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VANESSA ANDRADE DE BARROS

EFEITO DA DISPONIBILIDADE HÍDRICA NA EFICIÊNCIA ENERGÉTICA E NO METABOLISMO PRIMÁRIO DE ESPÉCIES NATIVAS E INVASORAS DA CAATINGA

Recife - PE
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Orientador: Prof. Dr. Mauro Guida dos Santos

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Vanessa Andrade de Barros

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RESUMO

O déficit hídrico é o principal fator limitante para o ganho de biomassa dos vegetais no mundo. Espécies invasoras possuem muitos mecanismos de tolerância a situações de estresse, e isso pode conferir altos potenciais de estabelecimento. As espécies invasoras representam impactos negativos sobre a biodiversidade, a composição de espécies, a estrutura e a função dos ecossistemas invadidos e podem causar grandes perdas econômicas. Diante da necessidade de se entender melhor os mecanismos que as plantas invasoras possuem para obter maior sucesso ecológico, o presente estudo vem com o objetivo de compreender o efeito da disponibilidade hídrica na eficiência energética e no metabolismo primário de espécies nativas e invasoras da Caatinga. Medimos sob estresse hídrico controlado, características fisiológicas, bioquímicas, crescimento vegetal e o uso de recursos em três espécies de plantas invasoras e três espécies nativas, que têm uma grande ocorrência em uma região semiárida. Os resultados mostraram que plantas arbóreas invasoras apresentaram baixo custo de construção foliar, altos teores de fósforo e nitrogênio, redução da perda instantânea de eficiência no uso de energia e menor área foliar específica quando comparadas às espécies nativas. Esta estratégia levou a um maior ganho de biomassa e uma alta razão raiz / parte aérea em ambos os tratamentos de água. Após a reidratação, as plantas invasoras apresentaram recuperação mais rápida e maiores taxas de assimilação de CO_2. As plantas invasoras arbustivas bem regadas sempre tiveram maiores taxas de assimilação de CO_2 e menores custos de construção da folha do que plantas nativas, enquanto a condutância estomática foi a mesma. Por outro lado, em condições de déficit hídrico, as plantas invasoras toleraram mais dias de seca e apresentaram maior biomassa radicular, conteúdo relativo de água, área foliar específica e menores custos de construção da folha do que as espécies nativas. Após a reidratação, as plantas invasoras apresentaram maior assimilação de CO_2, eficiência no uso do nitrogênio fotossintético, valores instantâneos de eficiência no uso de energia, menores custos de construção da folha e tempo de retorno em comparação com as espécies nativas. Esses resultados sugerem que as invasoras apresentaram um comportamento mais aquisitivo, investindo mais em crescimento, e uma maior tolerância ao défice hídrico em relação as nativas.

Palavras-chave: biomassa; caatinga; estresse hídrico; metabolismo fotossintético; nutrientes.

ABSTRACT

The water deficit is the main limiting factor for the biomass gain of vegetables in the world. Invasive species have many mechanisms of tolerance to stressful situations, and this can confer high establishment potentials. Invasive species have negative impacts on biodiversity, species composition, the structure and function of invaded ecosystems and can cause major economic losses. In view of the need to better understand the mechanisms that invasive plants have to achieve greater ecological success, the present study aims to understand the effect of water availability on energy efficiency and primary metabolism of native and invasive species in the Caatinga. We measure under controlled water stress, physiological, biochemical characteristics, plant growth and the use of resources in three species of invasive plants and three native species, which have a high occurrence in a semiarid region. The results showed that invasive tree plants had a low cost of leaf construction, high levels of phosphorus and nitrogen, reduction of the instant loss of efficiency in the use of energy and less specific leaf area when compared to native species. This strategy led to a higher biomass gain and a high root / shoot ratio in both water treatments. After rehydration, the invasive plants showed faster recovery and higher CO_2 assimilation rates. Well-watered invasive shrub plants have always had higher CO_2 assimilation rates and lower leaf construction costs than native plants, while stomatal conductance was the same. On the other hand, in conditions of water deficit, the invasive plants tolerated more drought days and presented higher root biomass, relative water content, specific leaf area and lower leaf construction costs than native species. After rehydration, the invading plants showed greater CO_2 assimilation, efficiency in the use of photosynthetic nitrogen, instantaneous values of efficiency in the use of energy, lower leaf construction costs and turnaround time compared to native species. These results suggest that the invaders showed a more acquisitive behavior, investing more in growth, and a greater tolerance to the water deficit in relation to the native ones.

Keywords: biomass; caatinga; hydraulic stress; photosynthetic metabolism; nutrients.

SUMÁRIO

1 INTRODUÇÃO

As espécies invasoras representam impactos negativos sobre a biodiversidade, a estrutura e a função dos ecossistemas invadidos e podem causar grandes perdas econômicas (NORMILE, 2010). Em ambiente tropical semiárido, os eventos de seca prolongada têm favorecido a proliferação de espécies invasoras devido ao alto desempenho fisiológico quando comparadas a nativas (FROSI et al., 2012).

O déficit hídrico é o principal fator limitante para o ganho de biomassa dos vegetais no mundo (SANTOS et al., 2014). A restrição na disponibilidade de água acarreta uma série de mudanças morfológicas, fisiológicas, bioquímicas e moleculares em todos os órgãos da planta, afetando negativamente o crescimento e a produtividade (CRAMER et al., 2011; FROSI et al., 2016; WANG et al., 2001). Os estômatos são os principais responsáveis pela manutenção do status hídrico foliar da planta. Plantas que não tenham um bom investimento nesses aparatos estão vulneráveis à sazonalidade climática, sobretudo em ambiente semiárido (FIGUEIREDO et al., 2012).

Outra resposta adaptativa é o acumulo de solutos como ácidos orgânicos, açúcares e aminoácidos, que servem como mecanismo de ajustamento osmótico de determinadas plantas, para manutenção do potencial hídrico (SAFFELL et al., 2014; SALA; WOODRUFF; MEINZER, 2012). Em termos de alterações bioquímicas, tem sido observado que açúcares e aminoácidos podem assumir papeis diferenciados das suas funções base, principalmente para espécies do semiárido, que habitualmente crescem em condições de seca. Os açúcares solúveis e aminoácidos de modo geral podem chegar a atuar como moléculas sinalizadoras em situação de estresse e também interagir com hormônios, fazendo parte da rede de sinalização da planta (SANTOS; PIMENTEL, 2009).

Diante das condições adversas, algumas espécies também são capazes de ajustar seus atributos funcionais de forma que consigam suportar as mudanças no ambiente. Essa capacidade é denominada de plasticidade fenotípica – uma alteração no fenótipo expresso por um único genótipo em ambientes diferentes (GRATANI, 2014). É através de medidas dos atributos funcionais que se pode mensurar a plasticidade fenotípica de um indivíduo. Esses atributos funcionais são características que afetam o desempenho individual de uma espécie sob determinadas condições ambientais através dos seus efeitos no crescimento, na reprodução e sobrevivência do organismo (VIOLLE et al., 2007).

Plantas invasoras possuem alta capacidade de crescimento, dispersão, maior número de sementes, alta taxa de germinação, sendo capazes de modificar a composição, estrutura ou função do ecossistema (LUZ, 2009). A presença de mecanismo de tolerância a situações de estresse pode conferir às plantas invasoras altos potenciais de estabelecimento. O entendimento desses atributos que fazem uma espécie invasora tornar-se mais tolerante a essa condição adversa do que uma nativa é muito importante com vistas ao seu controle. Diante da necessidade de se entender melhor os mecanismos que as plantas invasoras possuem para obter maior sucesso ecológico, o presente estudo vem com o objetivo de compreender o efeito da disponibilidade hídrica na eficiência energética e no metabolismo primário de espécies nativas e invasoras da Caatinga.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 ESPÉCIES ESTUDADAS

2.1.1 *Myracrodruon urundeuva* M. Allemão

Myracrodruon urundeuva M. Allemão é uma espécie arbórea e pertence à família das Anacardiaceae, que reúne aproximadamente 600 espécies e 70 gêneros (LORENZI; MATOS, 2008). A família Anacardiaceae no Brasil, está representada por 14 gêneros, 53 espécies e 8 variedades, das quais 13 são endêmicas, distribuídas em todos os domínios fitogeográficos (LORENZI; MATOS, 2008).

M. urundeuva possui vários nomes populares, como: aroeira-preta, aroeira-do-campo, aroeira vermelha, aroeira- do-cerrado e urundeúva, entre outros (CARVALHO, 2003). No Brasil, a espécie ocorre desde o Ceará até o Paraná e Mato Grosso do Sul, sendo mais frequente na Região Nordeste. É uma árvore caducifólia de 5 a 10 m de altura com muitas variações entre regiões, o seu caule pode atingir 1 metro de diâmetro, sua copa é ampla, com folhas compostas, alternas, imparipinadas, com 5 a 7 pares de folíolos ovados obtusos (VIANA et al., 2007). É uma planta dióica, alógama, cuja incidência em florestas primárias pode ocorrer com diversas espécies, ao contrário das florestas secundárias, onde é de ocorrência, quase que homogeneamente, em áreas perturbadas (FREITAS et al., 2006). Geralmente, a espécie floresce de julho a setembro e a maturação dos frutos ocorre de setembro a outubro (NUNES et al., 2008).

M. urundeuva apresenta uma gama de utilizações. É considerada umas das principais plantas com potencial farmacológico. Suas cascas, folhas e raízes são bastante utilizadas para prevenir e curar diferentes enfermidades. A mesma possui propriedades anti-inflamatórias, adstringentes, antialérgicas e cicatrizantes, suas raízes são usadas no tratamento de reumatismo e as folhas são indicadas para o tratamento de úlceras (FIGUEIRÔA; BARBOSA; SIMABUKURO, 2004). Pode ser também utilizada como planta ornamental, na restauração de florestas, em sistemas agroflorestais, na apicultura e meliponicultura, alimentação animal e na indústria de curtumes (MAIA, 2004).

2.1.2 *Mimosa caesalpiniifolia* Benth.

Mimosa caesalpiniifolia Benth. é uma planta arbórea nativa, considerada endêmica da Caatinga (MAIA, 2004). Pertence à família Leguminosae e subfamília Mimosoideae, comumente conhecida como sabiá, sansão-do-campo, unha-de-gato, cebiá e angiquinho-sabiá, que exibe resistência à seca e desenvolve-se bem em áreas degradadas (BALBINOT et al., 2010; MENDONÇA et al., 2008; STAMFORD; SILVA, 2000).

Ocorre naturalmente nos estados do Rio Grande do Norte, Piauí e Ceará (RIBASKI et al., 2003). O sabiá é uma espécie pioneira, com alta capacidade de regeneração e resistência à seca (BALBINOT et al., 2010). Ocorre espontaneamente em áreas de Caatinga semi-úmidas, também sendo encontrada em áreas mais secas. Nesse caso, apresenta forma mais arbustiva, com tronco polifurcado (RIBASKI et al., 2003).

Geralmente vai da forma de arbusto a árvore perenifólia, com as árvores maiores na idade adulta atingindo dimensões próximas a 10 m de altura por 30 cm de diâmetro a 1,30 m do solo. Tem aspecto entouceirado e apresenta boa capacidade de rebrota (CARVALHO, 2007; LORENZI; MATOS, 2008). O tronco geralmente apresenta acúleos em maior ou menor grau e o caule espinhoso na idade jovem vai perdendo os espinhos à medida que a casca engrossa (CARVALHO, 2007). A planta possui folhas bipinadas, as flores são brancas, monóclinas, pequenas e axilares, reunidas em espigas cilíndricas de 5 a 10 cm de comprimento. No Nordeste do Brasil, a floração geralmente ocorre de março a junho com as plantas geralmente florescendo antes de completar um ano de idade (SILVA et al., 2009). A espécie possui um sistema radicular bem desenvolvido, apropriado para absorver e reciclar nutrientes mais profundos do solo, sendo acumulados na superfície na forma de serapilheira, expressa por uma baixa relação C/N, sendo fonte eminente de matéria orgânica (CARVALHO, 2003).

Graças à sua forma entouceirada, sua madeira é empregada como cerca viva, e devido à sua rusticidade, é amplamente cultivada para fins de estacas e caibros (CARVALHO, 2007). O sabiá possui grande importância na medicina caseira (MAIA, 2004), é considerada uma planta que representa importante fonte de pólen e néctar para as abelhas (FIGUEIRÔA;

BARBOSA; SIMABUKURO, 2004), e é utilizada na alimentação animal (LIMA et al., 2008).

2.1.3 *Cenostigma microphyllum* (Mart. ex G.Don) Gagnon & G.P.Lewis

Cenostigma microphyllum (Mart. ex G.Don) Gagnon & G.P.Lewis é uma espécie nativa, endêmica do Brasil (FLORA DO BRASIL 2020). É popularmente conhecida na região Nordeste como "catingueira", devido ao odor desagradável que exala das folhas (AGRA et al., 2008). A espécie possui um hábito arbóreo ou arbustivo e ocorre no domínio fitogeográfico da Caatinga e Cerrado no estado de Minas Gerais, leste de Goiás, Tocantins, Alagoas, Bahia, Maranhão, Pernambuco, Piauí, Sergipe (QUEIROZ, 2009).

