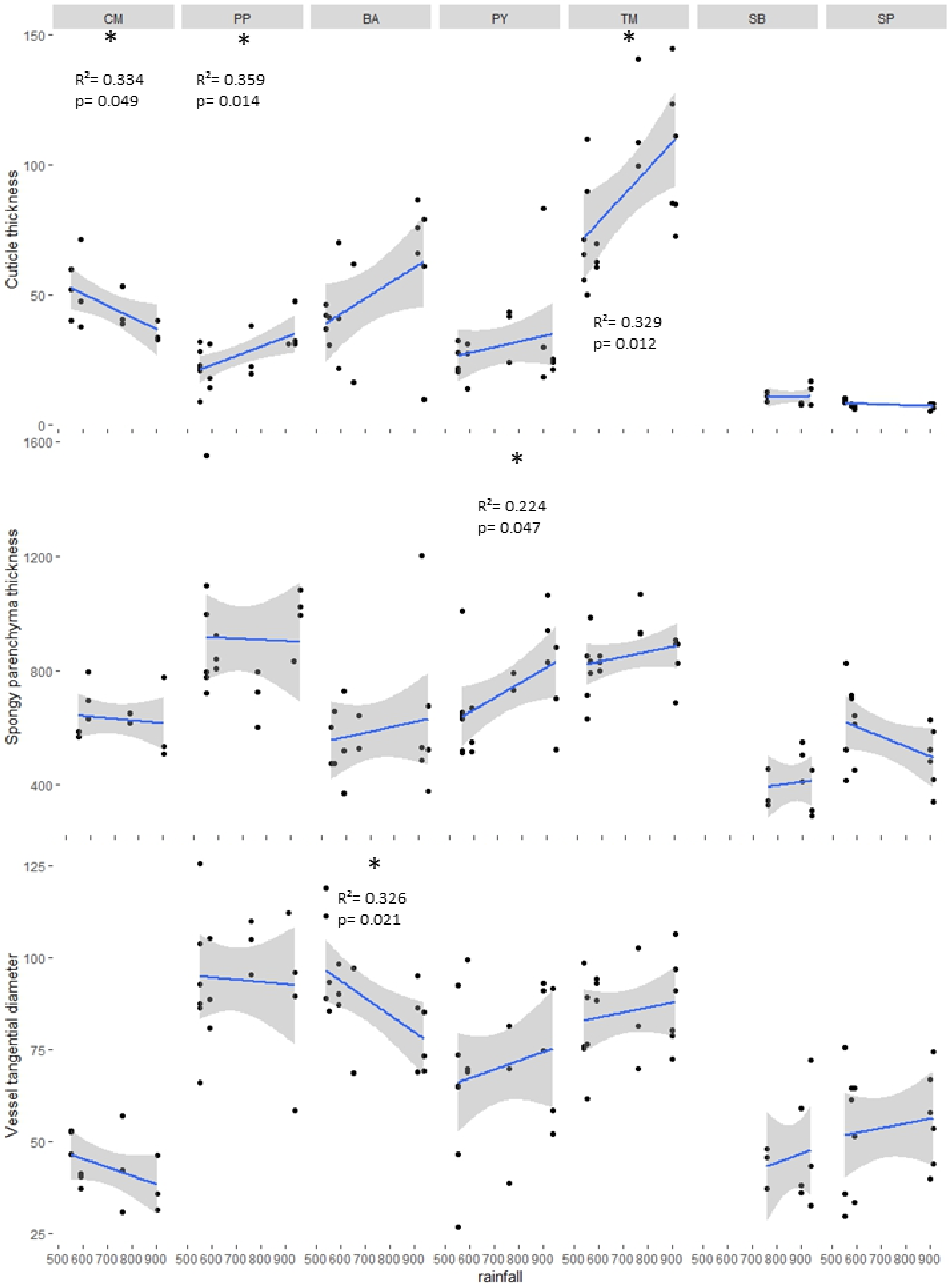
CM
PP
BA
PY
TM
SB
SP
*
*
*
R²= 0.334
p= 0.049
R²= 0.359
p= 0.014
R²= 0.329
p= 0.012
Cuticle thickness
150
100
50
0
1600
*
R²= 0.224
p= 0.047
Spongy parenchyma thickness
1200
800
400
*
R²= 0.326
p= 0.021
Vessel tangential diameter
125
100
75
50
25
500 600 700 800 900
rainfall

Fig. 3 Leaf traits variation due to rainfall in legumes of Catimbau National Park. Cuticle thickness (Ct-µm), Spongy parenchyma thickness (SPt- µm), and Vessel diameter (VD- µm). Each point represents an individual. The blue line represents the trend line of the average of individuals. The grey area represents the 95% confidence interval around the mean. CM- *Cenostigma microphyllum,* PP- *Peltogyne pauciflora*, BA- *Bauhinia acuruana*, PY- *Pityrocarpa moniliformis*, TM- *Trischidium molle*, SB- *Senegalia bahiensis*, SP- *Senegalia piauhiensis*. The * indicates species in which traits varied with rainfall, according to the R^2 and p-value accompanying.

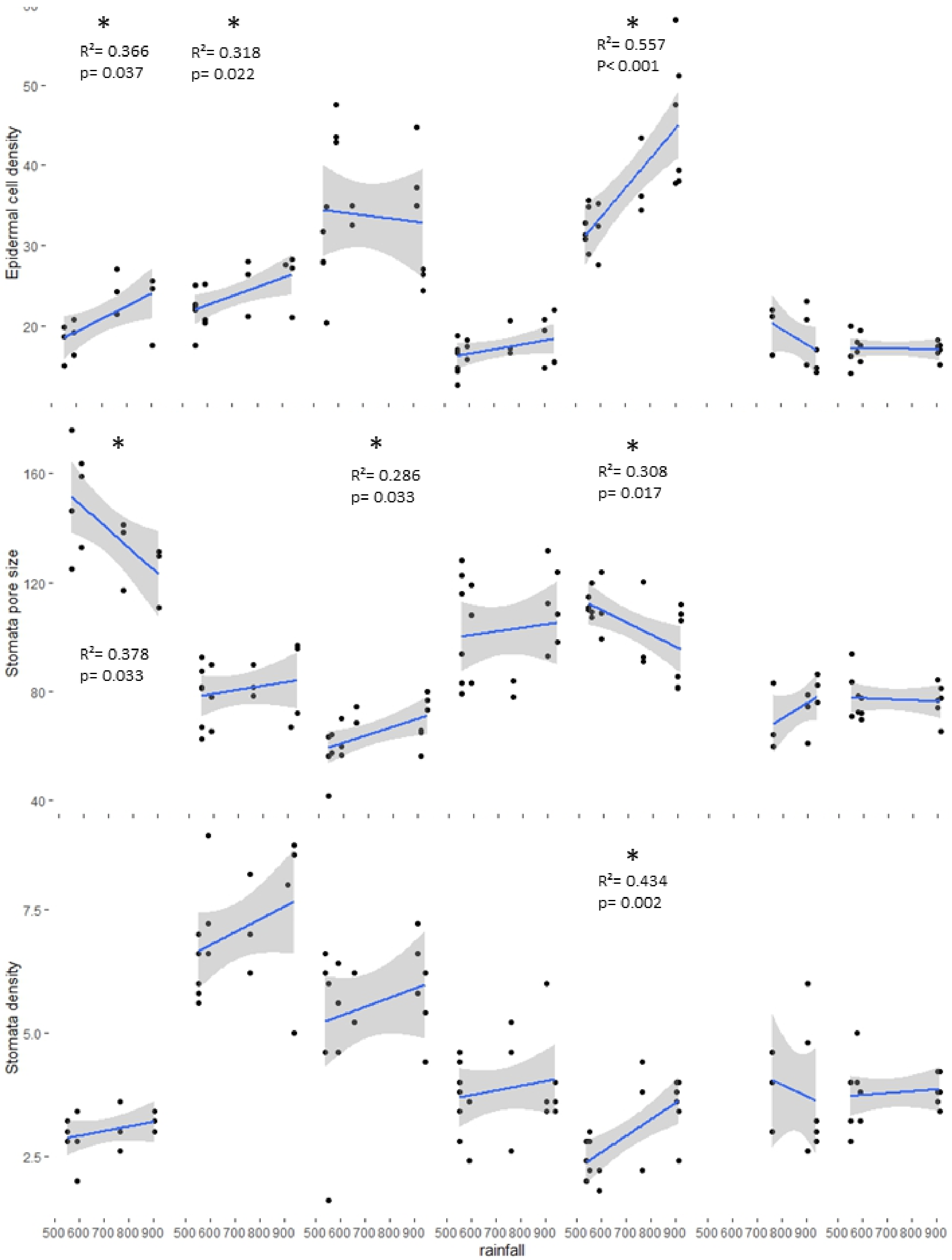
*
R²= 0.366
p= 0.037
*
R²= 0.318
p= 0.022
*
R²= 0.557
P< 0.001
50
40
30
20
Epidermal cell density
*
*
R²= 0.286
p= 0.033
*
R²= 0.308
p= 0.017
R²= 0.378
p= 0.033
160
120
80
40
Stomata pore size
*
R²= 0.434
p= 0.002
7.5
5.0
2.5
Stomata density
500 600 700 800 900
rainfall

Fig. 4 Epidermal leaf traits variation due to rainfall in legumes of Catimbau National Park. Epidermal Cell density, Stomata density, and Stomata pore size (Sps- µm). Each point represents an individual. The blue line represents the trend line of the average of individuals. The grey area represents the 95% confidence interval around the mean. CM- *Cenostigma microphyllum,* PP- *Peltogyne pauciflora*, BA- *Bauhinia acuruana*, PY- *Pityrocarpa moniliformis*, TM- *Trischidium molle*, SB- *Senegalia bahiensis*, SP- *Senegalia piauhiensis*. The * indicates species in which traits varied with rainfall, according to the R^2 and p-value accompanying.

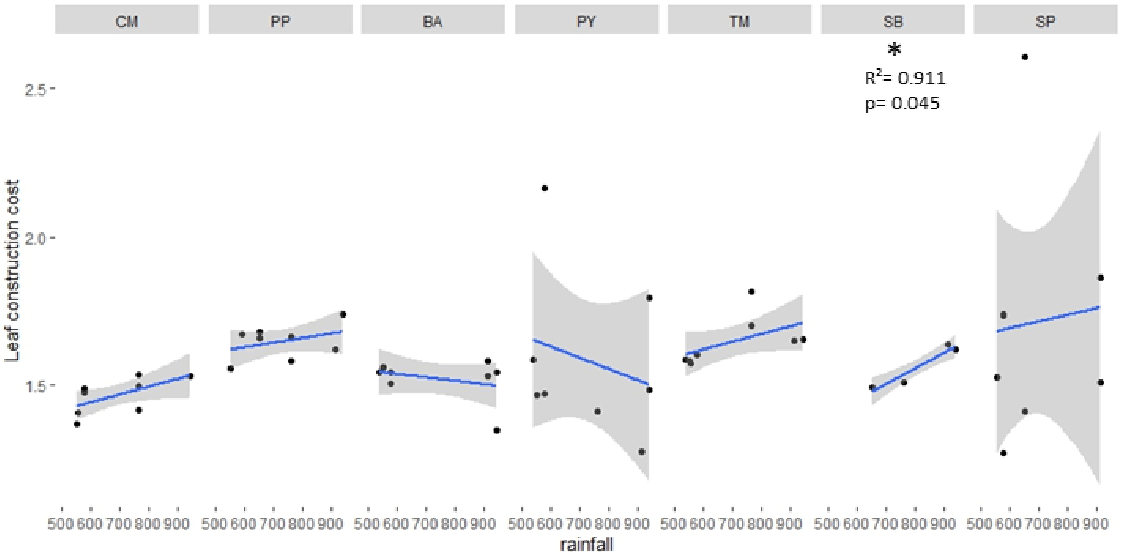

Fig. 5 Leaf construction cost (Ccarea) (g glucose m^{-2}) variation due to rainfall in legumes of Catimbau National Park. Each point represents an individual. The blue line represents the trend line of the average of individuals. The grey area represents the 95% confidence interval around the mean. CM- *Cenostigma microphyllum,* PP- *Peltogyne pauciflora*, BA- *Bauhinia acuruana*, PY- *Pityrocarpa moniliformis*, TM- *Trischidium molle*, SB- *Senegalia bahiensis*, SP- *Senegalia piauhiensis*. The * indicates species in which traits varied with rainfall, according to the R^2 and p-value accompanying. SB was the only species which varied against rainfall

Epidermis

Frontal views of the epidermis on both surfaces revealed epidermal cells with rectilinear anticlinal walls in *Pityrocarpa moniliformis* and *Peltogyne pauciflora* (Fig. 6a), corrugated in *Bauhinia acuruana* (Fig. 6b), and sinuous in *Cenostigma microphyllum*, *Senegalia bahiensis*, *Senegalia piauhiensis,* and *Trischidium molle* (Fig. 7c). *Peltogyne pauciflora* was the only species with glabrous leaflets (Fig. 6a). All other species had fewer or more non-glandular trichomes (Data S2); *B. acuruana*, *C. microphyllum,* and *T. molle* also had characteristic glandular trichomes (Fig. 6c,d). In addition, we observed anomocytic stomata in *B. acuruana*, *C. microphyllum,* and *T. molle* (Fig. 6c-e) and paracytic stomata in the other species (Fig. 6f). *B. acuruana* and *T. molle* had stomata grouped in patches between the larger secondary veins (Fig. 6d,e).

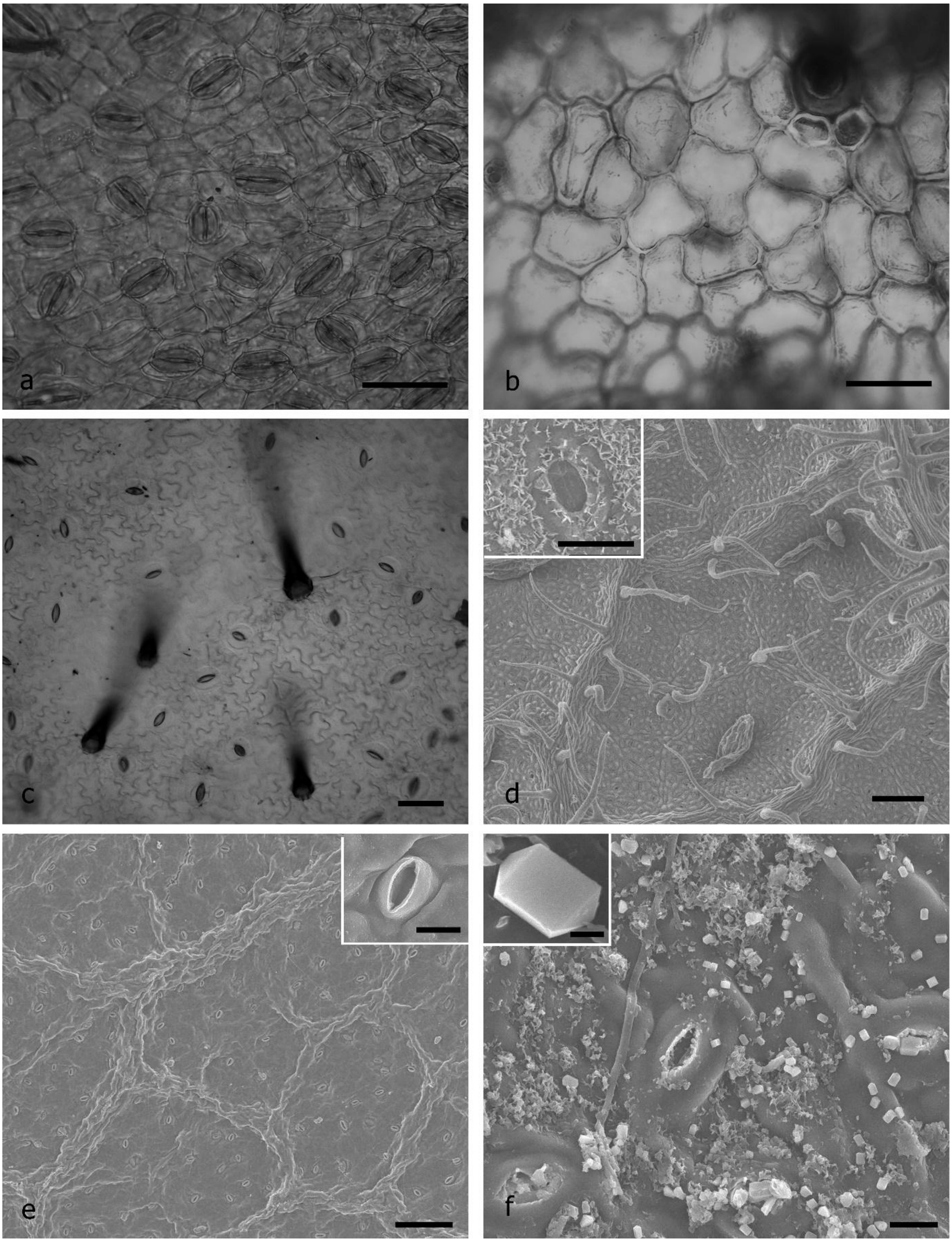
a
b
c
d
e
f

Fig. 6 Abaxial epidermis features of legumes of Catimbau National Park. Retilineous epidermis of *Peltogyne pauciflora* (a), corrugated of *Bauhinia acuruana* (b), and sinuous of *Cenostigma microphyllum* (c). Scale= 50µm. Anomocytic stomata in *C. microphyllum* (c) and paracytic in *P. pauciflora* (f). Scale= 50µm and 10µm, respectively. The epidermis of *B. acuruana* (d) and *Trischidium molle*) with secondary veins dividing the leaf into sub-areas and the stomata in clusters. Scale= 100µm. Details of anomocytic stomata of *B. acuruana* (d) and *T. molle* (e). Scale= 10µm. The epidermis of *P. pauciflora* with paracytic stomata and prismatic crystals (detail) on the surface of the cuticle (f). Scale= 10µm and 1µm, respectively.

In transverse sections, we observed a uniseriate epidermis in all species (Fig. 7). *Bauhinia acuruana* had phenolic compounds in the epidermal cells (Fig. 7a), and *C. microphyllum* had mucilage in some cells of the epidermis (Fig. 7b). A thick cuticle occurred in *C. microphyllum*, *P. pauciflora*, *P. moniliformis,* and *T. molle*, which have an epidermis with rectilinear periclinal walls (Fig. 7a,b, Data S2). In contrast, papillary epidermis, with a thin cuticle, occurred on both surfaces in *Senegalia bahiensis* and *S. piauhiensis* (Fig. 7c, Data S2). In addition, prismatic crystals were observed in the epidermis of *C. microphyllum*, *S. piauhiensis,* and *P. pauciflora*. In the latter, they may also have occurred on the surface of the cuticle (Fig. 7f).

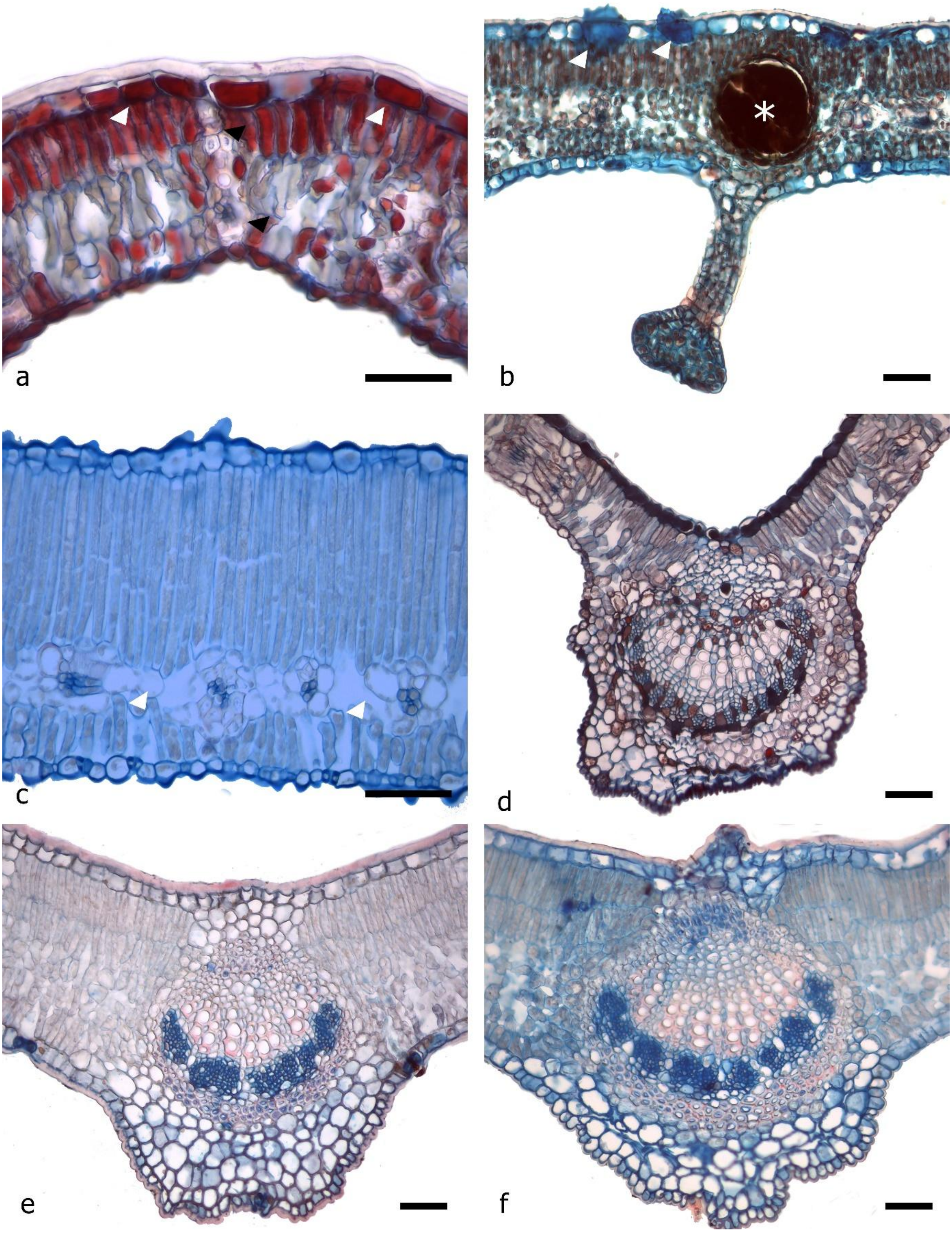
a
b
*
c
d
e
f

Fig. 7 Anatomical features of legumes of Catimbau National Park. Cross-section of mesophyll with rectilinear periclinal epidermal cells, and evident phenolic compounds (white arrows), and extended bundle sheath (black arrow), in *Bauhinia acuruana* (a) and *Cenostigma microphyllum* (b), with mucilage (arrows) and a secretory cavity full of phenolic compounds (*) adjacent to a secretory trichome. Cross-section of mesophyll with thin cuticle, papillary epidermis, and paraveinal parenchyma (arrows) in *Senegalia bahiensis* (c). Collateral vascular bundles with reniform shape in *B. acuruana* (d) and broad-elliptical in *Trischidium molle* (e), and bi-collateral circular in *P. moniliformis* (f). Scale= 50µm

Mesophyll

All analyzed species presented a dorsiventral mesophyll (Fig. 7). Palisade parenchyma with two layers of cells occurred in *B. acuruana*, *P. moniliformis,* and *T. molle* (Fig. 7a, d), whereas one layer was observed in the other species (Fig. 7b,c,e,f). In some individuals of *S. bahiensis,* the spongy parenchyma was compact, similar to palisade parenchyma (Fig. 7c). Both *Senegalia* species presented a paraveinal mesophyll, with large and some globose cells distributed transversally between the minor ribs (Fig. 7c). The spongy parenchyma presented two or three layers in all species (Fig. 7). The average thicknesses of both tissues are shown in Data S2. *B. acuruana*, *P. moniliformis,* and *T. molle* had extended bundle sheaths that divided the leaves into sub-areas between the larger secondary ribs (Fig. 6d,e, and 7a). Secretory cavities occurred in *P. pauciflora* and *C. microphyllum*, as well as in idioblasts containing phenolic compounds, which also occurred in *B. acuruana* and *P. moniliformis* (Fig. 7a,b).

