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ADGLECIANNE DE SOUSA MELO

PRODUÇÃO, ALOCAÇÃO E USO DE AÇÚCARES EM ESPÉCIES CADUCIFÓLIAS LENHOSAS NA CAATINGA, UMA FLORESTA TROPICAL SAZONALMENTE SECA

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal, da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutora em Biologia Vegetal.
Área de concentração: Ecologia e Conservação

Orientador: Prof. Mauro Guida dos Santos

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O caminho me fez doutora.

Sou grata por absolutamente tudo.

RESUMO

Com as previsões de intensificações de seca e aumento de temperatura global, esforços para prever como as florestas irão responder a essas novas condições têm sido incentivados, especialmente em ambientes tipicamente secos como a Caatinga pois estão entre os ambientes mais ameaçados diante desse cenário. Nesse contexto, o presente trabalho acessou informações sobre como espécies decíduas respondem a variação sazonal em termos de dinâmica de produção e partição dos carboidratos. O estudo foi realizado no Parque Nacional do Catimbau onde coletamos material vegetal de *Commiphora leptophloeos*, *Peltogyne pauciflora*, *Cenostigma microphyllum* e *Pityrocarpa moniliformes* para quantificação de carboidratos não estruturais (NSC) ao longo de oito meses de 2020 a 2021. A presente versão da tese está dividida em dois capítulos, onde no primeiro manuscrito confirmamos a existência de fotossíntese corticular para *C. leptophloeos*, estratégia que contribuiu para a manutenção do pool constante de NSC durante os períodos de seca. No segundo capítulo, testamos se as espécies decíduas sem a fotossíntese corticular variam drasticamente em relação à concentração de NSC apresentando maiores concentrações em períodos chuvosos e reduções nos períodos secos, devido ao uso das reservas nos períodos de limitação da fotossíntese. Os resultados refutam essa hipótese uma vez que para as três espécies o pool de NSC foi constante ao longo dos meses, não havendo reduções nem aumentos drásticos entre períodos secos e chuvosos. O principal aspecto observado foram respostas espécie-específica para as estratégias de alocação e particionamento dos NSC entre os órgãos.

Palavras-chave: árvores decíduas; floresta seca; fotossíntese corticular; mudanças climáticas; tolerância.

ABSTRACT

With predictions of increased drought and global temperature rise, efforts to predict how forests will respond to these new conditions have been encouraged, especially in typically dry environments like the Caatinga, as they are among the most threatened environments in this scenario. In this context, the present study accessed information on how deciduous species respond to seasonal variations in terms of carbohydrate production and partitioning dynamics. The study was conducted in Catimbau National Park, where we collected plant material from *Commiphora leptophloeos*, *Peltogyne pauciflora*, *Cenostigma microphyllum*, and *Pityrocarpa moniliformis* for the quantification of non-structural carbohydrates (NSC) over eight months from 2020 to 2021.The current version of this thesis is divided into two chapters. In the first one, we confirmed the existence of corticular photosynthesis (CP) for *C. leptophloeos*, a strategy that contributed to the maintenance of a constant NSC pool during dry periods. In the second chapter, we tested whether deciduous species without CP vary significantly in terms of NSC concentration, showing higher concentrations in rainy periods and reductions in dry periods due to the use of reserves during photosynthesis limitations. The results refute this hypothesis, as for all three species, the NSC pool remained constant throughout the months, with no drastic reductions or increases between dry and rainy periods. The main observation was species-specific responses in the allocation and partitioning strategies of NSC among the organs.

Keywords: climate change; corticular photosynthesis; deciduous tree; drought tolerance; dry forest.

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SUMÁRIO

1 INTRODUÇÃO

Dentre os processos fisiológicos fundamentais para a sobrevivência das plantas está o armazenamento de carbono na forma de compostos transitórios, os quais sustentam, principalmente, o metabolismo vegetal durante o período noturno, quando a produção de carboidratos está temporariamente estagnada. Além dessa dinâmica diária da mobilização do estoque de carbono, o acúmulo de carboidratos não estruturais (NSC) também desempenha papel crucial na sobrevivência de plantas expostas às condições ambientais limitantes como disponibilidade de água e nutrientes, temperatura ou algum fator biótico (PALACIO et al., 2018).

Os carboidratos não estruturais são conhecidos principalmente por seu envolvimento na tolerância de plantas sob condições de seca e salinidade, sendo importante para o ajustamento osmótico, sequestro de espécies reativas de oxigênio, bem como atuando como moléculas sinalizadoras do estresse (SANTANA-VIEIRA et al., 2016). Em espécies perenes, tais como as árvores, vários estudos tentam elucidar o que determina a alocação de carbono, seria um processo passivo ou ativo? Além disso, como se daria o uso desse pool armazenado sob condições ambientais limitantes? (SALA; WOODRUFF; MEINZER, 2012).

A falta de carbono e a falha hidráulica são apontadas como as possíveis causas primordiais de mortalidade de árvores em consequência da seca (LANDHÄUSSER et al., 2018). Desta maneira a dinâmica de estoque de carbono é crucial para a sobrevivência de espécies em Florestas Tropicais Sazonalmente Secas (FTSS), tal como a Caatinga no semiárido brasileiro, uma vez que há limitação da disponibilidade hídrica nesses ambientes colocando-as em situação de vulnerabilidade. Para espécies caducifólias, em especial, o estoque de NSC passa então a ser uma importante fonte de energia disponível durante todo o período de estação seca devendo sustentar o metabolismo básico até a chegada da estação chuvosa. Desta maneira um possível esgotamento dessas reservas durante este período pode levar essas plantas à morte (MARTÍNEZ-VILALTA et al., 2016). Sobretudo sob condições climáticas cada vez mais limitantes, com secas mais prolongadas (MARENGO; BERNASCONI, 2015)

No contexto das mudanças climáticas que alertam para a tendência de aumento de temperatura e da intensidade e duração dos eventos de seca é importante compreender como a sazonalidade regula essa dinâmica do estoque de carboidratos nas espécies lenhosas, como proxy de suscetibilidade ou resiliência de espécies arbóreas frente ao cenário futuro. Entretanto, justamente para espécies de FTSS essas informações são escassas. Estudos climatológicos

(MARENGO E BERNASCONI, 2015) apontam que a Caatinga, uma das maiores FTSS no mundo, é uma das regiões ecológicas mais suscetíveis às mudanças climáticas (LAPOLA et al., 2020). Nossa proposta, portanto, é compreender como se dá essa dinâmica de produção, uso e estoque de açúcares em árvores decíduas nativas da Caatinga em função da sazonalidade.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 ECOLOGIA E FISIOLOGIA DE ESPÉCIES DECÍDUAS LENHOSAS EM FLORESTAS TROPICAIS SECAS

2.1.1 Florestas Secas e a deciduidade

As florestas tropicais são ambientes extremamente diversos e complexos (WITHMORE, 1998; HAN et al., 2022). Nesse contexto, as Florestas Tropicais Secas (FTS) representam quase metade de todos os tipos de florestas tropicais do mundo, abrangendo aproximadamente 40%, com uma presença de cerca de 20% na América do Sul (MURPHY e LUGO, 1986; MILES et al., 2006). Essas florestas se caracterizam por uma sazonalidade bem definida, com períodos de seca e chuvas abundantes, sendo influenciadas pela frequência e duração do período seco (MOONEY, BULLOCK, MEDINA, 1995; MILES et al., 2006; LUO et al., 2024). São, na sua maioria, ecossistemas decíduos, em comparação com as florestas tropicais úmidas (MURPHY e LUGO, 1986; BRAGA et al., 2016) com relevância global, tendo em vista ocupam uma grande área nos trópicos e desempenham um papel importante no ciclo do carbono da Terra (ALSTRÖM et al., 2015).

A sazonalidade climática leva a ocorrência de variações ambientais, influenciando diretamente a disponibilidade de água, a irradiação, a temperatura e, consequentemente, os padrões fenológicos. Para as FTS a literatura clássica considera as espécies sempre verde e decíduas como as duas principais categorias funcionais para essa vegetação (MOONEY, BULLOCK, MEDINA, 1995; EWEL e HIREMATH, 2005), assumido serviços ecossistêmicos distintos e complementares dentro da mesma assembleia (DING et al., 2020).

Espécies sempre verde ou brevemente decíduas retém um número substancial de folhas ao longo de todos os períodos estacionais em FTS (LIMA et al., 2021). Devido a isso, tem grande importância na estabilização dos solos, devido a suas raízes profundas e duradouras (FRANCO et al., 2005) e no sequestro de carbono de forma contínua durante todo o ano (DING et al., 2020). Essas espécies podem manter uma estabilidade fotossintética mesmo sob flutuações de água no solo (FIGUEIREDO-LIMA et al., 2018), bem como apresentam alta eficiência na recuperação do potencial hidrico do xilema (PEREIRA et al., 2019). Por outro lado, durante a estação seca, algumas espécies arbóreas adotam a deciduidade foliar como uma estratégia para evitar danos causados pela falta de água, sendo comum a perda total ou parcial de folhas (MUNNÉ- BOSCH e ALEGRE 2004; SANTOS et al., 2014). Devido à queda de suas folhas, essas espécies contribuem anualmente com o ciclo de nutrientes no solo devido ao aumento da serrapilheira (LIMA et al 2021; MONTANEZ, AVELLA e CAMACHO, 2023), bem como são importantes espécies enfermeiras durante o período seco, devido a regulação do microclima abaixo da copa (VALIENTE-BANUET e VERDÚ, 2008). Ambos os tipos funcionais coexistem nessas florestas e são fundamentais para a manutenção dos serviços ecossistêmicos como ciclagem de nutrientes, regulação hídrica e sequestro de carbono em FTS.

Os modelos de alterações climáticas globais preveem significantes alterações na temperatura e pluviosidade nas próximas décadas para as regiões tropicais (PAINEL INTERGOVERNAMENTAL SOBRE ALTERAÇÕES CLIMÁTICAS, 2015). As FTS ao redor do globo e especialmente as que ocorrem no Nordeste da Região Brasileira são especialmente vulneráveis às mudanças climáticas, e os efeitos combinados de alta temperatura e menor precipitação projetam pra essa região uma expansão de zonas mais secas (SALAZAR et al., 2007; MARENGO e BERNASCONI, 2015). No entanto, ainda não está claro como as espécies destas regiões responderão às mudanças climáticas, especialmente as espécies decíduas que apresentam uma janela de oportunidade muito mais curta para ganho de carbono e perda de água do que as espécies sempre verdes.

2.1.2 Estratégias fisiológicas e implicações de espécies decíduas em FTS

As diferenças funcionais entre espécies decíduas e sempre verdes geralmente derivam do balanço entre os custos e benefícios da formação das folhas (SOBRADO, 1991; WRIGHT et al., 2004). Embora os processos que levam a queda das folhas em espécies decíduas ainda não sejam totalmente conhecidos, algumas hipóteses destacam a deciduidade como resultado de diversos processos e respostas fisiológicas foliares (DEXTER et al., 2018), como a percepção das plantas às alterações na umidade do solo (ARDIEU e SIMONNEAU, 1998), processos endógenos, como a reidratação do caule (MOREL et al. 2015).) e fotoperíodo (WAY e MONTGOMERY, 2014).). No entanto, sabe-se que a sazonalidade é um importante driver na seleção de estratégias fenológicas distintas.

Em espécies decíduas, o menor tempo de vida foliar pode estar associado a outros dois mecanismos importantes: a queda das folhas, atuando como um "fusível hidráulico" ao evitar danos no xilema vulnerável durante a seca (LIMA et al., 2018; SOUZA et al., 2020), e raízes profundas, que permitem o acesso a fontes de água mais profundas, prolongando a duração da folhagem na copa das árvores durante a estação seca (HASSELQUIST et al. 2010, SOUZA et al., 2020). Estes mecanismos combinados à características funcionais/estruturais como maior investimento fotossintético, devido a menor expectativa de vida da folha e menores massas foliares (i.e menor utilização de energia) (SOBRADO et al., 1991; FU et al., 2012; SOUZA et al., 2020) podem apresentar vantagens adaptativas nesses grupos funcionais. Por exemplo, em FTS, espécies decíduas apresentam estratégias menos conservadoras, com maior capacidade de trocas gasosas, maior taxa de assimilação de carbono e maior eficiência no uso da água em comparação com espécies sempre-verdes (WORBES et al., 2013; FIGUEIREDO-LIMA et al., 2018; PEREIRA et al., 2019). Essas estratégias podem favorecer o balanço hídrico e de carbono nessas espécies.

No entanto, espécies decíduas podem exibir variações fenológicas associadas a características do caule, como densidade de madeira e potencial hídrico do xilema (CHOAT et al., 2006; WORBES et al., 2013), importantes preditores do funcionamento hidráulico das plantas em climas sazonais (SOUZA et al., 2020). Plantas com baixa densidade de madeira tendem a produzir folhas novas e entrar em fases reprodutivas durante a estação seca, enquanto aquelas com madeira de alta densidade geralmente perdem folhas e voltam a brotar dependendo da disponibilidade de água no solo. Dessa forma, os dados sugerem que para além da estratégia de deciduidade, a combinação de diferentes traços pode determinar subgrupos de espécies caducifólias (LIMA et al. 2012; OLIVEIRA et al. 2015) com diferentes estratégias para enfrentar os períodos secos.

Espécies decíduas que possuem tecidos lenhosos com capacidade fotossintética demonstram comportamentos distintos frente à seca devido à sua capacidade de realizar fotossíntese corticular. que atua como um mecanismo de regulação local. Este processo ajuda a mitigar o estresse hídrico ao regular a concentração de oxigênio e dióxido de carbono (CO2) no caule, promovendo a adaptação a ambientes áridos e semiáridos. A fotossíntese corticular está associada a uma menor densidade de madeira, facilitando a difusão de gases e a eficiência metabólica em condições adversas (ROSELL e OLSON, 2014)

2.2 FOTOSSÍNTE CORTICULAR

A capacidade de realizar fotossíntese através do tecido lenhoso é uma vantagem evolutiva presente em algumas espécies vegetais. É considerada uma importante fonte local de carbono para o funcionamento da planta, principalmente em situações de déficit hídrico, quando a fotossíntese foliar é limitada após o fechamento estomático ou queda foliar (PFANZ et al., 2002; DE ROO et al., 2020; NATALE et al., 2023) especialmente em espécies de florestas secas.

A fotossíntese corticular parece ser um método eficiente de (re) fixação de carbono sem grande perda de água, em comparação com a fotossíntese foliar. Ou seja, há uma diferença clara entre a fotossíntese nas folhas e no caule: para absorver o CO2, as folhas precisam abrir seus estômatos e ficam expostas à perda de água para o ambiente; já o tecido lenhoso, é abastecido com CO2 liberado pela respiração de tecidos não fotossintéticos (PFANZ et al., 2002; ÁVILA et al., 2014). Sendo assim, a reassimilação interna de CO2 nos tecidos do caule é considerada uma estratégia importante na economia de carbono da planta inteira (ASCHAN e PFANZ, 2003; ÁVILA et al., 2014).

Portanto, a fotossíntese corticular é capaz de promover significativamente o acúmulo de carboidratos, que auxiliam no reabastecimento dos vasos embolizados e na recuperação da condutividade hidráulica (CHEN et al., 2018; LIU et al., 2019). Nesse sentido, espécies decíduas com essa capacidade fotossintética podem apresentar uma maior resiliência à seca em razão dessa fonte adicional de carboidratos devido ao potencial de assimilação de carbono em outro tecido verde não foliar fornecendo fontes significativas e alternativas de fotoassimilados, essenciais para um rendimento ideal (SIMKIN, 2019; DE ROO et al., 2020).