A espécie possui folhas com lâminas bipinadas, inflorescência ramificação(ções) do tipo racemo(s), indumento do tipo pubérulo(s), bráctea(s) no formato lanceolada(s); bráctea(s) comprimento 2 - 5 mm; pedicelo(s) articulação(ções) abaixo do hipanto 2 - 2.5 mm. Apresenta polinização predominante xenogâmica, sistema reprodutivo dicogâmico e protogínico (FLORA DO BRASIL 2020).

C. microphyllum é tida como planta facilitadora, apresentando potencial para a recuperação de áreas degradadas (PEREIRA et al., 2015). A espécie também pode ser utilizada em projetos de recuperação de áreas degradadas. Além disso, por essa espécie ser comum em áreas degradadas, possui um potencial como aceleradora do processo sucessional e de restauração ecológica (PATERNO et al., 2010). Suas flores, folhas e frutos são usados na medicina popular para tratar doenças gastrointestinais, estomacais e respiratórias (AGRA et al., 2008).

2.1.4 *Prosopis juliflora* (Sw) DC.

O gênero Prosopis faz parte da família leguminosae, o qual é constituído por volta de 44 espécies localizadas nos continentes americano, asiático e africano (SILVA et al., 2003). *Prosopis juliflora* (Sw) DC. É uma arbórea, xerófita, perenifólia, heliófila, que pode atingir até 18 m de altura e apresenta um sistema radicular axial ou pivotante, capaz de alcançar grandes profundidades em busca d'água e nutrientes (DE ANDRADE; FABRICANTE; DE OLIVEIRA, 2010).

Prosopis juliflora é uma árvore abundante e nativa das regiões de pastagem da América do Sul, América Central e Caribe e está presente nas regiões áridas e semiáridas. A maioria concentra-se em zonas áridas e secas da América do Sul, sendo a Argentina o centro de maior diversidade, com 27 espécies, das quais 8 são árvores e 11 espécies são endêmicas (DE SOUZA NASCIMENTO et al., 2014; LÓPEZ-FRANCO et al., 2013). A *Prosopis juliflora* foi introduzida na Caatinga no início dos anos 1940 como fonte de alimento para pecuária e se espalhou com sucesso pela região, invadindo e formando povoamentos, principalmente em antigas terras agrícolas ao longo das margens dos rios e planícies aluviais (ALMEIDA; LOPES, 2015; DE SOUZA NASCIMENTO et al., 2014; OLIVEIRA et al., 2017). *Prosopis* forma povoamentos densos, aparentemente excluindo ou impelindo o restabelecimento de conjuntos de espécies de árvores e arbustos ricas em espécies, particularmente no rio bancos degradados pela agricultura itinerante e pelo sobrepastoreio da pecuária (DE SOUZA NASCIMENTO et al., 2014; OLIVEIRA-BENTO, 2012; PEGADO et al., 2006).

As folhas são compostas bipinadas, inflorescências em espigas axilares, hermafroditas, de coloração branca-esverdeada, medindo 14 cm de comprimento. Os frutos são legumes indeiscentes em forma de lomento drupáceo, lineares ou curvos, apresentando o exocarpo estriado, mesocarpo carnoso de coloração amarelada, com 40% de sacarose e endocarpo dividido em segmentos coriáceos com uma semente; medindo 10 a 40 cm de comprimento, 15 a 20 mm de largura e 4 a 5 mm de espessura, com média de 20 sementes. Adaptada às condições adversas da Caatinga, cresce sob a forma de arbustos e árvores que podem atingir alturas superiores a 12m e diâmetro do tronco superior a 1m de circunferência (BHATIA; GUPTA; SONI, 2014).

Apesar do efeito negativo do perfil invasor da algaroba, aspectos positivos foram relatados em solos degradados na Índia, ao longo das laterais de estradas e pastagens, fornecendo importante fonte de madeira e forragem para animais (SÁTIRO; ROQUE, 2008). Os frutos da algaroba, com a morfologia clássica das vagens produzidas pelas Fabaceae, são historicamente utilizados como alimento por seres humanos em regiões onde a planta é nativa, principalmente devido ao seu sabor, aroma, e os seus elevados níveis de sacarose e proteínas semelhante ao milho e cevada (BORGES, 2004). Há o consumo difundido da algaroba na alimentação humana e como fonte de madeira para combustível dentre os nativos nas Américas, datando milhares de anos atrás (GUILHERME et al., 2009). Em relação ao aspecto tecnológico, a algaroba (*Prosopis juliflora*) é uma planta que quando cultivada de forma controlada proporciona diversos benefícios à sociedade, como: uso da madeira para construção rural e produção de carvão; vagens, caules e folhas para produção de biocombustíveis, bebidas e alimentos (PASIECZNIK et al., 2003).

2.1.5 *Leucaena leucocephala* (Lam.)

Leucaena leucocephala (Lam.), pertence à família Leguminosae, subfamília Mimosoidae, nome popular leucena, é originária da américa Central e foi introduzida no Brasil na década de 1940, para fins de produção de madeira, forragem e recuperação de áreas degradadas (FABRICANTE, 2014). No Brasil foram confirmadas a ocorrência desta espécie no Norte, Nordeste, Centro-Oeste, Sudeste e Sul do país (FLORA DO BRASIL 2020). Apresenta indivíduos com porte arbustivo e arbóreo, alturas variando entre cinco e 18m, são espécies perenes de crescimento rápido e adaptadas às regiões secas tropicais que requerem temperaturas entre 25 e 30ºC para um crescimento ótimo (MENDES, 2006). A respectiva espécie é uma leguminosa com floração durante o ano todo; a floração maior ocorre nos meses com índice pluviométrico mais elevado (COSTA; DURIGAN, 2010).

Adapta-se a solos calcários e ambientes secos, sendo amplamente utilizada em reflorestamento de áreas degradadas. Também na agricultura é amplamente utilizada em pastagens, como adubo verde e alimentação animal. Essa espécie pode formar aglomerado monoespecífico, substituindo a vegetação natural e expondo o solo à erosão, e compõe a lista das 100 espécies invasoras mais agressivas do mundo (LUQUE et al., 2014). A dominância exercida também impede a regeneração natural e estabelecimento de espécies nativas (LEÃO et al., 2011). Essa espécie além de apresenta uma capacidade de afetar ecossistemas nativos de forma rápida e gradual, promovendo a homogeneização da flora onde está inserida, também reduz o potencial germinativo por meio de alelo químicos, intoxicando animais, diminuindo a qualidade de pastagens, além de ser hospedeira de pragas e doenças (FABRICANTE, 2014).

Na região Nordeste do Brasil, a Leucena apresenta alto potencial econômico para a região devido a rica fonte de proteínas é oferecido alimento para os animais, além disso, o fuste é utilizado na produção de madeira, na construção de cercas, e nos abrigos para pequenos animais (DANTAS et al., 2016). A lenha, é utilizada para o cozimento de alimentos. Além de ser uma leguminosa, responsável por estabelecer uma relação simbiótica com bactérias do gênero Rhizobium, responsável por fornecer nitrogênio ao solo, o que representa uma boa opção fertilização natural do solo e consequentemente favorecer na recuperação de áreas degradadas (BAYÃO et al., 2016).

2.1.6 *Calotropis procera* (Aiton) W. T. Aiton

Calotropis procera (Aiton) W. T. Aiton (Apocynaceae) é uma espécie invasora (ALMEIDA et al., 2014), de hábito arbustivo perene (BOUTRAA, 2010), sempre verde, com metabolismo C3 (TEZARA et al., 2011), nativa do noroeste e norte da África e sudoeste da Ásia (BRANDES, 2005). *Calotropis procera* é popularmente conhecida como algodão-de-ceda, flor-de-seda, leiteira, ciúme,queimadeira, janaúba, paininha-de-seda (RANGEL; NASCIMENTO, 2011; GALLEGOS-OLEA et al., 2008).

Calotropis procera é nativa da África e Ásia, abrangendo desde do Noroeste (Senegal e Mauritânia) e Norte (Marrocos, Argélia, Líbia e Egito) da África e se estendendo até Península Arábica, Afeganistão, Paquistão e Índia (BOUTRAA, 2010; BRANDES, 2005). No Brasil, a *C. procera* foi introduzida no início do século XX na cidade do Recife (OLIVEIRA-BENTO, 2012), primeiro com intenção ornamental em seguida sendo usada como forragem (SOBRINHO et al., 2013). *Calotropis procera* é bem distribuída na região Nordeste, mas também é encontrada em outros estados como Minas Gerais, São Paulo, Espírito Santo, Mato Grosso, Rio de Janeiro, Goiás e no Distrito Federal. *Calotropis procera* habita áreas abertas, onde há pouca concorrência de outras plantas, como por exemplo áreas degradadas, terrenos baldios, beira de estrada, em áreas abandonadas, geralmente em solos arenosos em áreas de baixa pluviosidade (MUTWAKIL et al., 2017). Contudo não é encontrada em florestas densas.

Calotropis procera é uma planta perene, arbustiva ou semi-arbórea, medindo por volta de 2 - 4 m, podendo alcançar 6 m de altura (BOUTRAA, 2010). Possui um sistema radicular bem desenvolvido, com raiz principal pivotante, podendo chegar 4 m em solos arenosos de desertos (BARBOSA et al., 2013). Possui fácil propagação através de suas sementes aladas devido a excelente germinação, sem haver necessidade de pré-tratamentos, pois não apresentam dormência, podendo ser plantadas diretamente no solo (ULHÔA; FERNANDES; ALMEIDA-CORTEZ, 2007). *Calotropis procera* apresenta crescimento rápido e com florescimento e frutificação durante todo o ano (SOBRINHO et al., 2013), entretanto a maior incidência é na estação seca como observado por Sobrinho et al. (2013). *Calotropis procera* ocorre em áreas áridas e semiáridas com precipitação anual variando de 150 a 1000 mm, sendo tolerante à seca e a salinidade (KHAN et al., 2007). Embora preferindo habitats de baixa precipitação, *C. procera* pode persistir nas áreas mais úmidas, desde que o solo seja bem drenado (por exemplo, areia). Essa alta tolerância aos fatores abióticos, associados à manutenção das suas folhas e atividade fotossintética torna a *C. procera* uma espécie de interesse de investigação ecofisiológico, anatômico e molecular (RIVAS et al., 2017, 2020; TEZARA et al., 2011).

Apesar de ser uma exótica invasora, *C. procera* já está bastante presente nas paisagens do nordeste brasileiro. A sua alta capacidade de tolerar um amplo espectro de condições edafoclimáticas, mantendo ótimo desempenho sob condições estressantes, faz com que ela produza fitomassa durante todo o ano, tornando-se uma fonte alternativa de importância para fins de uso como forragem animal durante os períodos de seca no semiárido (FROSI et al., 2012). As propriedades medicinais, fitoquímicas e farmacológicas dos compostos de *C. procera*, bem como sua atividade biológica, são bastante pesquisadas e a maioria dos trabalhos acerca dessa espécie são com essa abordagem (AWAAD et al., 2018; CHUNDATTU; AGRAWAL; GANESH, 2016; SHARMA et al., 2019). Entretanto, o seu notável desempenho sob condições ambientais extremas tem atraído o foco de pesquisas na área de ecofisiologia, as quais buscam compreender as bases da sua tolerância e desta forma avançar no conhecimento das repostas das plantas aos estresses abióticos.

2.2 INVASÃO BIOLÓGICA

Invasão biológica refere-se à extensão de um determinado organismo da área de distribuição original para uma nova área, geralmente remota (HUAN; FENGLAN, 2017)**.** As invasões biológicas são cada vez mais comuns em todo o mundo devido às transformações contínuas que os ambientes vêm sofrendo (CHAFFIN et al., 2016). As invasões biológicas são consideradas a segunda maior causa de perda de biodiversidade no mundo e isso afeta diretamente a biodiversidade, a economia e a saúde (FUNK, 2013).

A partir do momento que uma espécie invade um ambiente de forma natural ou não, ela precisa estabelecer-se sob as novas condições ambientais (espécie casual), gerar indivíduos férteis e populações autossustentáveis (espécie naturalizada), e ao passar a expandir-se além do local de sua introdução, ser considerada invasora (COLAUTTI; MACISAAC, 2004; OLIVEIRA et al., 2017). Para que isso aconteça as espécies precisam superar um conjunto de barreiras bióticas (ALPERT; BONE; HOLZAPFEL, 2000) e abióticas (LEVINE; ADLER; YELENIK, 2004) para seu estabelecimento, proliferação e disseminação no novo habitat (PYŠEK et al., 2008). Nesta sequência de etapas do processo de invasão, as espécies ultrapassam consecutivamente barreiras geográficas, reprodutivas e de dispersão até chegarem à fase de invasão (RICHARDSON et al., 2000). Estima-se que apenas entre 1 e 5% de todas as espécies introduzidas tornem-se invasoras (RICHARDSON; PYŠEK, 2006). Embora apenas uma pequena fração do pool de espécies alienígenas se tornam invasivas, as forças que promovem a introdução de espécies determina o tamanho e a natureza do pool de espécies exóticas e, consequentemente, a chance de eventos bem-sucedidos de invasão (CHAPPLE; SIMMONDS; WONG, 2012).