Vascular system

The main vascular bundle was bicollateral in *P. pauciflora* and *P. moniliformis* (Fig. 7f) and collateral in all other species (Fig. 7c,d). Two or three layers of fibers formed a sheath surrounding the bundle in *C. microphyllum*, *S. bahiensis*, *S. piauhiensis*, *P. pauciflora,* and *P. moniliformis* (Fig. 7f). In other species, these cell layers may be incomplete or contain collenchyma (Fig. 7d,e). Prismatic crystals may have occurred in *B. acuruana*, *C. microphyllum*, *P. moniliformis*, *Senegalia* spp., and *T. molle* (Fig 7f). Based on shape, we classified the bundles of *B. acuruana* as reniform (Fig. 7c), *T. molle* as broad-elliptical (Fig. 7e), and the other species as circular (Fig. 7f). Vessel and sieve tube tangential diameters ranged from 2.85 to 19.51µm and from 1.51 to 20.75µm, respectively, between the species (Data S2).

Discussion

The analysis of leaves of seven legume species distributed along a rainfall gradient in a seasonally dry tropical forest revealed that dry species perform more conservative strategies in individuals living in higher levels of annual rainfall, for example, presenting thicker cuticles with denser and smaller stomata and narrower vessels when compared with individuals living under lower rainfall levels. In the same context, wet and indifferent species in areas with higher rainfall show less investment in security, presenting a thicker spongy parenchyma and higher leaf construction costs. The main source of photoassimilate production, the leaves in wet and indifferent deciduous woody species with a short annual rainy season, does not seem to be able to invest in safer structures when subjected to severe conditions. The positive and negative aspects of this behavior are discussed. Identifying leaf structure, behavior, and dynamics in dry forests contributes to understanding community composition and provides additional resources for future scenario prediction studies. In addition, our study provides new data on the anatomy and ecophysiology of species of the most representative family in a seasonally dry tropical forest. Considering the great biodiversity of this environment, a gap exists in knowledge about the biology of the species that comprise it, which, with our data, we seek to reduce.

Higher abundance in lower rainfall: dry species

Cenostigma microphyllum and *Bauhinia acuruana*, two of the three most abundant species in lower rainfall areas (below 762 mm/year rainfall average), presented smaller stomata and narrower vessels, respectively, when living in areas with higher levels of rainfall. *Peltogyne pauciflora*, the second most abundant species in lower rainfall areas, adopts a different strategy; it has a wider average vessel tangential diameter. However, it is a more deciduous species, flushing almost all leaves for a longer period during the dry season. In addition, these species showed strategies to avoid the risk of hydraulic failure, even in higher rainfall plots, either with epidermal strategies to avoid dehydration or with reduced transpiration through the flushing of leaves. These behaviors make them more likely to grow in drier areas because they are more efficient in the transport and assimilation apparatus.

Bauhinia acuruana showed a contrasting response to higher rainfall, adopting conservative strategies, such as reducing vessel diameter, a trait related to water flow security (Hacke et al. 2016). In contrast, it also increased stomatal pore size, indicating a greater water loss during transpiration (Li & Liu 2016), compared with low rainfall areas. This species seems to take advantage of increased water availability to invest in conservative strategies, and once seasonality is strongly marked in the Caatinga domain, it invariably faces stress due to a lack of water. Notably, *B. acuruana* was more abundant in the driest sampled plots, suggesting a high tolerance under low water availability. This species has a heterobaric leaf with a high density of trichomes organized in clusters, a common strategy for reducing transpiration water loss (Bosabalidis and Kofidis 2002). These results suggest that *B. acuruana* has an efficient water-use strategy, and additional physiological studies are necessary to better identify these mechanisms.

Higher abundance in higher rainfall: wet species

Trischidium molle, *Senegalia piauhiensis*, and *Senegalia bahiensis* were the most abundant species in wetter areas (average rainfall above 762 mm/y). *T. molle* was the most plastic species, with four traits varying depending on rainfall. It adopts a similar strategy in dry species, creating a safer epidermis with smaller and denser stomata and thicker cuticles. In contrast, *S. bahiensis* had thinner leaves and narrower vessels and sieve tubes than the Caesalpinioideae mimosoid clade species (*Pityrocarpa moniliformis* and *Senegalia* spp.) but increased LCC in wetter areas. This species used some strategies with greater assimilation efficiency when more water was available. However, these changes have rendered them less secure. Moreover, this species had fewer variable traits than the dry species, adding to its smaller distribution and absolute abundance, suggesting its security is limited. *Senegalia bahiensis* and *S. piauhiensis* have leaves composed of tiny leaflets but only a few tector trichomes, as well as a papillary epidermis with a fine cuticle. These features do not indicate a high tolerance to drought, although small leaf areas and papillary cuticles are related to water-loss strategies (Li and Liu 2016). In addition to the restricted distribution of *S. bahiensis* and the predilection of *S. piauhiensis* for areas with greater water availability, our results suggest a risk to this species facing climate change. In a niche modeling study (Yule and Santos, unpublished data), we found a niche reduction for *S. bahiensis* and, despite increasing fragmentation for *S. piauhiensis* in future climate change scenarios (PBMC 2014; Fick and Hijmans 2017), these results indicate a worrisome situation for these species.

High abundance and wide distribution: indifferent species

Pityrocarpa moniliformis was the most abundant and widely distributed species in this study. However, only one trait changed due to rainfall: the spongy parenchyma thickness (SPt) increased with increasing rainfall. This feature, added to heterobaric leaves with bundle sheath extension (BSE) and a thick cuticle, for example, promotes a high level of transpiration control and thus conditions to grow well in different levels of rainfall.

Some anatomical characteristics observed in the present study were previously related to the studied genus or other members of the family Leguminosae, such as the shape of the main vascular bundle and epidermal cells (Bento et al. 2020), type of stomata (Maiti et al. 2016) and glandular trichomes (Roth 1990; Marinho et al. 2016). They are phylogenetically related and may not vary in appearance depending on the environmental conditions. However, this may vary in number, as observed in our results. Variations in stomatal and epidermal cell densities and stomatal pore size are commonly associated with the control of transpiration and CO_2 uptake (Bosabalidis and Kofidis 2002; Bertolino et al. 2019). Likewise, stomatal aspects and cuticles showed differences in the four analyzed species. The cuticle is formed by waxes, polysaccharide microfibrils, and cutin, providing mechanical protection against water loss through the epidermis. In Caatinga species, it plays an important role in controlling transpiration (Figueiredo et al. 2015; Medeiros et al. 2017; Pereira et al. 2019).

The paraveinal mesophyll (PV) and extended bundle sheath (BSEs), as observed in *Senegalia* spp., *Bauhinia acuruana, P. moniliformis*, and *Trischidium molle*, have been previously described in legumes (Wylie 1952; Rutten et al. 2003), deciduous species (McClendon 1992) and trees and shrubs growing under high irradiance and low precipitation (Zsögön et al. 2015). These structures reduce the hydraulic resistance from the bundle sheath to the epidermis, optimizing lateral air transport in the mesophyll, rate of stomatal opening, and stomatal conductance (Buckley et al. 2011; Zsögön et al. 2015). In addition, paraveinal mesophyll promotes changes between neighboring bundles outside the hydric tissues (Weston and Cass 1973; McClendon 1992), guaranteeing faster rehydration and improved photoassimilate transport (Kevekordes et al. 1988; Zsögön et al. 2015). These tissues are formed from layers of ground meristems that are different from those that form the palisade and spongy parenchyma, performing specific roles in leaf physiology (Weston and Cass 1973; Kevekordes et al. 1988). Consequently, BSEs consist of colorless tissue and surrounding bundles and extend from one epidermis to the other, completely or not, creating compartments in the mesophyll (McClendon 1992; Rodrigues et al. 2017). *B. acuruana, P. moniliformis,* and *T. molle* are classified as heterobaric based on the presence of BSEs tissue (Rodrigues et al. 2017) as the CO_2 pressure varies between different parts of the leaf (Zsögön et al. 2015). This reduces air diffusion and allows the leaf to open or close groups of stomata in different regions, and consequently, has more control over water loss.

Woody species tend to allocate more biomass to the leaves and phloem to ensure transport and resources for assimilation under drought (Kiorapostolou and Petit 2019). We believe that in these organs, in addition to hydraulic tissues, the epidermis play an important role in maintaining the function of the leaves, as demonstrated in experimental and modeling studies (Dayer et al. 2020). The investment and adjustment of vascular and epidermal traits is mainly reasonable for deciduous and sub-shrubby species, whose leaves usually have lower construction costs (Falcão et al. 2017) and can flush in the case of conductivity failure (de Lima et al. 2012). For these species, in these conditions, leaf construction cost only varies among rainfall events in *S. bahiensis*, and this may be explained by the predominance of habit, phenological behavior, and phylogenetic relationships: all species are deciduous woody (trees or shrubs) legumes. Additional studies on species biology are necessary to understand why *S. bahiensis* invests in more expensive leaves.

There was no direct relationship between low rainfall and the adoption of more conserved and secure traits in the leaves of five of the seven woody legumes evaluated. Studies on recurrent stress have revealed that severe events tend to reduce response capacity (Camarero et al. 2018), deplete productivity, increase water evapotranspiration loss, and lead to death (Fleta-Soriano and Munné-Bosch 2016). In contrast, moderating drought events promote a stress "memory" producing epigenetic changes and accumulating singling proteins or transcription factors, affecting persistent gene expression changes (Li and Liu 2016). Individuals, populations, and species distributed in wetter areas of the Caatinga experience seasonality with the same drought intensity as those occurring in drier areas but with a greater amplitude of water availability. We suggest that this method can recover from drought damage more effectively and quickly after stress and is a more persistent community component. However, the adoption of less conservative strategies indicates a process of acclimatization that promotes a reduction in the safety margin for the operation of species under similar conditions (Tombesi et al. 2018), increasing the risks for leaves and, consequently, for the entire plant. To better understand how these species respond to the trade-off of security versus productivity, further studies are necessary, with pluriannual sampling, including other organs, in vivo analyses, and the "omics" approach.

The abundance of the species observed in this study was related to the rainfall gradient, which is an important record of its behavior. Functional traits related to drought sensitivity have proven to be good predictors of species distribution in tropical forests (Engelbrecht et al. 2007). Based on our results that plants subjected to lower water availability showed less secure anatomical changes, we are concerned about populations in the face of climate change predictions. Climate change intensifies the water stress due to the lack of water inherent to the Caatinga, as an increase of 1.5 ºC to 3.5 °C in the average temperature is expected, accompanied by a 20% to 60% reduction in rainfall, still in this century, to the Northeast region of Brazil (Rodrigues-Filho et al. 2016; Torres et al. 2017). It promotes changes in vegetation dynamics, increases hydraulic insecurity, delays responses to recovery from damage, and increases the risk of mass mortality, which are related to increasingly frequent and severe drought events (Anderegg *et al.* 2015a; Anderegg *et al.* 2015b). Our results corroborate the risk of vegetation with niche loss, depletion of assimilation and growth rates, and hydraulic failure, but collaborate to understand future scenarios once vegetation responses are species-specific (Camarero et al. 2018; Kiorapostolou et al. 2020).

In conclusion, rainfall range promotes anatomical variations in Leguminosae leaves distributed along different levels in the Caatinga, mainly affecting mesophyll, followed by epidermal and conductive traits, especially those related to the xylem. Changes caused by environmental variations are related with the abundance of species along the rainfall gradient. However, in contrast to what was expected for species distributed in restrictive environments, intraspecific variation did not occur the sense of adopting relatively more conservative traits in environments with reduced water availability. Our results corroborate the risks to vegetation under future climate change scenarios as stressed species and populations may not endure even more severe conditions. Finally, it is important to know the responses of other organs to effectively understand plant strategies against stress due to lack of water, both now and in the future.

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Declarations

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Tamires Soares Yule, Mauro Guida dos Santos and Rosani do Carmo de Oliveira Arruda. The first draft of the manuscript was written by Tamires Soares Yule and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Competing interests

On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Anderegg WRL, Flint A, Huang CY, et al (2015a) Tree mortality predicted from drought-induced vascular damage. Nat Geosci 8:367–371. https://doi.org/10.1038/ngeo2400

Anderegg WRL, Schwalm C, Biondi F, et al (2015b) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science (80-) 349:528–532. https://doi.org/10.1126/science.aab1833

Bento JPSP, Scremin-Dias E, Alves FM, et al (2020) Phylogenetic implications of the anatomical study of the Amburaneae clade (Fabaceae: Faboideae). Bot J Linn Soc 1–15. https://doi.org/10.1093/botlinnean/boaa019

Bertolino LT, Caine RS, Gray JE (2019) Impact of Stomatal Density and Morphology on Water-Use Efficiency in a Changing World. Front Plant Sci 10:. https://doi.org/10.3389/fpls.2019.00225

Bosabalidis AM, Kofidis G (2002) Comparative effects of drought stress on leaf anatomy of two olive cultivars. Plant Sci 163:375–379. https://doi.org/10.1016/S0168-9452(02)00135-8

Brodribb TJ, Mcadam SA, Carins Murphy MR (2017) Xylem and stomata, coordinated through time and space. Plant Cell Environ 40:872–880. https://doi.org/10.1111/pce.12817

Bucci SJ, Goldstein G, Meinzer FC, et al (2004) Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. Tree Physiol 24:891–899. https://doi.org/10.1093/treephys/24.8.891

Buckley TN, Sack L, Farquhar GD (2017) Optimal plant water economy. Plant Cell Environ 40:881–896. https://doi.org/10.1111/pce.12823

Buckley TN, Sack L, Gilbert ME (2011) The role of bundle sheath extensions and life form in stomatal responses to leaf water status. Plant Physiol 156:962–973. https://doi.org/10.1104/pp.111.175638

Camarero JJ, Gazol A, Sangüesa-Barreda G, et al (2018) Forest growth responses to drought at short- and long-term scales in Spain: Squeezing the stress memory from tree rings. Front Ecol Evol 6:1–11. https://doi.org/10.3389/fevo.2018.00009

Carmona CP, de Bello F, Mason NWH, Lepš J (2016) Traits Without Borders: Integrating Functional Diversity Across Scales. Trends Ecol Evol 31:382–394. https://doi.org/10.1016/j.tree.2016.02.003

Cavalcanti LC de S, Corrêa AC de B (2014) Pluviosidade no parque nacional do Catimbau (Pernambuco): seus condicionantes e seus efeitos sobre a paisagem. Geografia 23:133–156

Cosme LHM, Schietti J, Costa FRC, Oliveira RS (2017) The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. New Phytol 113–125. https://doi.org/10.1111/nph.14508

Dayer S, Herrera JC, Dai Z, et al (2020) The sequence and thresholds of leaf hydraulic traits underlying grapevine varietal differences in drought tolerance. J Exp Bot 71:4333–4344. https://doi.org/10.1093/jxb/eraa186

de Lima ALA, de Sá Barretto Sampaio EV, de Castro CC, et al (2012) Do the phenology and functional stem attributes of woody species allow for the identification of functional groups in the semiarid region of Brazil? Trees - Struct Funct 26:1605–1616. https://doi.org/10.1007/s00468-012-0735-2

Domec J-C, Smith DD, McCulloh KA (2016) A synthesis of the effects of atmospheric carbon dioxide enrichment on plant hydraulics: implications for whole-plant water use efficiency and resistance to drought. Plant Cell Environ 921–937. https://doi.org/10.1111/pce.12843

Engelbrecht BMJJ, Comita LS, Condit R, et al (2007) Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447:80–82. https://doi.org/10.1038/nature05747

Falcão HM, Medeiros CD, Almeida-Cortez J, Santos MG (2017) Leaf construction cost is related to water availability in three species of different growth forms in a Brazilian tropical dry forest. Theor Exp Plant Physiol 29:95–108. https://doi.org/10.1007/s40626-017-0087-9

Falcão HM, Medeiros CD, Silva BLR, et al (2015) Phenotypic plasticity and ecophysiological strategies in a tropical dry forest chronosequence: A study case with Poincianella pyramidalis. For Ecol Manage 340:62–69. https://doi.org/10.1016/j.foreco.2014.12.029

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315

Figueiredo K V., Oliveira MT, Arruda ECP, et al (2015) Changes in leaf epicuticular wax, gas exchange and biochemistry metabolism between Jatropha mollissima and Jatropha curcas under semi-arid conditions. Acta Physiol Plant 37:. https://doi.org/10.1007/s11738-015-1855-2

Fleta-Soriano E, Munné-Bosch S (2016) Stress memory and the inevitable effects of drought: A physiological perspective. Front Plant Sci 7:1–6. https://doi.org/10.3389/fpls.2016.00143

Franklin GL (1945) Preparation of Thin Sections of Synthetic Resins and Wood-Resin Composites, and a New Macerating Method for Wood. Nature 155:51–51. https://doi.org/10.1038/155051a0

Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. Perspect Plant Ecol Evol Syst 4:97–115

Hacke UG, Spicer R, Schreiber SG, Plavcov?? L (2016) An ecophysiological and developmental perspective on variation in vessel diameter. Plant, Cell Environ 831–845. https://doi.org/10.1111/pce.12777

IBGE (2002) Mapa de Solos Brasileiros - IBGE .pdf

Johansen DA (1940) Plant Microtechnique. New York

Kevekordes KG, McCully ME, Canny MJ (1988) The occurrence of an extended bundle sheath system (paraveinal mesophyll) in the legumes. Can J Bot 66:94–100. https://doi.org/10.1139/b88-014

Kiorapostolou N, Camarero JJ, Carrer M, et al (2020) Scots pine trees react to drought by increasing xylem and phloem conductivities. Tree Physiol 40:774–781. https://doi.org/10.1093/treephys/tpaa033

Kiorapostolou N, Petit G (2019) Similarities and differences in the balances between leaf, xylem and phloem structures in Fraxinus ornus along an environmental gradient. Tree Physiol 39:234–242. https://doi.org/10.1093/treephys/tpy095

Kottek M, Grieser J, Beck C, et al (2006) World Map of Köppen − Geiger Climate

Classification. Meteorol Z 15:259–263. https://doi.org/10.1127/0941-2948/2006/0130.