2.3. DINÂMICA DE CARBONO (C) NAS PLANTAS E OS CARBOIDRATOS NÃO-ESTRUTURAIS (CNE)

2.3.1 Geral

A fração do C assimilado que será utilizado pelas plantas, depende da eficiência do uso de CO2, na divisão entre o incremento de biomassa (i.g crescimento primário e secundário) e a respiração (DANNOURA et al., 2016). A fotossíntese é o processo que reduz o carbono inorgânico atmosférico em compostos orgânicos e, os carboidratos são os produtos finais desse processo. Em algumas espécies esse processo de produção pode acontecer também em tecidos lenhosos, por meio da refixação do CO2 proveniente da respiração nas células clorofiladas da casca, parênquima radial e medula do caule (LIU et al., 2018). Essas moléculas produzidas fornecem substratos para construção das estruturas das plantas (carboidratos estruturais), bem como a energia necessária para as reações biológicas das células e a síntese de outros compostos orgânicos (carboidratos não estruturais). (DANNOURA et al., 2016).

Os carboidratos não estruturais (CNE), são os principais substratos para o metabolismo primário e secundário das espécies vegetais. São divididos em classes que vão de acordo com a natureza das moléculas. Os monossacarídeos são moléculas simples, que contém entre 3 e 5 átomos de carbono (i.g glicose, frutose, arabinose e galactose). Esses carboidratos, como a glicose e frutose, funcionam principalmente como osmólitos e substratos para respiração celular. A glicose é principal produto da fotossíntese, é convertida para a síntese de muitas outras moléculas. Já a frutose, é também um importante CNE na respiração celular e atua como molécula de reserva energética rápida em algumas plantas. Os dissacarídeos e oligossacarídeos (i.g sacarose, rafinose, estaquiose), são moléculas compostas, por três a nove açúcares simples, em média. Podem ser hidrolisados a moléculas menores e assim, utilizados como substratos. A sacarose é um dos principais açúcares de transporte nas plantas (HARTMANN; TRUMBORE, 2016). Já os polissacarídeos são cadeias longas de monossacarídeos, seus representantes mais comuns são a amilopectina e amilose, que formam o amido, os carboidratos de reserva mais comum em plantas. A natureza osmoticamente inativa desse carboidrato, permite que sejam armazenados em grandes quantidades pelas plantas (HARTMANN; TRUMBORE, 2016).

Os CNEs estão presentes em todos os tecidos vegetativos vivos das plantas. Entretanto, a distribuição desses compostos ao longo da planta ocorre de maneira assincrônica entre os órgãos, mesmo sob condições consideradas favoráveis (STITT et al., 2012). Durante o dia, nas folhas, os carboidratos excedentes resultantes da fotossíntese são armazenados nos cloroplastos na forma de amido. Durante a noite, para a manutenção dos processos vitais, o amido é hidrolisado em glicose ou exportado para outros órgãos na forma de sacarose. O floema é o principal tecido de condução e, devido às suas propriedades anatômicas e funcionais, consegue controlar a quantidade de carboidratos diários alocados para os tecidos dreno (EPRON et al., 2016). As raízes recebem cerca de 31% da produção primária, e suas funções são fortemente dependentes dos recursos fotossintéticos (LITTON et al., 2007).

Tais moléculas são fundamentais para a sobrevivência das plantas (SALA; WOODRUFF; MEINZER, 2012) e, estima-se que os CNE produzidos pela fotossíntese representem metade do carbono assimilado pelas plantas. Portanto, uma eventual limitação de carbono proveniente da fotossíntese afetaria não somente o incremento de biomassa, mas a manutenção de processos metabólicos básicos como a respiração.

2.3.2 O papel dos CNEs na tolerância ao estresse hídrico

Os CNE desempenham papel importante na vida das plantas expostas a condições ambientais estressantes, como seca (PALACIO et al., 2018), atuando como moléculas sinalizadoras do estresse, osmoreguladores, e no sequestro de espécies reativas de oxigênio – ROS (PIPER; FAJARDO; HOCH, 2017; MARTÍNEZ-VILALTA et al., 2016). Além disso, discussões crescentes apontam que o acúmulo de carboidratos pode visar estrategicamente a formação de uma reserva para tempos difíceis em termos de aquisição de carbono pelas plantas. Essa reserva seria utilizada quando a demanda por carbono não pudesse ser atendida pela fotossíntese (SALA; WOODRUFF; MEINZER, 2012; CHUSTE et al.,2020).

Durante um estresse hídrico, a regulação da abertura estomática, que visa a manutenção do conteúdo de água na planta, afeta diretamente a assimilação de C (TANG et al., 2002; FLEXAS et al., 2006). Devido a isso, hipóteses clássicas associam a morte de plantas sob condições de déficit hídrico à redução da disponibilidade de carbono, seja pela diminuição na produção de CNE (hipótese de esgotamento de carbono) ou pela dificuldade de alocação desses compostos para os tecidos vegetais (hipótese de falha hidráulica) (SALA et al., 2010; MILLARD et al., 2007). No entanto, na última década, pesquisas têm demonstrado que os CNE desempenham um papel significativo na tolerância das plantas a diversos estresses abióticos (ROSA et al., 2000; RIGIER et al., 2009; PIPER, 2011).

2.3.3 CNE e as espécies decíduas

Dada a relevância dessas reservas como fonte de carbono, estudos indicam que particularmente para as espécies decíduas, o acúmulo de CNE pode ser determinante durante as secas sazonais (PALACIO et al., 2018). Diante da estratégia adaptativa de eliminar as folhas, essas espécies caducifólias obrigatoriamente precisam remobilizar os carboidratos armazenados para manutenção básica durante todo o período de seca (MARTÍNEZ-VILALTA et al., 2016). Os CNE devem ainda ser suficientes para dar início ao desenvolvimento de novas folhas com a chegada da estação chuvosa, e a produção dessas estruturas são um dos principais drenos de carbono (PALACIO et al., 2018). Desse modo, as espécies caducifólias precisam particionar de maneira deliberada o uso do pool de NSC entre a manutenção metabólica básica e a rebrota da copa, visando a retomada da fotossíntese e crescimento no período favorável de chuvas (BLUMSTEIN et al., 2020).

As espécies podem, contudo, diferir quanto ao padrão da dinâmica de produção e alocação de carboidratos mesmo ocorrendo em ambientes semelhantes, o que pode estar ligado principalmente as diferenças no tipo funcional. Árvores decíduas podem ser mais dependentes de reservas de CNE do que espécies sempre verdes, por exemplo, devido a manutenção de área fotossintética nestas, o que pode levar a flutuações menos dramáticas no seu pool de CNE durante a seca (PALACIO et al., 2018). O mesmo vale para espécies que possuem tecidos lenhosos com capacidade fotossintética, as quais encontram nessa estratégia uma fonte significativa de carbono sob condições limitadas, configurando como uma alternativa crucial de sobrevivência durante a seca (ROO et al., 2020).

Esse tipo de fotossíntese caulinar é menos afetado pela disponibilidade hídrica do que a fotossíntese foliar (ROO et al., 2020), inclusive, e dados recentes revelam a contribuição substancial dessa fotossíntese sobre o balanço de carbono em algumas espécies como o álamo (Populus tremula) sob déficit hídrico nas regiões temperadas (ROO; SALOMÓN; STEPPE, 2020). À luz disso, a presença de tal estratégia em espécies arbóreas de ambientes vulneráveis a severidade das secas, como a floresta seca Caatinga, pode ser o fator chave na resiliência de árvores desses ecossistemas.

Entretanto, as implicações graves da seca não consistem apenas na limitação fotossintética e provoca também consequências hidráulicas nas plantas, como embolia dos vasos condutores, podendo acarretar em falhas no sistema de transporte e conduzir à mortalidade dos indivíduos (SAVI et al., 2019). Dentro desse contexto também, os CNE podem ser decisivos atuando na regulação osmótica, a fim de evitar falhas hidráulicas drásticas durante o estresse hídrico (SALA; WOODRUFF; MEINZER, 2012). O que traz à luz outro ponto de bastante interesse dos ecofisiologistas frente o cenário de mudanças climáticas: desvendar o mecanismo que dirige a mortalidade das árvores em condições de seca, isto é, se ela é determinada pela depleção de carbono ou pela falha hidráulica. Essa compreensão permanece obscura (PIPER, 2011) e dados recentes sugerem que as duas causas podem estar interconectadas (SAVI et al., 2019).

3 ARTIGO 1 - GREEN STEM WATER STORAGE AND BEHAVIOR OF NON-STRUCTURAL CARBOHYDRATES IN A DECIDUOUS WOODY TREE IN A DRY TROPICAL FOREST

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Green stem water storage and behavior of non-structural carbohydrates in a deciduous woody tree in a dry tropical forest

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Abstract

We investigate the strategy in *Commiphora leptophloeos*, a dry tropical forest deciduous tree that exhibit green stems. The main objective of this work was to understand how non-structural carbohydrates (NSC) vary throughout the plant during both seasons under a semi-arid climate. Thus, we evaluated photochemical activity in green stem and leaves, collecting leaves, twigs, and roots to quantify the NSC content. We also assessed the stomatal conductance (g_s) in leaves and xylem water potential (Ψ_x) of plants. We found that the maximum quantum efficiency of PSII indicate a photochemical activity in the stems and no difference to leaves or throughout months. In the leafless months the concentration of soluble sugars decreased by half in the twigs and roots. The NSC concentration was stable during dry periods and the partitioning was consistent among organs throughout months, however during transition from rainy to dry season, the SS roots concentration increase while the starch reduced. This can indicate plants could be interconverting this non-soluble sugar to optimize their metabolism in response to incoming drought. Plants also sustained high Ψ_x even in dry months, which can be explained by both the water storage capacity due to low wood density of this species and by the consistence of NSC. However, g_s values showed a relationship with Y_x. A slight reduction in water status led to strong control of the stomatal pore.

Keywords: Caatinga; drought tolerance; green stem; NSC dynamic; woody species

Introduction

Tree mortality is an increasing problem in forests around the world for drought consequences (Hammond et al. 2019, Blumstein et al. 2020). The warnings show that environments already sensitive to dry events will be much more affected (Marengo and Bernasconi 2015, IPCC 2022). Drought stress is a causal factor to plants survival with effects on uptake resources such as photosynthetic carbon and nutrients (Falcão et al. 2017). In the face of the changing scenario of the global climate, tree species survival could be in danger (Savi et al. 2019).

Under limited water soil conditions, plants could face a critical reduction in xylem water potential that may lead to vessel cavitation and threaten hydraulic integrity on a scale of the whole plant (De Baerdemaeker et al. 2017, Savi et al. 2019). It also could affect the dynamic of carbon in the plant, by changing process of synthesis and mobilization of Non-Structural Carbohydrates (NSC) impairing the homeostasis of the plant metabolism (Sala et al. 2012). Thus, trees under drought conditions may collapse because of either hydraulic issues or carbon starvation (Sala et al. 2012, Hammond et al. 2019).

Species living in dry environments show adaptations to face those limited conditions. One of these adaptive traits commonly found in plants of tropical dry forests (TDF) such as the Brazilian one named Caatinga, is the defoliation strategy during dry seasons (Santos et al. 2022). In this domain most species are deciduous, which helps to control the transpiration rate during periods of reduced water availability (Falcão et al. 2017, Barros et al. 2021). On the other hand, it implies adverse effects on carbon gain along months of drought since the most crucial photosynthetic tissue is absent (Palacio et al. 2018). To evaluate the effect of this on carbon balance, and the impact on tree mortality in dry environments is essential to assess how the NSC pools vary over time (Chuste et al. 2020).

To avoid carbon starvation during these times plants must produce and store NSC during rainy seasons. Thus, they should be able to survive accessing the store and also use it for leaf sprouting at the starting rains (Sala et al. 2012, Piper et al. 2017, Blumstein et al. 2020, Furze et al. 2021). Although, little is known about how seasonality drives the regulation of this NSC dynamic, especially in woody plants of dry forests (Santos et al. 2021). Besides, studies are reporting species with a particular compensatory way to deal with the issue of carbon gain under drought. There are mature trees with the ability to do photosynthesis in non-leaf tissues, such as the stems (Ávila-Lovera et al. 2017, Burrows and Connor 2020). This strategy is reported for species that have a layer of chlorophyll tissue under the periderm and it is named Corticular Photosynthesis (Liu et al. 2019, De Roo, Salomón, Oleksyn, et al. 2020).

That another path to obtaining carbohydrates is less impacted by the reduction of water than the conventional one by leaf (De Roo, Salomón, and Steppe 2020). Studies have shown a significant contribution of this path to carbon balance in species from temperate regions under drought stress (De Roo, Salomón, Oleksyn, et al. 2020). In light of this, a reasonable question is whether these plants that can take this pathway under water-limited environments, might better resist this emergent climate change (Simkin et al. 2019). In this context, it has been seen that in Caatinga dry forest, there is a deciduous species that shows a conspicuous green tissue, especially in drought season (Araújo, Castro, Albuquerque 2007). Nevertheless, none is known about the contribution of this feature to active photosynthesis, and how it impacts the dynamic of NSC over seasons.

Therefore, we have been investigating this strategy in *Commiphora leptophloeos*, this species has a very low wood density, high water storage capacity throughout the year (Lima et al. 2012) and presents changes in the phenological cycle independent of water availability in the soil between DTF seasons (Lima et al. 2021). It is a tree native to Caatinga Brazilian dry forest, in effect one of the biggest tropical dry forests in the world (Pereira et al. 2020). Besides, one of the most susceptible to climate change consequences as well (Lapola et al. 2020, IPCC 2022). We hypothesized that: 1) the fluctuations in NSC dynamics throughout seasonal variation would not be pronounced in this species as it can count with the contribution of the corticular tissue activity; 2) having wood with very low density would support the maintenance of tissue hydration throughout the seasons, going through the entire dry season with high xylem potential and consuming stored NSC from twigs and roots.

Material and methods

Study site and focal species

We conducted the study in an area for conservation of Caatinga, which is a domain of Seasonally Dry Tropical Forest in Brazil. The site is located on Catimbau National Park, city of Buíque, state of Pernambuco, Northeast of the country (8°24′00″ and 8°36′35″ S; 37°0′30″ and 37°1′40″ W). The park comprises a vast territorial extension of 607-km^2. The region's climate is semiarid, characterized by temperature averages around 23º C and annual rainfall ranging from 480mm to 1000mm (Pereira et al. 2020, Vanderlei et al. 2021). Our focal species for this study is *Commiphora letophloeos* (Mart.) J.B. Gillett (Burseraceae), one of the most representative species of Caatinga dry forest (Medeiros et al. 2022). It is a deciduous tree that belongs to family Burseraceae which along with Fabaceae, Euphorbiaceae and Boraginaceae are the most abundant families of the woody species in that area (Pereira et al. 2020).

Field conditions and sample design

Field assessments and plant material collections were carried out over a 17-month space-time window to cover a spectrum of varied environmental conditions experienced by trees at the study site over time. Eight sampling collections were performed in this study time range, starting in 2020, in November (Nov20), and repeating throughout 2021 in the months of April (Apr21), August (Aug21), October (Oct21), December (Dec21) and finally, in 2022 in January (Jan22), April (Apr22) and November (Nov22). These months, according to the seasonal characteristics of the region, include dry seasons, rain, and the transition periods between them.