O aumento da perturbação pelas crescentes populações humanas fará com que biotas tropicais terrestres sejam mais vulneráveis a invasões (MCGEOCH et al., 2016; ROY et al., 2014). Esta vulnerabilidade aumentada é devido ao benefício de espécies exóticas e invasoras aos distúrbios humanos, como limpeza e degradação do solo pela agricultura e pecuária. Os humanos, intencionalmente ou não, favorecem as espécies invasoras através da criação de habitats alterados ou novos (ALMEIDA et al., 2014). Muitos estudos foram realizados no intuito de identificar quais atributos biológicos são responsáveis pelo sucesso de invasão das espécies vegetais (BARROS et al., 2020; LLORET et al., 2005; OLIVEIRA et al., 2017). De um modo geral, os atributos biológicos correlacionados com a invasividade das espécies incluem traços de história de vida ruderal, sementes de pequeno tamanho, alta plasticidade genotípica e fenotípica, alta taxa de crescimento, além da alta e rápida fecundidade e fertilidade (BARROS et al., 2020; HEBERLING; FRIDLEY, 2013; LLORET et al., 2005). De acordo com estes resultados, dentre os atributos citados como promotores da capacidade de invasão estão aqueles que conferem alta habilidade competitiva e que são fortemente envolvidos nas etapas de estabelecimento e expansão da espécie na nova área (LLORET et al., 2005).

A estratégia de história de vida ou pacote de traços exibidos por espécies exóticas e invasoras também afetam seu desempenho competitivo ou adaptabilidade, enquanto condições ambientais, regimes de perturbação, degradação de habitat e a estrutura de comunidades nativas (por exemplo, padrões de riqueza de espécies e composição funcional) são forças externas controlando o sucesso da invasão (BANERJEE; DEWANJI, 2017; GILIOLI et al., 2014; NASCIMENTO et al., 2020). Os fatores intrínsecos e externos coletivamente podem definir o potencial de invasão bem-sucedida e delimitar seu contexto ecológico, a cobertura geográfica e potenciais danos à biodiversidade nativa. Apenas invasões bem-sucedidas ocorrem quando espécies exóticas podem superar forças externas (LI et al., 2014; SVENNING et al., 2014). Esses fatores explicam porque uma pequena fração de espécies exóticas introduzidas tornam-se invasoras, independentemente do tipo de ecossistema ou integridade do habitat (NOVOA et al., 2015; VAN WILGEN; RICHARDSON, 2014).

Quando bem estabelecidas algumas espécies invasoras apresentam características como: baixo custo de construção foliar, alto teor de fósforo e nitrogênio, alta eficiência no uso da energia fotossintética, maior biomassa, alta sobrevivência, maior eficiência no uso da água, assimilação de CO_2 e razão de massa radicular em resposta a mudanças nos fatores ambientais (BARROS et al., 2020; DAVIDSON; JENNIONS; NICOTRA, 2011; DYDERSKI;

JAGODZIŃSKI, 2019; VALLANO; SELMANTS; ZAVALETA, 2012). Essas características permitem que as espécies invadam novos habitats e tenha rápida evolução após naturalização levando à invasão em uma variedade maior de habitats (DRENOVSKY et al., 2012).

Em ambientes semiáridos tropicais, eventos prolongados de seca favoreceram a proliferação de espécies invasoras espécies devido ao alto desempenho fisiológico quando comparadas às espécies nativas (FUNK et al., 2016; OLIVEIRA et al., 2014). O mecanismo de tolerância ao estresse pode conferir às plantas invasoras a capacidade de estabelecer em diferentes ambientes (FUNK, 2013; OLIVEIRA et al., 2017). Ainda não está totalmente claro como as espécies invasoras atingem um alto desempenho sob restrição hídrica quando comparado a espécies nativas da regiões semiáridas (OLIVEIRA et al., 2014, 2017).

A vegetação da Caatinga representa um singular região biogeográfica e uma das maiores sazonalmente florestas tropicais secas do continente americano (NASCIMENTO et al., 2020; PENNINGTON; LAVIN; OLIVEIRA-FILHO, 2009). Com milhares de espécies de plantas nativas, incluindo algumas endêmicas, a biota da Caatinga tem enfrentado intensas degradações do habitat, variando da exaustão do solo a introduções deliberadas de plantas exóticas para apoiar atividades baseadas na agricultura (CAVALCANTE; MAJOR, 2006; LEAL et al., 2005). Alguns desses exóticos são agora invasores e ameaçam a biodiversidade nativa (SOUZA NASCIMENTO et al., 2014).

Segundo Almeida et al. (2014), um total de 205 espécies de plantas exóticas foram registradas para o ecossistema da Caatinga. Das 57 (27,8) espécies apresentando informações históricas, 54 (26,34%) eram introduzidos deliberadamente e três (1,46%) foram introduzidos não intencionalmente. 69 espécies (33,66%) exibiram uso econômico, sugerindo introduções deliberadas, enquanto 79 (38,54%) espécies exóticas não têm uso econômico; ou seja, introduções não intencionais. Introduções de plantas para alimentação humana (28 espécies), ornamentais (15), têxteis (5) e silvicultura (4) finalidades também foram documentadas. As espécies de plantas exóticas foram distribuídas em 135 gêneros e 48 famílias. Maior número de espécies estavam nas famílias Poaceae (61 spp.) e Fabaceae (33). Outras dez famílias representavam 27,8% de todas espécies listadas, enquanto 36 famílias (26,3%) foram representadas por três ou menos espécies.

2.3 INFLUÊNCIA DA SECA NAS PLANTAS

A seca é um dos principais fatores que limita a produção e o crescimento vegetal, tanto na agricultura como em condições naturais, bem como influencia a distribuição de espécies e a biodiversidade dos ecossistemas (MANAVALAN et al., 2009; FROSI et al., 2016). A cutícula e os estômatos são os principais responsáveis pela manutenção do status hídrico foliar da planta. Juntos, eles formam um sistema integrado de funções fisiológicas que aperfeiçoa a atividade fotossintética e as trocas gasosas como um todo (PINHO; OLIVEIRA; SILVA, 2009), sendo os estômatos os maiores responsáveis pelo controle dos processos vitais da planta. Assim, a condutância estomática, moldada de acordo com as condições ambientais, é uma estratégia evolutiva da planta para maximizar sua eficiência do uso da água, controlando a transpiração e a absorção de CO_2, bem como definindo a estratégia de sobrevivência da planta (CHAVES et al., 2016).

Os açúcares solúveis e aminoácidos de uma forma geral também apresentam alterações sob deficiência hídrica, podendo atuar como moléculas sinalizadoras em situação de estresse, além de interagir com hormônios como parte da rede de sinalização (ROLLAND; BAENA-GONZALEZ; SHEEN, 2006; SANTOS; PIMENTEL, 2009). Tanto os açúcares como os aminoácidos desempenham papel importante no aumento da tolerância ao déficit hídrico por serem osmoprotetores, sinalizadores e eliminadores de espécies reativas de oxigênio (ŁABANOWSKA et al., 2013). O amido transitório é o primeiro produto da fotossíntese das plantas. O consumo de amido pode ser umas das respostas iniciais à seca, permitindo a manutenção do suprimento do carbono em uma condição de reduzida fixação de CO_2 atmosférico (PINHEIRO; CHAVES, 2011).

Dentre os aminoácidos, a prolina é um dos mais reportados na literatura como envolvido nas respostas a diferentes estresses abióticos, atuando na osmorregulação e osmoproteção celular (MUNNS; TESTER, 2008). A quantidade de açúcares e aminoácidos nos órgãos das plantas pode regular a atividade fotossintética (HARA; PAUL; WINGLER, 2013). Dessa forma, a habilidade da espécie em armazenar os açúcares e aminoácidos chaves durante a restrição hídrica pode auxiliar no controle e manutenção do crescimento. Por outro lado, os fatores ambientais também regulam a atividade fotossintética, e por sua vez, regulam a produção de açúcares e aminoácidos, o que influencia uma rede metabólica através da planta (EVELAND; JACKSON, 2012). Assim, açúcares e aminoácidos atuam como fonte de reserva energética, nutricional e moléculas sinalizadoras, regulando o crescimento das plantas tanto em condições favoráveis quanto adversas (HARA; PAUL; WINGLER, 2013).

É através de medidas dos atributos funcionais que se pode mensurar a plasticidade fenotípica de um indivíduo. Esses atributos funcionais são características que afetam o desempenho individual de uma espécie sob as condições ambientais através dos seus efeitos no crescimento, na reprodução e sobrevivência do organismo (VIOLLE et al., 2007). Atributos relacionados às folhas são comumente utilizados, pois as folhas são órgãos plásticos e sua estrutura interna adapta-se facilmente às condições do ambiente. Os atributos funcionais fisiológicos, principalmente os relacionados à aquisição e utilização de carbono, formam o Espectro de Economia Foliar (EEF) (POORTER et al., 2006). Dentre os atributos que formam o EEF, o custo de construção foliar é importante, pois fornece informações relevantes acerca do uso da energia adquirida da folha nos diferentes cenários, e também está relacionado à eficiência do uso de recursos e à taxa de crescimento do organismo. Além disso, o custo de construção foliar está associado ao tempo de compensação, e.g. o tempo que a planta necessita fotossintetizar para compensar os gastos da produção das folhas e que é um importante parâmetro de avaliação na determinação da eficiência energética das plantas sob condições adversas (POORTER et al., 2006).

2.4 CRESCIMENTO VEGETAL, CUSTO DE CONSTRUÇÃO FOLIAR E ÁREA FOLIAR ESPECÍFICA

Na maioria das vezes, a sobrevivência e a reprodução dependem do tamanho da planta e, por conseguinte, a taxa de crescimento (SHIPLEY, 2006). A taxa de crescimento superior facilita a captura dos recursos disponíveis e dá à planta uma vantagem competitiva sobre as demais (GROTKOPP; REJMÁNEK, 2007). O sucesso das espécies depende do uso eficiente de recursos disponíveis. Uma baixa exigência de recursos pode aumentar a capacidade competitiva das espécies. A exigência de uma espécie pode ser influenciada pela quantidade de energia necessária para executar funções de crescimento (NAGEL; GRIFFIN, 2001). Uma economia de energia permite as espécies alocar recursos em estratégias de crescimento tais como incremento de biomassa, alta taxa de crescimento relativo, crescimento da raiz e produção de sementes (SONG et al., 2007).

Em muitos estudos, o crescimento das plantas é simplesmente considerado como a acumulação de biomassa, sem considerar a composição química da biomassa construída. No entanto, a maneira que uma planta investe os fotoassimilados e os minerais absorvidos em diferentes compostos químicos influencia diretamente o seu desempenho de crescimento, o custo de construção foliar (CC) e os custos de manutenção (CM) (VILLAR et al., 2006).

O CC é definido pela quantidade de glicose utilizada para a construção de um grama de biomassa (WILLIAMS et al., 1987), ou seja, a quantidade de glicose necessária a construção de esqueletos de carbono, poder redutor na forma de NADPH e energia para a síntese de compostos orgânicos e normalmente variam de cerca de 1,1 a cerca de 1,9 g de glicose g-1 para as folhas de diferentes espécies (POORTER et al., 2006; VILLAR et al., 2006). O CC está indiretamente relacionado com a taxa de crescimento relativo (WILLIAMS et al., 1987), e pode ser usado para avaliar as diferenças no uso dos recursos, indicando a eficiência entre espécies de plantas (NAGEL; GRIFFIN, 2001).

Geralmente, um baixo CC está associado a taxa de crescimento relativo alta e até mesmo pequenas diferenças no CC podem levar a diferenças substanciais na taxa de crescimento (GROTKOPP; REJMÁNEK, 2007). Para as plantas com o custo de construção foliar baixo, é mais vantajoso e mais econômico bioquimicamente e estruturalmente o investimento de energia na construção de uma nova folha, em vez de investir em estratégias para manter as folhas velhas (ZHU et al., 2013). Por outro lado, as plantas com os custos de construção foliar alto, podem investir os seus recursos em metabólitos de defesa, que são caros em termos de energia (WESTOBY et al., 2002).

Outra característica funcional chave que pode permitir a compreensão dos comportamentos ecofisiológicos das plantas e do crescimento, é a área foliar específica. Ela influencia diretamente no uso da capacidade fotossintética e na eficiência de recursos, tais como luz, água e nutrientes (NOUVELLON et al., 2010). Em geral, a área foliar específica tende a ser mais elevada nas plantas que colonizam áreas que estão no início dos estágios sucessionais. Nessas áreas sucessionais iniciais, o investimento no crescimento é mais importante do que o investimento em atributos que permitem, a longo prazo, a persistência das plantas, como a produção de compostos de defesa (ZHU et al., 2013). Geralmente, plantas que possuem elevadas de área foliar específica têm maior conteúdo de nitrogênio na folha, o que sugere que a maior parte da energia é utilizada para a síntese de proteínas, principalmente sob a forma de Rubisco, que contribui para taxas fotossintéticas mais elevadas (VILLAR; MERINO, 2001). Por outro lado, plantas que possuem folhas menores podem utilizar isso como uma estratégia para diminuir o tempo que foi necessário para recuperar os custos de construção da folha (POORTER et al., 2006).

Embora já haja alguns estudos disponíveis a respeito CC e área foliar associados a parâmetros ecofisiológicos (OSUNKOYA et al., 2010), ainda pouco se sabe sobre a relação desses parametros funcionais em plantas nativas e invasoras.

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3 MANUSCRITO I

O conteúdo dessa seção consiste em um artigo intitulado "Different resource-use strategies of invasive and native woody species from a seasonally dry tropical forest under drought stress and recovery" publicado na revista *Plant Physiology and Biochemistry*. A formatação do artigo segue as normas estabelecidas pela revista disponíveis no anexo A deste documento.