Kraus JE, De Sousa HC, Rezende MH, et al (1998) Astra blue and basic fuchsin double staining of plant materials. Biotech Histochem 73:235–243. https://doi.org/10.3109/10520299809141117

Li L, McCormack ML, Ma C, et al (2015) Leaf economics and hydraulic traits are decoupled in five species-rich tropical-subtropical forests. Ecol Lett 18:899–906. https://doi.org/10.1111/ele.12466

Li X, Liu F (2016) Drought Stress Memory and Drought Stress Tolerance in Plants: Biochemical and Molecular Basis. In: Drought Stress Tolerance in Plants, Vol 1. Springer International Publishing, Cham, pp 17–44

Maiti R, Rodríguez HG, Balboa PCR, et al (2016) Leaf surface anatomy in some woody plants from northeastern Mexico. Pakistan J Bot 48:1825–1831

Marinho CR, Oliveira RB, Teixeira SP (2016) The uncommon cavitated secretory trichomes in Bauhinia s.s. (Fabaceae): The same roles in different organs. Bot J Linn Soc 180:104–122. https://doi.org/10.1111/boj.12354

McClendon JH (1992) Photographic Survey of the Occurrence of Bundle-Sheath Extensions in Deciduous Dicots. Plant Physiol 99:1677–1679. https://doi.org/10.1104/pp.99.4.1677

Medeiros CD, Falcão HM, Almeida-Cortez J, et al (2017) Leaf epicuticular wax content changes under different rainfall regimes, and its removal affects the leaf chlorophyll content and gas exchanges of Aspidosperma pyrifolium in a seasonally dry tropical forest. South African J Bot 111:267–274. https://doi.org/10.1016/J.SAJB.2017.03.033

PBMC (2014) Avaliação de modelos globais e regionais climáticos. In: Base científica das mudanças climáticas. pp 278–319

Pereira S, Figueiredo-Lima K, Oliveira AFM, Santos MG (2019) Changes in foliar epicuticular wax and photosynthesis metabolism in evergreen woody species under different soil water availability. 192–201. https://doi.org/10.32615/ps.2019.013

Pivovaroff AL, Cook VMW, Santiago LS (2018) Stomatal behavior and stem xylem traits are coordinated for woody plant species under exceptional drought conditions. Plant Cell Environ. https://doi.org/10.1111/pce.13367

Rasband W (2018) ImageJ. U. S. National Institutes of Health, Bethesda, Mar

Rito KF, Arroyo-Rodríguez V, Queiroz RT, et al (2017) Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. J Ecol 105:828–838. https://doi.org/10.1111/1365-2745.12712

Rodrigues-Filho S, Junior DSR, Martins E, et al (2016) Implicações Para a Sustentabilidade

Regional No Brasil

Rodrigues TM, Esteves Amaro AC, Fernandes Boaro CS, et al (2017) Four distinct leaf types in the Brazilian cerrado, based on bundle sheath extension morphology. Botany 95:1171–1178. https://doi.org/10.1139/cjb-2017-0073

Roeser K (1972) Die Nadel der Schwarzkiefer - Massenprodukt und Kunstwerk der Natur. Mikrokosmos 61:33–36

Roth I (1990) Peculiar Surface Structures of Tropical Leaves for Gas Exchange, Guttation, and Light Capture. 185–238. https://doi.org/10.1007/978-94-009-1872-6_3

Rutten T, Krüger C, Melzer M, et al (2003) Discovery of an extended bundle sheath in Ricinus communis L. and its role as a temporal storage compartment for the iron chelator nicotianamine. Planta 217:400–406. https://doi.org/10.1007/s00425-003-1010-y

Salisbury EJ (1928) I. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. Philos Trans R Soc London Ser B, Contain Pap a Biol Character 216:1–65. https://doi.org/10.1098/rstb.1928.0001

Santos MG, Oliveira MT, Figueiredo K V., et al (2014) Caatinga, the Brazilian dry tropical forest: Can it tolerate climate changes? Theor Exp Plant Physiol 26:83–99. https://doi.org/10.1007/s40626-014-0008-0

Sevanto S (2014) Phloem transport and drought. J Exp Bot 65:1751–1759. https://doi.org/10.1093/jxb/ert467

Silva AC, Souza AF (2018) Aridity drives plant biogeographical sub regions in the Caatinga, the largest tropical dry forest and woodland block in South America. PLoS One 13:e0196130. https://doi.org/10.1371/journal.pone.0196130

Silva JMC da, Barbosa LCF (2017) Impact of Human Activities on the Caatinga. In: Silva JMC da, Leal IR, Tabarelli M (eds) Caatinga, 1st edn. Springer International Publishing, Cham, pp 359–368

Silva PF da, Lima JR de S, Antonino ACD, et al (2017) Seasonal patterns of carbon dioxide, water and energy fluxes over the Caatinga and grassland in the semi-arid region of Brazil. J Arid Environ. https://doi.org/10.1016/j.jaridenv.2017.09.003

Speckmann GJ, Post J, Dijkstra H (1965) The length of stomata as an indicator for polyploidy in rye-grasses. Euphytica 14:225–230. https://doi.org/10.1007/BF00149503

Sperry JS, Venturas MD, Anderegg WRL, et al (2016) Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost. Plant Cell Environ 816–830. https://doi.org/10.1111/pce.12852

Tomás M, Flexas J, Copolovici L, et al (2013) Importance of leaf anatomy in determining mesophyll diffusion conductance to CO2 across species: Quantitative limitations and scaling up by models. J Exp Bot 64:2269–2281. https://doi.org/10.1093/jxb/ert086

Tombesi S, Frioni T, Poni S, Palliotti A (2018) Effect of water stress "memory" on plant behavior during subsequent drought stress. Environ Exp Bot 150:106–114. https://doi.org/10.1016/j.envexpbot.2018.03.009

Torres RR, Lapola DM, Gamarra NLR (2017) Future Climate Change in the Caatinga. In: Silva JMC da, Leal IR, Tabarelli M (eds) Caatinga. Springer International Publishing, Cham, pp 383–410

Villar R, Merino J (2001) Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. New Phytol 151:213–226. https://doi.org/10.1046/j.1469-8137.2001.00147.x

Weston GD, Cass DD (1973) Observations on the Development of the Paraveinal Mesophyll of Soybean Leaves. Bot Gaz 134:232–235. https://doi.org/10.1086/336708

Williams K, Percival F, Merino J, Mooney HA (1987) Estimation of Tissue Construction Cost from Heat of Combustion and Organic Nitrogen Content. Plant, Cell Environ 10:725–734. https://doi.org/10.1111/1365-3040.ep11604754

Wispelaere L De, Bodé S, Hervé-Fernández P, et al (2017) Plant water resource partitioning and isotopic fractionation during transpiration in a seasonally dry tropical climate. Biogeosciences 14:73–88. https://doi.org/10.5194/bg-14-73-2017

Wylie RB (1952) The bundle sheath extension on leaves of dicotyledons. Am J Bot 39:645–651. https://doi.org/10.1086/336403

Yin H, Tariq A, Zhang B, et al (2021) Coupling Relationship of Leaf Economic and Hydraulic Traits of Alhagisparsifolia Shap. in a Hyper-Arid Desert Ecosystem. Plants 10:1867. https://doi.org/10.3390/plants10091867

Zsögön A, Alves Negrini AC, Peres LEP, et al (2015) A mutation that eliminates bundle sheath extensions reduces leaf hydraulic conductance, stomatal conductance and assimilation rates in tomato (Solanum lycopersicum). New Phytol 205:618–626. https://doi.org/10.1111/nph.13084

Supplementary data

Table S1. Minimum, maximum, mean, and standard deviation trait values in legumes due to rainfall categories in Catimbau National Park. BA- Bauhinia acuruana, CM- Cenostigma microphyllum, PP- Peltogyne pauciflora, PY- Pityrocarpa moniliformis, SB- Senegalia bahiensis, SP- Senegalia piauhiensis, and TM- Trischidium molle. Td- Trichome density, Sd- Stomata density, Ecd- Epidermal cell density, Si- Stomata index, Sf- Stomata frequency, Ct- Cuticle thickness, Etad- Adaxial epidermis thickness, Etab-Abaxial epidermis thickness, Lt- leaf thickness, PPt- Palisade parenchyma thickness, SPt- Spongy parenchyma thickness, VD- vessel diameter, and STD- sieve tube diameter.

Species	**Category**	**Statistics**	**Td**	**Sd**	**Ecd**	**Si**	**Sf**	**Ct**	**Etad**	**Etab**	**Lt**	**PPt**	**SPt**	**Spl**	**VD**	**STD**
BA	Dry	min	3.000	1.000	17.000	5.000	0.053	12.490	8.764	6.725	801.200	200.000	62.530	28.520	37.190	16.200
		max	54.000	8.000	49.000	22.222	0.286	82.070	21.378	13.828	1708.490	596.960	879.360	97.350	153.200	77.060
		mean	13.120	5.300	34.440	13.391	0.157	40.848	13.203	9.330	1110.813	360.168	560.843	61.297	93.949	35.965
		sd	12.358	1.729	8.574	4.209	0.057	17.265	2.605	1.480	212.846	89.042	144.425	12.995	24.257	11.906
	Wet	min	5.000	4.000	21.000	9.615	0.106	5.440	9.220	6.266	783.340	218.750	327.160	40.340	38.790	15.270
		max	26.000	8.000	49.000	22.581	0.292	106.250	18.286	13.020	1877.520	469.790	1230.150	99.830	140.450	90.190
		mean	13.800	5.933	32.467	15.913	0.191	63.097	12.630	9.217	1151.861	309.513	633.257	69.488	79.696	37.665
		sd	5.235	1.258	8.772	3.384	0.048	27.398	2.174	1.659	338.432	66.560	280.537	12.842	19.682	17.623
CM	Dry	min	0.250	2.000	12.000	8.333	0.091	31.250	9.718	9.005	1250.000	443.750	506.250	90.760	22.220	11.860
		max	15.000	4.000	23.000	20.000	0.250	81.250	28.857	18.068	1978.130	912.500	875.000	195.180	71.910	50.560
		mean	5.842	2.867	18.300	13.631	0.159	51.452	16.319	13.473	1601.271	692.292	645.084	150.381	45.147	27.026
		sd	4.423	0.571	2.628	2.551	0.034	13.276	4.376	2.317	232.401	135.029	92.545	23.130	12.603	7.175
	Wet	min	5.000	2.000	15.000	6.667	0.071	25.000	11.415	8.582	1200.020	456.250	493.750	85.800	13.890	16.200
		max	22.000	4.000	33.000	18.182	0.222	56.250	22.352	18.862	1887.500	775.000	843.750	161.470	82.910	42.950
		mean	12.200	3.133	23.400	12.113	0.139	39.896	16.271	12.744	1462.655	584.342	617.536	128.016	40.501	27.353
		sd	6.042	0.629	4.538	3.002	0.039	9.037	3.116	2.528	156.152	66.746	99.608	18.725	15.905	6.230
PP	Dry	min	0.000	4.000	15.000	12.121	0.138	6.250	8.732	8.286	1381.250	468.750	643.750	51.020	44.760	14.930
		max	0.000	11.000	30.000	34.483	0.526	37.510	23.799	15.017	2550.030	912.500	1650.000	115.500	151.600	62.930

		mean	0.000	6.711	22.022	23.526	0.314	21.979	15.682	11.195	1893.541	700.784	946.117	78.362	93.030	33.292
		sd	0.000	1.632	3.434	5.532	0.096	8.462	3.200	1.693	269.280	119.399	256.650	14.963	23.918	9.469
	Wet	min	0.000	4.000	14.000	11.905	0.135	18.750	9.296	5.303	1101.600	370.650	531.250	51.420	23.000	9.720
		max	0.000	12.000	38.000	46.154	0.857	50.020	19.299	14.003	2562.500	1350.000	1200.000	114.980	153.930	52.300
		mean	0.000	7.400	25.657	22.734	0.305	31.756	12.901	10.043	1887.483	773.110	866.275	83.070	95.281	28.067
		sd	0.000	2.018	5.455	6.630	0.130	10.084	2.200	2.230	454.983	323.840	185.055	14.205	26.689	9.351
PY	Dry	min	5.000	1.000	9.000	4.348	0.045	10.890	10.009	8.182	1187.500	368.750	418.750	62.810	16.900	15.710
		max	44.000	6.000	22.000	40.000	0.667	40.340	21.161	16.301	1971.880	1000.000	1100.020	149.300	146.690	63.400
		mean	21.444	3.622	16.178	18.753	0.241	25.588	15.723	12.202	1551.125	681.179	633.725	103.579	67.508	31.286
		sd	12.330	1.173	2.766	7.215	0.119	7.056	2.620	2.302	236.177	161.196	157.646	20.801	27.250	9.203
	Wet	min	12.000	2.000	12.000	10.526	0.118	10.890	12.326	9.028	1412.510	462.500	487.540	62.810	23.730	13.350
		max	87.000	7.000	26.000	31.579	0.462	87.500	23.573	18.598	2487.530	1237.500	1093.770	159.950	125.790	48.210
		mean	35.200	4.044	18.044	18.415	0.231	34.553	18.031	13.395	1804.868	714.867	807.310	100.843	72.335	27.058
		sd	20.967	1.242	3.496	5.077	0.080	20.307	2.799	2.547	248.979	180.695	155.265	22.457	24.731	6.939
SB	Wet	min	0.000	2.000	10.000	11.111	0.125	4.080	5.303	4.000	756.280	312.500	231.250	45.990	16.670	14.160
		max	9.000	8.000	26.000	33.333	0.500	19.250	17.571	16.016	1775.400	1072.160	606.380	103.030	95.880	49.690
		mean	0.822	3.778	18.289	16.897	0.207	10.602	10.176	9.297	1188.685	602.893	406.404	73.953	45.741	30.862
		sd	1.918	1.412	3.865	4.271	0.068	3.747	2.816	2.598	332.194	248.546	96.001	13.104	16.116	8.009
SP	Dry	min	0.000	1.000	12.000	7.143	0.077	4.110	6.857	6.429	1206.690	560.000	326.670	54.120	14.960	18.890
		max	8.000	6.000	23.000	28.571	0.400	11.620	17.618	14.728	2286.670	1253.330	893.330	109.730	111.110	91.100
		mean	2.100	3.725	17.200	17.785	0.220	8.050	11.723	10.858	1724.050	907.938	611.926	77.340	52.012	39.657
		sd	2.073	1.037	2.681	4.413	0.066	2.017	2.642	2.146	284.668	190.078	148.535	12.360	22.554	10.978
	Wet	min	0.000	2.000	14.000	10.000	0.111	3.490	8.949	8.291	860.030	346.670	313.330	49.810	23.730	23.900
		max	7.000	6.000	21.000	27.273	0.375	11.290	18.020	16.571	1780.000	1020.000	780.000	105.570	132.430	59.960
		mean	2.600	3.833	17.000	18.376	0.228	7.136	12.890	11.704	1429.186	719.317	497.677	76.605	56.037	40.044
		sd	1.589	0.874	1.838	3.802	0.057	2.021	2.718	2.582	301.822	223.699	112.365	11.099	21.164	9.006
TM	Dry	min	0.000	1.000	25.000	2.703	0.028	33.740	8.469	9.857	1525.200	575.000	580.400	77.850	32.520	22.400
		max	24.000	4.000	39.000	12.121	0.138	121.190	22.167	19.769	2034.480	950.000	1109.720	155.180	141.610	72.720
		mean	8.644	2.378	32.178	6.803	0.074	70.561	14.299	14.974	1772.804	693.076	810.258	111.497	83.698	43.678

	sd	5.955	0.984	3.505	2.585	0.030	21.026	3.559	2.311	126.008	70.375	109.660	13.744	22.076	10.652
Wet	min	0.000	1.000	25.000	1.639	0.017	49.990	8.812	9.959	1441.360	510.200	618.630	57.750	37.190	21.600
	max	26.000	6.000	60.000	14.286	0.167	166.670	20.161	18.028	2449.030	982.160	1237.270	131.320	162.600	92.460
	mean	9.589	3.511	42.911	7.698	0.085	107.944	14.690	13.663	1934.684	766.405	892.481	97.532	86.658	47.894
	sd	8.636	1.325	8.652	2.993	0.035	28.190	2.077	2.074	220.573	119.724	122.172	17.290	24.249	12.633

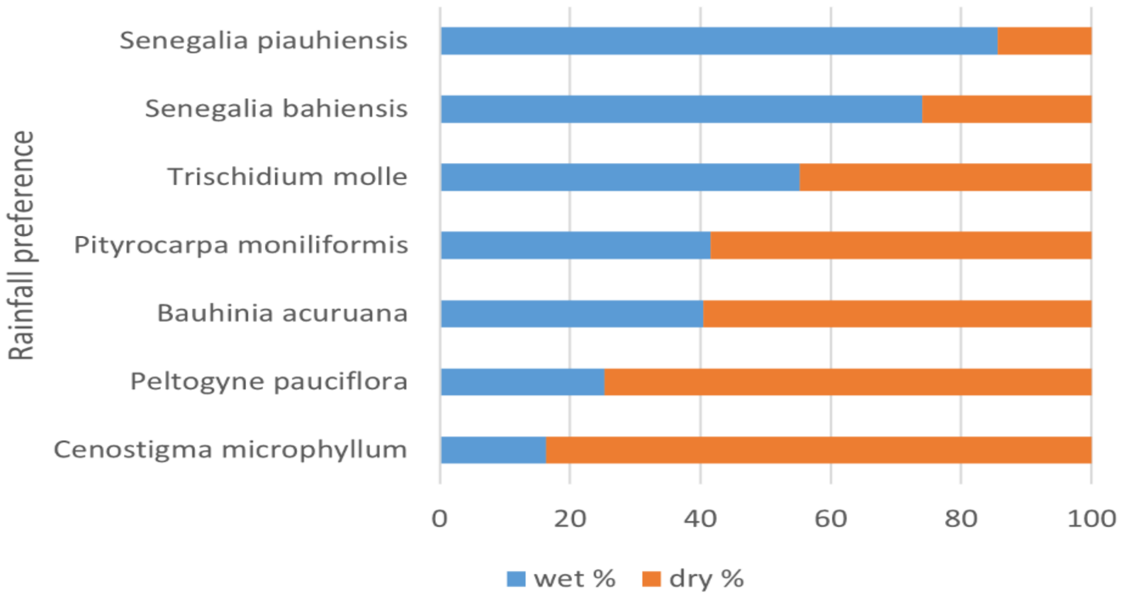

Fig. S2 Rainfall preference of legumes due to rainfall in Catimbau National Park. Wet species group is composed by *Trischidium molle* (Benth.) H.E. Ireland, *Senegalia bahiensis* (Benth.) Seigler & Ebinger, and *Senegalia piauhiensis* (Benth.) Seigler & Ebinger that are more abundant in higher rainfall average plots. Indifferent species is *Pityrocarpa moniliformis* (Benth.) Luckow & R. W. Jobson which is widely distributed and have similarly abundant under both conditions. Dry species group is composed by *Cenostigma microphyllum* Mart. Ex G. Don) E. Gagnon & G.P. Lewis, *Peltogyne pauciflora* Benth., and *Bauhinia acuruana* Moric. that are more abundant in low rainfall average plots.

Capítulo II

Bark and phloem are protagonists under different water availability in tropical dry forest

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Abstract

Climate change scenarios predict that severe droughts and increases in average temperatures in seasonally dry tropical forests will occur. This means that plant communities will be subjected to even more severe conditions than they have already adapted to. Understanding the mechanisms that these species use to withstand stressful conditions will enable us to estimate their responsiveness to future situations. We selected seven legume species from the Caatinga and carried out a quantitative study of stem and root bark and wood of individuals growing under conditions of higher and lower average rainfall. The most demanding species in terms of water requirements exhibited different behaviors from all other species. Their wood and bark in the roots and stems adjusted differently. As rainfall increased, the less demanding species invested in changes in bark and transport efficiency, whereas the most demanding species invested in changes in wood and reducing wood-specific gravity. The indifferent species was the most plastic one, providing more storage and transport capacity to the stems. These results demonstrated the importance of the bark and phloem in these species and suggest that small changes in the xylem may increase efficiency under water deficit.

Keywords*:* Caatinga; dry environments; stem; root; phloem; xylem

1.1 Introduction

Increases in global average temperature and changes in rainfall distribution patterns are predicted effects of climate change of anthropogenic origin, which the planet has been going through (Torres, Lapola and Gamarra, 2017). However, the response of tropical ecosystem vegetation to these changes remains unclear (Santos *et al.*, 2014; Silva *et al.*, 2017). Hydraulic tissues are directly linked to environmental conditions, making them good predictive models for understanding present functioning and assessing future scenarios impacted by climate change (Lourenço *et al.*, 2022).

Tracheophytes have developed mechanisms and hydraulic architectures that optimize photosynthesis and water conductivity, minimizing the vulnerability of carbon assimilation and conducting tissues along their evolutionary course in diverse and changing global environmental conditions (Hacke and Sperry, 2001; Chaves, Flexas and Pinheiro, 2009). Vessel width and density are related to xylem capacity and the efficiency of water transport, but also to a greater or lesser risk of embolism (Davis, Sperry and Hacke, 1999). Similarly, the parenchyma and fiber fractions are related to hydraulic capacitance, efficiency, resilience, and security against mechanical damage (Meinzer *et al.*, 2009). Additionally, the phloem changes owing to water availability (Salmon *et al.*, 2018). The functional attributes related to these mechanisms are reflected in the distribution of species, in different ecosystems and over time (Falcão *et al.*, 2015; Cosme *et al.*, 2017) and their variations occur at different approaches among the woody components of a community (Woodcock, 2000; Fortunel, Paine, *et al.*, 2014; Plourde, Boukili and Chazdon, 2015).

The integrity of the plant hydraulic system depends on the forming of a soil–plant–atmosphere continuum to function properly (Milburn, 1966). However, every plant organ experiences different environmental conditions that may determine its structural and physiological characteristics (Aroca, Porcel and Ruiz-Lozano, 2012). Despite their importance in the uptake, storage, and maintenance of water supply, belowground organs have received less attention in hydraulic system studies (Brunner *et al.*, 2015). In woody species, roots and stems may present different arrangements of hydraulic tissues to optimize their security and guarantee the functioning of the whole plant (Brodribb, Mcadam and Carins Murphy, 2017; Wu *et al.*, 2020). This adds one more approach to understanding species performance and strategies and plant community composition in forests.