Rainfall (mm) and soil water balance (WB)

Meteorological data records for the region were extracted from the databases of the Agronomic Institute of Pernambuco – IPA and the National Institute of Meteorology - INMET. We used the average monthly precipitation and temperature to calculate the soil water balance, drawing data from the year preceding the start of our study (November 2019) up to the study's final year (November 2022). This approach provided us with a more comprehensive overview of the water conditions that the plants might have encountered before data collection began, not only during the study evaluation period (Fig. 1).

Xylem water potential (Ψ_x) and stomatal conductance (g_s)

At 4:00 AM, branches from four individuals were collected to determine the pre-dawn water potential of the xylem using a Scholander pressure chamber (Model 3035, Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Stomatal conductance was assessed in five individuals of each species during seasonal periods when leaves were present (Apr21, Aug21, Jan22, and Apr22). Measurements were taken at 9:00 AM using a leaf porometer (SC – 1 Leaf Porometer, METER Group).

Chlorophyll a fluorescence and chlorophyll content

The functionality of the photosynthetic apparatus (PSII) in both leaves (n = 3) and stems (n = 3) was assessed through chlorophyll fluorescence analysis, using a portable fluorometer (FP 100, Photon Systems Instruments, Brno, Czech Republic). Following the OJIP measurement protocol of the equipment and the calculations outlined by Baker (2008), key parameters such as the maximum quantum efficiency of PSII (Fv/Fm), operational efficiency of PSII (ΦPSII) and electron transport rate (ETR) were determined.

For the measurement of minimum chlorophyll fluorescence (F_o) and maximum fluorescence (F_m) values, both leaves and stems underwent a dark adaptation for a minimum of 30 minutes. The dark adaptation for *C. leptophloeos* stems was achieved using self-manufactured adapted material, following the approach by Johnstone et al. (2012) (Fig. 2a). For the leaves, we utilized the specialized adapting tweezers provided with the measuring device (Fig. 2b).

Approximately, 200 mg of fresh leaves were homogenized with 80% acetone and total chlorophyll was extracted according to the method described by Lichtenthaler and Wellburn (1983) with some changes. Chlorophylls a and b and total carotenoids were throughout spectrophotometric quantification by analyses of their absorbance at 664, 646 and 470 nm wavelengths, respectively. Each photosynthetic pigment was expressed in milligrams per gram of dry weight, transformed from the equivalent in fresh weight and estimated using the following equations, where A means absorbance: Chl *a* (mg l^{-1}) = 12.21. A664—2.81. A646; Chl *b* (mg l^{-1}) = 20.13. A646—5.03. A664; Carotenoids (mg l^{-1}) = (1,000. A470—3.27 [Chl *a*] - 104 [Chl *b*])/227.

NSC concentration

To determine the SS (soluble sugar) content, leaf samples (when present), stems, and roots of five individuals were collected according to the methodology of Quentin et al. 2015, where the material collected in the field is placed in a microwave oven for 180 seconds to stop the enzymatic activity, preserving the tissue biochemistry in the closest state to that collected until further analysis in the laboratory. The samples were kept in paper bags and stored in airtight containers until analysis. The following criteria were considered: fully expanded and healthy leaves, distal branches of the individuals, and roots with a diameter of up to 0.7 cm. Non-Strutuctural Carbohydrates were quantified following the protocols of Dubois et al. (1956) and Santana-Vieira et al. (2016).

For starch concentration, the insoluble fraction (*Pellet*) of ethanolic extraction was incubated for 60 min with ten units of amyloglucosidase (from *Aspergillus niger* ammonium sulfate suspension, Sigma – Aldrich®), then the soluble sugar resultant of the reaction was determined by the same protocol mentioned to SS. Non-structural carbohydrates (NSCs) concentration was calculated by adding the SS and starch values, taking into account the mass of the tissue samples used.

Leaf Construction Cost (LCC)

Healthy and expanded leaves were collected from four individuals during each collection period. The ash content (g kg^{-1}) was obtained from 200 mg of dry matter of leaves, dried in a muffle at 500 °C for 6 h. The ash content was determined from the difference between pre and post muffle weighing (Li et al., 2011). The calorific measurement (ΔHC, kJ g^{-1}) was obtained by burning 200 mg of dry leaf matter in a calorimetric bomb (IKA C-200) according to Villar and Merino (2001). The calorific value (ΔHC) was calculated using: ΔHC = calories/(1-ash). The leaf construction costs (LCC) per unit mass (mass LCC) (g glucose g^{-1} DM) was determined based on the ash content, nitrogen concentration and ΔHC, according to Williams et al. (1987). The formula used to calculate the mass LCC: mass LCC = [(ΔHC 0.06968 - 0.065) (Ash - 1) + 7.5 (*k*N/14.0067)], where *k* is the oxidation state of nitrogen to nitrate (+5) and ammonium (-3) (Penning De Vries et al., 1974).

Data analysis

To analyze our data, we fitted Generalized Linear Mixed Models (GLMMs) and used the Akaike Information Criterion (AIC) as a guide for selecting the most appropriate model. After evaluating the models, we identified that the gamma family with a log-link function was the most suitable. To verify how the stomatal conductance, water potential, the leaf construction cost and the chlorophyll parameters changed over the months, we fitted a unique model for each. The months sampled were used as the fixed effects, and the individuals sampled (ID) as a random effect (response ~ months + (1| ID)). To comprehend the dynamic of NSC regarding partitioning among the organs (leaves, branches and roots) and the concentration over the months, we used the two categories: organs and months as fixed effects (response ~ organs*months + (1| ID)). All the data were analyzed on RStudio software (R 4.1.0).

Results

Environmental conditions

Rainfall (mm), soil water balance (WB)

The soil water balance in the studied area was most of the time negative, or the precipitation that occurred only recovered the system water lost to the atmosphere. Few moments of water accumulation throughout the experimental period (Fig. 1). Regarding the precipitation data and

WB in the sampled years, we can observe that 2021 was drier compared to 2020 and 2022. There is precipitation recorded from March to September 2021 but no water surplus until mid-2022. When the study sampling began in Nov20, even though there was recorded rainfall for that month, it did not result in a positive water balance. Furthermore, the water balance had been negative in the preceding months. The year 2022 had atypical rainfall for the region. It records rainfall from November 2021 until the same month of 2022. A positive water balance is presented from May to November of that year.

Xylem water potential (Ψ_x) e Stomatal conductance (g_s)

Regarding Ψ_x, plants did not show drastic fluctuations over months (Fig. 3). Interestingly, in Oct21, which is typically the driest month, plants did not exhibit a significant reduction in their water potential, with values remaining high (around -0.4 MPa), like those observed during rainy months. Regarding the g_s responses, data were collected exclusively during months with leaf presence (Apr21, Aug21, Jan22, Apr22, and Nov22) and they were correlated with the Y_x of the plants (Fig. 3a). We observed that although there were all rainy periods, plants exhibit differences in the g_s responses (Fig. 3c). Specifically, when comparing the same month between the two different years (2021 and 2022). For instance, plants in Apr21 exhibited higher g_s values than any other month including Apr22.

Pigments and chlorophyll a fluorescence

The content of photosynthetic pigments between leaves and stem was measured in Apr22, middle of rainy season, and demonstrated that all pigments are found in greater abundance in leaves, except carotenoids (Table 1).

The chlorophyll fluorescence parameters are shown in Table 2. Similar to g_s, data for chlorophyll *a* fluorescence of leaves were collected only when they were present on the trees. However, in two months (Apr21 and Nov22), due to technical problems with the equipment, we were unable to perform the measurements. No difference is observed in any of the fluorescence parameters measured on leaves over the months. The operational efficiency of PSII (ΦPSII) and the maximum quantum efficiency (F_v/F_m) data indicate functional PSII operation for the stems. This parameter showed no significant differences throughout the year, and modeling revealed no differences in photosynthetic parameters between stems and leaves.

NSC concentration

The dynamics of SS and starch among different plant organs over the months are presented in Figure 4. In general, plants showed a consistent pattern of partitioning among organs over the months. In most of the months the plant had the same concentration of SS in leaves, twigs and roots. We observed a difference in this pattern only in AG21 where SS twigs concentrations were lower than leaves and roots (- 0.75 and - 0.71 times, respectively). That means that compared to the other months, in August plants increase the SS concentration in roots rather than branches. Regarding the variation throughout the months, no difference can be found for SS leaves concentration. Plants exhibit different concentrations at the organs throughout months only for twigs and roots considering those months in which there were leaves in the trees. That is, in AG21 when plants start to shed their leaves, we observed that the SS concentrations increase in roots and twigs become less concentrated. When leaves are absent on the trees (N20, OC21, and DE21), plants exhibit higher root SS concentration in N20 (Fig. 4a). For twigs, the SS concentration in N20 was higher only compared to those collected in DE21 (0.72 times). Consequently, N20 shows an overall higher SS concentration, even though there is no difference in the partitioning pattern between these two organs over the months. In fact, twigs and roots consistently maintain similar concentrations regardless of the month. However, the concentration of SS in both organs decreased more than 50% compared to the months when there were leaves on the plants (Fig. 4a).

Regarding starch concentration, in terms of partitioning among the three organs, we only noticed a change in the pattern from one year to the other (Fig.4b). While in the months from 2021, the starch concentration in the three organs were the same, for the second year there was a reduction in twigs concentration compared to leaves. However, twigs were the only organ that did not show any change in its concentration across months when leaves were present. In general, roots have the same partitioning pattern then twigs and leaves. Despite the starch concentration among twigs and roots being the same regardless of the month, it can be observed that in AG21 there is a reduction of about 53% in the root starch concentration meanwhile an increase of about 36% in root SS concentration.

Leaf Construction Cost (LCC)

The leaf construction cost showed only small fluctuations during the study period (Fig. 1 Supp.). The range of values occurred within found for other deciduous woody species in the Caatinga.

Discussion

Our results suggest that: 1) the low wood density allows the species to maintain a high water status during both seasons in the DTF; 2) g_s has a quick response to changes in Y_x; 3) there is photochemical activity in the green tissue of the stem in the rainy and dry seasons, without sudden changes; 4) when the leaves are dropped, the concentration of soluble sugars in the roots increases, on the other hand, the concentration of starch is reduced by half. Furthermore, in the leafless months the concentration of soluble sugars is reduced by around 50% in the twigs and roots. The main aspect occurring is adjustments in the partition between organs in strategic moments. Before entering the dry season, specifically in August, trees accumulate SS in roots, which appear as priority organs in partitioning and storing of SS, over branches. This appears to be a strategy to prepare for the upcoming dry months as this species begins to lose its leaves in August, remobilizing soluble sugars from this organ in abscission.

Water is a transient resource in semiarid regions, which means that trees in this site must optimize their strategy to uptake resources while being available (Wright et al. 2021). The leaf fall during drought periods creates a trade-off between preserving water and carbon uptake in general deciduous species (Palacio et al. 2018). In the present study, *C. leptophloeos*, in addition to being deciduous, has a low wood density, with a high capacity to store water (Lima et al. 2012). However, these species tend to have larger diameter xylem vessels and their susceptibility to embolism is greater (Borchert 1994a,b). This fact may explain the high sensitivity of stomatal conductance to variations in xylem water potential in *C. leptophloeos*.

Storing NSC is an efficient strategy as a crucial source for not impacting vital functions dependent on carbon during drought (Sala et al. 2012, Chuste et al. 2020, Blumstein et al. 2020). In addition, NSC are known for their key role in hydraulic maintenance, due to their osmoregulation properties, helping to prevent critical problems with embolism and xylem vessel refills (Secchi and Zwieniecki 2011; Sala et al. 2012). There is a prevailing hypothesis that deciduous species might be more susceptible to carbon (C) starvation mortality due to reduced C fixation during leaf fall. Consequently, effective NSC storage and a well-regulated dynamic seem even more crucial in those species (Santos et al., 2021). Some deciduous species, the stem plays a substantial role in maintaining carbon balance during drought through Corticular Photosynthesis, thereby enhancing the species tolerance to arid environments and providing a carbohydrate source for plant survival (De Roo et al., 2019). C. *leptophloeos* showed strong stability for NSC concentration in twigs and roots through the study period, which could be supported by the maintenance of elevate water status and the efficient distribution of NSC between twigs and roots. However, these organs showed a reduction by half in the concentration of soluble sugars in those months when the trees are leafless.

This study represents the first investigation into the dynamics of NSC over the months and years for a deciduous tree species with green stem in the Caatinga dry forest. This kind of approach in mature trees is still rare, despite its importance in understanding how trees respond to increasingly extreme environments (Hartmann et al., 2018). *C. leptophloeos* is the first woody species in the Caatinga region known to have this green stem strategy (Araújo, Castro, Albuquerque 2007), and our study support their stem photochemical activity and discuss its potential contribution to the dynamics of NSC.

Since the most significant parameters of stem fluorescence did not differ over months, it indicates that corticular tissue is photochemical active not only in the dry season, but all over the year. Although with a lower concentration of photosynthetic pigments than leaves. It may explain the consistency of NSC in the plants. The F_v/F_m and ΦPSII are the most predictive fluorescence parameters of the functionality of photosynthetic apparatus (Johnstone et al. 2012). The first one reveals the maximum quantum yield of photosystem II (ΦPSII) that could be achieved, and the second shows how much the proportion of light absorbed is being used in the photochemistry process (Maxwell and Johnson 2000, Kalaji et al. 2014). Therefore, the photochemical capacities are consistent between the leaves and stems of *C. leptophloeos,* contrasting with data for other species in temperate climates that have less activity in the stem (Johnstone et al., 2014). In effect, leaves face more restrictions regarding the photo-assimilate process than stems, due to limitations in carbon uptake by stomata (Melo et al. 2021, Santos et al. 2022), which respond to hydraulic signals (Chen et al. 2020). This adds another dimension to the contributions of corticular photosynthesis, the stems may offset the carbon uptake losses by the leaf when stomatal conductance is a restriction factor. Since the process involves recycling internal CO_2, and is not directly dependent on leaf gas exchange (Chen et al. 2018).

C. leptophloeos has a very low wood density, which means it is vulnerable to wide variations in Ψ_x and susceptible to cavitation (Borchert 1994; Lima et al. 2012). Among dozens of deciduous woody species from the Brazilian TDF, *C. leptophloeos,* showed the lowest wood density and greatest capacity to store water (Lima et al. 2012), which may explain the upkeep of high potential water even under drought. Moreover, the consistency of an NSC pool in organs over the dry months plays a crucial role in improving hydraulic resistance, helping the plant detect and reverse embolisms (Epron et al. 2012, De Roo et al. 2019, Santos et al. 2021). Tropical species demonstrate this relationship; plants with higher NSC concentrations tend to maintain higher water potentials during the dry season (Blumstein et al. 2020). The local input of carbohydrates by corticular photosynthesis may help this, being used by plants for the maintenance of hydraulic integrity (Chen et al., 2018, De Roo et al., 2019). The stable concentration of SS and Starch throughout months of the dry season serves as strong evidence for the beneficial role of non-foliar photosynthesis in deciduous trees (Ávila-Lovera et al. 2017). That means that this species did not experience the drastic fluctuations in NSC pools that were expected based on the literature for deciduous trees under drought (Palacio et al., 2018).