Different resource-use strategies of invasive and native woody species from a seasonally dry tropical forest under drought stress and recovery

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Abstract

Exotic plants in semiarid region have developed strategies for efficient use or capture of resources. They have become invasive and outperform native species. To understand which factors could explain the success of invasive woody species in a semiarid region, several physiological traits were analyzed in young plants of two invasive and two native species exposed to different water availability. Invasive plants showed low leaf construction cost, high phosphorus and nitrogen contents, reduced loss of instantaneous energy use efficiency, and smaller specific leaf area when compared to native species. This strategy led to a higher biomass gain and a high root/shoot ratio in both water treatments. After rehydration, invasive plants showed faster recovery and higher rates of CO_2 assimilation. This resilience is fundamental for species in semiarid regions, and also increase uptake of nutrients. Maintaining a high photosynthetic rate, whenever there is water availability is a strategy that increases the performance of the species in relation to biomass gain. The low leaf construction cost and the fast recovery of the photosynthetic metabolism of invasive plants after limiting water resources explains the success of these species, and suggests that their potential may increase under prolonged and severe drought seasons.

Keywords: invasive success; leaf construction cost; photosynthetic capacity; water deficit

1. Introduction

Invasive species are the second largest cause of species extinction on the planet (Funk, 2013). They have a negative impact on biodiversity, species composition, and ecosystem structure. They can cause great economic losses (Normile, 2010). In tropical semiarid environments, prolonged drought events have favored the proliferation of invasive species due to high physiological performance when compared to native species (Oliveira et al., 2014).

Water deficit is the main limiting factor for plant biomass gain in different ecosystems, as well as in semiarid regions, such as the Brazilian northeast region (Oliveira et al., 2014). The restriction of water availability leads to a series of morphological, physiological, biochemical and molecular changes in all plant organs, negatively affecting growth and productivity (Cramer et al., 2011; Frosi et al., 2016; Wang et al., 2001). Among the changes that allow plants to survive in adverse environments, the gas exchange behavior is the main responsible for maintaining the status of plant leaf water content (Santos et al., 2014; Oliveira et al., 2017). Moreover, there are changes in organic solutes, such as acids, sugars and amino acids, which play important role in osmotic adjustment, a mechanism to keep water potential high (Saffell et al., 2014; Sala et al., 2012).

Semiarid woody species change their functional attributes in different seasons (Falcão et al., 2017; Santos et al., 2014; Oliveira et al., 2014). Attributes related to leaves are changed quickly due to organ plasticity. Thus, their anatomical structure easily adapts to the environment (Oliveira et al., 2017). Physiological functional attributes related to carbon uptake and assimilation, form the leaf economic spectrum (Poorter et al., 2006). Among those that form this spectrum, the leaf construction cost plays a decisive role by characterizing the energy use captured by leaves, thus, can change nitrogen use efficiency and specific leaf area (Falcão et al., 2017).

The tolerance mechanism to stress can confer to invading plants the ability to establish in different environments to invading plants (Funk, 2013; Oliveira et al., 2017). Thus, the identification of a group of traits that explain the ability to invade is a challenge since the characteristics of these species depend on the invaded habitats (Pysek and Richardson, 2007; Tecco et al., 2010). In poor resource environments, measurements related to uptake are relevant since the competitive capacity will be influenced by these strategies (Craine et al., 2005; Funk, 2013).

It is not yet clear how invasive species reach a high performance under water restriction when compared to native species of the semiarid regions (Oliveira et al., 2014). This Brazilian region is dominated by the seasonally dry tropical forest, Caatinga, named after the first inhabitants of the South American continent, meaning white forest, due to the aspect that dominates the landscape during the dry season, where most plants are deciduous. It has three to four months of concentrated and irregular rainfall and the rest of the period without precipitation. The annual average for the region is around 750 mm. This semiarid region has one of the largest populations in the world for this type of climate. Thus, leads to a high anthropic disturbance, which has as one consequence the unsustainable use of the ecosystem. Once devastated, the forest has many limitations to recover, such as low rainfall, large herbivores, and soil characteristics. This scenario becomes a favorable environment for exotic species with high ability to tolerate local conditions and may become invasive (to see more Santos et al., 2014). From this point of view, the present study investigates whether four species, two invasive and two native have different efficiency during the uptake of light and nutrients even under water deficit and after recovery. We had two main hypothesis: (H1) Under water limited and recovery period among the chosen species, invasive species *Prosopis juliflora* and *Leucaena leucocephala* maintain greater performance with high use of photosynthetic energy and lower leaf construction costs, which would allow a higher photosynthetic rate compared with native species *Mimosa caesalpiniifolia* and *Myracrodruon urundeuva*. (H2) On the other hand, the well-watered condition differences in traits may not be noted among the species.

2. Materials and methods

2.1. Plant material and growth conditions

The experiment was conducted in a greenhouse in northeast Brazil (8°08'58"S, 34°56'55"W). The average temperature was 30 ± 2°C and 50–60% relative humidity. Plants were maintained under ideal hydration (pot capacity - 450 mL) until the application of the water deficit. The experimental design was completely randomized, with a factorial arrangement of 4×2, corresponding to the different species studied (2 native and 2 invasive) and to the water deficit (irrigated and suspended), with 15 replicates available for each treatment. From these 15 replicates, 5 were destined to evaluate the biomass, cost of foliar construction and nutrients, 5 to evaluate the relative water content foliar, gas exchanges and the other 5 for the biochemistry.

The soil used in the experiment was a mixture of 3:1 black soil and washed sand, respectively, presenting the following characteristics P: 23 $mg.dm^{-3}$; pH: 7.1 H_2O; Ca: 5.40 $cmol_c.dm^{-3}$; Mg: 0.7 $cmol_c.dm^{-3}$; Na: 0.35 $cmol_c.dm^{-3}$; K: 0.69 $cmol_c.dm^{-3}$.

Plant species were chosen because they belong to widely distributed families in semiarid regions, with the same lifestyle and habit (Giulietti et al., 2004). Seeds of the native species *Mimosa caesalpiniifolia* Benth. and *Myracrodruon urundeuva* Allemão were donated by the Núcleo de Ecologia e Monitoramento Ambiental (NEMA) and the invasive species *Prosopis juliflora* (Sw.) DC. and *Leucaena leucocephala* (Lam.) de Wit (Almeida and Lopes, 2015) were collected in the metropolitan region of Recife-PE, Brazil. The seeds were disinfected with sodium hypochlorite (0.5%) and germinated in trays containing vermiculite. When the seedlings presented the first leaf pair, they were transferred to pots containing approximately 5 kg of soil, being kept under pot capacity hydration.

2.2. Experiment design

The water deficit was imposed when the plants completed 4 months of development. Plants were divided in 2 treatments: control (irrigated with 250 mL of water once a day) and drought (suspension) for each species. Watering suspensions was kept until the maximum stress [stomatal conductance (g_s) close to zero], being rehydrated soon afterwards. The rehydration was carried out by re-watering the plants of the water deficit treatment with the pot capacity until the plants reached their net photosynthetic rates similar to the control plants. All measurements were performed on the day of maximum stress (gs close to zero) and on rehydration (A of the dry plants near the control).

2.3. Relative leaf water content (RWC) and soil moisture

Leaf discs approximately 3 cm were collected in the maximum stress and rehydration at 06:00 a.m. and weighed immediately on a precision scale (AND H200, Tokyo, JP) to obtain fresh weight (FW). Then, the discs were soaked for 24 h in deionized water and weighed again to obtain turgid weight (TW). Later, leaf discs were dried in a stove for 48 h at 60 °C, and weighed to obtain dry weight (DW). The leaf RWC was calculated according to Barrs and Weatherley (1962): RWC (%) = [FW-DW/TW-DW] x 100. Soil moisture content was obtained using a soil moisture meter (v/v) measuring approximately 30cm (HFM 2030 Falker, Porto Alegre, BR).

2.4. Gas Exchange

Gas exchange was measured in the maximum stress and rehydration in expanded and non-senescent leaves by infrared gas analyzer (IRGA, ADC, model LCi-Pro; Hoddesdon, UK), obtaining stomatal conductance (g_s) and net photosynthetic rate (A). The water use efficiency (WUE - A/E) was also calculated, where E is transpiration rate. The measurements were performed between 09:00 a.m. and 10:00 a.m., and the photosynthetic photon flux density (PPFD) was determined according to the global radiation incident at the time of measurements, ranging from 700 to 900 μmol $m^{-2}s^{-1}$ during experiment. The vapor pressure deficit (VPD) was calculated in parallel with gas exchange measurements using the es-ea formula, where (es) is the saturating vapor pressure and (ea) is the ambient vapor pressure (Campbell and Norman, 1998), using temperature and air humidity obtained by digital thermo hygrometer (Thermo-Higro SH 122, J. Prolab, São José dos Pinhais, BR). The VPD ranged from 1.12 to 1.64 during experiment.

2.5. Biomass

Five individuals per treatment were collected on the last day of rehydration, that is, when each species recovered at least its gas exchange when compared to the control plants. The shoots and roots were separated and placed in a stove at 70 °C for 5 days. Subsequently, the material was weighed in precision scale (AND H200, Tokyo, JP), to obtain the dry weight of each part. The Shoot/ Root ratio was calculated as well.

2.6. Nutrients

To measure leaf and root content of nitrogen (N), phosphorus (P) and potassium (K^+), 200 mg for dry mass of tissue were collected during the last day of rehydration of five plants of each treatment. The material was digested in sulfuric acid solution (H_2SO_4) in a digester block at 350 °C to obtain the samples extract (Thomas et al., 1967). The total N content was determined by extract titration using HCl after adding boric acid and a colorimetric indicator (Thomas et al., 1967). The P content was determined spectrophotometrically (Spectrophotometer 600S, FEMTO, São Paulo, BR) according to Murphy J and Riley JP (1962) using a P-concentration curve. The K^+ content was determined by flame photometry (DM-62, Digimed, São Paulo, BR) using a 5 ppm K^+ solution as standard. The photosynthetic efficiency of nutrient use (PENU) was determined by the ratio of net photosynthetic rate and each of nutrient content (PNUE- N, PPUE-P, PKUE-K)

2.7. Leaf construction cost, photosynthetic energy use efficiency and specific leaf area

All leaves of five individuals per treatment were collected on the last day of rehydration. Leaves were scanned for calculation of leaf area using Image Pro Plus 4.5 program (Media Cybernetics, Inc., Rockville USA). Afterwards, the leaves were dried at 60 °C for 72 h and weighed on a precision scale (HR-200, E, Tokyo, JP) to obtain dry biomass. The specific leaf area (SLA) was determined by the ratio of leaf area and leaf dry biomass.

The ash content (g kg^{-1}) of 100 mg of dry matter was obtained by muffle at 500°C for 6 h to calculate the cost of foliar construction. The ash content was determined by the pre and post-muffle weight difference (Li et al., 2011). The calorific value (ΔHC kj g^{-1}) was obtained by the combustion of 100 mg dry matter in calorimeter (C200, IKA, Heiters-Heim, DE) according to Villar and Merino (2001) using the formula: $\Delta HC = calories/(1\text{-}ashes)$.

The leaf construction cost per unit mass (CCmass) (g glucose DW^{-1}) was calculated using the results of ash, nitrogen concentration and ΔHC according to Williams et al. (1987): $CCmass = [(0.06968\ \Delta HC - 0.065)\ (1 - Ash) + 7.5\ (kN/14.0067)]/GE$, Where k is the oxidation state of nitrogen for nitrate (+5) and ammonium(-3), and GE represents the growth efficiency estimated to be 0.87 m (De Vries et al., 1974). The leaf construction cost per unit area (CCarea) (g glucose m^{-2}) was calculated as the ratio between CCmass and SLA.

The photosynthetic efficiency of use energy (PEUE) was calculated by the ratio of CO_2 assimilation (*A*) and CCarea (Nagel et al., 2005).

2.8. Leaf content of sugars, proteins and proline

Leaves were collected (~ 3g) at 15:00 h during maximum stress, when the stomatal conductance of each species was around zero, and on the last day of rehydration, at this time the gas exchange did not present significant difference for the always well hydrated control plants. Thus, all the leaves were immediately frozen in liquid nitrogen and stored in a freezer at -20°C. The leaves were used to determine the content of total soluble carbohydrates (SS), sucrose, proline, total soluble proteins (TSP). For extraction, 100 mg of fresh material mass was used to prepare the ethanol extract. TSP and proline were quantified according to Bradford (1976) and Bates (1973), respectively. All measurements were performed on a double beam spectrophotometer (Geneses 10S UV-Vis, Thermo Scientific, Waltham, USA). SS were measured according to Dubois et al. (1956), using D (+) glucose as standard and the absorbance read at 490 nm. Sucrose was measured according to Handel (1968) using sucrose as the standard and the absorbance read at 660 nm.

2.9. Chloroplastic pigments

For chlorophyll a chlorophyll b and carotenoids, 100 mg of leaf fresh material was macerated in 2 mL of acetone (80%) with calcium carbonate (CaCO3) to prevent the chlorophyllase activity. Samples were filtered and read at 470.0; 648.8 and 663.2 nm absorbance. Additionally, a 710 nm nonspecific absorbance was read to correct color, turbidity and contaminating compounds, since pigments are not read in this wavelength. Final pigment concentrations were calculated as described by Lichtenthaler and Buschmann (2005).