Exchanges among traits explain the performance of species in the composition of communities between different congeners across the landscape or even populations of the same species in different landscapes (Reich, 2014). Trade-offs that determine the distribution of individuals in space and time are caused by the allocation of limited resources for one purpose versus another at the physiological level. According to Reich (2014), the known choices for a species in one place are predictably similar to those in other places at different scales (local, regional, and even global). This effect has been observed in Caatinga species by Vieira and Lisi (2019), who demonstrated a relationship between anatomical characteristics and environmental conditions (temperature and precipitation), distinguishing woody species from different functional groups in the community.

Variations in weather patterns directly influence the functioning of vegetation, altering the hydraulic balance, and consequently, carbon assimilation, resulting in changes in the dynamics and composition of communities and species distribution (Seddon *et al.*, 2016). Understanding the mechanisms and strategies, as well as the capacity to tolerate higher temperatures and lower water availability, helps predict future community composition, establish measures for the conservation of ecosystems, and control or mitigate the effects of climate change (Wright, 2010). Although responses to even more severe changes and conditions are still uncertain (Anderegg *et al.*, 2015), the capacity to tolerate drought and high assimilation, even under greater water restriction, makes dry forests key ecosystems for carbon storage, reduction of atmospheric levels, and consequently, global climate change (Santos *et al.*, 2014; Silva *et al.*, 2017).

In this context, the aim of the present study was to evaluate the relationship between the attributes of secondary conductive tissues in the stems and roots and to identify variations in the functional attributes of wood and bark due to water availability in a seasonally dry tropical forest (SDTF). Our main goals were to (1) describe and quantify the quantitative trait variation due to rainfall, (2) infer the influence of the variation in attributes within the rainfall preference categories, and (3) identify and describe the resource allocation strategies and adaptations adopted by species in different organs according to their categories of rainfall preferences. We hypothesized that (1) species would adjust wood and bark traits to make them more secure when less water is available, i.e., in lower rainfall areas, (2) the capacity of adjustment would be different between the rainfall preference categories, (3) the more plastic species would be better equipped to occupy drier areas, and (4) roots would be more stable organs than stems once they experience less environmental variation, i.e., occupying a more constant microhabitat.

1.2 Materials and Methods

1.2.1 Study area

We conducted the study in an area of dry tropical forest (DTF) in the Caatinga domain at Catimbau National Park, located in Pernambuco state, Brazil 8°24′0″–8°36′35″S; 37°0′30″–37°1040″W), covering an area of 62,300 ha. The climate is semi-arid BSh type with a transition to tropical rainy type As’ (Kottek *et al.*, 2006). In this region, the soil is sandy, well-drained, and with low fertility. Natric Planossols are characterized by high sodium saturation and great susceptibility to erosion, and Chromic Luvissols have high base saturation in the subsurface horizons, easily weathered primary minerals (nutritional reserve). There are large amounts of stones in the surface horizon (IBGE, 2002). The annual temperature average is 23

°C (73.4 °F) and the annual rainfall average varies from 400 to 940 mm (Cavalcanti and Corrêa, 2014) (Fig. 1). In total, 20 plots were randomly established throughout the different rainfall rates recorded in this area, and 10 were visited to collect samples for the present study (Fig. 2).

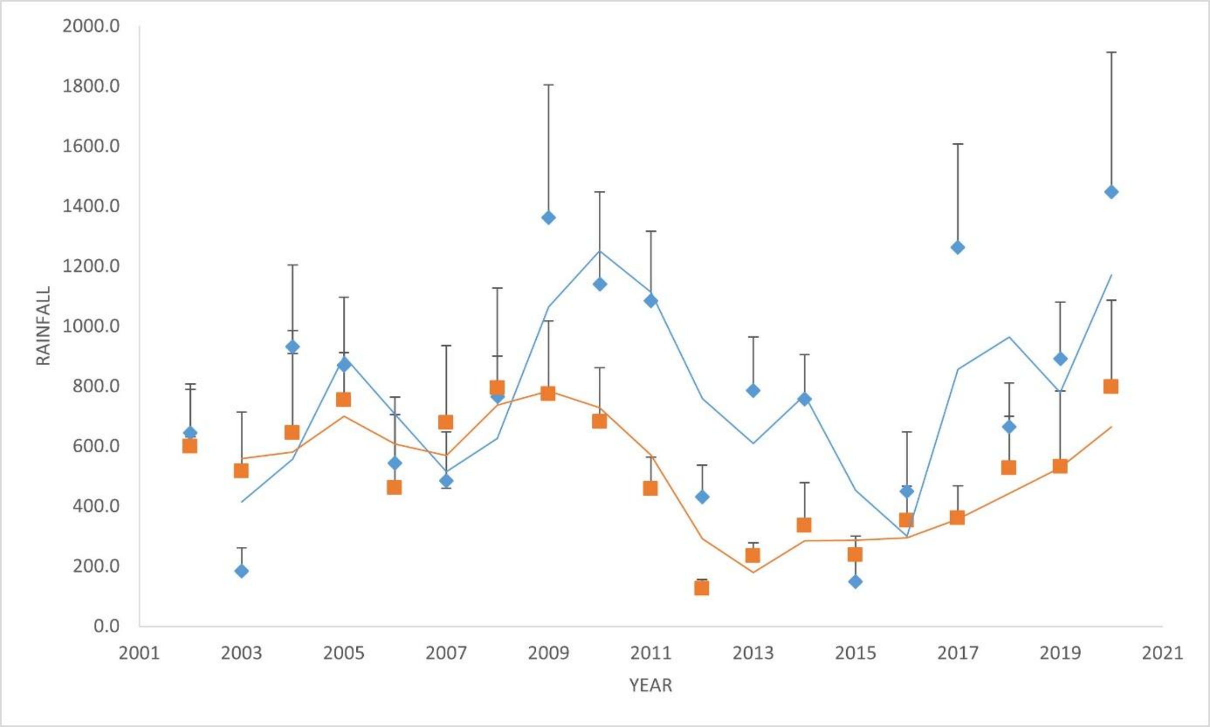

Figure 1. Annual rainfall average in Catimbau National Park, Pernambuco, Brazil. Blue line represents the average (mm/year) of the last seventeen years of wet area, and red line represents the average of dry area, in the same period.

The highest annual average temperature and the lowest and most irregular rainfall in Brazil occur in the Caatinga domain, which is normally concentrated over a short period of the year (2–5 months) (Prado, 2003). It also has the highest rates of solar radiation and lowest relative humidity (Kottek *et al.*, 2006; Andrade *et al.*, 2017). Extreme events, such as great droughts and floods, are common in the region and are caused by climatic dynamics governed by cyclical and multi-annual events, which over time have selected for and modulated local biodiversity (Prado 2003). These environmental conditions result in SDTF with a predominance of steppe savanna vegetation within a mosaic of arboreal and shrubby deciduous landscapes (IBGE, 2012). The most representative families in the Caatinga plant communities are Fabaceae, Euphorbiaceae, Cactaceae, Bromeliaceae, Anacardiaceae, Apocynaceae, Bignoniaceae, Burseraceae, Arecaceae, Rhamnaceae, Malvaceae, and Portulacaceae (Prado, 1991).

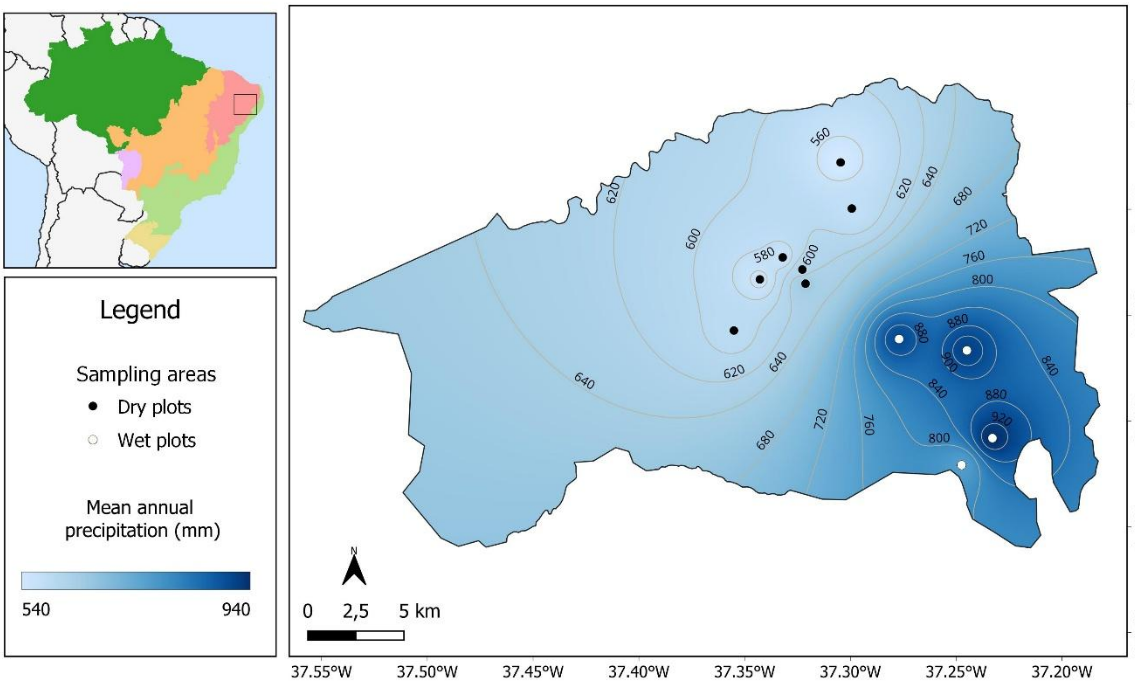

Figure 2. Catimbau National Park, Pernambuco State, Brazil. White dots correspond to the wetter plots with high rainfall annual average (above to 762 mm/year) and black dots corresponds to the dryer plots, with low rainfall annual average (below to 591mm/year).

1.2.2 Selected species and sampling

We selected seven legume trees and shrubby species with different abundances as models based on previous community data (Rito *et al.*, 2017; Oliveira *et al.*, 2021) and the National Park rainfall gradient. *Cenostigma microphyllum* Mart. ex G. Don), E. Gagnon & G.P. Lewis, and *Peltogyne pauciflora* Benth. are trees while *Bauhinia acuruana* Moric. is a climbing shrub. They were more abundant in lower average rainfall plots (below 653 mm). We referred to these as the preferentially dry species (DS). *Pityrocarpa moniliformis* (Benth.) Luckow &

R.W. Jobson is a tree that was widely distributed and abundant under both conditions, and we classified it as an indifferent species (IS). *Trischidium molle* (Benth.) H.E. Ireland is a shrub whereas *Senegalia piauhiensis* (Benth.) Seigler & Ebinger is a tree, and both were more abundant in high rainfall average plots but also occurred in low rainfall plots. *Senegalia bahiensis* (Benth.) Seigler & Ebinger is a tree and was exclusively found in higher average rainfall plots (above 762 mm) (Rito *et al.*, 2017). The last three species were classified as preferentially wet species (WS). Species classification, habitat, rainfall preference, rainfall, and abundance are shown in Table 1.

Table 1. Legumes species sampled, classification, habit, rainfall preference category, rainfall category, and abundance in Catimbau National Park

Species	**Subfamily**	**Habit**	**Rainfall preference category**	**Rainfall category**	**Abundance** (individuals/ category)
Cenostigma microphyllum	Caesalpinioideae	Tree	DS	low	369
				high	72
Peltogyne pauciflora	Detarioideae	Tree	DS	low	130
				high	44
Bauhinia acuruana	Cercidoideae	Shrub	DS	low	59
				high	40
Pityrocarpa moniliformis	Caesalpinioideae -Mimosoid clade	Tree	IS	low	365
				high	260
Trischidium molle	Papilionoideae	Shrub	WS	low	58
				high	47
Senegalia bahiensis	Caesalpinioideae -Mimosoid clade	Tree	WS	low	157
				high	55
Senegalia piauhiensis	Caesalpinioideae -Mimosoid clade	Tree	WS	low	160
				high	27

We collected three individuals per plot in three plots per rainfall level, i.e., high (above 762 mm/year) and low (below 653 mm/year), for nine (9) individuals per condition and eighteen (18) in total. The individuals had a diameter at breast height (DBH) of at least 3 cm, from which wood and bark samples were collected at DBH level (±1.3 m) for the stems, and 30 cm below the soil for the roots. We standardized the size of individuals by species, always trying to collect individuals with similar DBH to avoid allometric variations. The non-destructive collection was carried out with the aid of a portable drill and chisel to collect a 2.5 × 6 cm sample containing bark and sapwood. The collected material was used for anatomical analysis and to determine wood-specific gravity (WSG). The WSG was determined by obtaining the volume of water displaced by samples of fresh wood saturated in water for 4 to 5 days (FV), subsequently dried in an oven at 100 °C for 24 h, to determine the dry mass (DM). WSG was calculated as the ratio of the two values: WSG = DM/FV (Williamson and Wiemann, 2010). All samples were placed in plastic tubes from the field to the laboratory, where the collected material was fixed in FAA_{50} for 48 h, rinsed in water, and stored in 70% ethanol for anatomical study.

1.2.3 Anatomical study

In this study, we considered bark as a group of tissues external to the cambium (Rosell, 2016) whereas the inner bark is the phloem, the cortex, when present, and the phellodermis (Rosell, Olson and Anfodillo, 2017).

To obtain histological sections, we selected small samples of wood and bark (approximately 0.5 × 0.5 cm), dehydrated in ethanol (70%–100%), and embedded in Historesin (Leica), following the manufacturer's guidelines. Transversal sections were made using a Leica RM2145 rotary microtome at 5–7 μm thickness and stained with 0,05% Toluidine Blue (O’Brien, Feder and McCully, 1964).

Fragments of wood were dissociated in a solution of acetic acid and hydrogen peroxide (1:1) in an oven at 60 °C (Franklin, 1945). After approximately 48 h, it was rinsed thoroughly in water, stained with 5% aqueous Basic Fuchsin, and mounted in 50% glycerin semi-permanent slides (Kraus *et al.*, 1998).

We proceeded with the observations and photographic registration using a Nikon Eclipse Ci light microscope coupled with a Motic MoticamPro 252 B capture system. Counts and measurements were performed using ImageJ software (Rasband, 2018).

The wood samples were also analyzed using a JEOL Model JSM-6380LV scanning electron microscope (Tokyo, Japan). The samples were previously oven-dried at 60 °C for 48 h and then sputtered with gold using Denton Vacuum Desk III (Moorestown, Nova Jersey, EUA).

1.2.4 Statistical analyses

We performed a permutation multivariate analysis of variance using distance matrices to infer the rainfall influence over the measured traits, as well as the abundance, using the "adonis2" function in the "vegan" package (Oksanen *et al.*, 2022). We considered traits as dependent variables, and rainfall, abundance, and species as independent variables. We performed a linear mixed-effects model (LMM) test for each analyzed attribute using species, plots, and individuals as fixed variables, and organ and rainfall as random variables. We used the "lmer" function of the "lme4" package (Bates *et al.*, 2015). All analyses were performed using the R software [version 4.2.0] (R Core Team, 2022).

1.3 Results

In the present study, we analyzed the variation in 15 wood and bark attributes of the stems and roots of seven legume species. The sampled populations were distributed under different rainfall levels in an SDTF.

The analysis of variance of all variables showed differences among the seven evaluated species for both stems (Df = 6, $\underline{R}^2 = 0.4814$, $p = 0.0002$) and roots (Df = 6, $R^2 = 0.48192$, $p =$

0.0002). For stems, there was also a difference in abundance (Df = 1, $R^2 = 0.02679$, $p = 0.0008$), rainfall (Df = 1, $R^2 = 0.02368$, $p = 0.001199$), and the interaction between rainfall and species (Df = 5, $R^2 = 0.04745$, $p = 0.0043991$). Root abundance (Df = 1, $R^2 = 0.01436$, $p = 0.018396$), rainfall (Df = 1, $R^2 = 0.01887$, $p = 0.005799$), and the interaction between rainfall and species (Df = 5, $R^2 = 0.03667$, $p = 0.04639$) also differed.

Among the 15 attributes evaluated in bark and wood, inter-vessel pore size (Po) showed no variation due to species, organs, or rainfall. All other attributes showed differences in species, organs, rainfall, and interactions between factors (Fig. 3) (Supplementary data S1-S3). Bark and phloem attributes responded similarly to wood and xylem attributes under environmental conditions, with 67% and 70% of the evaluated attributes showing positive results for rainfall and interactions, respectively (Fig. 4). Bark thickness (Bt) and vessel length (Vl) were the most plastic attributes in the evaluated species, varying among the seven and six species, organ, and rainfall categories, respectively (Fig. 4 and 8). Stems responded more to rainfall variations (Fig. 5–8, Supplementary data S1-S3). *P. moniliformis* and *S. piauhiensis* were the most plastic species, with nine attributes varying through organs and/or rainfall (Fig. 5–8). Contrary to the expected results, mesomorphy and vulnerability was suggested for major species and organs, except for *B. acuruana* stems and roots in both conditions and *T. molle* in the dry plots (Supplementary data S1–S3).

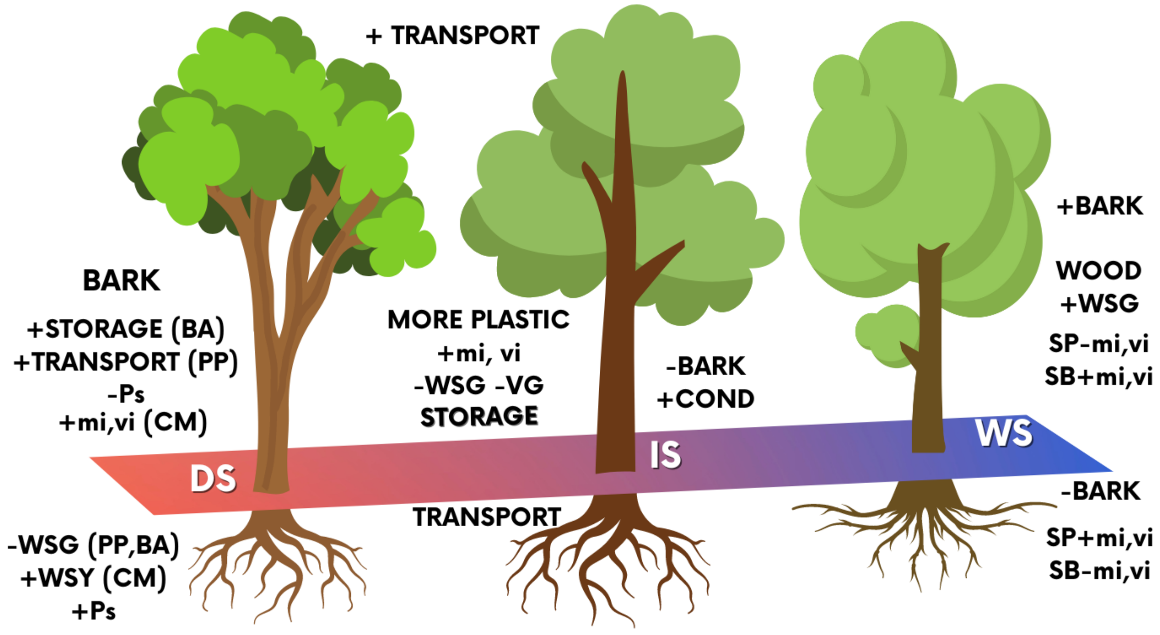

Figure 3. General behavior of legumes due to rainfall and abundance in Catimbau National Park. The species are distributed due to rainfall preference: *Cenostigma microphyllum* Mart. ex G. Don) E. Gagnon & G.P. Lewis, *Peltogyne pauciflora* Benth., and *Bauhinia acuruana* Moric. are DS. *Pityrocarpa moniliformis* (Benth.) Luckow & R. W. Jobson is IS. *Trischidium molle* (Benth.) H.E. Ireland, *Senegalia piauhiensis* (Benth.) Seigler & Ebinger, and *Senegalia bahiensis* (Benth.) Seigler & Ebinger are WS.

1.3.1 Preferentially dry species (DS)

The three species in this category, *C. microphyllum*, *P. pauciflora*, and *B. acuruana*, changed their bark and wood features. Bark thickness (Bt) tended to decrease with the rainfall increase in all roots and *P. pauciflora* stem, increasing only in *B. acuruana* stems (Fig. 4a). Despite the thickness reduction, the bark features of the species were adjusted to optimize conduction and storage. In *C. microphyllum* roots, the total phloem (Pt) (Fig. 4b) was reduced, but the sieve tube area (Sa) and length (Sl) increased in the stems and roots (Fig. 5a), optimizing both functions. *P. pauciflora* also showed reduced stem Bt (Fig. 4a), concentrating storage in the roots. Once in this organ, it also increased the total phloem thickness (Pt) and conducting phloem percentage (Pc) (Fig. 4b,c). In the stem, it decreased Pt and increased Pc, sacrificing and storing areas and prioritizing transport (Fig. 4b,c). *B. acuruana* stems was the only DS organ in which Bt increased with increasing rainfall (Fig. 4a), whereas Pt exhibited the same behavior (Fig. 4a,b). In both organs, Pc decreased with an increase in rainfall, suggesting less investment in transport and security than in storage (Fig. 4c). All DS species adjusted the WSG with an increase in rainfall (Fig. 6b): *B. acuruana* was reduced in the roots, *P. pauciflora* was reduced in both organs, and *C. microphyllum* was increased in the roots. In *B. acuruana* this change was accompanied by a decrease in Vl and an increase in inter-vessel pit size (Ps) (Fig. 7 b,c). Ps also changed in other species, with a reduction in stems and an increase in roots of *P. pauciflora* and *C. microphyllum*. The mesomorphy index (Mi) and vulnerability index (Vi) increased with increasing rainfall in *C. microphyllum* but not in the other species, similar to the vessel grouping index (Vg) (Fig. 8a-c).