Droughts are becoming more intense and longer in many regions of the world (Piper 2011, Hartmann et al. 2018, IPCC 2022). Based on the information presented here, one might conclude that the strategy of corticular photosynthesis is a crucial trait for resilience, potentially enhancing the survival of this species compared to other community members in the face of changing climate scenarios. Indeed, *C. leptophloeos* could exhibit greater resistance compared to deciduous counterparts that lack this specific strategy (De Roo et al. 2019). Nevertheless, it is essential to consider other important ecophysiological traits of this species, particularly those related to phenology triggers, which could become problematic with changing rainfall regimes. The need for this species to maintain a high water status may be a weakness under future semi-arid climate conditions. High hydration maintains high metabolism, which could explain the 50% drop in soluble sugars in stems and roots when there were no leaves, without an increase in starch concentration.

It has been shown that the phenology phases of *C. leptophloeos* are dictated by photoperiod rather than soil water availability, in contrast to species with high wood density (Lima et al., 2021). Maintaining a high water supply in tissues can favor this behavior regardless of soil water availability. When considering the future climate scenario in the semi-arid region, with longer droughts and more irregular rainy seasons, this species may be more harmed than those that respond to the soil's water potential. By reducing the NSC concentration by half during the leafless period and regrowing its new leaves during the dry season (Lima et al. 2021), this species would use a large part of the immediate NSC reserve. If the next rainy season takes longer to arrive, NSC consumption will be kept high and production low. Further investigations in this respect would be very welcome to our understanding of the ability of species to survive in a plot of changing climate.

Maintaining a high water supply in tissues can favor this behavior regardless of soil water availability. When considering the future climate scenario in the semi-arid region, with longer droughts and more irregular rainy seasons, this species may be more harmed than those that respond to the soil's water potential. Decreasing NSC concentration by half during the leafless period and regrowing its new leaves during the dry season (Lima et al. 2021), this species would use a large part of the immediate NSC reserve. Whether the next rainy season takes longer to arrive, NSC consumption would be kept high and production low. Therefore, a scenario like this could harm the complete annual cycle of this species, such as the entry into flowering and fruit production.

In summary, the present work showed that the first hypothesis was partially confirmed, the fluctuation in NSC concentration was accentuated, only when the plants were without leaves, at least in relation to the soluble sugar content; however, it confirms the second hypothesis, where xylem water potential was kept high throughout the study period, which favors the consumption of NSC stored in the twigs and roots, when the leaves are not present. This would support the regrowth of new leaves at the end of the dry season.

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Figures Legends

Figure 1. Soil Water Balance and Rainfall across months from one year prior to the beginning of the study (2019) and during the study (2021 and 2022). Region of the Catimbau National Park, City of Buíque, northeastern Brazil.

Figure 2. Fluorescence measurement on green stem and leaves of *Commiphora leptophloeos*. A- Own-manufactured structure to dark adaptation. B- Tweezer adaptation for leaves. C- Dark adapt structure placed on stem and demonstration of measurements (in the right up corner picture). D- Green stem of *Commiphora leptophloeos* totally exposure during drought season.

Figure 3. Relationship between Xylem water potential (Ψ_x) and Stomatal conductance (g_s) from *Commiphora leptophloeos* and the responses of these parameters of the over the months

Figure 4. The NSC (Soluble sugars – SS, and starch) dynamics trough months among leaves (L), twigs (T) and roots (R) of *Commiphora leptophloeos* in Caatinga dry forest.

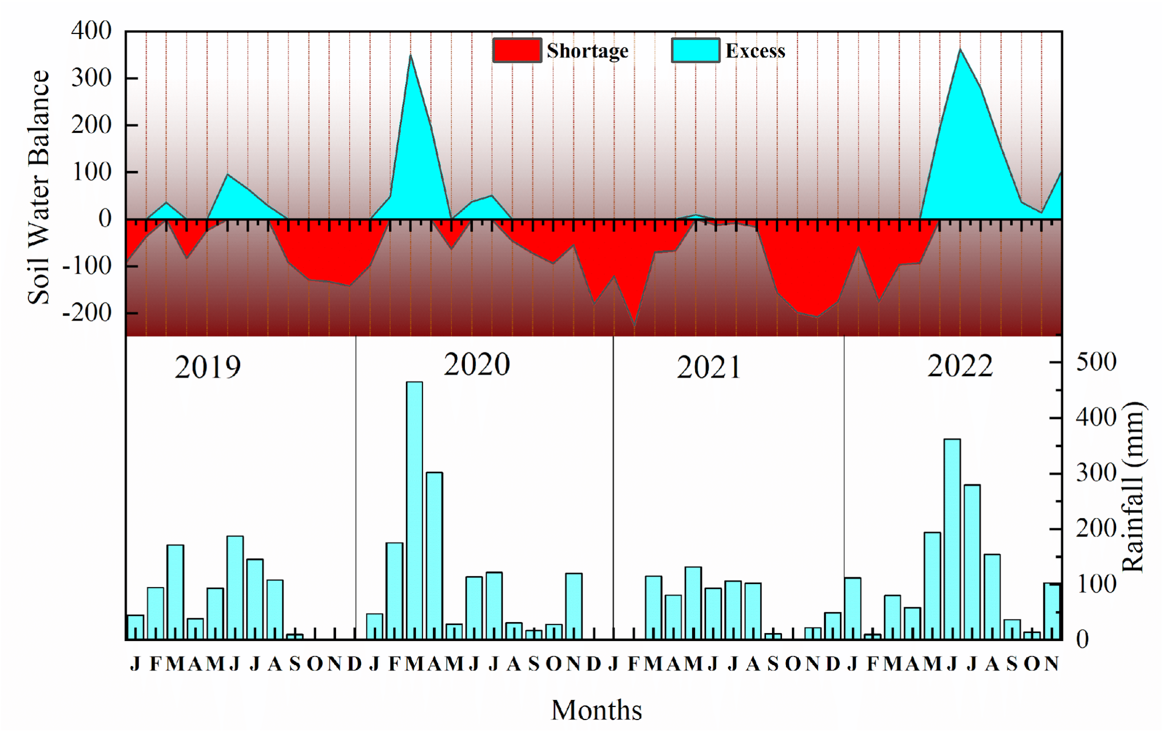
Shortage
Excess
Soil Water Balance
400
300
200
100
0
-100
-200
2019
2020
2021
2022
500
400
300
200
100
0
Rainfall (mm)
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N
Months

Figure 1

Figure 2

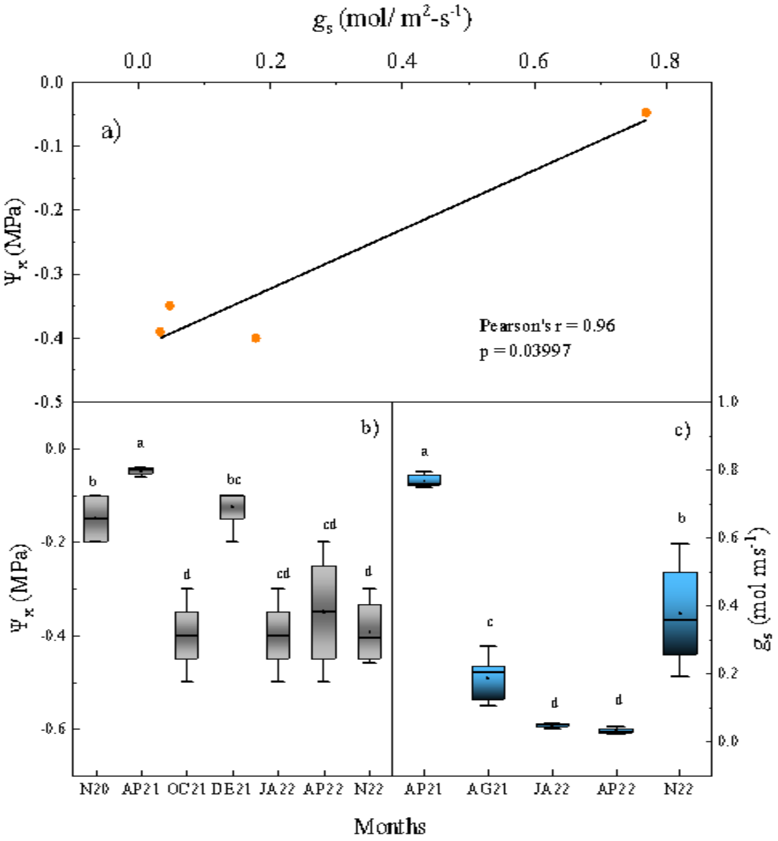
gs (mol/ m2-s-1)
0.0
0.2
0.4
0.6
0.8
a)
Ψx (MPa)
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
Pearson's r = 0.96
p = 0.03997
b)
c)
0.0
-0.2
-0.4
-0.6
b
a
d
bc
cd
cd
d
N20
AP21
OC21
DE21
JA22
AP22
N22
a
c
d
d
b
AP21
AG21
JA22
AP22
N22
1.0
0.8
0.6
0.4
0.2
0.0
gs (mol ms-1)
Months

Figure 3

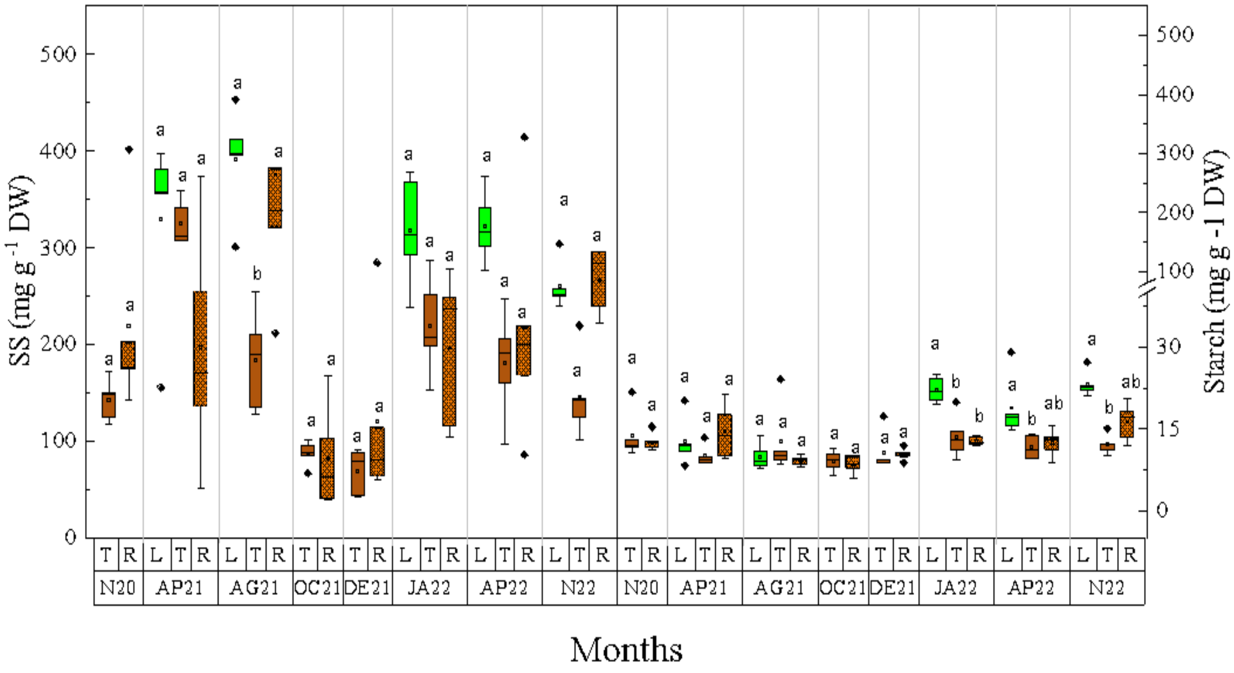
SS (mg g-1 DW)
Starch (mg g -1 DW)
0
100
200
300
400
500
0
15
30
100
200
300
400
500
T R L T R L T R L T R T R T R L T R L T R L T R T R L T R L T R L T R T R T R L T R L T R L T R
N20
AP21
AG21
OC21
DE21
JA22
AP22
N22
N20
AP21
AG21
OC21
DE21
JA22
AP22
N22
a
b
ab
Months

Figure 4

Table 1. Chlorophyll and carotenoids content at leaves and main stem with green tissue (corticular) (g kg^{-1}DM). Mean values (n = 4±SE). Values compared between organs in the columns.

Tissue	**Chlorophyll *a***	**Chlorophyll *b***	**Total chlorophyll**	**Carotenoids**
Leaves	$0.755 \pm 0.023^{***}$	$0.247 \pm 0.011^{*}$	$1.002 \pm 0.033^{***}$	0.266 ± 0.008^{ns}
Stem	0.371±0.047	0.174±0.018	0.545±0.065	0.325±0.023

*difference to 5%; *** to 1%.

Table 2. Chlorophyll fluorescence. F_v/F_m – Maximum quantum efficiency of the PSII (Photosystem II); ϕPSII – PSII Operational Efficiency, ETR – Electron Transport Rate. Mean values (n = 4±SE). There are no significant differences for any parameter, either throughout the months or among the organs.

Parameters/Month	**Aug21**	**Oct21**	**Dec21**	**Jan22**	**Apr22**
		LEAVES			
Fv/Fm	0.75±0.0^{ns}	-	-	0.76±0.0	0.72±0.0
ϕPSII	0.46±0.1^{ns}	-	-	0.33±0.0	0.32±0.1
ETR	300±43^{ns}	-	-	233±37	242±30
		STEM			
Fv/Fm	0.76±0.0^{ns}	0.59±0.1	0.68±0.0	0.66±0.1	0.76±0.0
ϕPSII	0.36±0.1^{ns}	0.30±0.0	0.40±0.0	0.37±0.1	0.49±0.1
ETR	238±47^{ns}	210±24	261±51	263±58	369±58

4 ARTIGO 2 - XYLEM WATER POTENTIAL DOES NOT EXPLAIN THE DYNAMICS OF NON-STRUCTURAL CARBOHYDRATES IN WOODY SPECIES UNDER THE SEASONALITY OF A TROPICAL DRY FOREST

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Xylem water potential does not explain the dynamics of non-structural carbohydrates in woody species under the seasonality of a tropical dry forest

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Abstract

Facing the climate changes, it becomes imperative to comprehend how seasonality regulates the dynamics of non-structural carbohydrates (NSC) storage in wood species because they are critical for plant survival strategy under drought conditions. We approach this issue by studying three representative deciduous woody species from the Caatinga dry forest: *Peltogyne pauciflora*, *Pityrocarpa moniliformis* and *Cenostigma microphyllum*. We tested if the NSC pool will vary according to the season, being higher in wet periods and lowering in dry ones independent of the species. During eight months we collected leaves, twigs, and roots to quantify NSC concentrations, along with measurements of stomatal conductance (g_s), chlorophyll fluorescence, and water potential (Ψ_x). The results show that regarding g_s, *P. pauciflora* was the only species that did not show differences in stomatal behavior throughout the months. Additionally, this species was the only one in which chlorophyll fluorescence parameters did not show significant differences between consecutive months. Concerning Ψ_x, we observed fluctuations throughout months for all three species, where the lowest Ψ_x values was found for the typical dry periods compared to the others. Regarding the overall NSC concentration among the three species, *P. pauciflora* had the highest concentration surpassing its counterparts. *C. microphyllum* and *P. moniliformis* did not exhibit differences in their NSC concentration. Furthermore, we found no significant differences in the dynamics of total NSC throughout the months for any of the species. This suggests that there was no drastic reduction in the NSC pool from rainy to dry months, nor a significant increase from dry to wet months.