2.10. Statistical analysis

Data were submitted to factor analysis of variance (ANOVA), where the different species and the water deficit were considered as factors. When necessary, means were checked by the Student Newman Keuls test at 5% using the Statistica 8.0 program (StatSoft, Inc., Tulsa, OK 74104, USA).

Principal Component Analysis (PCA) was performed to check possible clusters and define the most important variables in group separation under maximum stress and rehydration. Data were transformed (ranging) for standardization due to different scale of magnitudes. The importance level of each variable was determined by the coefficient of correlations values ($r \geq 0.7$) of each attribute in relation to principal components (PC). The importance of each PC was determined by the Broken-stick method. The PC with eigenvalues that exceeded the expected was kept for interpretation. Analyses were performed using the Fitopac 2.1.2.85 program.

3. Results

3.1. Relative leaf water content (RWC) and soil moisture (SM)

At maximum stress, with g_s near zero, all plants submitted to water deficit (drought) presented a reduction in the RWC in relation to control plants (Fig. 1a). After rehydration, with A in stressed plants without difference when compared to well-hydrated plants, all plants that suffered water deficiency recovered their water content, not differing from their respective controls, with a mean of 65% among the four species (Fig. 1b), except *M. caesalpiniifolia*, which showed treated plants with lower values.

The moisture at maximum stress was lower 71% and 80% in the soil of plants under drought conditions compared to the controls of native and invasive plants.

3.2. Gas exchanges

The maximum stress of *M. caesalpiniifolia*, *P. juliflora* and *L. leucocephala* occurred after seven days of drought, and for *M. urundeuva* after 11 days. The rehydration was carried out by re-watering the plants of the water deficit treatment with the pot capacity until the plants reached their net photosynthetic rates with the Control plants. For native species this occurred during four days following maximum stress. However, for the invasive plants the recovery of net photosynthetic rates occurred after 10 days, since they lose their leaves after the maximum stress, being necessary to wait for the appearance of new leaves and totally expanded to carry out the measurements.

At maximum stress, the plants under drought showed a decrease in all parameters of gas exchange in relation to the control (Fig. 2a, c, e). *L. leucocephala* showed the highest rates of A (11.6 μmol.m^{-2}s^{-1}). Under the control WUE values from well-watered plants of *M. urundeuva* had the highest values, followed by invasive plants (Fig. 2e).

After rehydration, all plants submitted to drought showed recovery of gas exchange parameters. The g_s was higher 30% in *M. caesalpiniifolia* and *L. leucocephala* for both treatments. The reduction was approximately 55% in *P. juliflora* (Fig. 2b) when compared with other invasive species *L. leucocephala*. The rate of A was approximately 50% higher in invasive species. *L. leucocephala* presented the highest values (Fig. 2d). The invasive plants showed a WUE increase of approximately 27% when compared with their maximum stress values, and *M. caesalpiniifolia* presented a 24% reduction in rates (Fig. 2e-f) if compared with all the others species after recovery.

3.3. Biomass

The biomass measurements were performed on plants collected on the last day of recovery, established when the CO_2 assimilation values of the plants that were stressed were without significant difference in relation to the always well hydrated plants, the control. For native species this occurred during four days following maximum stress. However, for the invasive plants the recovery of net photosynthetic rates occurred after 10 days, since they lose their leaves after the maximum stress, being necessary to wait for the appearance of new leaves and totally expanded to carry out the measurements. *P. juliflora* and *L. leucocephala* (invasive) presented higher shoot and root biomass compared to *M. caesalpiniifolia* and *M. urundeuva* (native) in both treatments. Under drought conditions, invasive plants had a reduction of approximately 40% in shoots and 37% in roots. *L. leucocephala* had the highest investment in root biomass, followed by *P. juliflora* and *M. caesalpiniifolia* and *M. urundeuva* (Table 1). This greater investment of *L. leucocephala* in the underground part reflected in a higher root/shoot ratio, compared to other species. On the other hand, both native species did not show difference between drought and well-watered plants for shoot and root biomass.

3.4. Nutrients and photosynthetic nutrient use efficiency

L. leucocephala presented a higher content of shoot nitrogen and phosphorus under drought than under the control. As for potassium, the plants of *M. caesalpiniifolia* of the control and drought treatments presented a greater accumulation in shoots, compared to other species. In roots, there was a reduction in K^+ concentrations in plants of all species under drought (Table 2), except for *M. caesalpiniifolia* which did not show any difference between treatments.

In relation to the photosynthetic nutrient use efficiency, *M. urundeuva* plants presented higher PNUE, PPUE and PKUE in both treatments. *P. juliflora* plants had the lowest efficiencies of all nutrients in both treatments (Table 3).

3.5. Leaf construction cost, photosynthetic energy use efficiency and specific leaf area

The CC was higher in all plants submitted to drought in relation to the control plants, especially *M. urundeuva*, which had CC five times larger than control plants, while had showed a lower PEUE. On the other hand, under control treatment, invasive plants had the lowest CC values. In addition, *L. leucocephala* presented a lower CC and a higher PEUE (Fig. 3a-b) when compared to other species. Just as CC, the SLA was higher in invasive plants compared to native plants in both treatments. *L. leucocephala* and *P. juliflora* had higher SLA than native species after hydration. The lowest SLA was observed for plants of *M. caesalpiniifolia* in both the control and water deficit treatments (Fig. 3c).

3.6. Organic solutes

At maximum stress, a higher accumulation of soluble sugars was observed for *M. urundeuva* plants in both treatments (Fig. 4a). Plants of *P. juliflora* under drought showed a significant reduction in TSP and sucrose concentrations (83% and 76%, respectively). In both water conditions, *P. juliflora* presented the highest accumulations of proline (Fig. 4e-f). *L. leucocephala*, in both treatments, together with hydrated plants of *P. juliflora*, presented the highest rates of sucrose (Fig. 4g).

In rehydration, as well as at maximum stress, *P. juliflora* presented the highest concentrations of proline (Fig. 4f). Under drought, the sucrose had a reduction of 79% compared to control plants (Fig. 4h).

3.7 Chloroplast pigments

At maximum stress, *P. juliflora* under drought showed about 90% of reduction in Car, Chl *a* and Chl *b* (Fig. 5a-c-e).

After rehydration, the invasive plants submitted to drought were unable to recover carotenoids rates (Fig. 5b). The Chl *a* was higher in *L. leucocephala* plants previously submitted to drought compared to the other plants and treatments. There was an increase of approximately 44% when compared to well hydrated plants (Fig. 5d) and higher CO_2 assimilation. The plants under drought always showed lower concentration of chlorophyll *b* (Fig. 5f) compared to the control plants.

3.8. Principal components analyses

The PCA was performed for periods of maximum stress and rehydration (Fig. 6). At maximum stress, the ordering comprising all variables represented 61.73% of the total data variation. For PC1, the most relevant attributes were TSP (r = 0.80), sucrose (r = 0.71), Car (r = 0.82), Chl *a* (r = 0.83), and Chl *b* (r = 0.81). For PC2, the most relevant attributes were RWC (r = -0.70), g_s (r = -0.73), and WUE (r = -0.72). The irrigated plants formed a single group, independent of species. Under drought conditions, the native and invasives species presented a similar behavior. There was no separation of groups. However, a separation was evidenced for the invasive control species. *P. juliflora* presented a greater accumulation of proline, photosynthetic pigments, sucrose and TSP, where as *L. leucocephala* had the highest gas exchange rates and higher RWC, forming a distinct group (Fig. 6a).

In rehydration, the ordering comprising all variables represented 75.5% of the total variation. In PC1, there was a separation between native and invasive species, since in PC2, there was no clear distinction between water treatments. For PC1, the most relevant attributes were Car (r = 0.90), Chl *a* (r = 0.90), Chl *b* (r = 0.87), SLA (r = -0.70), shoot biomass (r = 0.86), root biomass (r = 0.90). For PC2, the most relevant attributes were g_s (r = 0.86) and K (root) (r = 0.74). Throughout PC1, it was possible to observe faster recovery of leaf metabolism for native species, since there is less distinction between the symbols representing hydrated plants and drought plants. In PC2, the invasive plants differed in both groups because *L. leucocephala* presented a higher biomass and *P. juliflora* had higher photosynthetic pigment content (Fig. 6b).

4. Discussion

In a semiarid environment, the main limiting factor to the increase in biomass of plants is the seasonality of water availability. Exotic species that have become invasive species need some competitive advantage in using available resources to gain predominance over native species. The invasive species, *P. juliflora and L. leucocephala,* chosen for this study showed low leaf construction cost under both conditions of hydration, high instantaneous energy-use efficiency, and fast recovery of the photosynthetic metabolism after rehydration. The possible advantages of these traits, and the influence at devastated Caatinga environment are discussed below.

Under low soil water availability, the RWC decreased for native *M. caesalpiniifolia and M. urundeuva* and invasive *P. juliflora and L. leucocephala* similarly. In most species, the water content in the soil may influence all metabolic processes, especially gas exchange, as observed in the present study and previous research (Chaves et al., 2009; Oliveira et al., 2014). In general, the reduction in gas exchange is related to stomatal resistance, which reduce water loss by remaining less open (Barros et al., 2018; Hessini et al., 2017, Rivas et al., 2016). The ability to regulate stomatal pore and maintain CO_2 assimilation was different among species in the present study. When well hydrated, plants of both native and invasive groups have similar g_s. The invasive species *L. leucocephala* reached the highest *A* rates, suggesting a greater resource use efficiency among the species studied. Previous works had the same behavior of higher photosynthetic rates in invasive species compared to native species (Feng, 2008; Matzek, 2011; Oliveira et al., 2014).

The invaders, *P. juliflora and L. leucocephala* plants showed a higher shoot and root biomass in relation to *M. caesalpiniifolia and M. urundeuva* native plants in both treatments (Table 1). This greater investment in biomass provides the invaders with a competitive advantage over native plants since the higher growth rate would improve the uptake of resources available in the soil and light for leaves (Grotkopp and Rejmánek, 2007). On the other hand, under drought conditions, only invasive plants reduced the shoot biomass, which could maintain a lower transpiration. There was a strong investment in root biomass in both treatments in *L. leucocephala*. Previous studies have also shown high investments in roots of invasive species (Grotkopp and Rejmánek 2007; DeFalco et al., 2003). This can lead to competitive advantages for the uptake of water and nutrients, mainly under semiarid conditions (Grotkopp and Rejmánek 2007).

The strong investment in root biomass in *L. leucocephala* supported the higher uptake of macronutrients under the drought treatment, increasing average values of leaf nitrogen and phosphorus contents (Table 2). Phosphorus plays an important role in the conservation and transfer of energy in cell metabolism (Jin et al., 2006). It is a frequent limiting factor for plant development in arid ecosystems (Oliveira et al., 2004; Sardans and Peñuelas, 2004). The most common mineral nutrient in plant biomass is nitrogen. It constitutes several organic molecules, such as proteins, nucleic acids, amino acids, and vitamins (Hu and Schmidhalter, 2005). This nutrient, just as P, is directly involved with photosynthesis. Thus, if the nitrogen supply is not sufficient, the photosynthetic rate and leaf area decrease, and leaf senescence and chlorosis increase (Mahieu et al., 2009). The higher nutrient uptake efficiency by invasive species has been discussed, and it leads species to a more competitive advantage over native species (Godoy et al., 2011; Matzek, 2011). In fact, alien species that become invasive have a high biomass gain capacity even under limited resource conditions such as nutrient and water (Oliveira et al., 2014).

To have a competitive advantage over other species, it is not enough to have a high efficiency to acquire resources, but also a high ability in using them. Thus, low resource requirements can increase competitive capacity (Falcão et al., 2017). In fact, this requirement can be influenced by the amount of energy required to increase biomass (Nagel and Griffin, 2001). The CC resulting from the photosynthetic process is an important trait regarding an efficient energy use (Poorter et al., 2006). In this work, when all species were submitted to water deficit, the instantaneous use of energy (PEUE) decreased (Fig. 3b). This result represents less CO_2 assimilation per unit of energy, reflecting in higher costs for leaf construction (Zhu et al., 2013). Among native species *M. caesalpiniifolia and M. urundeuva*, the drought affected less *M. caesalpiniifolia* in relation to PEUE, leading to a lower CC when compared to the other native species. The lower efficiency of *M. urundeuva* provided a five-time increase when compared to control CC values (Fig 3a-b). The strategy of investing in leaves with greater robustness to survive the water deficiency period may have led to higher CC values in detriment of investing energy in new leaves (Barros et al., 2018; Villar et al., 2006). For leaves to have a long life, plants need to invest in secondary metabolites synthesis, which are expensive in energy. On the other hand, these secondary metabolites can prolong the useful life of leaves (Westoby et al., 2002). In the group of invader species, *L. leucocephala* under drought showed a decrease in PEUE, leading to a low CC and a higher SLA in relation to *P. juliflora*. Investing in SLA supports greater photosynthetic area, which could then lead to strong carbon assimilation (Barros et al., 2018; Zhu et al., 2013). In general, the invader species, *P. juliflora and L. leucocephala* had higher PEUE values when compared with native species under drought conditions. This could be an advantage under semiarid conditions due to more energy investment in root biomass growth during irregular rainfall periods and fast recovery after soil rehydration.