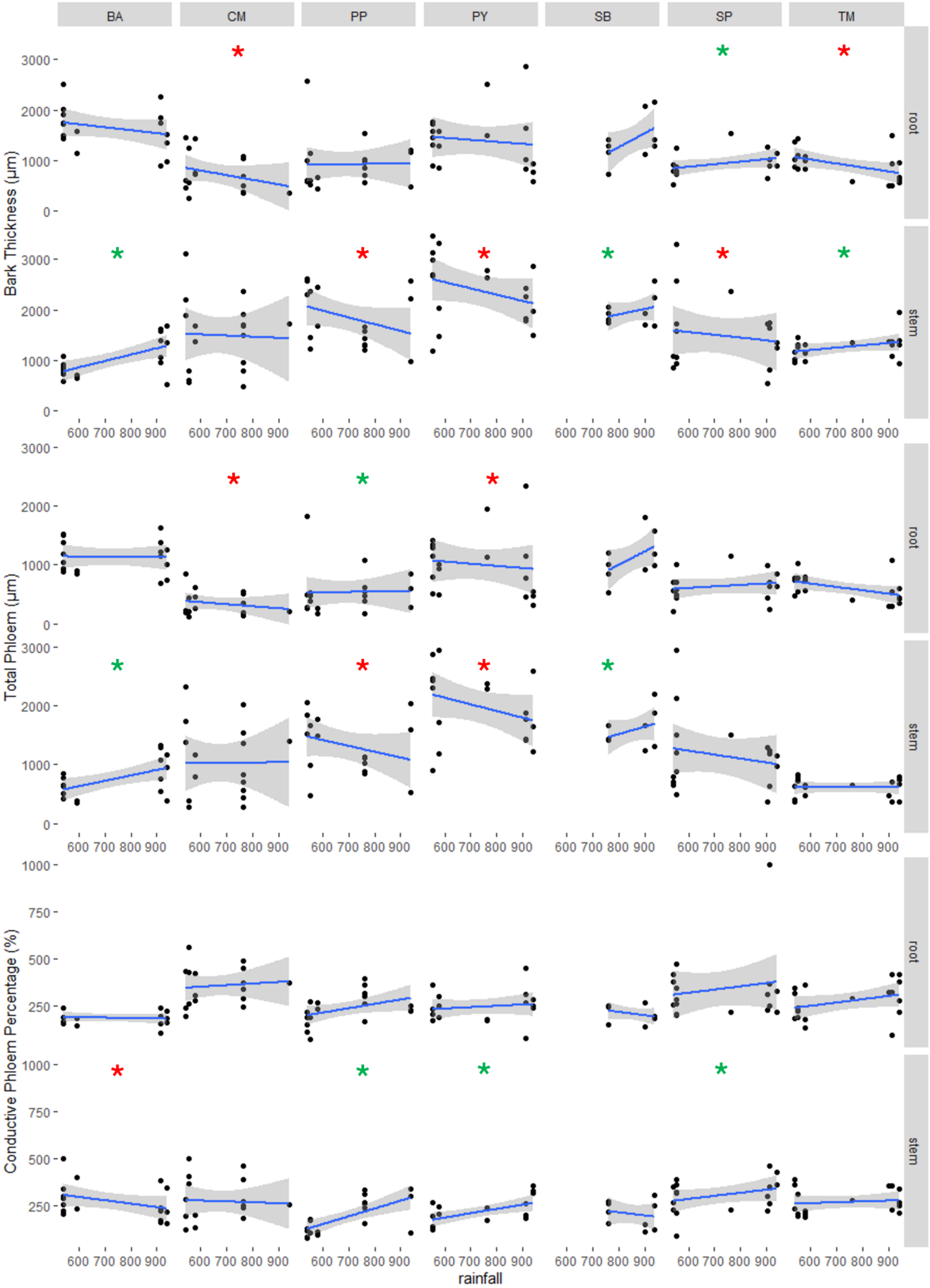
BA
CM
PP
PY
SB
SP
TM
root
stem
Bark Thickness (µm)
Total Phloem (µm)
Conductive Phloem Percentage (%)
0
1000
2000
3000
250
500
750
1000
600 700 800 900
rainfall
*

Figure 4. Species averages of **a**-bark thickness (Bt) (µm), **b**-total phloem thickness (Pt) (µm), and **c**-conductive phloem percentage (Pc) (%) in stems and roots, across the rainfall gradient, demonstrated per species, in Catimbau National Park, Pernambuco, Brazil. Data obtained from linear mixed-effect model (LMM), with eighteen (18) individuals sampled per species, being nine in each rainfall preference category, except SB (*Senegalia bahiensis*), from which only nine (9) individuals were sampled in wetter areas. The * indicates species with significant p value difference among rainfall and/or organ.

1.3.2 Indifferent species (IS)

P. moniliformis is one of the most plastic species with only 5 (five) unchanged features. In this species, the stems and roots adopted different strategies in response to increased rainfall. *P. moniliformis* stem bark (Bt) became less thick (Fig. 4a), with less Pt (Fig. 4b), more conductive phloem percentage (Pc) (Fig. 4c), and longer sieve tubes (Sl) (Fig. 5b) when compared with stems in lower rainfall areas. The roots of this species had smaller Bt (Fig. 4a) and Pt (Fig. 4b), as well as larger Pc (Fig. 4c) and sieve tube area (Sa) (Fig. 5a), and shorter sieve tube length (Fig. 5b) under the same conditions. This demonstrated the concentration of the storage effort in the stem and the investment of both organs in transport.

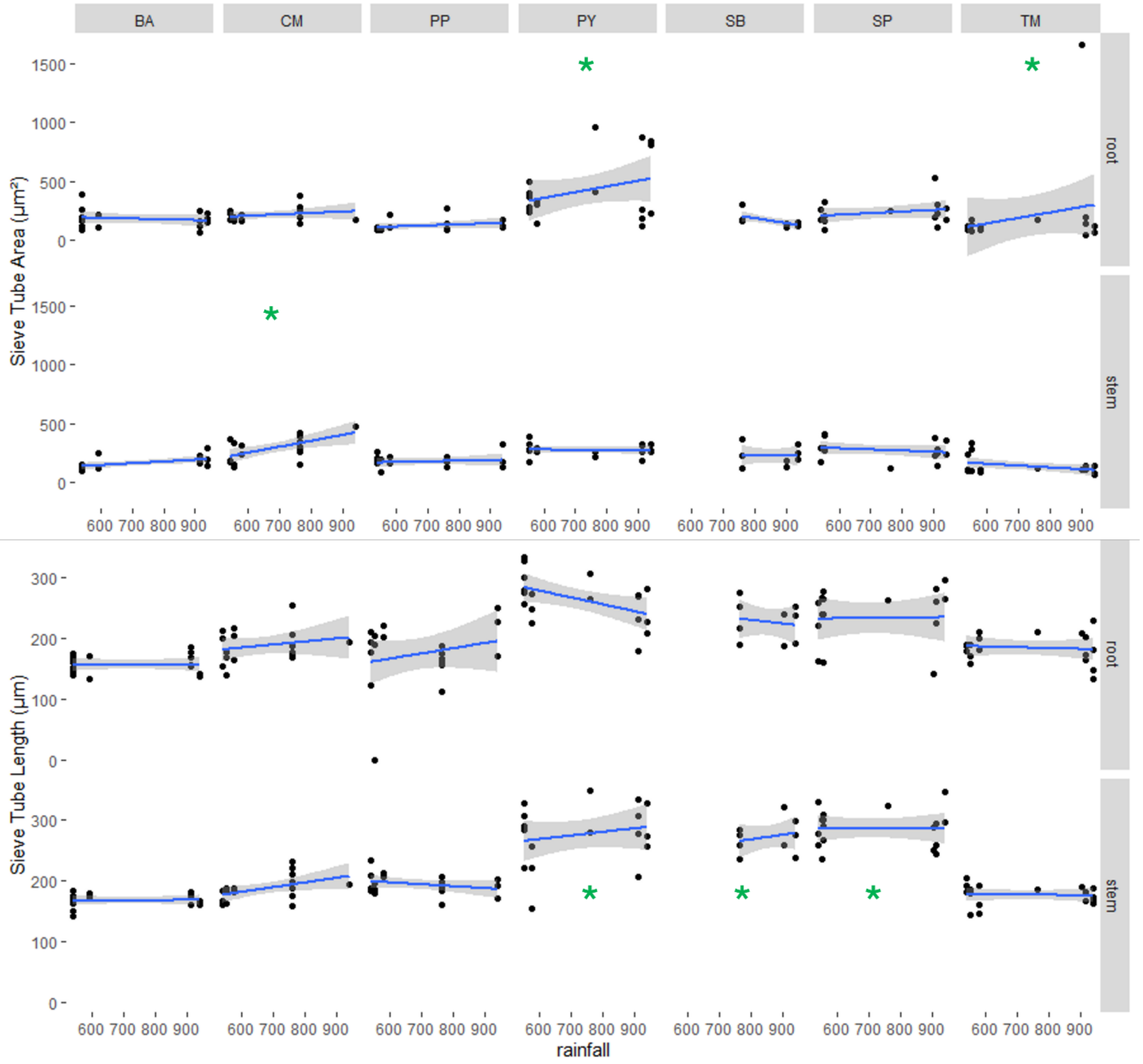

Figure 5. Species averages of **a**-sieve tube area (Sa) (µm) and **b**-sieve tube length (Sl) (µm), in stems and roots, due the rainfall gradient, demonstrated per species, in Catimbau National Park, Pernambuco, Brazil. Data obtained from linear mixed-effect model (LMM), with eighteen (18) individuals sampled per species, being nine in each rainfall preference category, except SB (*Senegalia bahiensis*), from which only nine (9) individuals were sampled in wetter areas. The * indicates species with significant p value difference among rainfall and/or organ.

Wood-specific gravity (WSG) varied among organs and rainfall in this species. The stems and roots showed reduced WSG with increasing rainfall (Fig. 6b). Changes occurred with increasing Vl in both organs (Fig. 7b). The mesomorphy (Mi) and vulnerability indices (Vi) increased in *P. pauciflora* stems as a function of rainfall (Fig. 8a,b), whereas the vessel grouping index (Vg) decreased under the same conditions (Fig. 8c).

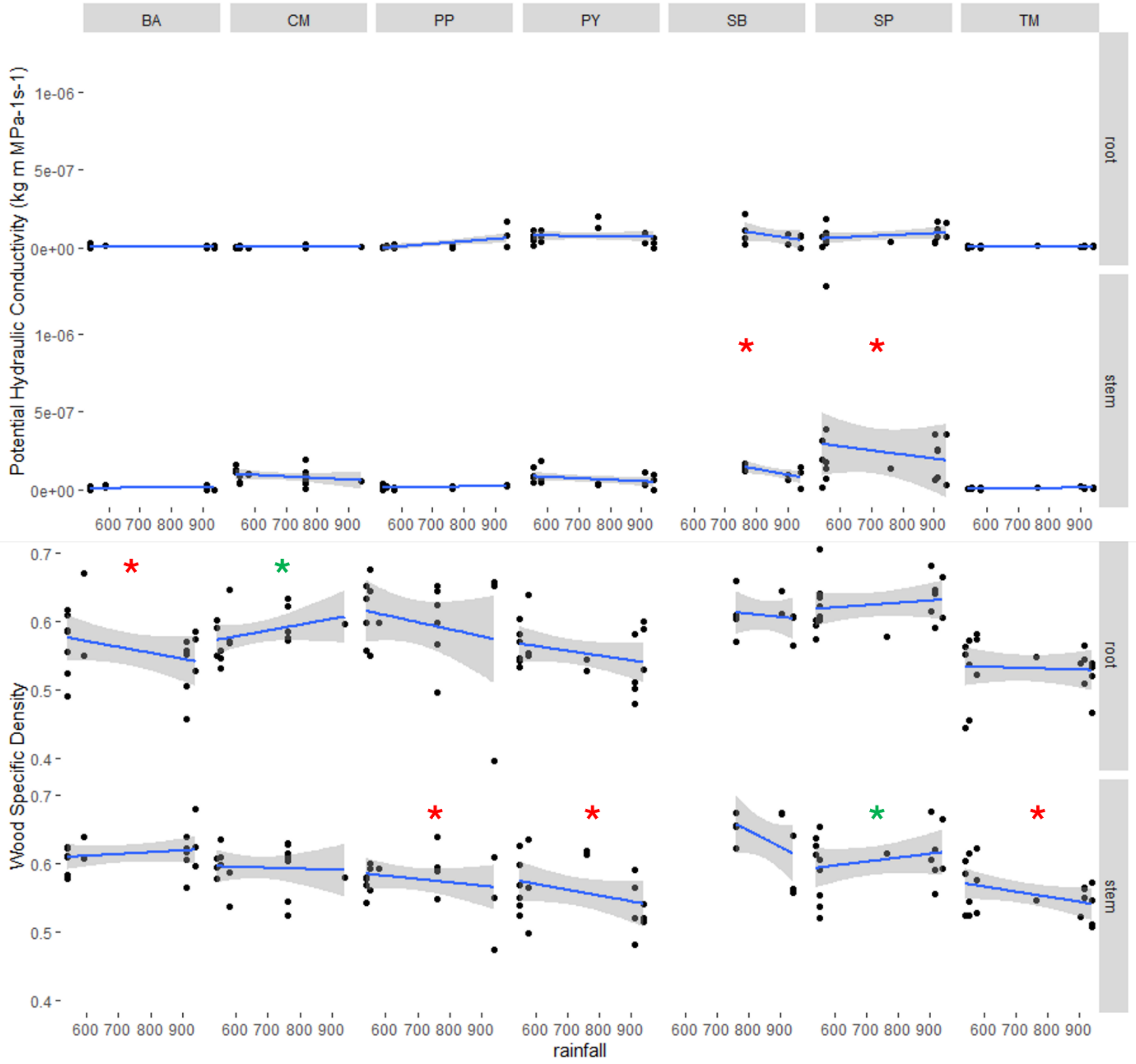

Figure 6. Species averages of a- potencial hydraulic conductivity (Kp) (kg m MPa^{-1} s^{-1}) and b- wood specific gravity (WSG) in stems and roots, across the rainfall gradient, demonstrated per species, in Catimbau National Park, Pernambuco, Brazil. Data obtained from linear mixed-effect model (LMM), with eighteen (18) individuals sampled per species, being nine in each rainfall preference category, except SB (*Senegalia bahiensis*), from which only nine (9) individuals were sampled in wetter areas. The * indicates species with significant p value difference among rainfall and/or organ.

1.3.3 Preferentially wet species (WS)

More wood than bark attributes changed in WS. This occurred in both *Senegalia* species, while *T. molle* had the same number of traits varying between bark and wood, and similar behavior was observed in DS and IS: stems increased the bark thickness (Bt) and reduced the sieve tube area (Sa), and the opposite occurred in roots (Fig. 4a, 5a). *S. bahiensis* increased Bt and Pt but had no difference in Pc, unlike *S. piauhiensis*, which decreased stem Bt and increased root Bt but had no statistical difference in Pt but increased Pc for both organs (Fig. 4a,b). None of these species presented differences in Sa, but *S. piauhiensis* had the longest sieve tubes among all the analyzed species, and *S. bahiensis* adjusted differently in each organ, increasing in stems and reducing in roots (Fig. 5b).

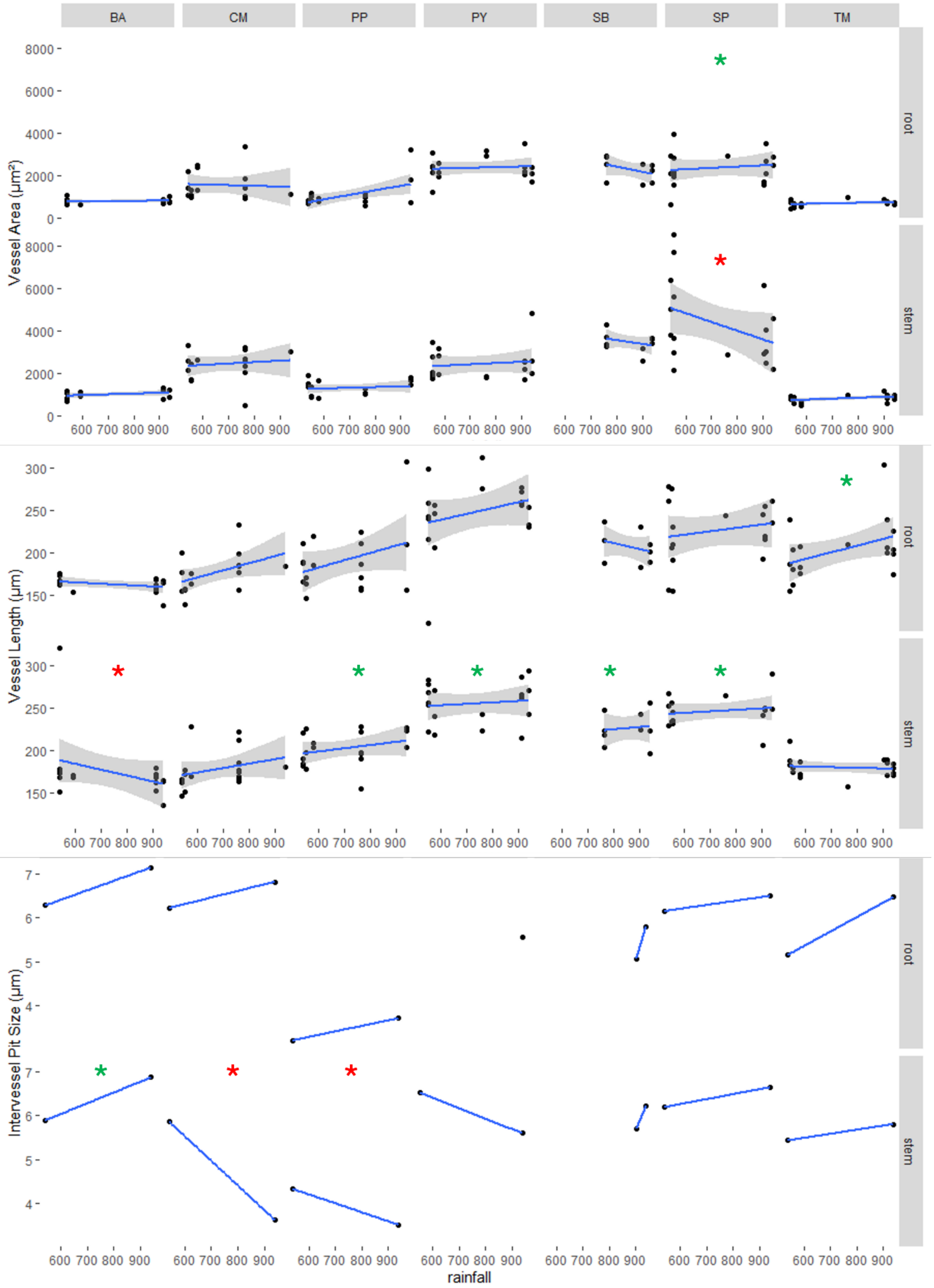
BA
CM
PP
PY
SB
SP
TM
root
stem
Vessel Area (µm²)
0
2000
4000
6000
8000
Vessel Length (µm)
150
200
250
300
Intervessel Pit Size (µm)
4
5
6
7
600 700 800 900
rainfall
*

Figure 7. Species averages of **a**-vessel tangential area (Va) (µm), **b**-vessel length (Vl) (µm) and **c**- intervessel pit size (µm) in stems and roots, across the rainfall gradient, demonstrated per species, in Catimbau National Park, Pernambuco, Brazil. Data obtained from linear mixed-effect model (LMM), with eighteen (18) individuals sampled per species, being nine in each rainfall preference category, except SB (*Senegalia bahiensis*), from which only nine (9) individuals were sampled in wetter areas. The * indicates species with significant p value difference among rainfall and/or organ.

WSG, which was greater in stems, also decreased with an increase in rainfall in this species for both organs (Fig. 6b). These changes demonstrated the preferential stem investment in this species, concentrating resources on its structure and storage.

S. piauhiensis and *S. bahiensis* showed opposite behaviors when comparing the organs of the two species. *S. piauhiensis* stems reduced Mi (Fig. 8a), Vi (Fig. 8b), potential hydraulic conductivity (Kp) (Fig. 6a) and vessel area (Va) (Fig. 7a) with rainfall raise, while roots discretely increased all these features plus conductive phloem percentage (Pc) (Fig. 4c) and sieve tube length (Sl) (Fig. 5b). In this species, WSG and Vl increased with rainfall in both organs (Fig. 6a, 7b). In contrast, the Mi (Fig. 8a), Vi (Fig. 8b), Sl (Fig. 5b), and Vl (Fig. 7b) increased with rainfall in *S. bahiensis* stems and decreased in roots. In this species, Bt (Fig. 4a) and Pt (Fig. 4b) increased and Kp decreased (Fig. 6a) with rainfall in both organs. The opposite strategies for *Senegalia* species demonstrated security investment in *S. piauhiensis* wood stem and *S. bahiensis* root wood, while both roots also invest in phloem conductivity efficiency.