Keywords: Drought tolerance, Nonstructural carbohydrates, Seasonality, Tropical dry Forest

Introduction

Carbohydrates are a vital currency in plant metabolism, encompassing a family of macromolecules primarily composed of soluble sugars and starch. These macromolecules are collectively referred to as Non-Structural carbohydrates (NSCs) and play a fundamental role in both primary and secondary plant metabolism (Hartmann and Trumbore 2016). Plants can accumulate these molecules daily or even decades and can use this store to support the vital process in unfavorable conditions when photosynthesis is impacted (Blumstein et al. 2020). The accumulation of NSCs strategy, therefore, emerges as a key factor in enhancing species' drought tolerance, particularly for perennial life forms like trees (Epron et al. 2012). Research has indicated that, especially for deciduous species, the NSCs can be critical during seasonal droughts (Palacio et al. 2018). Because these species employ the adaptive strategy of shedding leaves, they must inevitably mobilize stored carbohydrates for basic maintenance throughout the entire dry period. Consequently, a massive depletion of these reserves during this period could lead to the death of these plants (Martínez-Vilalta et al. 2016).

The serious implications of drought extend beyond limitations in photosynthesis and also encompass hydraulic consequences in plants, such as vessel embolism, which can result in transport system failures and lead to individual mortality (Savi et al. 2019). Within this context, NSCs can also play a decisive role in osmotic regulation, aiming to prevent drastic hydraulic failures during water stress (Sala et al. 2012). This raises a point of great interest to eco-physiologists in the face of climate change which is unraveling the mechanism driving tree mortality under dry conditions: whether it is determined by carbon depletion or hydraulic failure. This understanding remains unclear (Piper 2011), and recent data suggest that the two causes may be interconnected (Savi et al. 2019). Such interconnections underscore the complexity of tree responses to changing environmental conditions. Given the preceding discussion, one might question whether, for example, among deciduous species, those that delay leaf shedding, thus maintaining photosynthesis for an extended period before losing leaves entirely, could exhibit a trend of stability of NSC compared to the counterparts deciduous, under water limited availability, such as under drought season in a dry tropical forest (DTF).

Therefore, the dynamic of carbohydrate storage is important for DTF woody species, particularly in regions like the Caatinga, which face limited water availability, rendering them highly vulnerable. Decrease soil water availability, reduce xylem water potential and, in general lead to reduced stomatal conductance in these woody species under this environmental (Souza et al. 2010; Santos et al. 2021), avoiding excessive transpiration. Thus, when the stomata close, gas exchanges are limited (Chaves et al. 2002; Ferreira-Neto et al. 2022), with consequent negative feedback in photochemical efficiency (Baker and Rosenqvist 2004).

Given the current climate change scenarios, including rising temperatures and extended drought events (Marengo and Bernasconi 2015), it becomes imperative to comprehend how seasonality regulates the dynamics of carbohydrate storage in wood species from these ecosystems. Thus, we bring this approach about how seasonality impacts NSC dynamics in three different wood deciduous species from Caatinga dry forest: *Peltogyne pauciflora*, *Pityrocarpa monilifmoris* and *Cenostigma microphyllum.* Considering the pivotal role of NSCs in plant survival during drought, we formulate the following hypotheses for our study: 1) The NSc pool will vary according to the season, being higher in wet periods and lowering in dry ones independent of the species, and 2) among the three deciduous species under investigation, *Peltogyne pauciflora* employing a late deciduous strategy may display greater stability in NSC levels during drought compared to their counterparts. This knowledge serves as a proxy for assessing the susceptibility or resilience of tree species and could be used to improve model predictions regarding plant survival in the face of the climate changing challenges.

Material and methods

Study site and focal species

We conducted the study in an area for conservation of Caatinga, which is a domain of Seasonally Dry Tropical Forest in Brazil. The site is located on Catimbau National Park, city of Buíque, state of Pernambuco, Northeast of the country (8°24′00″ and 8°36′35″ S; 37°0′30″ and 37°1′40″ W). The park comprises a vast territorial extension of 607 km^2. The region's climate is semiarid, characterized by temperature averages around 23º C and annual rainfall ranging from 480mm to 1000mm (Pereira et al. 2020; Vanderlei et al. 2021). Our focal species for this study are tree species that belong to Fabaceae, the most abundant family of woody species in that area (Pereira et al. 2020): *Peltogyne pauciflora* (Benth.), *Cenostigma mycrophyllum* (Mart. Ex G. Don) E. Gagnon & G.P. Lewis and *Pityrocarpa moniliformis* (Benth.) Luckow & R. W. Jobson. The three species have high wood density, that is, above 0.5 g cm^{-3} (*P. pauciflora* 0.8±0.04; *C. microphyllum* 0.6±0.03 and *P. moniliformis* 0.6±0.05 g cm^{-3} (Trugilho et al. 1990; Lima et al. 2021).

Field conditions and sample design

Field assessments and plant material collections were carried out over a 17-month space-time window to cover a spectrum of varied environmental conditions experienced by trees at the study site over time. Eight sampling collections were performed in this study time range, starting in 2020, in November (Nov20), and repeating throughout 2021 in the months of April (Apr21), August (Aug21), October (Oct21), and December (Dec21) and finally, in 2022 in January (Jan22), April (Apr22) and November (Nov22). These months, according to the seasonal characteristics of the region, include dry seasons, rain, and the transition periods between them.

Rainfall (mm) and soil water balance (WB) and Soil moisture (SM)

Meteorological data records for the region were extracted from the databases of the Agronomic Institute of Pernambuco – IPA and the National Institute of Meteorology - INMET. We used the average monthly precipitation and temperature to calculate the soil water balance, drawing data from the year preceding the start of our study (November 2019) up to the study's final year (November 2022). This approach provided us with a more comprehensive overview of the water conditions that the plants might have encountered before data collection began, not only during the study evaluation period (Fig. 1).

Soil moisture measurements were conducted throughout the months using the gravimetric method. Soil samples (n=2) from the vicinity of each individual will be collected at depths ranging from 60 to 100 cm (Costa et al. 2014). The fresh weight (FW) and dry weight (DW), after 24 hours of drying in an oven at 105 °C, were determined for these samples. Gravimetric moisture content (%) was calculated as the ratio of water mass to dry soil mass (Viana et al., 2017).

Xylem water potential (Ψ_x) and stomatal conductance (g_s)

At 4:00 AM, branches from four individuals were collected to determine the pre-dawn water potential of the xylem using a Scholander pressure chamber (Model 3035, Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Stomatal conductance was assessed in five individuals of each species during seasonal periods when leaves were present (Apr21, Aug21, Jan22, and Apr22).

Measurements were taken at 9:00 AM using a leaf porometer (SC – 1 Leaf Porometer, METER Group).

Chlorophyll fluorescence

The functionality of the photosynthetic apparatus (PSII) in leaves (n = 4) was assessed through chlorophyll fluorescence analysis, using a portable fluorometer (FP 100, Photon Systems Instruments, Brno, Czech Republic). Following the OJIP measurement protocol of the equipment and the calculations outlined by (Baker 2008), key parameters such as the maximum quantum efficiency of PSII (F_v/F_m), operational efficiency of PSII (ΦPSII) and electron transport rate (ETR) were determined. For the measurement of minimum chlorophyll fluorescence (F_o) and maximum fluorescence (F_m) values, leaves underwent a dark adaptation for a minimum of 30 minutes.

NSC concentration

To determine the SS (soluble sugar) content, leaf samples (when present), stems, and roots of five individuals were collected according to the methodology of (Quentin et al. 2015), where the material collected in the field is placed in a microwave oven for 30 seconds to cease the enzymatic activity, preserving the tissue biochemistry in the closest state to that collected until further analysis in the laboratory. The samples were kept in paper bags and stored in airtight containers until analysis. The following criteria were considered: fully expanded and healthy leaves, distal branches of the individuals, and roots with a diameter of up to 0.7 cm. The Soluble sugar (SS) components of Non-Strutuctural Carbohydrates components were analyzed following the steps: to extract the SS from the dry material, the samples were ground using a mortar and pestle and suspended in 1,200 µl of 80% ethanol (Farrar, 1995). Subsequently the samples were vortexed, ant the suspension was incubated for 90 minutes in a water bath at 70°C., the material was centrifuged at

12,500 g, and the supernatant was collected. This process was repeated using 600 µl of 80% ethanol for an additional 30 minutes. Soluble sugars were analyzed by the phenol-sulfuric acid method, adding 0.5ml 5% phenol and 2.5 ml of sulfuric acid to the extract aliquot, SS were measured at 487 nm using a dual-beam spectrophotometer (Geneses 10S UV–Vis, Thermo Scientific), according to the methodology described by (Dubois et al. 1956).

For the starch component quantification, the insoluble fraction (*Pellet*) of ethanolic extraction was resuspended in 800uL of 0.2 M KOH solution, vortexed and carried to a water bath at 95°C for 120 minutes. After that, to adjust the pH of the samples to 5.5 we added 200uL of acetic acid and samples were centrifuged at 12,500 G. Subsequently, the resultant supernatant was collected and was hydrolyzed with 10 units of amyloglucosidase (A1602, Sigma-Aldrich) for 60 minutes in a thermal bath at 55°C to digest the gelatinized starch to glucose. SS and starch concentrations (measured as glucose equivalents) were measured at 487 nm using a dual-beam spectrophotometer (Dubois et al. 1956). To obtain the total NSC value, the measurements of SS and starch in the leaves of each species were summed.

Prior to the analyses, a mass test was carried out for each species to determine the dry weight (mg) to be used in the extraction. The test consisted of measuring the SS of 10mg, 20mg and 40mg of dry material of three aleatory individuals per species and verifying whether the SS concentration value increased proportionally to the mass. This allowed us to analyze the saturation level of the extracts. Thus, the masses were determined and for the three species we used 20mg.

Data analysis

To analyze our data, we fitted Generalized Linear Mixed Models (GLMMs) and used the Akaike Information Criterion (AIC) as a guide for selecting the most appropriate model. After evaluating the models, we identified that the gamma family with a log-link function was the most suitable. To verify how the stomatal conductance, water potential and the chlorophyll parameters changed over the months, we fitted a unique model for each. The months sampled were used as the fixed effects, and the individuals sampled (ID) as a random effect (response ~ months + (1| ID)). To comprehend the dynamic of NSC regarding partitioning among the organs (leaves, branches and roots) and the concentration over the months, we used the two categories: organs and months as fixed effects (response ~ organs*months + (1| ID)). All the data were analyzed on RStudio software (R 4.1.0).

Regression analysis

To evaluate how tree responses were related to the environmental conditions we performed regression analyses between some plant parameters such as NSC, Water Potential in function of Water Balance parameters and Soil Moisture. We also performed Person's correlation analysis to evaluate the relationship between Precipitation, Soil water balance parameters and Soil moisture.

Results

Environmental conditions

Rainfall (mm), Soil water balance (WB) and Soil moisture (SM)

The meteorological data accessed since 2019 (Fig. 1), the year before the study began, until the last month sampled, provided us with a better overview of the conditions that trees had been experiencing. Figure 1 illustrates the pattern of water excess and shortage in the soil over the months. It's evident that even when a rainfall rate is recorded, it doesn't necessarily imply a positive water balance in the soil.

Regarding the precipitation data and WB in the sampled years, we can observe that 2021 was drier compared to 2020 and 2022. There is precipitation recorded from March to September 2021 but no water surplus until mid-2022. When the study sampling began in Nov20, even though there was recorded rainfall for that month, it did not result in a positive water balance. Furthermore, the water balance had been negative in the preceding months. The year 2022 was a year with atypical rainfall for the region. It records rainfall from November 2021 to November 2022. A positive water balance is presented from May to November of this year. Concerning Soil moisture, the most interesting difference is found comparing Oct21 to Ap21 and Nov20 (- 1.5 lower than both). Oct21 used to be a typical dry month in the area, and Ap21 the wet one. Nov20 was supposed to be dry too, but it was a little rainier than Oct21.

Xylem water potential (Ψ_x) e Stomatal conductance (g_s)

The trend for all the three species was for the water potential fluctuations throughout the months. The trees had especially lowest Ψ_x in the typical dry periods (Oc21) compared to the other months (Fig. 2). For *Peltogyne pauciflora*, plants reduced their Ψ_{wx} from Apr21 to Oct21 (- 0.97 MPa), but in Dec21 plants increased the Ψ_x in about 2.2 times higher than Oct21. In Jan22 and Apr21 there was further reduction about 0.9 and 1.2 times, respectively. For this species, the highest values Ψ_x was found in Dec21 compared to any other month (Fig. 2a). For *C. microphyllum* the trends reduction was almost the same from Apr21 through Dec21, except that the magnitude of the reduction in Oc21 compared to Apr21 was higher for this species, about 2.3 times (Fig.2c). The values remained stable through Jan22 and Apr22, reducing again only from Apr21 to Nov22 (0.9 times). For this species, the Ψ_x of Oc21 was the lowest compared to any other month (-3.75 MPa). In the case of *Pityrocarpa moniliformis*, trees exhibited a different pattern in the relationship between Ψ_x values for Oct21 and Dec21 compared to the other species (Fig.2b). In this species, the plants in Dec21 had significantly lower Ψ_x values, approximately 1.5 times less, than in Oct21. From Dec21 to Jan22 plants increased their water potential 1.0 times, reducing once further in Apr22 (1.3 times) and in Nov22 (1.0 times).

Concerning stomatal conductance (g_s), among the three species, *P. pauciflora* was the only species that did not show differences in stomatal behavior throughout the months and neither between the same months through the two years of sampling (Fig.2d). The g_s was consistent in the trees with an average of 0.3 mol $m^{-2}s^{-1}$. However, for *P. moniliformis* and *Cenostigma. microphyllum*, there were variations in g_s over the months. For *P. moniliformis* (Fig.2e) it was observed a reduction in g_s from Apr21 to Aug21(-0.6 times), from Aug21 to Oct21 (-0.8 times), followed by an increase in Jan22 (-0.5 times). *C. mycrophyllum* (Fig.2f) also exhibited a decrease in g_s from Apr21 to Aug21 (- 0.9 times), followed by an increase in Jan22 (1.1 times), and another decrease in Apr22 (0.5 times). Furthermore, when comparing the same month (April) in two consecutive years (2021 and 2022), there were differences in stomatal behavior observed for *P. moniliformis and C. microphyllum.* In April 2021, these trees showed higher g_s compared to April 2022 (0.7 times higher for both). Among the three species, only *C. microphyllum* showed g_s responses positively correlated with the Ψ_x (Fig.3).

Chlorophyll fluorescence

In a chronological sequence of the sampling, out of the three parameters we use to evaluate the functionality of the Photosystem, such as F_v/F_m, ΦPSII and ETR, *P. pauciflora* was the only specie in which none of the parameters differed in the consecutive months (Table 1). We observed differences when we looked through similar periods in different years, such as Nov20 to Oct21 and to Nov22. F_v/F_m was higher in Nov22 than Nov20 (0.4 times), the ΦPSII had more yield in Oct21 than in Nov20 (0.7 times) and the ETR was also higher in Oct21 (0.8 times) and in Nov22 compared to Nov20 (0.7 times). For *P. moniliformis* and *C. microphyllum*, the F_v/F_m was the only parameter to show difference in a chronological scale, from Apr22 to Nov22 (0.5 and 0.6 times, respectively). For the other parameters, such as ΦPSII and ETR, *P. moniliformis* had the lowest yield in Oct21 (ΦPSII = 0. 216 and ETR= 150) compared to most of the other months. Concerning *C. microphyllum* the ΦPSII and ETR do not show differences throughout months.