When well hydrated, the species showed different behavior as regards PEUE. *M. caesalpiniifolia* showed the same PEUE in both conditions, while the CC was lower in relation to *M. urundeuva*. *L. leucocephala* had the highest efficiencies and the lowest CC when compared to the other species (Fig 3a-b). These differences did not corroborate our second hypotheses, which states that no advantageous trait would differ between the species studied when under drought or well hydrated. This low CC is associated with high growth rate because there are more resources to produce more photosynthetic tissue, which maximizes carbon assimilation by the plant (Barros et al., 2018; Grotkopp and Rejmánek, 2007; Zheng et al., 2009). The low CC leads to biochemical and structural advantages to invest energy in new leaves (Villar et al., 2006; Zhu et al., 2013). In the present study, this was corroborated by the shift in *L. leucocephala* leaves at the maximum stress.

Plants whose growth investment is a priority can have larger leaf area, rather than expending energy on attributes that allow long-term plant resilience (Zhu et al., 2013). Species such as *L. leucocephala*, which have high rates of carbon assimilation, high leaf nitrogen content and short leaf life, have a fast return on carbon investment. This species was the only one to invest in higher chlorophyll *a* content in leaves after experiencing water deficiency. This higher content could support the higher photosynthetic rate observed in this species. In our study, this species, followed by *P. juliflora*, invested more in SLA than the native species (Fig

3b). Previous studies have discussed this competitive advantage in some invasive species (Ordonez and Olff 2013; Penuelas et al., 2010).

In relation to primary metabolites, the increase in carbohydrates by *M. urundeuva* could play an important role for the control of reactive oxygen species (Keunen et al., 2013), and increase water deficit tolerance because they are osmoprotectors (Barros et al., 2018). Furthermore, they can act as signaling molecules in stress situations, and interact with phytoregulators as part of the signaling network (Łabanowska et al., 2013). In addition, the high content of leaf SS and high WUE values may have been the main traits that supported *M. urundeuva* to tolerate drought when compared to *M. caesalpiniifolia*, due to maintenance of the RWC.

The invasive species *P. juliflora* and *L. leucocephala*, showed different biochemical patterns when compared to native species *M. caesalpiniifolia and M. urundeuva*. Under water deficiency, there were protein content reduction and maintenance of proline in *P. juliflora* (Fig 4c-e). Such behavior may have led to osmoprotection by the stabilization of membranes, proteins, and enzymes (Ashraf and Foolad, 2007). On the other hand, at maximum stress, *L. leucocephala* in both treatments invested in sucrose reserves, which could contribute to osmotic regulation, prevention of xylemic cell embolism, and energy reserve to accelerate metabolic recovery after stress (Bucci et al., 2003; Nardini et al., 2012). In fact, this species showed the fastest leaf photosynthetic metabolism recovery after rehydration.

Our results showed that without limitation of water resources, *L. leucocephala* outstrips *M. caesalpiniifolia* and *M. urundeuva* in relation to biomass increase and resource uptake. Thus, there is high CO_2 assimilation, higher energy efficiency, lower CC and higher SLA, conferring highly competitive advantage over native species *M. caesalpiniifolia* and *M. urundeuva*. On the other hand, *P. juliflora* invested mainly in the compounds of primary metabolism, proteins, proline, sucrose and all photosynthetic pigments when well hydrated. Under drought conditions, *P. juliflora* and *L. leucocephala* showed better maintenance of physiological functions, supporting higher biomass, higher uptake of N and P than native species *M. caesalpiniifolia* and *M. urundeuva*. Thus, there were higher values of the instantaneous energy-use efficiency and SLA when compared to native species under drought. This performance of the invasive species leads us to speculate that in a scenario where droughts may be more intense, higher average temperatures and more irregular rainy seasons, the native species of this study would be disadvantaged under field conditions as well. Which would lead to an imbalance of the landscape in the disturbed caatinga ecosystem.

5. Conclusion

In conclusion, invader species, *P. juliflora* and *L. leucocephala*, use and capture light and nutrients more efficiently than the native species studied, *M. caesalpiniifolia* and *M. urundeuva*, favoring growth and acquisition of other resources even when with limited water resources. Our PCA analyses showed in PC1 clearly that SLA and shoot and root biomass distinguished *P. juliflora* and *L. leucocephala* from *M. caesalpiniifolia* and *M. urundeuva* performance after drought stress. On the other hand, PC2 pointed out stomatal control as the most important variable with water limited conditions among the species, at maximum stress and rehydration. Thus, our hypothesis is partially corroborated, because these invasive species, *L. leucocephala* showed gas exchange advantages only after rehydration when compared to native species, *M. caesalpiniifolia* and *M. urundeuva*. After water limitation was removed, *L. leucocephala* had the highest CO_2 assimilation and instantaneous water use efficiency, showing resiliency under unfavorable conditions and fast resumption of growth. Finally, new studies under field conditions with adult plants of these species, and subject to seasonality with short rainy and long dry season could show other abilities that support the performance of each one in a semiarid environment.

Author contribution

V. Barros, L. Nogueira, M. Santos and A. Melo conducted the experiment, performed the measurements. V. Barros and G. Frosi analyzed the data and wrote the first version of the manuscript. M. Santos is an advisor of V. Barros and participated in the planning of the study, data analysis and writing of the manuscript.

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Figure Legends

Fig. 1. Leaf relative water content (RWC) and soil moisture (SM) in young *Mimosa caesalpiniifolia, Myracrodruon urundeuva, Prosopis juliflora* e *Leucaena leucocephala* plants submitted to two water levels (+H_2O and – H_2O) and different species under controlled conditions in maximum stress (MS) and rehydration (RE) days. (a) and (c)- maximum stress and (b) and (d)- rehydration (n=5, ±S.E.).

Fig. 2. Stomatal conductance (*g*s) – **(**a) and (b); net photosynthetic rate (*A*)- (c) and (d) and water use efficiency (WUE)- (e) and (f) in young *Mimosa caesalpiniifolia, Myracrodruon urundeuva, Prosopis juliflora* e *Leucaena leucocephala* plants submitted to two water levels (+H_2O and – H_2O) and different species under controlled conditions in maximum stress (MS) and rehydration (RE) days. a, c, e - maximum stress and b, d, f- rehydration (n=5, ±S.E.).

Fig. 3. Cost of foliar construction (CC)- (a); photosynthetic efficiency of use energy (PEUE)- (b) and leaf specific area (SLA)- (c) in young *Mimosa caesalpiniifolia, Myracrodruon urundeuva, Prosopis juliflora* e *Leucaena leucocephala* plants submitted to two water levels (+H_2O and – H_2O) and different species under controlled conditions (n=5, ±S.E.).

Fig. 4. Soluble sugars (SS)- **(**a) and (b); Total soluble protein (TSP)- (c) and (d); Proline (PL)- (e) and (f); Sucrose (SC)- (g) and (h) in young *Mimosa caesalpiniifolia, Myracrodruon urundeuva, Prosopis juliflora* e *Leucaena leucocephala* plants submitted to two water levels (+H_2O and – H_2O) and different species under controlled conditions in maximum stress (MS) and rehydration (RE) days. a, c, e, g - maximum stress and b, d, f, h- rehydration (n=5, ±S.E.).

Fig. 5. Carotenoid (Car)- **(**a) and (b); chlorophyll a (Chl *a*)- (c) and (d) and chlorophyll b (Chl *b*)- (e) and (f) in young *Mimosa caesalpiniifolia, Myracrodruon urundeuva, Prosopis juliflora* e *Leucaena leucocephala* plants submitted to two water levels (+H_2O and – H_2O) and different species under controlled conditions in maximum stress (MS) and rehydration (RE) days. a, c, e - maximum stress and b, d, f- rehydration (n=5, ±S.E.).

Fig. 6. Principal component analysis (PCA) based on the whole dataset of the study of young *Mimosa caesalpiniifolia, Myracrodruon urundeuva, Prosopis juliflora* e *Leucaena leucocephala* plants submitted to two water levels (+H_2O and – H_2O) and different species

under controlled conditions: (a) maximum stress (MS) and (b) rehydration (RE) days (n=5). Throughout PC1, separation among species. During PC2, separation related to water regime.