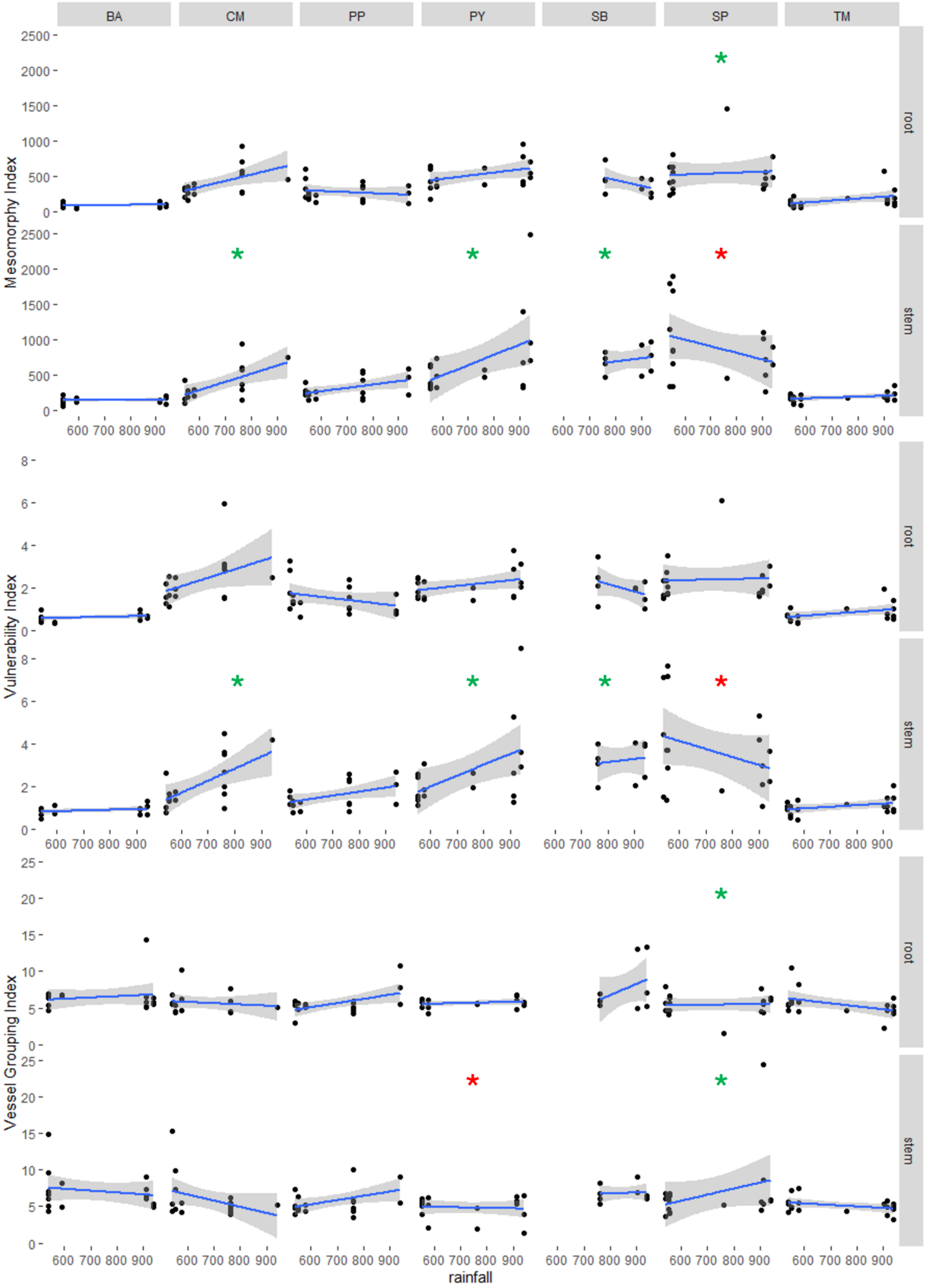
BA
CM
PP
PY
SB
SP
TM
root
stem
Mesomorphy Index
0
500
1000
1500
2000
2500
Vulnerability Index
0
2
4
6
8
Vessel Grouping Index
0
5
10
15
20
25
600 700 800 900
rainfall
*

Figure 8. Species averages of **a**-mesomorphy index (Mi), **b**-vulnerability index (Vi) and **c**-vessel grouping index (Vg) in stems and roots, across the rainfall gradient, demonstrated per species, in Catimbau National Park, Pernambuco, Brazil. Data obtained from linear mixed-effect model (LMM), with eighteen (18) individuals sampled per species, being nine in each rainfall preference category, except SB (*Senegalia bahiensis*), from which only nine (9) individuals were sampled in wetter areas. The * indicates species with significant p value difference among rainfall and/or organ.

1.4 Discussion

Our results reveal different behaviors among legume species in a SDTF under different conditions of water availability. These findings suggest that the species optimize their growth and permanence depending on water availability and changing morphological and/or anatomical parameters. Thus, abundant species in places with low water availability, when under high water availability, invest in storage and reduce protection measures such as root bark thickness and phloem traits. Furthermore, a greater transport capacity via the root phloem was suggested. Preferentially DS reduced bark thickness in the roots at higher rainfall levels, whereas *P. pauciflora* improves storage in the roots, *C. microphyllum* preferred to invest in phloem transport efficiency in the same organs, and *B. acuruana* increases storage in both organs. Under the same conditions, the IS *P. moniliformis* focuses on storage in stems and optimizes phloem transport in both organs. Preferentially WS has more changes in wood than the other groups, with *S. bahiensis* investing in traits changes for greater security in roots and *S. piauhiensis* in stems. *T. molle* adopt a strategy like that of DS: increasing storage in the stem and optimizing transport in the roots. In general, all analyzed species showed decreased wood density, indicating investment in growing under better water availability conditions.

The accumulation of carbohydrates and water is important for supporting metabolic processes in moments of scarcity and occurs in the parenchymatic tissues. This is particularly important in seasonal environments and in deciduous species that need to flush and support dry seasons (Rosell *et al.*, 2020). Except for *C. microphyllum*, *P. palciflora, P. moniliformis*, and *S. piauhiensis*, bark thickness increased when more water was available, and these species adjusted the total phloem thickness and conductive phloem percentage, increasing its efficiency. This behavior suggested that this species invests in areas for storage and transport when they have more resources. The opposite was observed in areas with less rainfall, which may have compromised the response after the dry season. The four cited species, which have thicker bark in dry areas, demonstrated coherent behavior; once they are, respectively, the first and second most abundant species in these areas, the more widely distributed species in general, and *S. piauhiensis*, where it occurs in the stem only, tend to invest in stem security.

Commonly neglected in studies related to plant–water relationships, the phloem has been more closely observed in recent years (Salmon *et al.*, 2018). It is the main transport route for long-distance photosynthates in plants and is regulated, according to Münch (1930), by the difference in hydrostatic pressure between the source (leaves) and drain organs (stem and root). It occurs throughout the body of the vegetable (Van Bel, 2003) and requires a large amount of energy, consuming part of the photoassimilates it transports (Willenbrink, 1957). The high investment and plasticity observed in the phloem attributes in this study corroborate the importance of this tissue in xerophytes and highlight its environmental sensitivity and response capacity, contrary to expectations. In general, the literature indicates that functional traits linked to phloem structure and patterns are more stable than xylem patterns, reflecting, comparatively, between tissues and evolutionary history rather than current environmental variations (Rosell, 2016; Prislan *et al.*, 2018).

Little is known about phloem responses to drought; however, the interdependence of xylem and phloem in maintaining flow under these conditions is known (Sevanto, 2014). The water potential in xylem can be affected by the transpiration rate, hydraulic conductance, or apoplastic osmolytes, and its variation influences the hydrostatic pressure in the phloem.

Thus, the local water potential exerts a significant effect on pressure gradients in the phloem, with consequences for carbon partitioning (Thorpe *et al.*, 2005). The connection between the two tissues is mainly formed by the radial parenchyma, which is continuous on both sides of the cambium (Pfautsch *et al.*, 2015). Therefore, reductions in xylem conductance are related to limitations in the productivity and phloem-carrying capacity of carbohydrates (Lens *et al.*, 2011; Epron, Dannoura and Hölttä, 2019). Dannoura et al. (2019) reported a reduction in the osmotic potential of the leaves as well as in the radius of the sieve tube elements in *Fagus sylvatica* under stress. This radius reduction led to a reduction in the phloem conductance in the stem. The authors concluded that prolonged droughts affect conductivity capacity through changes in the phloem anatomy. In addition, flow reduction reduces the effect of the hydrostatic pressure difference between the source and drain organs. The anatomical changes observed include a reduction in the percentage of conductive phloem, causing a reduction in the conductivity capacity of the tissue (Dannoura et al., 2019), similar to what we found here.

In lower rainfall areas, our species presented thicker bark but smaller conductive phloem percentage, which suggested a major investment in coating, storage, and protection, or a limited investment in transport. Since the apoplastic pathway is the main route of carbohydrate mobilization in mature tissues (Van, Justus and Van Bel, 1990; Thorpe *et al.*, 2005), these attributes may be very effective and important in the reserve, maintenance, and security of conductive tissues in plants subjected to hydraulic stress due to a lack of water. The rainfall responses of the evaluated species in the SDTF may suggest bark and phloem sensitivity to the environment, and it can indicate some difficulty in tolerating different climate change scenarios. However, once the conducting phloem corresponds to the newer part of the whole tissue, it is directly related to recent cambium activity, which in turn varies with the rainfall of the period. The SDTF may change during pluriannual cycles, which suggested that different results and bark responses may occur in different years. A long-term study may be necessary to understand these dynamics and relationships, which is a limitation of the present study.

Under low water availability, plants also adjust other properties of the xylem, promoting changes based on measurable parameters, such as vessel density per area and vessel composition (from many narrow to a few wide) (Zanne *et al.*, 2010). Because of effective communication among vessels, the xylem may change the grouping and density of vessels to create a net of support where different sizes of cells act together. Narrower and safer vessels maintain pressure to maintain the group filled with water, whereas wider and more efficient vessels promote more transport when conditions are favorable. In an anatomical study of stem wood with four species, Vieira and Lisi (2019), despite different functional groups of STDF, did not observe variations in qualitative attributes as a function of environmental conditions. However, the authors also found a strong correlation between variations in the quantitative parameters of the secondary xylem and environmental conditions. In the present study, the main environmental factors related to anatomical variations were temperature and precipitation, which affected and generated different responses among the functional groups. We also did not find many differences between the vessel grouping indices, which only varied in *P. pauciflora* compared to that in the other species, and between organs in *S. piauhiensis*. Thus, the species seems to be able to adjust xylem attributes in number but not in structure. This might demonstrate the high adaptability of these species to the environment and the efficiency of their hydraulic architecture.

The study of attributes at the cellular level allows for evaluating functional and structural scales, collaborating more accurately with an understanding of hydraulic conductivity dynamics in plants (Fonti and Jansen, 2012). As mentioned before, the occurrence of narrow vessels is common and expected in dry environments (Alves and Angyalossy-Alfonso, 2000; Evert and Eichhorn, 2006; Sonsin *et al.*, 2012). The minor tangential area promotes more tension to maintain the integrity of the water column under higher vapor pressures, which may cause cavitation and/or embolism events (Hacke and Sperry, 2001; Bucci *et al.*, 2004). This factor, combined with a longer length, optimizes the efficiency and safety of conductivity in the tissues of species subjected to stress due to a lack of water. These characteristics were observed in all the studied species, considering the values of Va and Vl. Although most studied species increased Vl, *B. acuruana* reduced it because of increased rainfall in both organs. Only *S. piauhiensis* presented differences in Va values, which differed between organs, with a reduction in stems and a discreet rise in roots. The small variation in Va indicates that other traits of the fibers or parenchyma may be related to density, as presented below.

Anatomical changes directly affect wood density, an attribute related to the growth of individuals, architecture, and mortality of species, its performance in environmental gradients and resource storage, and, therefore, the structure of communities (Fortunel, Ruelle, *et al.*, 2014). Wood density is highly influenced by the wall thickness × lumen ratio and increases with cavitation resistance (Lens *et al.*, 2011), which, in turn, is determined by the quantity and density of pits, quality (membrane thickness, size, and structure), and quantity and type of tissue surrounding the vessel (Lourenço *et al.*, 2022). According to Zanne et al. (2010), WSG is a good predictor of mechanical strength because the lumen spaces are disregarded in this measure. In the present study, WSG varied in almost all species owing to rainfall or even among species, not only *S. bahiensis*. In addition, except for *S. piauhiensis* and *C. microphyllum* roots, all other species had denser wood in dryer areas. Furthermore, *Senegalia* invested in security even in wetter areas, producing strengthened and safer wood. As this trait is widely used in functional studies, our data also contributes to studies performed with species and genera distributed worldwide in different biomes.

Inter-vessel pits promote communication between neighboring vessels, allowing the exchange of content and balance of the tissue's internal osmotic pressure (Jansen, Smets and Baas, 1998). In addition, they increase the adhesion of water molecules to the vessel wall, reducing the risk of column breakage during periods of lower vapor pressure and, therefore, the risk of embolism and cavitation (Alves and Angyalossy-Alfonso, 2000). In addition, the presence of vestured pits, which are common in Fabaceae species, was observed in this study and may have contributed to the success of the family in the Caatinga. The vested pits increase the adhesion of water molecules to the wall, thereby increasing the security of the vessels. *B. acuruana* is the only species that does not exhibit vestured pits, which is a feature of the genus (Quirk and Miller, 1985). All species presented minute inter-vessel pits (IAWA Commitee, 1989), vestured or not, that varied due to rainfall only in the DS. *B. acuruana* reduced pit size with increasing rainfall, whereas *C. microphyllum* and *P. pauciflora* reduced pit size in the stems and increased pit size in the roots. Once these last two species are invested in stem transport, the reduction in inter-vessel pit size may be a way of providing more secure vessels with less risk of air bubble entry. In contrast, larger pits in the roots provide more communication between vessels and efficiency in transport. The reduction observed in both organs of *B. acuruana* corroborates the conservative behavior adopted by the species. These results indicate the high efficiency of these structures and their phylogenetic relationships.

Four of the seven evaluated species presented differences in the Mi and Vi indices. *C. microphyllum, P. moniliformis, S. bahiensis* stems, and *S. piauhiensis* roots increased with increasing rainfall, whereas *S. bahiensis* roots and *S. piauhiensis* stems decreased. The construction of less dense wood under wetter conditions, as mentioned previously, followed by changes in Mi and Vi suggested faster growth, producing a less secure xylem. This is important for the plant to establish itself and occupy niches in the environment when conditions are favorable; however, it produces tissues and structures that are less able to withstand greater water restrictions.

1.5 Conclusions

The results obtained in the present study indicated the importance of bark and phloem attributes in legumes in an SDTF, as these tissues demonstrated a high sensitivity and adaptation capacity to rainfall variation. The xylem variation indicated high adaptation of species to environmental conditions and suggested that small changes, as observed, may provide a sufficient increase in efficiency and/or tolerance to stress. Our results also demonstrated the necessity of evaluating roots, their features, and behaviors, such as resprouting capacity, to effectively understand the role of the organ and, consequently, of the species in the community and its capacity to maintain more difficult future situations.

1.6 Abbreviations

Bt- Bark thickness
DBH- Diameter at breast height
DM- Dry mass
DS- Preferentially dry species
FAA$_{50}$- Formalin Acid Alcohol
FV- Fresh volume
IS- Indifferent species
Kp- Potential hydraulic conductivity
LMM- Linear mixed-effect model
Mi- Mesomorphy index
Pc- Conducting phloem percentage
Ps- Intervessel pit size
Po- Intervessel pore size
Pt- Total phloem thickness
Sa- Sieve tube area
Sl- Sieve tube length
Va- Vessel tangential area
Vd- Vessel density
Vg- Vessel group index
Vi- Vulnerability index
Vl- Vessel length
WS- Preferentially wet species
WSG- Wood specific gravity

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1.7 Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Tamires Soares Yule, Mauro Guida Santos and Rosani do Carmo de Oliveira Arruda. The first draft of the manuscript was written by Tamires Soares Yule and all authors commented on previous versions of the manuscript.

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1.9 Competing interests

The authors declare no conflict of interest.

2.0 Data availability

Data will be made available on request.

2.1 References

Alves, E. S. and Angyalossy-Alfonso, V., 2000. 'Ecological trends in the wood anatomy of some Brazilian species. 1. Growth rings and vessels', IAWA JOURNAL, 21(1), pp. 3–30. doi: 10.1078/0367-2530-0058.

Anderegg, W. R. L. et al., 2015. 'Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models', Science, 349(6247), pp. 528–532. doi: 10.1126/science.aab1833.

Andrade, E. M. de et al. , 2017. 'Water as Capital and Its Uses in the Caatinga', in Silva, J. M. C. da, Leal, I. R., and Tabarelli, M. (eds) Caatinga. Cham: Springer International Publishing, pp. 281–302. doi: 10.1007/978-3-319-68339-3_10.

Aroca, R., Porcel, R. and Ruiz-Lozano, J. M. , 2012. 'Regulation of root water uptake under abiotic stress conditions', Journal of experimental botany, 63(1), pp. 43–57. doi: 10.1093/jxb/err266.

Van Bel, A. J. E. , 2003. 'Transport Phloem : Low Profile , High Impact', Plant Physiology, 131(April), pp. 1509–1510. doi: 10.1104/pp.131.4.1509.

Brodribb, T. J., Mcadam, S. A. and Carins Murphy, M. R. , 2017. 'Xylem and stomata, coordinated through time and space', Plant Cell and Environment, 40, pp. 872–880. doi: 10.1111/pce.12817.

Brunner, I. et al. , 2015. 'How tree roots respond to drought', Frontiers in Plant Science, 6(July), pp. 1–16. doi: 10.3389/fpls.2015.00547.

Bucci, S. J. et al. , 2004.'Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant', Tree Physiology, 24(8), pp. 891–899. doi: 10.1093/treephys/24.8.891.

Carlquist, S. , 1977. 'Ecological factors in wood evolution: A floristic approach', American Journal of Botany, 64(7), pp. 887–896. doi: 10.1002/j.1537-2197.1977.tb11932.x.

Carlquist, S. , 2001. ‘Comparative wood anatmy: Systematic, ecological, and evolutionary aspects of dicotyledon wood’. Available at: http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=BRE.xis&method=post&formato=2&cantidad=1&expresion=mfn=005228 (Accessed: 4 January 2022).

Cavalcanti, L. C. de S. and Corrêa, A. C. de B. , 2014. ‘Pluviosidade no parque nacional do Catimbau (Pernambuco): seus condicionantes e seus efeitos sobre a paisagem’, Geografia, 23(2), pp. 133–156.

Chaves, M. M., Flexas, J. and Pinheiro, C. , 2009. ‘Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell’, Annals of Botany, 103(4), pp. 551–560. doi: 10.1093/aob/mcn125.

Cosme, L. H. M. et al. , 2017. ‘The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest’, New Phytologist, pp. 113–125. doi: 10.1111/nph.14508.

Dannoura, M. et al. , 2018. ‘The impact of prolonged drought on phloem anatomy and phloem transport in young beech trees’, Tree Physiology, 39(2), pp. 201–210. doi: 10.1093/treephys/tpy070.

Davis, S. D., Sperry, J. S. and Hacke, U. G. , 1999. ‘The relationship between xylem conduit diameter and cavitation caused by freezing’, American Journal of Botany, 86(10), pp. 1367–1372.

Epron, D., Dannoura, M. and Hölttä, T. , 2019. ‘Introduction to the invited issue on phloem function and dysfunction’, Tree Physiology, 39(2), pp. 167–172. doi: 10.1093/treephys/tpz007.

Evert, R. F. and Eichhorn, S. E. , 2006. Esau’s Plant Anatomy: Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development, 3rd Edition. Available at: http://www.amazon.com/exec/obidos/redirect?tag=citeulike07-

20&path=ASIN/0471738433.

Falcão, H. M. et al. , 2015. ‘Phenotypic plasticity and ecophysiological strategies in a tropical dry forest chronosequence: A study case with Poincianella pyramidalis’, Forest Ecology and Management, 340, pp. 62–69. doi: 10.1016/j.foreco.2014.12.029.

Fonti, P. and Jansen, S. , 2012. ‘Xylem plasticity in response to climate’, New Phytologist, 195(4), pp. 734–736. doi: 10.1111/j.1469-8137.2012.04252.x.

Fortunel, C., Paine, C. E. T., et al. , 2014. ‘Environmental factors predict community functional composition in Amazonian forests’, Journal of Ecology, 102(1), pp. 145–155. doi: 10.1111/1365-2745.12160.

Fortunel, C., Ruelle, J., et al. , 2014. ‘Wood specific gravity and anatomy of branches and roots in 113\rAmazonian rainforest tree species across environmental\rgradients’, New Phytologist, 202, pp. 79–94. doi: 10.1111/nph.12632.

Franklin, G. L. , 1945. ‘Preparation of Thin Sections of Synthetic Resins and Wood-Resin Composites, and a New Macerating Method for Wood’, Nature, 155(3924), pp. 51–51. doi: 10.1038/155051a0.

Hacke, U. G. and Sperry, J. S. , 2001. ‘Functional and ecological xylem anatomy’, Perspectives in Plant Ecology, Evolution and Systematics, 4, pp. 97–115.

IAWA Commitee , 1989. ‘IAWA list of microscopic features for hardwood identification’, Iawa Bulletin n.s, 10(3), pp. 219–332. doi: 10.2307/4110625.

IBGE , 2002. ‘Mapa de Solos Brasileiros - IBGE .pdf’.

IBGE , 2012. Manual Técnico da Vegetação Brasileira. doi: ISSN 0101-4234.

Jansen, S., Smets, E. and Baas, P. , 1998. ‘Vestures in woody plants: A review’, IAWA Journal. International Association of Wood Anatomists, pp. 347–382. doi: 10.1163/22941932-90000658.

Kottek, M. et al. , 2006. ‘World Map of Köppen − Geiger Climate Classification’, Meteorol.

Z., 15, pp. 259–263. doi: 10.1127/0941-2948/2006/0130.