When we compare the same months in the two different years Nov20 and Nov22, at least one parameter has a different response among months in each species (Table 1). Particularly for *P. moniliformis* and *P. pauciflora* the F_v/F_m and ΦPSII parameters showed lower yield comparing Nov20 to Nov22. The F_v/F_m and ΦPSII of *P. moniliformis* was 0.5 and 0.2 times lower, respectively and for *P. pauciflora* was - 0.4 for the F_v/F_m and 0.7 for the ETR parameter. For *C. microphyllum* only the F_v/F_m showed differences among Nov20 and Nov22, where the first one was 0.6 less than the second.

NSC concentration

Soluble Sugar (SS)

Concerning Soluble Sugars (Fig. 1 Supp.), *Peltogyne pauciflora* exhibited a remarkably consistent concentration across consecutive months. Although, the partitioning aspect demonstrated variations between roots and leaves (Fig. 1a Supp.). From Nov20, the first month of sampling, to Aug21, the trend was for leaves to exhibit average concentrations of 1.1mg/g DW ± 0.2 bigger than roots. However, by Oct21, a shift in the partitioning occurred between roots and leaves leading both to have equal concentrations (~214mg/g DW on average). This pattern remained the same through the following months. For the partitioning between leaves/twigs and twigs/roots the pattern was always the same throughout the months, where leaves were higher than twigs (0.9 mg/g DW ± 0.2) and twigs equal to roots. In Dec21, when leaves were absent, roots exhibited higher concentration than twigs (0.8mg/g DW ± 0.2).

Concerning *Cenostigma microphyllum* and *Pityrocarpa moniliformis* the partitioning pattern is equally consistent through the months between leaves and roots as it is between roots and twigs over months although the trends differ. For *C. microphyllum*, the overall trend is for the leaves to have concentration equal to roots, with roots being 1.0mg ± 0.1 higher in SS than twigs, on average (Fig. 1c Supp.). Only in Nov20 and Apr22 leaves had less concentration than roots (-0.65 mg/g DW ± 0.2 and -0.95 mg/g DW ± 0.2, respectively). For *P. moniliformis*, it's the opposite, where leaves are often higher than roots (1.3mg/gDW ± 0.2) and roots and twigs have the same concentration (Fig. 1b Supp.). The only difference in this partition pattern was found on Aug21, where the concentration between roots and leaves were equal. In Dec21 when leaves were absent the two species kept the pattern shown in the other months for roots and twigs. Looking at the responses among the three species, *P. pauciflora* was the only that changed the pattern in roots and twigs when leaves were absent.

Regarding the dynamic of concentration in the organ through the months, leaves did not differ for *P. moniliformis*, while the concentrations in twigs and roots did. Twigs concentration remains stable for most of the months, reducing only in the April months of the two years (2021 and 2022) compared to those who precedes them. For roots, there is an increase from Ap21 to Ag21 (1.3mg/g DW ±0.2), and a decrease from Ag21 to Oct21 (- 0.79 mg/g DW ±0.2). The concentration remains stable through Jan22, then decreases again in Apr22 (-1.0 mg/g DW ±0.2), thereafter no further changes are observed. For *C. microphyllum*, the concentration remains consistent across consecutive months, except for a decrease observed only in Nov22 for roots (-0.8 mg/g DW ±0.1).

The most significant fluctuation for both species is regarding the SS partitioning among leaves and twigs, specifically for *C. microphyllum*. This species switched between being more concentrated on leaves than twigs or equal in some months. In Aug21 and Oct21, *C. microphyllum* trees switched to have higher concentration on leaves than twigs (0.7 mg/gDW ±0.1 and 1.2 mg/gDW ±0.1, respectively), differing to the previous months. Then this changed in Jan22, where leaves and twigs became equal again, followed by another increase in leaves on Apr22 (0.8mg/g DW). For *P. moniliformis*, plants initially had equal concentrations in leaves and twigs, then they increased the concentration in leaves on Apr21 (0.8mg/g DW ±0.2), equalized again with twigs from Aug21 throughout Jan22, and become higher in leaves once more in Apr22 (1.8 mg/g DW ±0.2) and Nov22 (1.4mg/g DW ±0.2).

Starch

Among the three species, the starch partitioning dynamics over the months were most stable for the *C. microphyllum* species, followed by *P. moniliformis* (Fig. 1 Supp.). For *C. microphyllum*, a change in the overall pattern was only identified in Apr22, which was related to the leaf-to-twigs interaction, where leaves exhibited higher concentrations (0.4 mg/gDW ±0.1) (Fig. 1f Supp.). For all other months, the partitioning pattern remained consistent across the three organs. For *P. moniliformis*, the partitioning pattern differed only in Oct21 and Apr22 compared to the other months, concerning the root interaction with the other organs (Fig.1e Supp.). In Oct21 and Apr22, the roots showed lower concentrations compared to leaves (- 0.7 mg/g DW ±0.1 for both) and related to twigs/roots, twigs were higher 0.9 mg/g DW ±0.1 in Oct21 and 0.7 mg/g DW ±0.1 in Apr22. For all other months, the partitioning was equal among the three organs.

Regarding *P. pauciflora*, while the partitioning of soluble sugars (SS) remained relatively stable throughout all months, starch exhibited greater fluctuations in partition dynamics among the three species (Fig.1d Supp.). Particularly in the partition pattern among twigs and their counterparts. Twigs varied between having higher concentrations than both and being equal, but never lower. Regarding the interaction of twigs/leaves they were equal only in Nov20 and Jan22. Related to the partition among twigs and roots, they are higher in Apr21 and De21. Overall, the partitions among leaves/roots were consistent, differing only in Nov22, with roots having higher concentrations (0.6 mg/g DW ± 0.1).

In a chronological sequence, *C. microphyllum* was the only species that showed no variation in starch concentration across the months for any of the organs. That is, the concentrations in leaves, twigs, and roots remained consistent throughout the collections. For *P. pauciflora*, the starch concentration in leaves changed only from Oct21 to Jan22 (0.4 mg/g DW ±0.1). For twigs and roots, there was a decrease from Aug21 to Oct21 (-0.3mg/g DW ±0.0, and -0.4mg/g DW ±0.0 respectively), but there was an increase again from Oct21 to Jan22 (0.4 mg/g DW ±0.1 for both). In the case of *P. moniliformis*, there was a difference in leaves, with an increase from Apr21 to Aug21 (0.1 mg/g DW ±0.0), and again from Oct21 to Jan22 (0.5mg/g DW ±0.1). For roots, there was an increase from Apr21 to Aug21 (0.6 mg/gDW ±0.1), and another from Oct21 to Jan22 (1.0 mg/gDW ±0.1). Twigs concentrations did not differ across months.

NSC Pool

Concerning the overall total concentration of NSC among the three species, *Peltogyne pauciflora* had the highest NSC concentration than its counterparts. While *C. microphyllum* and *P. moniliformis* did not differ in their NSC. Considering the concentration in each organ among the species, the NSC in leaves was higher for *P. pauciflora* compared to both species. In case of NSC twigs *P. pauciflora* and *P. moniliformis* also have higher NSC concentration than *C. microphyllum* but *P. pauciflora* and *P. moniliformis* did not show a difference in this organ. *C. microphyllum* had a higher concentration in roots than both.

In terms of concentration within each species' organs (Fig. 4), *P. pauciflora* and *P. moniliformis* exhibited a consistent pattern in which leaves had higher concentrations compared to twigs and roots. For *P. pauciflora*, leaves were 0.95 higher than twigs and 0.65 higher than roots. For *P. moniliformis*, leaves were 0.5 and 1.02 higher than twigs and roots, respectively). Conversely, *C. microphyllum* showed an opposite trend regarding the interaction leaves and roots. Leaves had lower concentrations than roots (-0.4mg/g DM), while were higher than twigs (0.5 mg/gDM). When considering the interaction between roots and twigs, each species demonstrated a distinct pattern. *P. pauciflora* maintained consistent concentrations in both organs, while *P. moniliformis* had higher concentrations in twigs compared to roots (0.4mg/g DM). In contrast, *C. microphyllum* exhibited the opposite pattern, with roots having higher concentrations than twigs (0.9mg/gDM). Regarding the concentration of total NSC through the months for each specie, no significant differences were observed, except for *P. moniliformis* among Ag21 and Nov22, which was higher in the first one (0.7 mg/g DM). But no significant reduction in the NSC pool between wet and dry months specifically.

Regression and correlations analysis

In the regressions analysis we performed, only the component starch itself has a significant relationship with environmental conditions for *P. pauciflora* and *C. microphyllum.* The starch concentration in twigs and roots of *P. pauciflora* was positively correlated with the soil water balance (WB) ($R^2 = 0.76$, $p = 0.099$ and $R^2 = 0.75$, $p = 0.0111$, respectively). For *C. microphyllum* only starch concentration in twigs was positively correlated with the WB ($R^{2\,=}$ 0.85, $p = 0.002$). Correlations between the water potential of trees with NSC were also performed and only *P. pauciflora* (Fig. 5) did not show any relationship between these parameters. *C. microphyllum* showed significant relationship only in leaves (Fig. 6abc). Furthermore, only for this species there was a positive correlation between water potential and the soil moisture ($R^2 = 0.81$, $p = 0.014$), even though the soil moisture was not being correlated with the WB parameters. For *P. moniliformis* we observed that the SS concentration in leaves was negative correlated with Ψ_x while the starch shoed the inverse trend (Fig. 7 abc). For this specie the NSC in twigs was also positive correlated with Ψ_x (Fig. 7 df).

Discussion

Our results suggest that: 1) over the three years of collections, the soil water balance remained positive only on one collection date, and neutral at another time, which led to variations in xylem water potential differently among the species; 2) as for leaf behavior, stomatal conductance responds directly to Y_x in only one species, although NSC vary according to Y_x in more species; 3) furthermore, our data show that, in fact, there is a change in the concentration and partition pattern of the NSC components and not NSC pool concentration itself; 4) P. pauciflora, the only species with late deciduity, presents a different response under the same environment conditions as the other species, showing more stability for all parameters measured.

Species may differ in the pattern of carbohydrate dynamic of production and allocation even when occurring in similar environments. These differences can be primarily attributed to variations in functional types and phenology (Tixier et al. 2020). Deciduous trees, for instance, are believed to be more reliant on NSC stores compared to evergreen species due to the maintenance of photosynthetic areas in the latter. This can result in less dramatic fluctuations in their NSC pool during drought (Palacio et al. 2018). In the present study, *P. pauciflora*, the species that loses its leaves later than the other deciduous ones, that is, with the dry season already started, showed different behavior compared to the other two species. NSC allocation in no organ investigated showed correlation with the water status of the plant, which will be discussed later.

Our data corroborate the hypothesis that *P. pauciflora*, being a late deciduous species, would have more NSC concentrations. On the other hand, it does not entirely confirm the first one, that the fluctuation of the NSC would follow the seasons. In fact, what is shown from our data there is a change in the concentration and partition pattern of the NSC components and not the NSC pool concentration itself. The response is also species dependent, for instance, *C. microphyllum* do not change any of their NSC component concentration throughout the months while for *P. pauciflora* the Starch concentration in roots seems to follow the seasonality. For *P. moniliformis* both starch and soluble sugar in roots showed a seasonal pattern of changes.

In part, this study reinforces the aspect that less water availability in the soil reduces Y_x, and the species' first line of defense against water loss is the reduction of g_s (Santos et al. 2021; Ferreira-Neto et al. 2022). Such behavior was not observed in *P. pauciflora* plants, which maintained a strong stability of stomatal conductance throughout the study period and with the lowest variation in Y_x among the species studied, which can be supported by the thick cuticle of this species, as well as high epidermal cell density, and small, high-density stomatal pores (Yule et al. 2023).

The three species in the present study have a wide distribution in the DTF in the semi-arid region of northeastern Brazil (Yule et al. 2023). Previous studies discuss that woody species can be very stable in terms of their morpho-ecophysiological behavior (Yule et al. 2023), as well as in relation to the NSC stock in their organs (Sala et al. 2010; 2012), even under limited environmental resources, such as water availability (Martínez-Vilalta et al. 2019). Our data on $\square_x$, chlorophyll *a* fluorescence and NSC concentration throughout the study reflect this behavior. Although the three species are from the Fabaceae family, they have a different allocation pattern. *P. pauciflora*, late deciduous, during the dry season and late regrowth, with the rainy season underway, presented the highest NSC concentration for the three organs evaluated. On the other hand, *C. microphyllum* was the only species to present the highest NSC concentration in the roots, when compared to leaves and stems at same plants. Indeed, *C. microphyllum* had a direct relationship between g_s and the water status of the plant. Perhaps this is one of the reasons why it is the one that is least able to accumulate NSC in leaves and stems, when compared to other species, demonstrating greater sensitivity to variations in water availability, as shown by the lowest Y_x value among the three species. throughout the study period.

All forecasts for the Brazilian semi-arid region point to higher average temperatures and reduced precipitation (Marengo and Bernasconi 2015; IPCC 2021). In addition, greater irregularity in precipitation during the rainy season and longer dry seasons. This scenario, with greater or lesser intensity of climate change, should impact the growth dynamics of perennial species, especially deciduous ones. Having the ability to produce and store NSC during favorable periods can be a key factor for the establishment of new individuals and maintenance of the complete annual cycle, with seed production. Our data show three woody species, close in origin, but different in terms of their strategy for developing in the same environment. The three presented stability in terms of their respective NSC pool, but with different dynamics of the main components, soluble sugars and starch among the three organs evaluated and in terms of response to water availability. Two of the three species do not respond to xylem water potential to control their stomata, on the other hand, decrease water status leads to starch degradation and accumulation of soluble sugars in the leaves of both. This behavior was not observed for any investigated organ of *P. pauciflora*, which remains stable or with minimal variation in the evaluated parameters. This could be an advantage given the future climate scenario in the region.