Figures

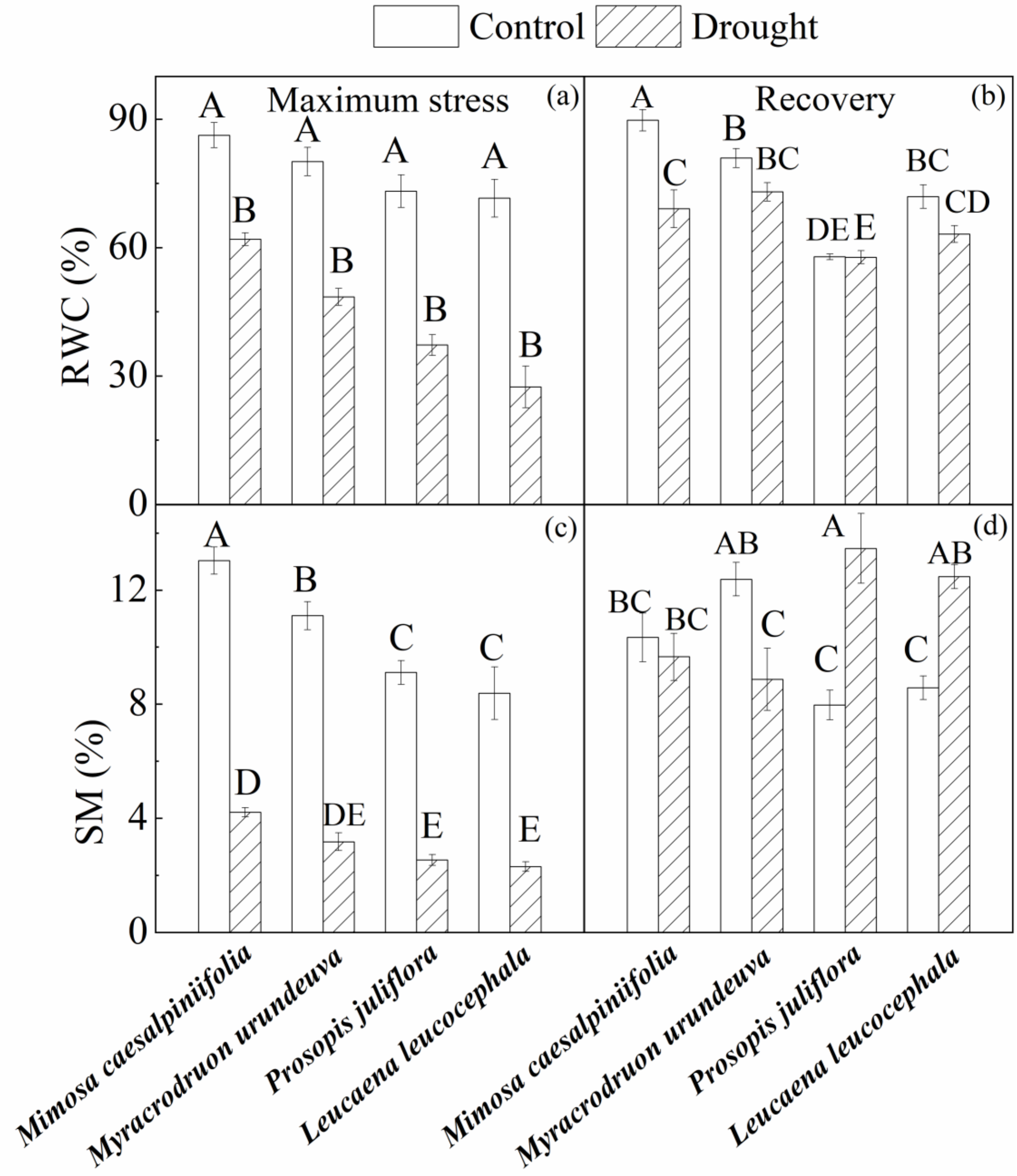

Fig. 1

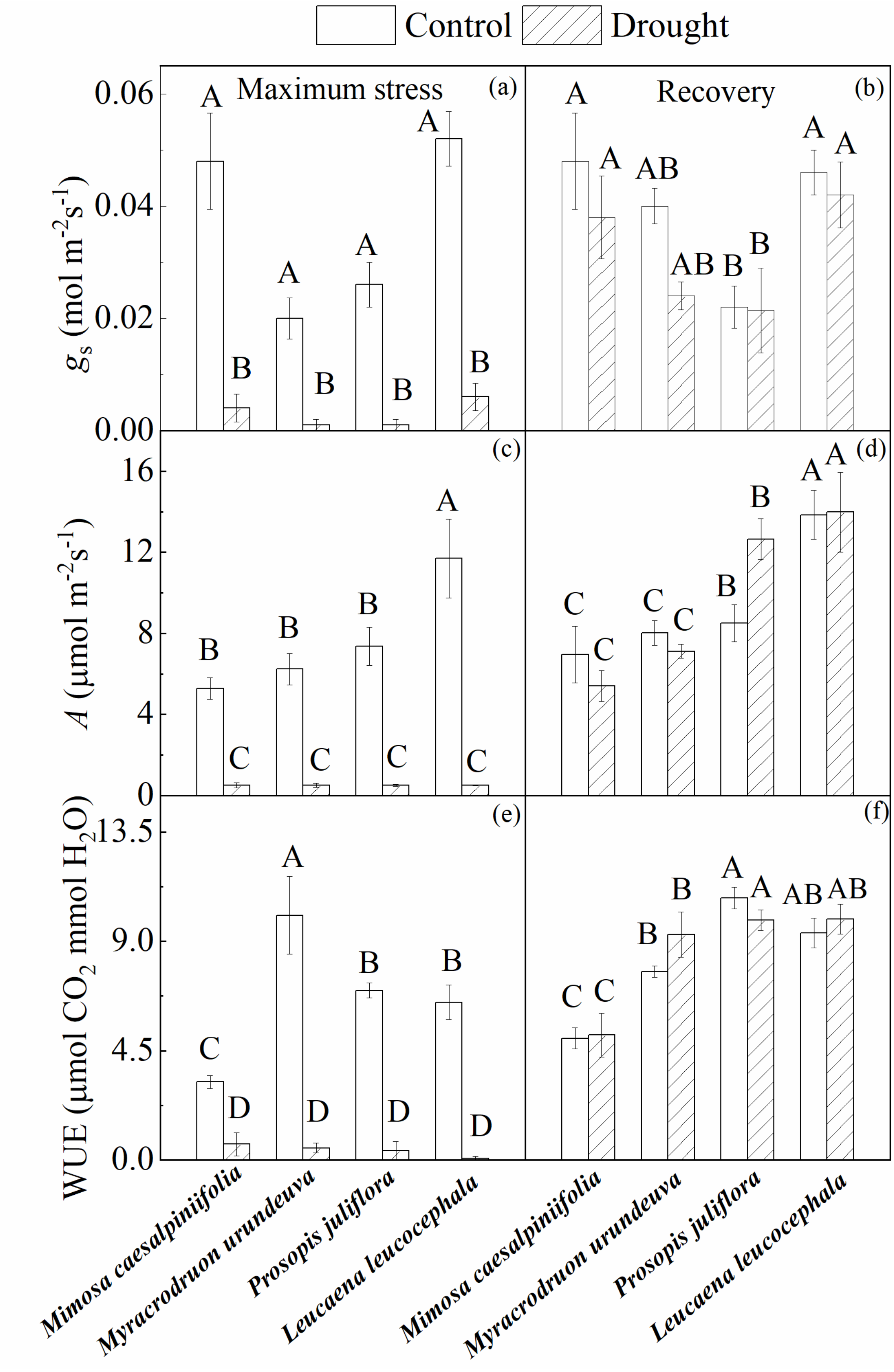
Control
Drought
Maximum stress
(a)
Recovery
(b)
(c)
(d)
(e)
(f)
g_s (mol m^{-2}s^{-1})
0.06
0.04
0.02
0.00
A (µmol m^{-2}s^{-1})
16
12
8
4
0
WUE (µmol CO$_2$ mmol H$_2$O)
13.5
9.0
4.5
0.0
A
B
AB
C
D
Mimosa caesalpiniifolia
Myracrodruon urundeuva
Prosopis juliflora
Leucaena leucocephala

Fig.2

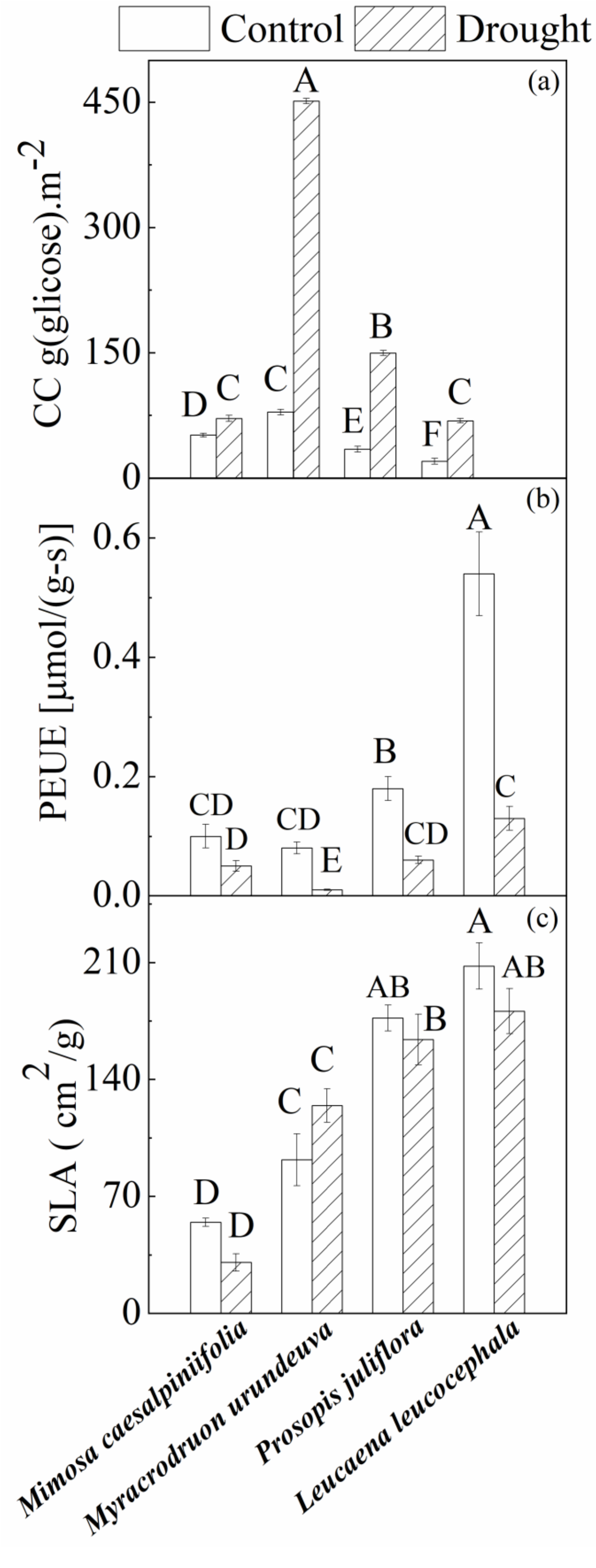
Control
Drought
(a)
CC g(glicose).m^{-2}
0
150
300
450
D
C
C
A
E
B
F
C
(b)
PEUE [µmol/(g-s)]
0.0
0.2
0.4
0.6
CD
D
CD
E
B
CD
A
C
(c)
SLA (cm^2/g)
0
70
140
210
D
D
C
C
AB
B
A
AB
Mimosa caesalpiniifolia
Myracrodruon urundeuva
Prosopis juliflora
Leucaena leucocephala

Fig.3

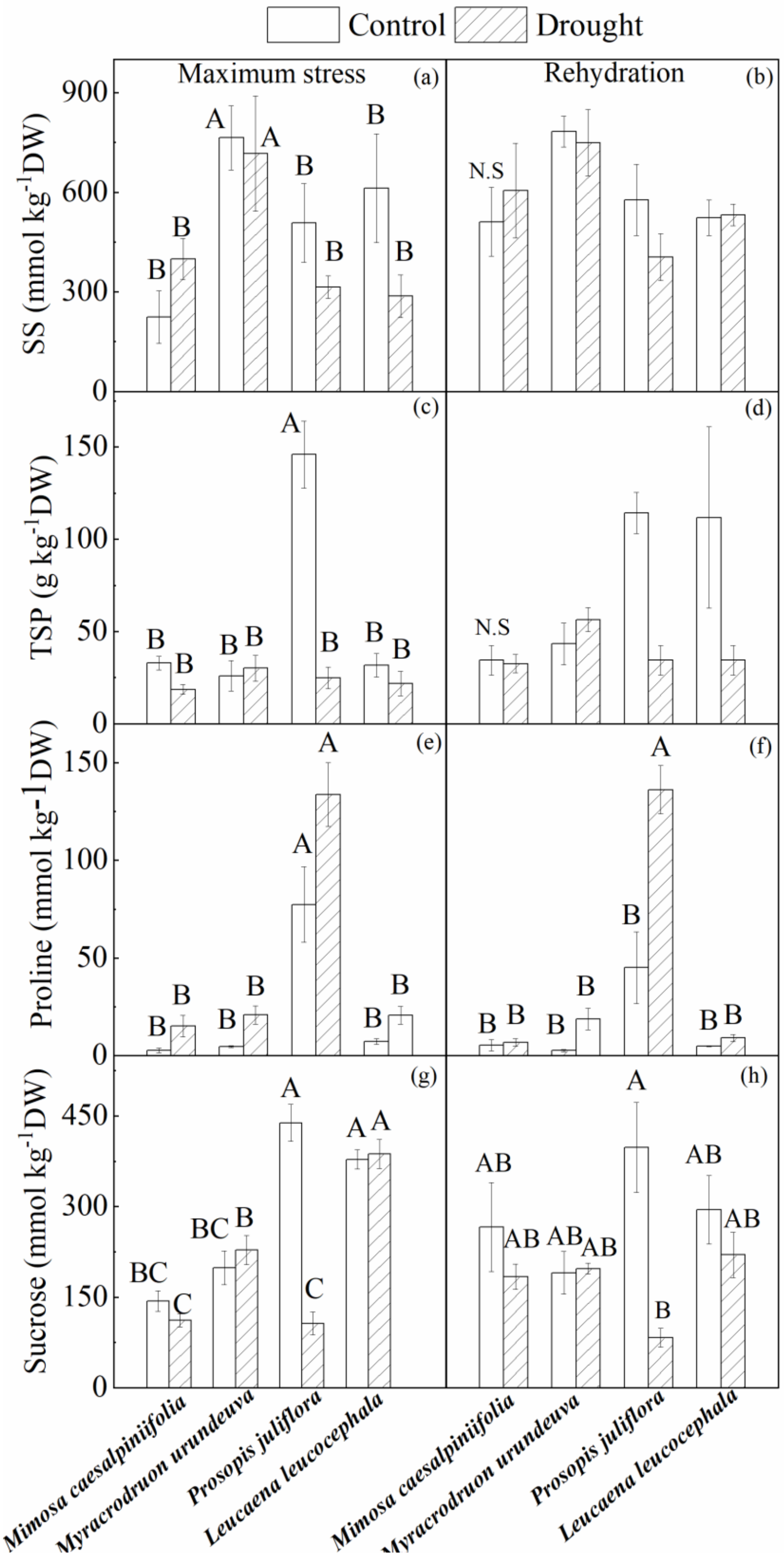
Control
Drought
Maximum stress
Rehydration
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
SS (mmol kg^{-1}DW)
TSP (g kg^{-1}DW)
Proline (mmol kg^{-1}DW)
Sucrose (mmol kg^{-1}DW)
0
300
600
900
0
50
100
150
0
50
100
150
0
150
300
450
N.S
A
B
Mimosa caesalpiniifolia
Myracrodruon urundeuva
Prosopis juliflora
Leucaena leucocephala
AB
BC
C

Fig.4

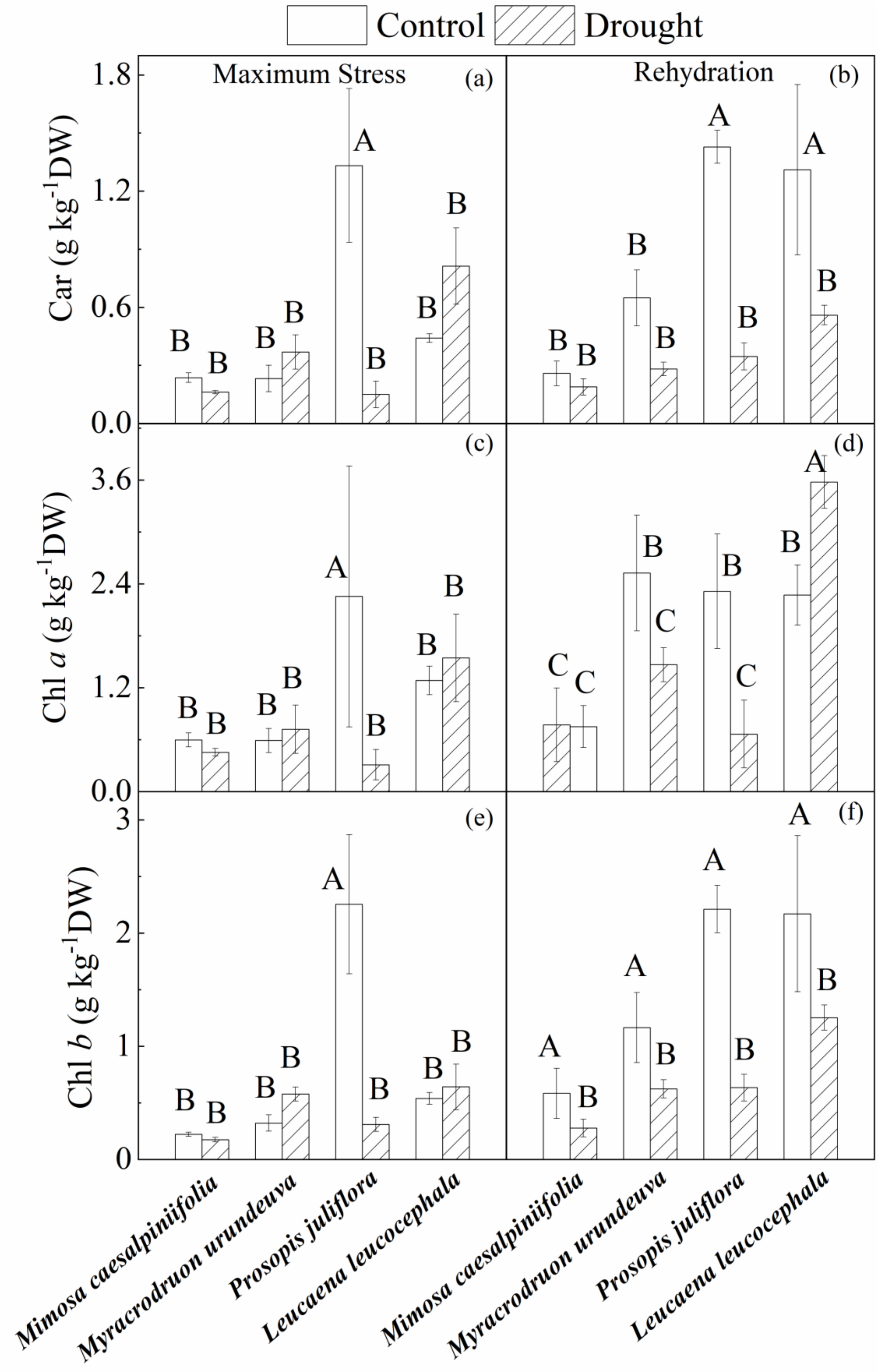
Control
Drought
Maximum Stress
Rehydration
(a)
(b)
(c)
(d)
(e)
(f)
Car (g kg-1DW)
Chl a (g kg-1DW)
Chl b (g kg-1DW)
1.8
1.2
0.6
0.0
3.6
2.4
1.2
0.0
3
2
1
0
A
B
Mimosa caesalpiniifolia
Myracrodruon urundeuva
Prosopis juliflora
Leucaena leucocephala