Kraus, J. E. et al. , 1998. ‘Astra blue and basic fuchsin double staining of plant materials’, Biotechnic and Histochemistry, 73(5), pp. 235–243. doi: 10.3109/10520299809141117.

Lens, F. et al. , 2011. ‘Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer’, New Phytologist, 190(3), pp. 709–723. doi: 10.1111/j.1469-8137.2010.03518.x.

Lourenço, J. et al. , 2022. ‘Hydraulic tradeoffs underlie local variation in tropical forest functional diversity and sensitivity to drought’, New Phytologist, 234(1), pp. 50–63. doi: 10.1111/nph.17944.

Meinzer, F. C. et al. , 2009. ‘Xylem hydraulic safety margins in woody plants: Coordination of stomatal control of xylem tension with hydraulic capacitance’, Functional Ecology, 23(5), pp. 922–930. doi: 10.1111/J.1365-2435.2009.01577.X.

Milburn, J. A. , 1966. ‘The conduction of sap’, Planta, 69(1), pp. 34–42. doi: 10.1007/bf00380208.

O’Brien, T. P., Feder, N. and McCully, M. E. , 1964. ‘Polychromatic staining of plant cell walls by toluidine blue O’, Protoplasma, 59(2), pp. 368–373. doi: 10.1007/BF01248568.

Oliveira, F. M. P. et al. , 2021. Plant protection services mediated by extrafloral nectaries decline with aridity but are not influenced by chronic anthropogenic disturbance in Brazilian Caatinga, Journal of Ecology. doi: 10.1111/1365-2745.13469.

Pfautsch, S. et al. , 2015. ‘Phloem as Capacitor: Radial Transfer of Water into Xylem of Tree Stems Occurs via Symplastic Transport in Ray Parenchyma’, Plant Physiology, 167(3), pp. 963–971. doi: 10.1104/pp.114.254581.

Plourde, B. T., Boukili, V. K. and Chazdon, R. L. , 2015. ‘Radial changes in wood specific gravity of tropical trees: Inter- and intraspecific variation during secondary succession’, Functional Ecology, 29(1), pp. 111–120. doi: 10.1111/1365-2435.12305.

Poorter, L. et al. , 2010. ‘The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species’, New Phytologist, 185(2), pp. 481–492. doi: 10.1111/j.1469-8137.2009.03092.x.

Prado, D. E. , 1991. ‘A critical evaluation of the floristic links between Chaco and Caatingas vegetation in South America’, p. 283. Available at: http://hdl.handle.net/10023/14121%0Ahttps://research-repository.st-andrews.ac.uk/handle/10023/14121.

Prado, D. E. , 2003. ‘As Caatingas da América do Sul’, in Ecologia e conservacão da Caatinga, pp. 3–73.

Prislan, P. et al. , 2018. ‘Intra-annual dynamics of phloem formation and ultrastructural changes in sieve tubes in Fagus sylvatica’, Tree Physiology, 39(2), pp. 262–274. doi: 10.1093/treephys/tpy102.

Quirk, J. T. and Miller, R. B. , 1985. ‘Vestured Pits in the Tribe Cassieae Bronn (Leguminosae)’, IAWA Journal, 6(3), pp. 200–212. doi: 10.1163/22941932-90000939.

Rasband, W. , 2018. ‘ImageJ’, p. U. S. National Institutes of Health, Bethesda, Mar.

Reich, P. B. , 2014. ‘The world-wide “fast-slow” plant economics spectrum: A traits manifesto’, Journal of Ecology, 102(2), pp. 275–301. doi: 10.1111/1365-2745.12211.

Rito, K. F. et al. , 2017. ‘Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation’, Journal of Ecology, 105(3), pp. 828–838. doi: 10.1111/1365-2745.12712.

Rosell, J. A. , 2016. ‘Bark thickness across the angiosperms: More than just fire’, New Phytologist, 211(1), pp. 90–102. doi: 10.1111/nph.13889.

Rosell, J. A. et al. , 2020. ‘Inner bark as a crucial tissue for non-structural carbohydrate storage across three tropical woody plant communities’, Plant, Cell & Environment, 44(1), pp. 156–170. doi: 10.1111/pce.13903.

Rosell, J. A., Olson, M. E. and Anfodillo, T. , 2017. ‘Scaling of Xylem Vessel Diameter with Plant Size: Causes, Predictions, and Outstanding Questions’, Current Forestry Reports. doi: 10.1007/s40725-017-0049-0.

Salmon, Y. et al. , 2018. ‘Drought impacts on tree phloem: From cell-level responses to ecological significance’, Tree Physiology, 39(2), pp. 173–191. doi: 10.1093/treephys/tpy153.

Santos, M. G. et al. , 2014. ‘Caatinga, the Brazilian dry tropical forest: Can it tolerate climate changes?’, Theoretical and Experimental Plant Physiology, 26(1), pp. 83–99. doi: 10.1007/s40626-014-0008-0.

Seddon, A. W. R. et al. , 2016. ‘Sensitivity of global terrestrial ecosystems to climate variability’, Nature, 531(7593), pp. 229–232. doi: 10.1038/nature16986.

Sevanto, S. , 2014. ‘Phloem transport and drought’, Journal of Experimental Botany, 65(7), pp. 1751–1759. doi: 10.1093/jxb/ert467.

Silva, P. F. da et al. , 2017. ‘Seasonal patterns of carbon dioxide, water and energy fluxes over the Caatinga and grassland in the semi-arid region of Brazil’, Journal of Arid Environments. doi: 10.1016/j.jaridenv.2017.09.003.

Sonsin, J. O. et al. , 2012. ‘A comparison of the wood anatomy of 11 species from two cerrado habitats (cerrado s.s. and adjacent gallery forest)’, Botanical Journal of the Linnean Society, 170(2), pp. 257–276. doi: 10.1111/j.1095-8339.2012.01282.x.

Thorpe, M. et al. , 2005. The Stem Apoplast: A Potential Communication Channel In Plant Growth Regulation, Vascular Transport in Plants. Elsevier Inc. doi: 10.1016/B978-012088457-5/50012-5.

Torres, R. R., Lapola, D. M. and Gamarra, N. L. R. , 2017. ‘Future Climate Change in the Caatinga’, in Silva, J. M. C. da, Leal, I. R., and Tabarelli, M. (eds) Caatinga. Cham: Springer International Publishing, pp. 383–410. doi: 10.1007/978-3-319-68339-3_15.

Van, A. J. E., Justus, B. and Van Bel, A. J. E. , 1990. ‘Xylem-Phloem Exchange Via the Rays: The Undervalued Route of Transport Carbohydrate transport, driving forces in the phloem and phloem-associated plant diseases and long-distance signals View project Arabidopsis-phytoplasma interactions View project Xylem-Phloem Exchange Via the Rays: The Undervalued Route of Transport’, Article in Journal of Experimental Botany, 41(227), pp. 631–644. doi: 10.1093/jxb/41.6.631.

Vieira, A. J. R. and Lisi, C. S. , 2019. ‘Caatinga Tree Wood Anatomy: Perspectives on Use and Conservation’, Floresta e Ambiente, 26(2). doi: 10.1590/2179-8087.099717.

Willenbrink, J. , 1957. ‘Über die Hemmung des Stofftransports in den Siebröhren durch lokale Inaktivierung verschiedener Atmungsenzyme’, Planta, 48(3), pp. 269–342. doi: 10.1007/BF01944847.

Williamson, G. B. and Wiemann, M. C. , 2010. ‘Measuring wood specific gravity...correctly’, American Journal of Botany, 97(3), pp. 519–524. doi: 10.3732/ajb.0900243.

Woodcock, D. W. , 2000. ‘Wood Specific Gravity of Trees and Forest Types in’, Acta Amazonica, 30(4), pp. 589–599.

Wright, S. J. , 2010. ‘The future of tropical forests’, Annals of the New York Academy of Sciences, 1195, pp. 1–27. doi: 10.1111/j.1749-6632.2010.05455.x.

Wu, M. et al. , 2020. ‘Root xylem in three woody angiosperm species is not more vulnerable to embolism than stem xylem’, Plant and Soil, 450(1–2), pp. 479–495. doi: 10.1007/s11104-020-04525-0.

Zanne, A. E. et al. , 2010. ‘Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity’, American Journal of Botany, 97(2), pp. 207–215. doi: 10.3732/ajb.0900178.

Attachments

Data S1. Stem descriptive statistics of wood and bark attributes in Legumes in Catimbau National Park, Pernambuco, Brazil. There are fourteen attributes: wood specific gravity (WSG), vessel tangential area (Va) (µm²), vessel length (Vl) (µm), vessel density (Vd) (vessel/mm²), intervessel pit size (Ps) (µm), mesomorphy index (Mi), vulnerability index (Vi), vessel group index (Vg), potential hydraulic conductivity (Kp), total bark thickness (Bt) (µm), total phloem thickness (Pt) (µm), conducting phloem percentage (Pc), sieve tube tangential area (Sa) (µm²) and sieve tube length (Sl) (µm).

Spp	**RC**	**Statistics**	**WSG**	**Va**	**Vl**	**Vd**	**Ps**	**Vi**	**Mi**	**Vg**	**Kp**	**Bt**	**Pt**	**Pc**	**Sa**	**Sl**
CM	Dry	min	0,536765	166,2	107,4	14,54690	2,314	0,7804810	113,891703	4,26315789	0,000000001935136	543,53	251,18	110,21177	63,758701	126,85
		max	0,664501	5025	317,43	79,98767	4,783	2,6263313	434,172839	15,2222222	0,000000162749202	3154,33	2488,75	538,85130	563,26274	238,59
		mean±	0,600264	2304,10	169,6241	52,93216	3,083	1,4398966	237,255094	7,09190828	0,000000086292127	1422,92	968,76933	291,77355	240,85671	176,92877
		SD	0,033639	939,732	31,74964	11,50424	0,6235354	0,5420838	94,5377805	3,5580113	0,000000050171609	850,046	702,18563	135,94955	114,71176	17,682367
	Wet	min	0,523872	92,4	124,42	10,84653	2,341	0,9386243	156,607601	3,97368421	0,000000008023171	470,29	257,64	173,87845	10,520879	124,1
		max	0,628540	7427,6	264,44	97,24769	6,704	4,4840231	948,163145	6,22222222	0,000000194016548	2473,36	2150,7	501,00304	943,51106	286,02
		mean±	0,595396	2461,87	183,2840	53,59178	4,091	2,6598419	494,128958	5,02046180	0,000000075742617	1455,29	1013,5026	267,26105	337,19345	195,72955
		SD	0,035279	1317,58	27,76579	16,23113	0,9261570	1,3515345	270,635291	0,67505575	0,000000053662114	568,956	560,23058	94,681015	148,78453	27,935173
PP	Dry	min	0,542936	369	75,71	21,67545	1,851	0,7544874	149,130981	3,97058823	0	1131,75	447,16	57,639747	32,979183	130,08
		max	0,600376	3267,6	306,19	64,50145	3,493	1,7895853	395,527596	6,28571428	0,000000026328104	2652,86	2202,86	199,31517	660,97546	293,46

		mean±	0,578413	1318,75	198,7582	40,12979	2,456	1,2472892	249,184416	4,87289419	0,000000014164994	2142,90	1543,1675	116,74815	172,98266	198,75944
		SD	0,019634	519,578	37,53657	8,303615	0,3320457	0,3503761	75,8843966	0,68803610	0,000000010064935	516,448	495,18056	37,364203	97,367805	29,755143
	Wet	min	0,474504	318,4	68,57	20,13453	1,656	0,8058274	153,435986	3,45833333	0,000000006812732	960,19	475,77	89,791383	39,147071	108,19
		max	0,639486	3152,3	346,91	63,35323	3,017	2,6602766	593,747136	10	0,000000033269414	2613,55	2078,93	353,04784	544,90579	273,87
		mean±	0,576098	1255,11	203,9633	39,39080	2,346	1,7931729	378,976471	6,40180711	0,000000017591826	1565,06	1102,185	244,97691	174,74724	189,41613
		SD	0,047223	422,414	40,65825	6,824985	0,3251246	0,7105474	175,070643	2,34658676	0,000000008902326	467,842	413,22717	82,123202	81,986501	27,647214
BA	Dry	min	0,577225	227,3	109,720	17,01197	1,308	0,451952	68,5421818	4,41304347	0,000000000307443	550,97	297,41	139,48884	45,723446	74,93
		max	0,637789	2244,6	445,050	53,45945	3,671	1,0929030	218,484574	14,9285714	0,000000029466241	1145,94	879,46	536,17187	842,90313	260,56
		mean±	0,61013	940,776	186,650	33,93504556	2,3787	0,8022901	148,590968	7,43822372	0,000000009700331	787,713	574,172	302,92706	140,26066	167,26011
		SD	0,019599	368,787	57,75201	6,813089	0.5496091	0,1937293	43,7029061	3,27270291	0,000000010852327	149,112	171,30319	94,613435	80,112031	25,329541
	Wet	min	0.56535	1.607	10.024	14,30418	0,997	0,6485987	88,0036098	4.94230769	3,40426E-	49.851	35.478	118,86683	60,407250	111,45
		max	0.68003	23.673	22.571	54,90118	2,524	1,2803822	209,564850	9.08695652	1,62749E-07	176.2	139.232	410,30776	440,03416	223,62
		mean±	0.61824	10.5824	16.24602	35,95459	1,6232666	0,9292230	1.3273E-05	151,031627	2,93193E-08	127.405	92.924289	238,16188	189,17726	168,81129

		SD	0.03327	4.22468	2.462504	7,408515	0,4578169	0,1918637	3.9775E-06	33,7547711	0,00000005174645678	36.5706	31.38059	78,044817	72,636437	19,836796
PY	Dry	min	0,498019	369,3	96,86	21,68426	2,303	1,1131890	314,330815	2,13333333	0,000000043098185	1116,02	865,38	101,36149	72,986737	107,06
		max	0,634129	6228,9	432,3	89,05549	4,417	3,0527106	732,522339	6,24242424	0,000000188869613	3524,4	3014,63	292,90021	830,59814	415,26
		mean±	0,566821	2405,60	253,9798	53,58890	3,214	1,8613291	469,07936	5,04593503	0,000000087399654	2550,57	2140,3064	179,25716	280,40401	260,436
		SD	0,045450	1212,35	63,52996	13,85119	0,5683282	0,6657331	160,719649	1,28380600	0,000000048944010	777,397	683,92447	53,229730	117,48204	69,005968
	Wet	min	0,482067	287,7	89,21	19,13925	3,008	1,2641800	331,020072	1,44680851	0,000000000803542	1389,05	1148,36	137,76815	56,345171	123,43
		max	0,618086	9137,6	418,01	107,8626	5,381	8,4875385	2491,70082	6,42857142	0,00000011593007	2874,69	2636	374,55262	912,73327	502,6
		mean±	0,551241	2438,30	255,2881	53,72597578	3,729	3,3585309	887,37647	4,62460227	0,000000050335355	2226,95	1845,0448	245,65561	270,37581	289,52766
		SD	0,047462	1363,84	62,37516	14,79446	0,5668216	2,2614373	686,229784	1,82728151	0,000000035065117	464,872	457,02796	70,376831	110,25902	67,049663
TM	Dry	min	0,524584	1	92,01	1,128379	1,407	0,4167094	71,6829079	4,2571428	0	904,15	339,34	150,2256	28,463143	81,09
		max	0,622092	1605,9	262,16	45,2183	4,065	1,3301242	235,351787	7,45454545	0,000000011542291	1641,32	1067,07	425,45295	589,64552	374,09
		mean±	0,571528	714,046	181,6661	29,50046	2,463	0,9040828	165,347186	5,51903947	0,000000008154200	1176,76	607,26844	255,36050	161,64055	175,40329
		SD	0,038173	280,451	31,14331	6,246561	0,5477819	0,3101926	58,8077149	1,13236379	0,000000003570318	182,390	166,21277	79,311250	114,40113	33,262215

	Wet	min	0,506714	242,6	69,83	17,57520	1,936	0,7837792	148,532389	3,23529411	0,000000005292888	810,6	336	171,70272	20,188581	107,61
		max	0,571331	1822,4	270,99	48,17002	3,878	2,0435786	352,928078	5,79310344	0,000000022282978	2155,88	885,74	422,45592	301,71855	241,75
		mean±	0,542463	893,562	177,6899	33,15699	2,625	1,1764845	208,053249	1,17648450	0,000000011090024	1343,423111	607,97488	277,45496	109,79109	176,50688
		SD	0,023666	327,469	33,15828	6,202873	0,5077887	0,4042312	68,0230415	0,79939718	0,000000005448502	282,0883095	155,51246	62,304151	54,550668	23,921307
SP	Dry	min	0,520894	788,2	90,47	31,67913	1,858	1,3413102	341,229778	3,64285714	0,000000015286953	716,43	410,2	85,311329	72,081016	160,53
		max	0,654147	17885,1	385,75	150,9039	2,971	7,6663239	1896,20646	6,75	0,000001310133743	3364,27	3001,56	443,68676	852,19125	402,94
		mean±	0,592699	5084,72	242,3357	75,14369	2,5355	4,3796970	1065,43840	5,40159062	0,000000297203885	1549,89	1256,5857	279,66803	300,57477	284,88607
		SD	0,046151	3968,99	56,14289	28,81963	0,2543910	2,4224348	605,438346	1,21545324	0,000000398318214	825,115	778,95740	102,19220	144,44602	49,918139
	Wet	min	0,555308	322	52,55	20,24804	1,976	1,0370363	263,542395	4,23076923	0,000000032366728	496,15	317,34	182,9251	48,89268	168,88
		max	0,674758	17091,9	418,37	147,52	7,830	5,3531620	1100,60303	24,4166666	0,000000353014544	2432,86	1865,38	506,69551	841,87426	460,96
		mean±	0,610692	3424,44	240,5537	62,51820	3,155	3,0613516	707,032023	7,49201891	0,000000186715724	1544,00	1180,4316	323,91518	242,62416	280,4645
		SD	0,038314	2524,25	63,02165	21,28678	1,0217975	1,5068943	281,123059	6,06451041	0,000000121594613	548,602	428,46394	80,108388	122,47514	54,096315
SB	Wet	min	0,557788	599,2	90,58	27,62109	1,549	1,9462746	475,036341	5,3	0,000000003523896	1610,77	1133,35	89,462833	45,126151	144,98
		max	0,674185	9469,7	441,54	109,8052	3,009	4,0441101	979,103897	9,06666666	0,000000165056452	2697,69	2306,18	319,51803	688,59948	406,43

	mean±	0,634784	3453,91	225,886	64,21374	2,228	3,1924529	715,231413	6,82861377	0,000000111766257	1960,57	1580,0795	202,99062	225,87449	271,29503
	SD	0,045402	1710,76	55,59429	16,59141	0,3993992	0,8664929	182,129221	1,16155216	0,000000051332576	289,700	301,64084	71,662955	120,48724	46,788825

Root descriptive statistics of wood and bark attributes in Legumes in Catimbau National Park, Pernambuco, Brazil. There are fourteen attributes: wood specific gravity (WSG), vessel tangential area (Va) (µm²), vessel length (Vl) (µm), vessel density (Vd) (vessel/mm²), intervessel pit size (Ps) (µm), mesomorphy index (Mi), vulnerability index (Vi), vessel group index (Vg), potential hydraulic conductivity (Kp), total bark thickness (Bt) (µm), total phloem thickness (Pt) (µm), conducting phloem percentage (Pc), sieve tube tangential area (Sa) (µm²) and sieve tube length (Sl) (µm).