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Figures and Tables

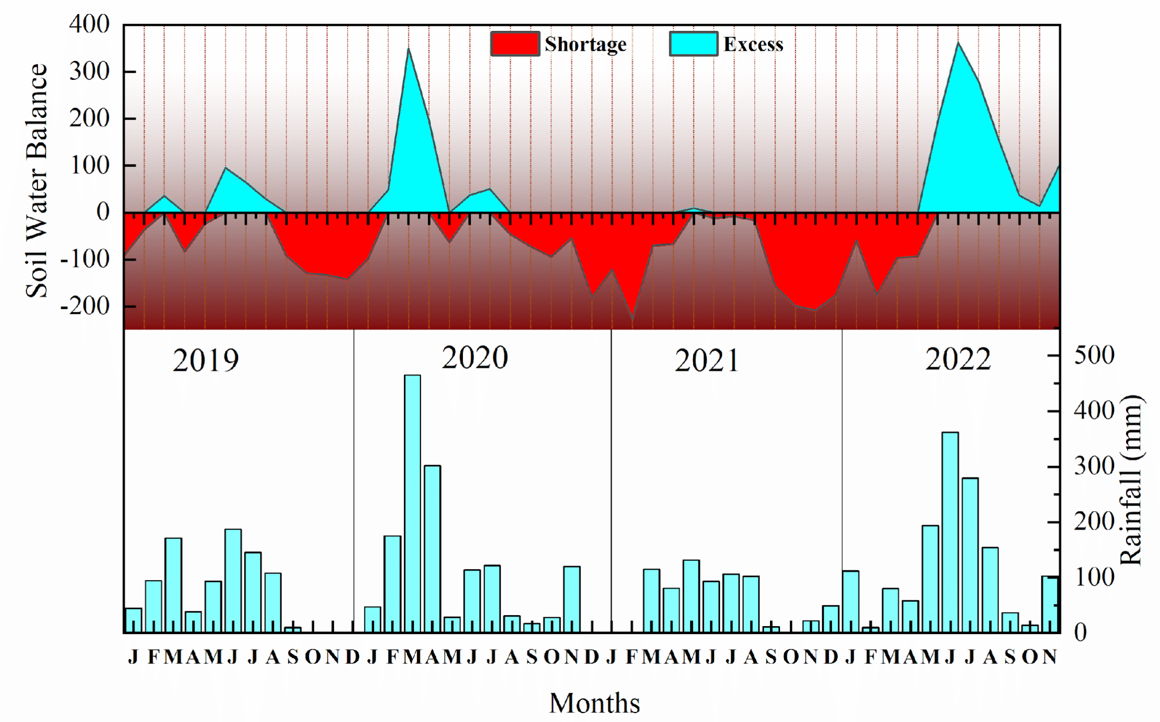

Figure 1. Soil Water Balance and Rainfall across months from one year prior to the beginning of the study (2019) and during the study (2021 and 2022).

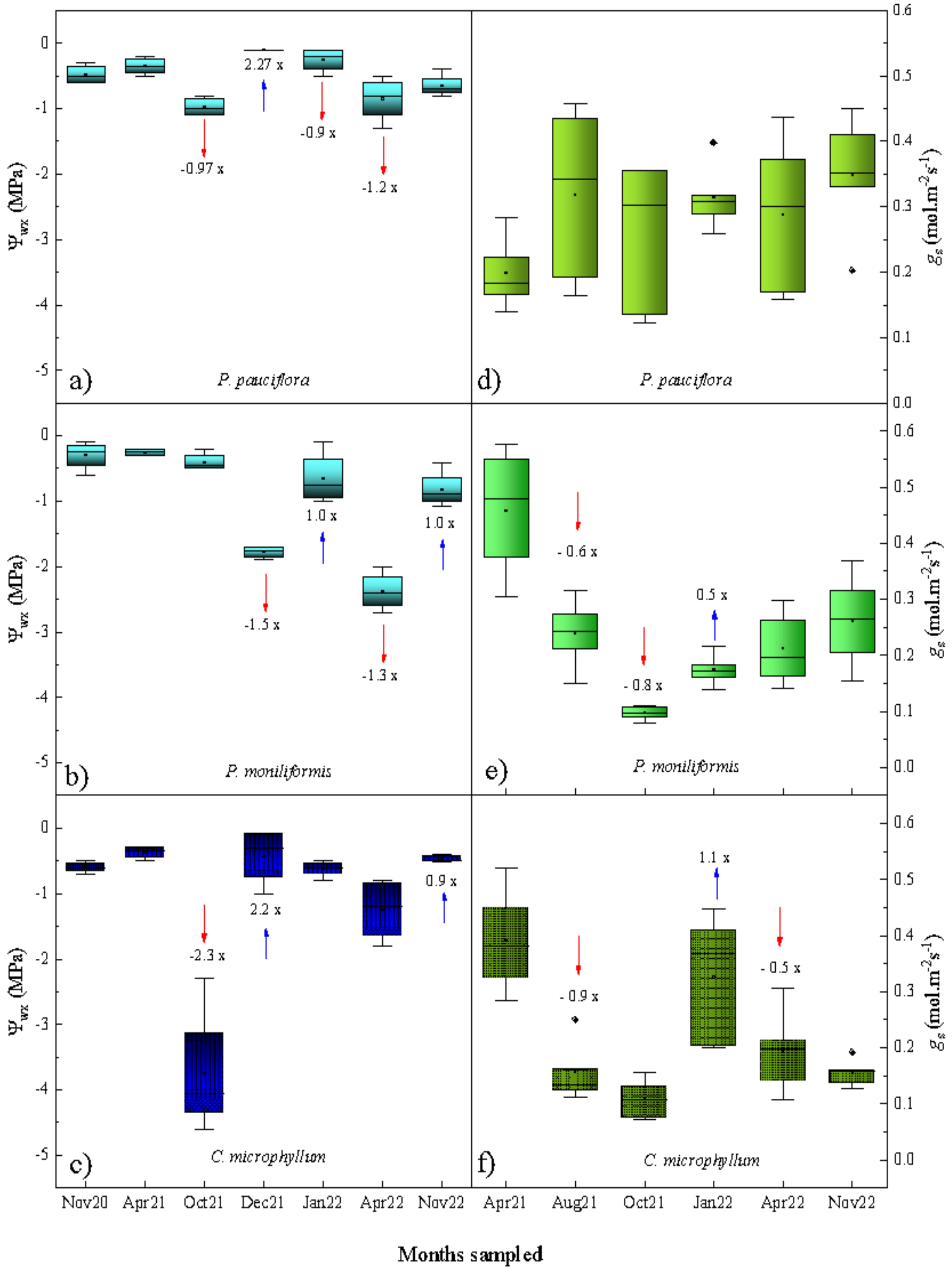

Figure 2. Xylem water potential Ψ_x (a-c) and stomatal conductance (g_s) (d-f) of individuals (*n*=5) from *Peltogyne pauciflora*, *Pityrocarpa moniliformis* and *Cenostigma microphyllum* throughout eight months across 2020, 2021, and 2022.

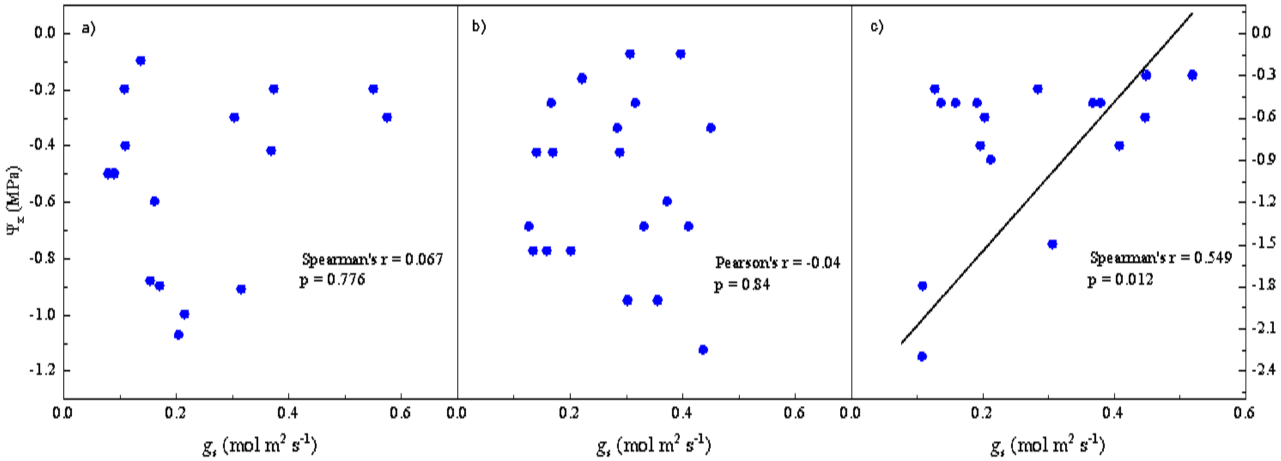

Figure 3. Relationship between xylem water potential (Ψ_x) and stomatal conductance (g_s) of individuals (n=5) from a) *Pityrocarpa moniliformis,* b) *Peltogyne pauciflora* and c) *Cenostigma microphyllum*

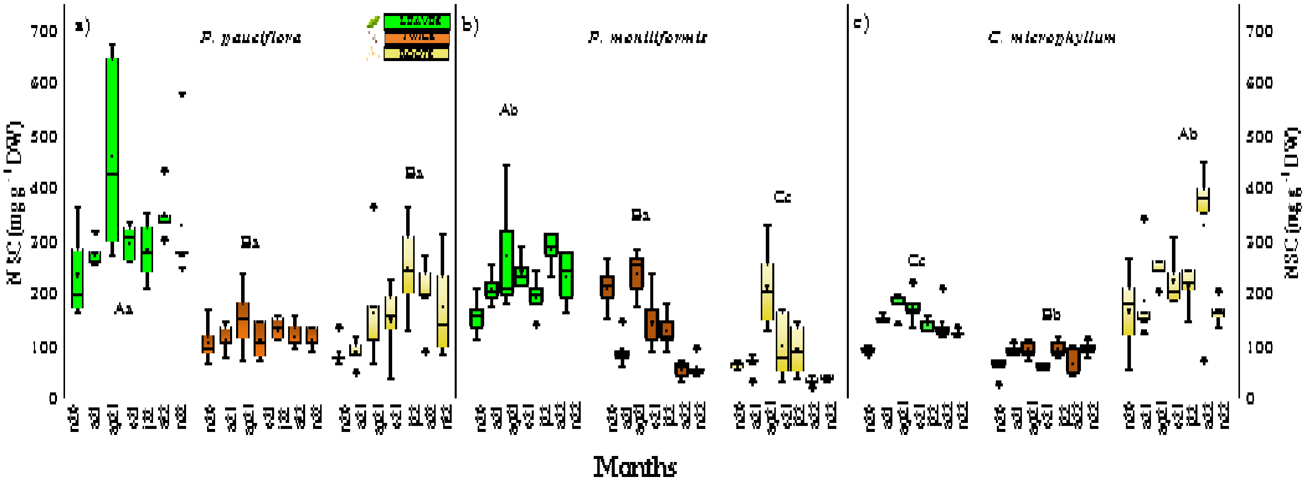

Figure 4. Total non-structural carbohydrates (NSC) (Soluble Sugar + Starch) in leaves, twigs and roots from individuals (n=5) of three deciduous species from Caatinga dry forest across months of sampling. Capital letter indicates differences among the three organs for each species individually and lowercase letters indicate difference among the same organ across species.

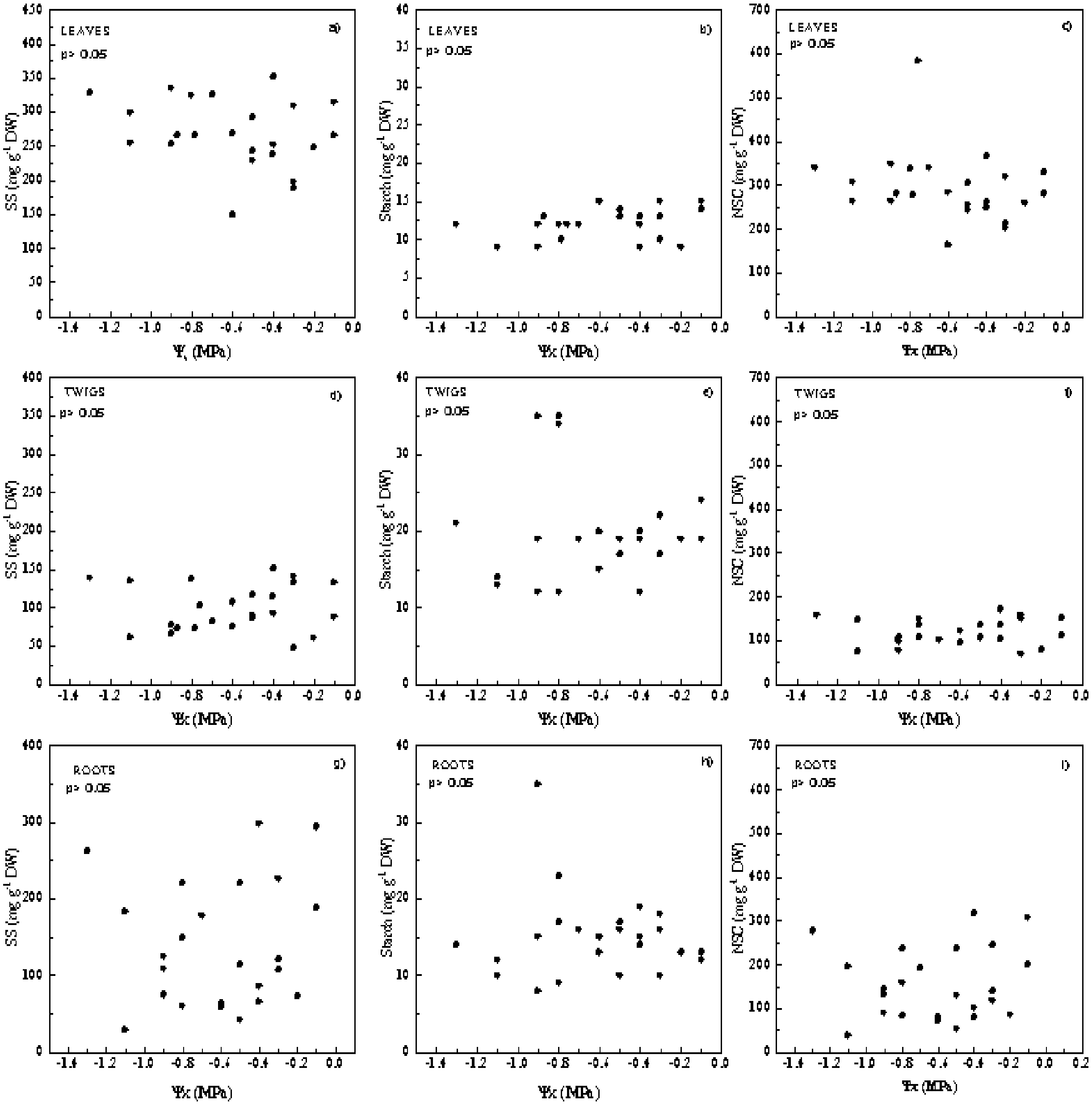

Figure 5. Correlation analyzes between non-structural carbohydrates (NSC) components concentration (SS = soluble sugars, Starch, and total NSC) and water potential (Ψ_x) for the specie *Peltogyne pauciflora*.