Spp	**RC**	**Statistics**	**WSG**	**Va**	**Vl**	**Vd**	**Ps**	**Vi**	**Mi**	**Vg**	**Kp**	**Bt**	**Pt**	**Pc**	**Sa**	**Sl**
CM	Dry	min	0,531330	184,5	72,97	15,32686	1,927	1,1223	173,293	4.32432	0	23.199	10.572	18.197366	0.43358	9.728
		max	0,670752	4218,1	24.534	73,28473	3,770	2,5377	400,328	10.1818	0,0000000190187498	156.932	90.172	64.015345	6.96061	26.457
		mean±	0,583463	15.7107	16.54	43,21607	2.72643	1,8053	295,638	5.89085	0,0000000033182439	83.34684	37.61393	34.575474	1.93597	18.18551
		SD	0,044939	8.44249	2.8937	11,54187	0.46944	0,5064	72,7394	1.79946	0,0000000065562426	41.86064	23.08007	11.887379	84,5932	3.282636
	Wet	min	0,560266	392,5	10.029	22,35501	1.218	1,1006	227,562	4.38462	0	21.825	8.486	18.956479	44,4145	9.515
		max	0,659253	72.088	32.917	95,80464	3.677	5,9297	937,545	7.625	0,0000000234904725	113.995	58.429	64.466967	8.84046	312.76
		mean±	0,596640	15.7325	19.399	42,95480	2.22513	2,7147	507,828	5.48977	0,0000000055899200	59.38644	27.44836	36.634104	229.785	185.4469
		SD	0,031661	9.86416	4.2974	12,59363	0.66283	1,5153	245,724	1.07795	0,0000000084011751	28.56321	15.49012	10.790093	117.903	40.61963

PP	Dry	min	0.549451	281,5	81,88	18,93190	1.026	0,6284	137,280	2.93333	0,0000000002039321581	412	171,45	56,3180539	27,5253	0
		max	0.675762	1887,3	281,48	49,02025	2.256	3,2611	606,424	5.88889	0,00000001945037064	2606,68	1853,4	303,353747	396,548	286,24
		mean±	0,611794	858,243	182,15	32,54028	1,518	1,6694	298,657	5.08844	0,000000008154232757	906,3702	519,9717	187,398321	110,843	168,9081
		SD	0,042704	305,861	38,156	5,831427	0.2809	0,8540	151,393	0.88881	0,00000000692648682	638,4364	482,8391	67,2218186	55,4950	69,35892
	Wet	min	0.397089	1.995	57,87	15,93773	1.225	0,7586	118,047	4.19512	0,000000002509575574	437,34	150,3	152,587212	32,9791	64,57
		max	0.658014	8267,4	423,12	102,5981	4.934	2,3569	431,400	10.7895	0,0000001725943872	1606,64	1083,91	49.723106	459,960	397,34
		mean±	0.587711	1225,41	196,73	37,61387	2,284	1,3453	263,465	6.04415	0,00000003719927597	935,3126	544,677	28.542478	132,383	177,9733
		SD	0.088612	917,615	58,314	12,08010	0.66591	0,5876	120,301	2.05902	0,0000000557230263	321,8968	268,5750	8.8912494	70,5873	52,17391
B	Dry	min	0.490984	215.8	59.79	16,57603	0,833	0,3364	52,2578	4.63793	0	1017.4	778.37	133.11092	14,0530	72
		max	0.670586	1743.3	291.36	47,11303	1.589	0,9507	155,614	6.92683	0,0000000340451163	2578.82	1603.73	253.49229	720,590	225,88
		mean±	0.576641	767.761	165.3	30,74843	1,193	0,5480	90,8724	6.12853	0,0000000097529522	1726.348	1131.384	188.4896	191,300	156,3988
		SD	0.053541	275.457	26.201	5,674223	0,16308	0,1836	30,9402	0.80903	0,0000000113965851	384.6699	270.3174	41.421997	119,710	25,49652
	Wet	min	0.456752	197,2	74,37	15,84559	1,848	0,4570	70,0479	5,125	0	843,72	638,022	43,1208402	12,0072	95,3
		max	0.585967	1676,7	242,63	46,20433	4,875	0,9652	152,966	14,2666	0,0000000149205943	2327,92	2025,7	300,612522	575,102	216,11

		mean±	0.541236	816,355	161,14	31,77191	3,1857	0,6655	107,440	6,80509	0,0000000069072732	1622,749	1195,315	171,661745	177,639	159,6189
		SD	0.042756	269,891	28,768	5,483929	0,91636	0,1558	26,9646	3,05483	0,0000000072142364	468,1917	361,3934	52,2857363	100,527	25,24509
PY	Dry	min	0,534028	4.395	7.673	7200	2.09	1,4638	183,390	4,23076	0,0000000169885363	762,32	43.252	13.341824	0.39147	15.044
		max	0,637954	64.483	48.596	17600	4.301	2,4964	656,600	6,2	0,0000001114937508	201.696	147.654	41.906304	11.145	42.465
		mean±	0,569044	22.3659	23.11	11173.33	2.99943	1,9196	450,874	5,51445	0,0000000679975062	138.424	99.7428	23.755189	3.15675	27.94735
		SD	0,033942	10.4411	7.3284	2635.975	0.58218	0,4270	156,021	0,69135	0,0000000307669380	33.82747	33.94247	6.8422119	1.67016	5.492951
	Wet	min	0,480555	5.074	7.361	3200	2.291	1,4192	385,234	4,82857	0,0000000010321598	49.43	25.472	6.896522	0.37937	11.978
		max	0,599653	72.392	42.668	23200	3.922	3,7329	963,094	6,76923	0,0000002030053235	292.143	241.286	51.415378	23.4569	39.402
		mean±	0,540882	24.8878	26.3	10604.44	2.92173	2,2768	593,210	5,80640	0,0000000824673154	140.7299	101.589	24.705697	5.20995	24.87965
		SD	0,041451	12.7563	6.2067	4120.567	0.43431	0,7985	198,053	0,61676	0,0000000598946265	77.3221	67.99284	10.343496	4.05231	5.808293
TM	Dry	min	0,444723	1.721	7.34	10000	1.429	0,3433	65,4928	4,58139	0,0000000005138616	760,29	425,82	116,844553	28,0861	114,29
		max	0.581172	15.484	30.505	39600	3.291	1,0643	221,16	10,4687	0,0000000172130324	1082,84	108.284	412,040494	318,256	260,43
		mean±	0.537128	6.32667	18.803	20684.44	2.24793	0,6072	115,70	6,25995	0,0000000078267717	712,8682	71.28682	239,259649	112,543	185,28
		SD	0.049391	2.25273	4.3893	7842.83	0.54885	0,2256	51,333	1,90410	0,0000000055246163	164,1208	16.41208	79,6105530	51,9338	28,87078

	Wet	min	0.46664	1.185	6.93	1100	1.267	0,5400	94,986	2,24324	0,0000000040544353	44.762	257,67	73,4159183	16,1883	9.6
		max	0.565547	32.204	39.401	28000	5.451	1,9453	583,41	6,34090	0,0000000136334276	1551,43	1148,77	492,248863	3391,19	28.8
		mean±	0.529592	7.52405	21.787	14024.44	2.6058	0,9628	221,45	4,67223	0,0000000091841591	763,7048	492,9693333	302,541018	294,960	183,2659
		SD	0.028693	3.00008	5.3429	6587.183	0.8652	0,4496	149,42	1,09804	0,0000000034375783	313,3509	232,8502849	107,574566	534,971	44,55293
SP	Dry	min	0,5742244914	155,8	60,69	14,08441412	2,094	1,5119	241,4107622	4,111111111	0,0000000032153877	501,75	191,33	150,27525	45,48405698	84,19
		max	0,705624	12448,7	380,3	125,8974	4,249	3,5193	820,414	7,94736	0,0000001865330994	1339,89	1087,13	665,353121	779,311	379,24
		mean±	0,620652	2243,27	218,11	49,73426	3,031	2,1604	481,334	5,57294	0,0000000633383034	821,6135	571,306	312,738322	206,681	232,3256
		SD	0,037957	1953,55	66,215	19,59967	0,53359	0,6421	194,200	1,22289	0,0000000556078904	192,6692	224,2082	109,130503	113,420	55,74853
	Wet	min	0,577243	392,5	81,62	22,35501	2,338	1,5925	334,315	1,58064	0	499,73	191,37	147,676442	39,9272	80,66
		max	0,681340	10323,3	377,43	114,6474	4,464	6,0644	1459,18	7,63157	0,0000001713097931	1743,19	1200,53	1000	1781,76	422,57
		mean±	0,628027	2299,78	227,90	50,97189	3,278	2,5946	611,518	5,26677	0,0000000795833508	1111,3194	715,1584	331,483212	260,517	236,0652
		SD	0,034064	1765,96	57,452	18,19737	0,53921	1,4779	369,844	1,81642	0,0000000607013219	294,2902	262,3989	234,415002	170,924	74,43127
SB	Wet	min	0,565160	316,4	77,83	20,07119	2,579	1,0154	215,483	4,89285	0,0000000018262603	625,48	474,98	110,949843	29,0333	120,2
		max	0,6597991	6015	331,67	87,51306	3,997	3,4352	745,883	13,3333	0,0000002203442601	2258,69	1867,15	713,471085	713,471	353,85

	mean±	0,6082331	2283,17	207,23	52,1889	3,07126	1,9678	406,427	7,54412	0,0000000767794980	1407,219	1118,724	164,417423	164,417	226,5634
	SD	0,0301946	1163,61	51,222	13,56549	0,31570	0,7459	160,133	3,27098	0,0000000648054662	438,6564	370,7838	94,8065030	94,8065	45,08002

Data S3. Linear mixed-effect model (LMM) test results, due to rainfall and organ, in Legumes in Catimbau National Park, Pernambuco, Brazil. There are fourteen attributes: wood specific gravity (WSG), vessel tangential area (Va) (µm²), vessel length (Vl) (µm), vessel density (Vd) (vessel/mm²), intervessel pit size (Ps) (µm), mesomorphy index (Mi), vulnerability index (Vi), vessel group index (Vg), potential hydraulic conductivity (Kp), total bark thickness (Bt) (µm), total phloem thickness (Pt) (µm), conducting phloem percentage (Pc), sieve tube tangential area (Sa) (µm²) and sieve tube length (Sl) (µm). The p values in bold represent those with significant results. NA is not applicable once *S. bahiensis* was not sampled in dry areas.

Spp	**Factor**	**Statistics**	**WSG**	**Va**	**Vl**	**Vd**	**Ps**	**Vi**	**Mi**	**Vg**	**Kp**	**Bt**	**Pt**	**Pc**	**Sa**	**Sl**
		F-statistics	4.711	19.95	11.75	2.524	1.728	6.022	5.15	1.09	5.585	8.351	10.08	3.758	3.506	17.97
		DF	25 and 200	25 and 200	25 and 200	25 and 200	25 and 200	25 and 200	25 and 200	25 and 200	25 and 200	25 and 200	25 and 200	25 and 200		
		R²	0.3706	0.7137	0.595	0.2398	0.954	0.4295	0.3917	0.1199	0.4111	0.5107	0.5575	0.3196	0.3047	0.692
CM	Rainfall	Estimated	-0.024420	1387.34	21.040	-11.6778	-3.23177	175.9848	0.958665	-1.623015	6.310e-08	181.93	74.59	31.411	145.22	28.50331
		Std. Error	0.020240	347.17	13.338	5.6241	0.63675	47.5153	0.220335	1.064287	4.363e-08	242.15	209.20	43.082	68.51	16.28660
		t-value	-1.207	3.996	1.577	-2.076	-5.075	3.704	4.351	-1.525	1.446	0.751	0.357	0.729	2.120	1.750
		p	0.229019	9.04e-05	0.11628	0.039129	0.03670	0.000274	2.16e-05	0.1288	0.149688	0.453360	0.721789	0.466789	0.035248	0.0816
		Estimated	0.077513	-682.03	7.352	-21.6990	2.90683	48.5176	0.219618	0.251571	-6.398e-08	-1092.98	-915.70	-129.030	-75.41	7.94786

	Organ	Std. Error	0.029569	507.21	19.487	8.2166	0.90049	69.4188	0.321905	1.554899	6.375e-08	353.78	305.63	62.942	100.09	23.79435
		t-value	2.621	-1.345	0.377	-2.641	3.228	0.699	0.682	0.162	-1.004	-3.089	-2.996	-2.050	-0.753	0.334
		p	0.009427	0.180249	0.70637	0.008919	0.08405	0.485415	0.495870	0.8716	0.316728	0.002289	0.003079	0.041664	0.452070	0.7387
PP	Rainfall	Estimated	-0.042141	205.07	42.414	-15.8222	-3.34697	87.5455	0.290580	-0.241670	4.951e-09	306.99	172.12	50.937	-12.49	21.17490
		Std. Error	0.020240	347.17	13.338	5.6241	0.63675	47.5153	0.220335	1.064287	4.363e-08	242.15	209.20	43.082	68.51	16.28660
		t-value	-2.082	0.591	3.180	-2.813	-5.256	1.842	1.319	-0.227	0.113	1.268	0.823	1.182	-0.182	1.300
		p	0.038596	0.555401	0.00171	0.005390	0.03434	0.066879	0.188733	0.8206	0.909769	0.206351	0.411630	0.238477	0.855547	0.1950
	Organ	Estimated	0.088616	232.06	-4.774	-1.5181	-0.07360	-19.5607	0.009137	-0.519273	2.534e-08	-906.74	-758.88	-101.003	-20.26	-0.28908
		Std. Error	0.028623	490.98	18.863	7.9536	0.90049	67.1968	0.311601	1.505129	6.171e-08	342.46	295.85	60.927	96.88	23.03273
		t-value	3.096	0.473	-0.253	-0.191	-0.082	-0.291	0.029	-0.345	0.411	-2.648	-2.565	-1.658	-0.209	-0.013
		p	0.002242	0.636976	0.80045	0.848825	0.94230	0.771279	0.976635	0.7305	0.681762	0.008746	0.011044	0.098925	0.834529	0.9900
BA	Rainfall	Estimated	0.618240	1074.53	162.244	40.9000	6.86357	91.7718	0.566979	6.643477	1.264e-08	1273.37	938.91	210.644	191.97	167.22625
		Std. Error	0.014726	252.61	9.705	4.0921	0.45025	34.5725	0.160317	0.774382	3.175e-08	176.19	152.21	31.347	49.85	11.85024
		t-value	41.982	4.254	16.717	9.995	15.244	2.654	3.537	8.579	0.398	7.227	6.168	6.720	3.851	14.112
		p	< 2e-16	3.22e-05	< 2e-16	< 2e-16	0.00428	0.008579	0.000503	2.58e-15	0.690945	1.01e-11	3.73e-09	1.83e-10	0.000158	< 2e-16
	Organ	Estimated	-0.077004	-257.27	-2.030	8.9625	0.27530	-25.2204	0.035448	0.161619	-5.733e-09	270.44	200.88	-15.533	-23.37	-9.70960
		Std. Error	0.020826	357.24	13.725	5.7871	0.63675	48.8928	0.311601	1.095142	4.490e-08	249.17	215.26	44.331	70.49	16.75877
		t-value	-3.697	-0.720	-0.148	1.549	0.432	-0.516	0.114	0.148	-0.128	1.085	0.933	-0.350	-0.332	-0.579
		p	0.000281	0.472259	0.88257	0.123027	0.70764	0.606539	0.909541	0.8828	0.898520	0.279070	0.351843	0.726422	0.740589	0.5630
PY		Estimated	-0.066998	1363.77	93.044	-20.2556	-1.26907	244.0813	0.716052	-2.018875	3.769e-08	953.58	906.14	236.407	78.40	122.30142

	Rainfall	Std. Error	0.020240	347.17	13.338	5.6241	0.63675	47.5153	0.220335	1.064287	4.363e-08	242.15	209.20	43.082	68.51	16.28660
		t-value	-3.310	3.928	6.976	-3.602	-1.993	5.137	3.250	-1.897	0.864	3.938	4.331	5.487	1.144	7.509
		p	0.001105	0.000118	4.31e-11	0.000399	0.18445	6.59e-07	0.001354	0.0593	0.388680	0.000113	2.34e-05	1.22e-07	0.253795	1.90e-12
	Organ	Estimated	0.066645	307.75	9.739	-3.0958	-0.30613	-82.9430	-0.249411	1.020184	3.787e-08	-1090.09	-1030.03	-229.906	273.99	-31.02154
		Std. Error	0.028623	490.98	18.863	7.9536	0.90049	67.1968	0.311601	1.505129	6.171e-08	342.46	295.85	60.927	96.88	23.03273
		t-value	2.328	0.627	0.516	-0.389	-0.340	-1.234	-0.800	0.678	0.614	-3.183	-3.482	-3.773	2.828	-1.347
		p	0.020886	0.531498	0.60623	0.697514	0.76627	0.218521	0.424414	0.4987	0.540160	0.001688	0.000611	0.000212	0.005157	0.1795
TM	Rainfall	Estimated	-0.075777	-180.97	15.446	-10.3667	-1.06127	25.8767	0.099935	-1.928758	-1.550e-09	70.05	-330.93	-48.469	-82.18	9.28064
		Std. Error	0.020240	347.17	13.338	5.6241	0.63675	47.5153	0.220335	1.064287	4.363e-08	242.15	209.20	43.082	68.51	16.28660
		t-value	-3.744	-0.521	1.158	-1.843	-1.667	0.545	0.454	-1.812	-0.036	0.289	-1.582	-1.125	-1.200	0.570
		p	0.000236	0.602754	0.24824	0.066762	0.23750	0.586634	0.650637	0.0714	0.971689	0.772668	0.115239	0.261910	0.231689	0.5694
	Organ	Estimated	0.064133	116.11	42.215	-3.0514	0.39807	3.8528	-0.083697	-0.204107	3.827e-09	-850.16	-315.89	-17.467	208.08	16.57213
		Std. Error	0.028623	490.98	18.863	7.9536	0.90049	67.1968	0.311601	1.505129	6.171e-08	342.46	295.85	60.927	96.88	23.03273
		t-value	2.241	0.236	2.238	-0.384	0.442	0.057	-0.269	-0.136	0.062	-2.483	-1.068	-0.287	2.148	0.720
		p	0.026146	0.813289	0.02632	0.701645	0.70166	0.954335	0.788512	0.8923	0.950605	0.013864	0.286926	0.774646	0.032926	0.4727
SP	Rainfall	Estimated	-0.003741	2449.57	87.125	-14.0500	-0.22600	198.6136	0.644297	1.528907	1.780e-07	154.62	103.70	122.374	57.40	119.62342
		Std. Error	0.020826	357.24	13.725	5.7871	0.63675	48.8928	0.226723	1.095142	4.490e-08	249.17	215.26	44.331	70.49	16.75877
		t-value	-0.180	6.857	6.348	-2.428	-0.355	4.062	2.842	1.396	3.965	0.621	0.482	2.760	0.814	7.138
		p	0.857607	8.47e-11	1.42e-09	0.016071	0.75658	6.97e-05	0.004949	0.1642	0.000102	0.535602	0.630514	0.006306	0.416477	1.69e-11

	Organ	Estimated	0.089790	-783.15	-13.825	-12.3375	-0.41830	-5.7039	0.050643	-3.067231	-9.539e-08	-643.62	-538.50	-108.860	31.19	-43.08398
		Std. Error	0.029453	505.21	19.410	8.1842	0.90049	69.1449	0.320635	1.548765	6.350e-08	352.38	304.43	62.694	99.69	23.70049
		t-value	3.049	-1.550	-0.712	-1.507	-0.465	-0.082	0.158	-1.980	-1.502	-1.826	-1.769	-1.736	0.313	-1.818
		p	0.002608	0.122682	0.47713	0.133259	0.68794	0.934337	0.874659	0.0490	0.134599	0.069262	0.078430	0.084029	0.754715	0.0706
SB	Rainfall	Estimated	0.016545	2379.38	63.642	-19.3667	-0.91143	227.4735	0.867511	0.185136	9.913e-08	687.20	641.17	105.306	33.90	104.06879
		Std. Error	0.020240	347.17	13.338	5.6241	0.55144	47.5153	0.220335	1.064287	4.363e-08	242.15	209.20	43.082	68.51	16.28660
		t-value	0.817	6.854	4.771	-3.444	-1.653	4.787	3.937	0.174	2.272	2.838	3.065	2.444	0.495	6.390
		p	0.414644	8.63e-11	3.51e-06	0.000699	0.24018	3.27e-06	0.000114	0.8621	0.024160	0.005007	0.002476	0.015375	0.621240	1.13e-09
	Organ	Estimated	0.050453	-913.47	-16.624	-0.1181	-0.78957	-97.2401	-0.320152	0.553894	-2.925e-08	-823.79	-662.23	-82.287	-38.09	-35.02199
		Std. Error	0.028623	490.98	18.863	7.9536	0.77985	67.1968	0.311601	1.505129	6.171e-08	342.46	295.85	60.927	96.88	23.03273
		t-value	1.763	-1.861	-0.881	-0.015	-1.012	-1.447	-1.027	0.368	-0.474	-2.406	-2.238	-1.351	-0.393	-1.521
		p	0.079476	0.064274	0.37920	0.988172	0.41788	0.149428	0.305448	0.7133	0.635968	0.017054	0.026291	0.178349	0.694643	0.1299

Conclusões

O presente estudo visou o entendimento das estratégias anatômicas e fisiológicas relacionadas à distribuição de espécies lenhosas de Fabaceae em uma floresta tropical sazonalmente seca, em diferentes níveis de disponibilidade hídrica. Para tanto consideramos a média de pluviosidade anual como proxy de disponibilidade hídrica e avaliamos atributos relacionados à evitação do estresse por falta d'água, bem como de uso eficiente deste recurso. Assim, avaliamos aspectos quantitativos de tecidos assimiladores, de revestimento, armazenamento e condutores, de todos os órgãos vegetativos: raiz, caule e folha.

A análise conjunta desses órgãos e tecidos nos permitiu compreender melhor as estratégias das espécies avaliadas, contribuindo principalmente com dados inéditos e escassos para o ambiente e em análises semelhantes: identificando variações em casca, floema e raízes. Foram nesses órgãos e tecidos onde encontramos parte das respostas mais significativas para as espécies em questão.

Enquanto as espécies investem em folhas mais conservativas e, portanto, menos eficientes, em condições de maior disponibilidade hídrica, o mesmo efeito não foi observado em caules e raízes. Nesses órgãos, os resultados obtidos indicam a importância dos atributos de casca e floema, uma vez que esses tecidos demonstram alta sensibilidade e capacidade de adaptação devido à variação das chuvas. A menor variação no xilema indica a alta adaptação das espécies às condições ambientais e sugere que pequenas alterações podem proporcionar um aumento suficiente na eficiência e/ou tolerância ao estresse. Dessa forma, considerando que todas as espécies avaliadas são caducifólias e, portanto, tem a oportunidade de ajustar suas folhas às necessidades da estação em que serão produzidas, os órgãos subterrâneos figuram como estruturas fundamentais para a manutenção das espécies no ambiente. Esses órgãos precisam ser mais bem explorados a fim de que seu papel na dinâmica de rebrota e reprodução assexuada, por exemplo, seja considerado nos estudos e previsões a nível de comunidade.

Nosso trabalho contribui com o conhecimento quanto à vegetação da Caatinga demonstrando que os órgãos aéreos das espécies estudadas, embora fortemente adaptados às condições ambientais locais, podem vir a sofrer danos e pressão de extinção em cenários mais severos de mudanças climáticas. Uma vez que as espécies demonstraram precisar de mais água para conseguir produzir folhas mais seguras e que os caules e raízes apresentam menor ajuste em xilema, concluímos que as populações atualmente submetidas à menores índices pluviométricos, poderão estar mais suscetíveis a falhas hidráulicas e outros danos causados por aumentos de temperatura e redução de pluviosidade, conforme esperado para a região.