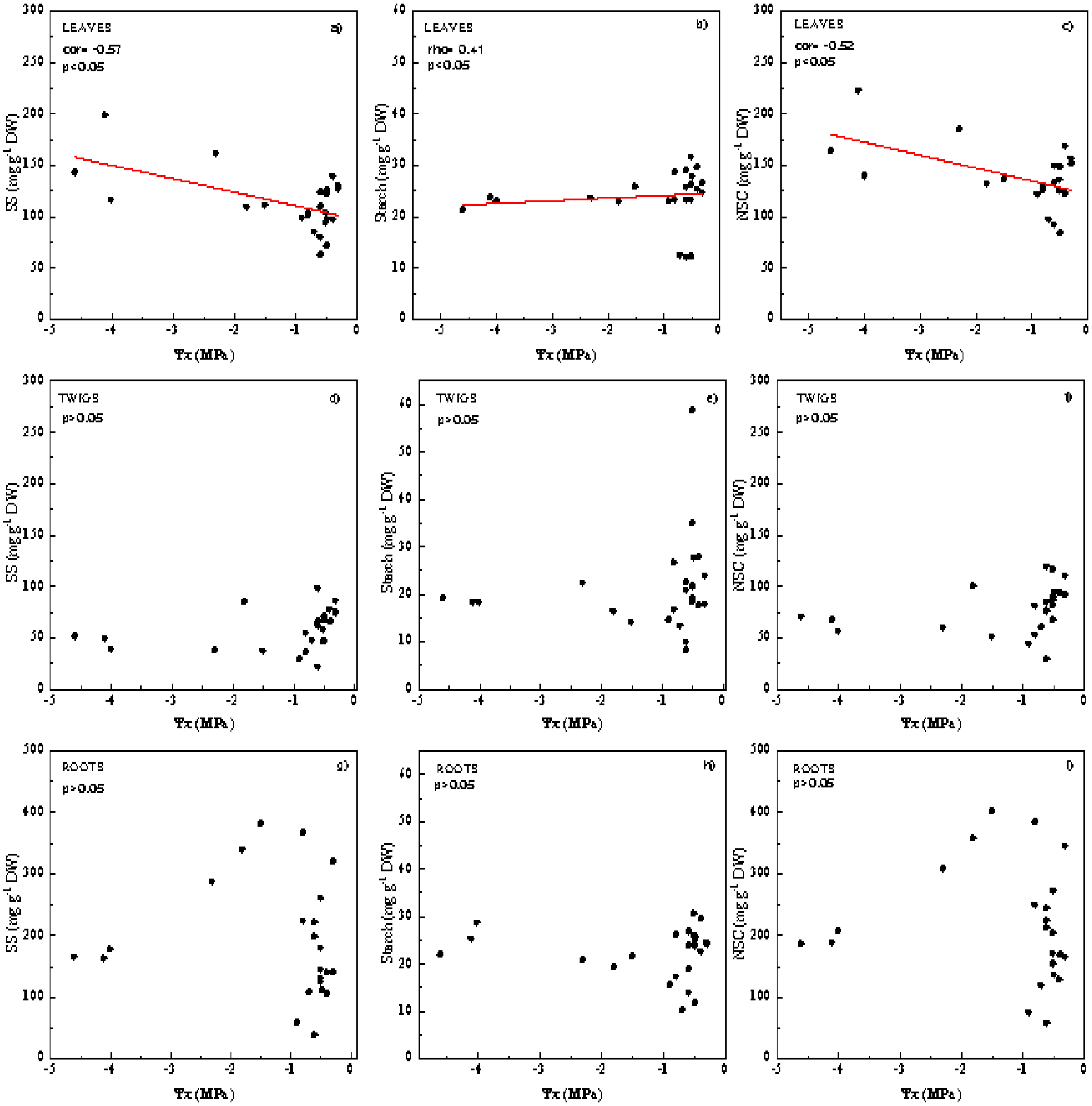

Figure 6. Correlation analyzes between non-structural carbohydrates (NSC) components concentration (SS = soluble sugars, Starch, and total NSC) and water potential (Ψ_x) for the specie *Cenostigma microphyllum*.

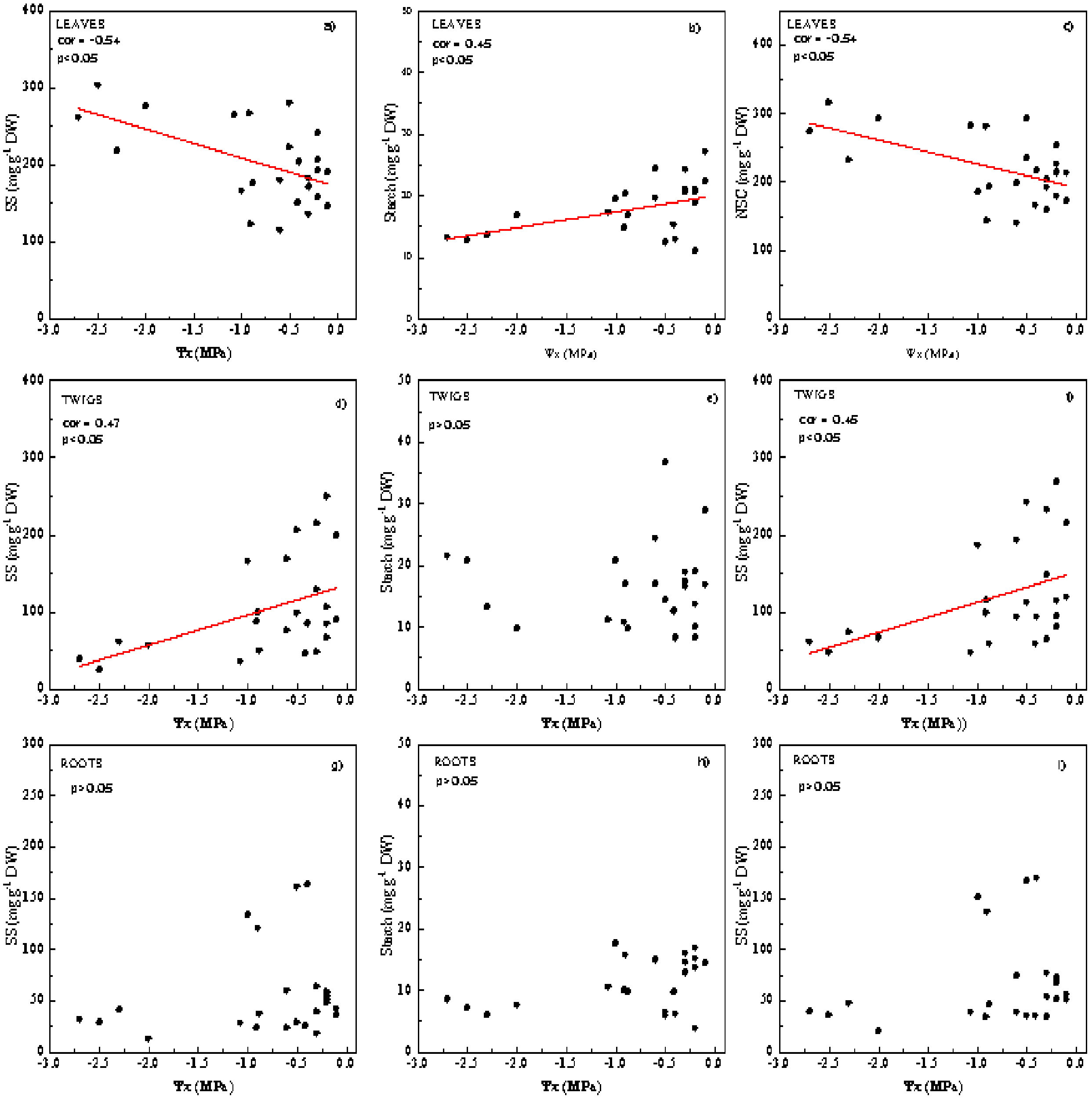

Figure 7. Correlation analyzes between non-structural carbohydrates (NSC) components concentration (SS = soluble sugars, Starch, and total NSC) and water potential (Ψ_x) for the specie *Pityrocarpa moniliformis*.

Table 1. Chlorophyll *a* fluorescence measurement in deciduous species from Caatinga Dry Forest across months over years (2020, 2021 and 2022). Different letters indicate differences across months for each parameter of each species.

Parameters/ Months	Nov20	Aug21	Oct21	Jan22	Apr22	Nov22
P. pauciflora						
Fv/Fm	0.62±0.0^{b}	0.63±0.1^{ab}	0.72±0.0^{ab}	0.77±0.0^{ab}	0.69±0.0^{ab}	0.97±0.1^{a}
ϕPSII	0.15±0.0^{b}	0.28±0.0^{ab}	0.33±0.0^{a}	0.38±0.0^{a}	0.22±0.0^{ab}	0.28±0.0^{ab}
ETR	99±25^{b}	184±27^{ab}	234±41^{a}	253±29^{a}	198±29^{a}	201±16^{a}
P. moniliformis						
Fv/Fm	0.75±0.0^{b}	0.76±0.0^{b}	0.73±0.0^{b}	0.80±0.0^{b}	0.76±0.0^{b}	1.3±0.1^{a}
ϕPSII	0.28±0.0^{bc}	0.32±0.0^{ab}	0.21±0.0^{c}	0.28±0.0^{ab}	0.28±0.0^{ab}	0.37±0.0^{a}
ETR	219±7.1^{ab}	215±5.2^{ab}	150±25^{c}	189±14^{bc}	251±27^{a}	263±30^{a}
C. microphyllum						
Fv/Fm	0.77±0.0^{b}	0.81±0.0^{bc}	0.70±0.0^{d}	0.77±0.0^{b}	0.75±0.0^{bcd}	1.43±0.0^{a}
ϕPSII	0.31±0.0^{ns}	0.34±0.0	0.43±0.0	0.27±0.0	0.24±0.0	0.36±0.0
ETR	207±13^{ns}	223±15	299±92	204±55	158±10	255±8.4

5 CONSIDERAÇÕES FINAIS

Neste estudo tínhamos dois grades objetivos a serem alcançados: primeiro, entender como se comporta a atividade fotoquímica no caule verde da espécie *Commiphora leptophloeos*, e se esta atividade influencia na dinâmica de carboidratos não-estruturais (CNE) ao longo da variação da sazonalidade em uma floresta tropical seca (FTS). Como principais respostas encontramos que esta espécie mantem o seu potencial hídrico do xilema elevado em qualquer estação do ano, o que pode ser consequência de dois fatores: a baixa densidade da madeira e o forte controle da condutância estomática. Além disso, a atividade fotoquímica do caule verde não apresentou diferença para a mesma atividade mensurada nas folhas. No início da estação seca as plantas decíduas, mostraram redução da concentração de amido e aumento de açúcares solúveis nas raízes. O segundo grande objetivo, foi avançar no entendimento da dinâmica de CNE em espécies decíduas sob a variação da sazonalidade em uma FTS. Três espécies arbóreas foram mensuradas *Peltogyne pauciflora*, *Pityrocarpa moniliformis* and *Cenostigma microphyllum*. *P. pauciflora* se mostrou uma espécie com condutância estomática e fluorescência da clorofila *a* extremamente estável ao longo das estações do ano. Bem como foi a espécie com a maior concentração de CNE. Nas outras duas espécies, embora o potencial hídrico do xilema tenha variado entre as estações seca e chuvosa, a condutância estomática não respondeu diretamente ao status hídrico das plantas. Porém sob as condições do início da estação seca, houve degradação de amido e aumento da concentração de açúcares solúveis nas folhas de *P. moniliformis* e *C. microphyllum*, sob as nossas condições de estudo. Em conclusão, somente a variação do potencial hídrico não deixa claro a dinâmica dos CNE em espécies lenhosas decíduas sob condições de FTS em plantas adultas.

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APÊNDICE A – FIGURA SUPLEMENTAR DO ARTIGO 2

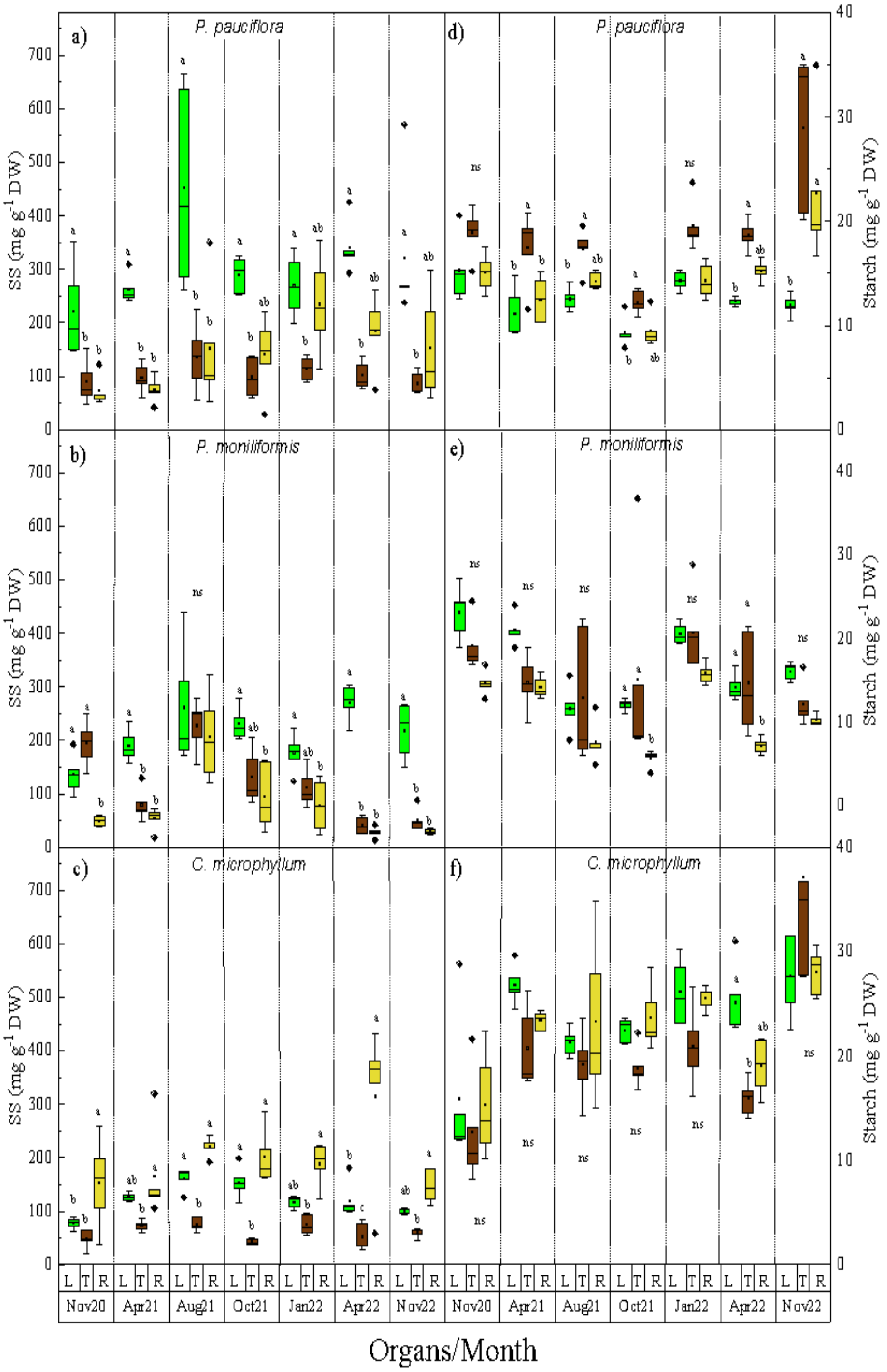

Figure 1 Supplementary. The Soluble Sugar (SS) and Starch dynamic in leaves, twigs and roots from individuals (n=5) of three deciduous species from Caatinga dry forest across months of sampling. Different letter indicates differences among the three organs for each month and specie individually.

ANEXO A – NORMAS PARA SUBMISSÃO

Periódico Theoretical and Experimental Plant Physiology – TxPP:

Disponível em: https://link.springer.com/journal/40626/submission-guidelines

Periódico Journal of Arid Environments:

Disponível em: https://www.sciencedirect.com/journal/journal-of-arid-environments/publish/guide-for-authors