Fig.5

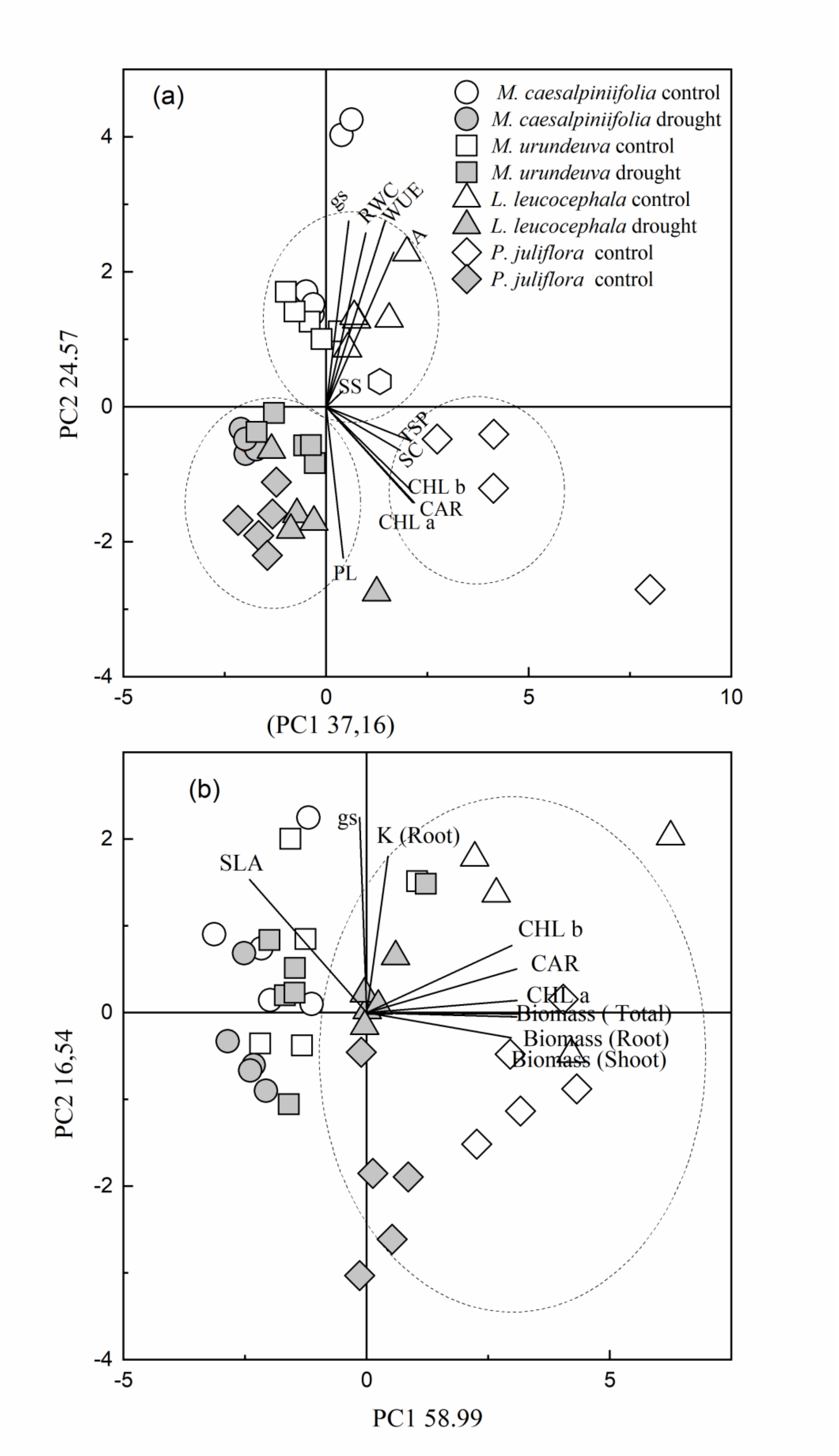
(a)
M. caesalpiniifolia control
M. caesalpiniifolia drought
M. urundeuva control
M. urundeuva drought
L. leucocephala control
L. leucocephala drought
P. juliflora control
P. juliflora control
gs
RWC
WUE
A
SS
TSP
SC
CHL b
CAR
CHL a
PL
PC2 24.57
(PC1 37,16)
4
2
0
-2
-4
-5
0
5
10
(b)
gs
K (Root)
SLA
CHL b
CAR
CHL a
Biomass (Total)
Biomass (Root)
Biomass (Shoot)
PC2 16,54
PC1 58.99
2
0
-2
-4
-5
0
5

Fig.6

Table 1

Biomass (Root, Shoot and Root/Shoot) in young *Mimosa caesalpiniifolia*, *Myracrodruon urundeuva*, *Prosopis juliflora* e *Leucaena leucocephala* plants submitted to water deficit under controlled conditions (n = 5 ± S.E).

		Biomass (g)		
Species	Treatments	Shoot	Root	Root/Shoot
Mimosa caesalpiniifolia	Control	3.77±0.57^{BC}	2.12±0.72^{C}	0.71±0.07^{B}
	Drought	3.59±0.61^{BC}	1.37±0.38^{C}	1.03±0.20^{B}
Myracrodruon urundeuva	Control	3.29±0.61^{BC}	2.29±0.39^{C}	0.55±0.14^{C}
	Drought	1.31±0.16^{C}	1.24±0.09^{C}	0.36±0.06^{C}
Prosopis juliflora	Control	8.36±0.62^{A}	9.20±1.55^{B}	1.14±0.22^{B}
	Drought	5.75±0.67^{B}	6.40±0.84^{B}	1.18±0.19^{B}
Leucanea leucocephala	Control	9.45±1.64^{A}	12.45±1.37^{A}	1.39±012^{A}
	Drought	4.68±0.36^{B}	7.34±0.43^{A}	2.05±0.19^{A}

Table 2

Nutrients (roots and shoot) in young *Mimosa caesalpiniifolia, Myracrodruon urundeuva, Prosopis juliflora* e *Leucaena leucocephala* plants submitted to water deficit under controlled conditions ($n = 5 \pm$ S.E).

		Nutrients (g kg^{-1})					
		N		P		K	
Species	Treatments	Shoot	Root	Shoot	Root	Shoot	Root
Mimosa caesalpiniifolia	Control	4.5±0.21^{B}	3.56±0.73^{NS}	1.4±0.15^{B}	1.2±0.25^{NS}	23.7±1.78^{A}	8.0±1.24^{A}
	Drought	4.7±0.44^{B}	3.86±0.30	0.9±0.19^{B}	0.9±0.08	27.0±2.6^{A}	9.0±0.76^{B}
Myracrodruon urundeuva	Control	4.7±0.19^{B}	2.8±0.82	1.9±0.14^{AB}	0.9±0.15	21.9±1.67^{B}	11.7±2.5^{A}
	Drought	5±0.53^{B}	2.9±0.68	1.2±0.13^{B}	2.1±0.25	16.1±0.99^{B}	9.1±1.89^{B}
Prosopis juliflora	Control	5.1±0.30^{B}	3.4±0.53	0.9±0.14^{B}	1.6±0.32	17.3±1.81^{B}	8.15±1.21^{A}
	Drought	5.6±0.41^{B}	3.8±0.52	0.9±0.05^{B}	0.9±0.04	16.9±1.17^{B}	5.6±0.90^{B}
Leucanea leucocephala	Control	5.8±0.45^{B}	3±0.08	1.5±0.21^{B}	0.9±0.01	18.8±1.27^{B}	15.0±1.93^{A}
	Drought	9.58±0.4^{A}	3.9±0.35	2.5±0.39^{A}	1.0±0.07	19.0±1.37^{B}	8.2±0.90^{B}

Table 3

Photosynthetic efficiency of use nutrients (N,P and K) in young *Mimosa caesalpiniifolia, Myracrodruon urundeuva, Prosopis juliflora* e *Leucaena leucocephala* plants submitted to water deficit under controlled conditions (*n* = 5 ± S.E).

Photosynthetic efficiency of use nutrients				
Species	Treatments	PNUE	PPUE	PKUE
Mimosa caesalpiniifolia	Control	0.2 ± 0.04^{B}	1.8 ± 0.26^{AB}	0.1 ± 0.03^{B}
	Drought	0.1 ± 0.03^{B}	2.1 ± 0.44^{AB}	0.1 ± 0.03^{B}
Myracrodruon urundeuva	Control	0.3 ± 0.07^{A}	2.0 ± 0.51^{A}	0.2 ± 0.03^{A}
	Drought	0.2 ± 0.04^{A}	3.5 ± 0.86^{A}	0.2 ± 0.02^{A}
Prosopis juliflora	Control	0.09 ± 0.08^{C}	1.1 ± 0.12^{B}	0.07 ± 0.09^{B}
	Drought	0.07 ± 0.01^{C}	0.5 ± 0.12^{B}	0.06 ± 0.01^{B}
Leucanea leucocephala	Control	0.2 ± 0.05^{B}	1.9 ± 0.56^{AB}	0.2 ± 0.04^{A}
	Drought	0.1 ± 0.03^{B}	1.7 ± 0.51^{AB}	0.2 ± 0.06^{A}

4 MANUSCRITO II

O conteúdo dessa seção consiste em um artigo intitulado "Low foliar construction cost and strong investment in root biomass in *Calotropis procera*, an invasive species under drought and recovery" publicado na revista *Flora*. A formatação do artigo segue as normas estabelecidas pela revista disponíveis no anexo A deste documento.

Low foliar construction cost and strong investment in root biomass in *Calotropis procera*, an invasive species under drought and recovery

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Abstract

The relationship between uptake and use of resources has always been highlighted among functional traits to explain the performance of invasive and native species. However, previous studies have shown that, under resource limitation, the species of both groups tend to have similar functional behavior. We measured a group of resource-use traits under controlled drought stress in *Cenostigma microphyllum* native to Caatinga of Brazil and the invasive species *Calotropis procera* that has a large occurrence in semiarid regions. The results showed that invasive well-watered plants always had higher CO_2 assimilation rates and lower leaf construction costs than native plants, while stomatal conductance was similar. On the other hand, under water deficit conditions, the invasive plants tolerated more days of drought and showed higher root/shoot biomass ratio, leaf relative water content, lower leaf construction costs and payback time than the native species. Moreover, seven days after stress, the invasive plants displayed higher CO_2 assimilation, photosynthetic nitrogen use efficiency, instantaneous efficiency of energy use and lower leaf construction costs compared with the native species. The ability to acquire and distribute resources among the different plant tissues at the right time seems to be a fundamental combination for the plants used in the experiment. Thus, a more acquisitive strategy is fundamental for having enough carbon to invest in the root biomass in *C. procera* under drought, which could contribute to maintain higher leaf water status for longer time compared with *C. microphyllum.*

Keywords:

Caatinga

Carbon metabolism

Gas exchange

Leaf economics

Resource-use efficiency

Specific leaf area

Water deficit

Abbreviations:

A	Net photosynthetic rate
CC	Leaf construction cost
CCmass	Leaf construction cost per unit mass
DW	Dry weight
ea	Ambient vapor pressure
es	Saturating vapor pressure
FW	Fresh weight
gs	Stomatal conductance
HC	Ash-free heat of combustion
K	Oxidation state of the N source
MS	Maximum stress
N	Nitrogen
NEMA	Núcleo de Ecologia e Monitoramento Ambiental
NM	Total N concentration
PC	Principal components
PCA	Principal component analysis
PBT	Payback Time
PEUE	Photosynthetic energy use efficiency
PNUE	Photosynthetic nitrogen-use efficiencie
PPFD	Photosynthetic photon flux density
RE	Rehydration
RWC	Relative leaf water content

SLA	Specific leaf area
SM	Soil moisture
TW	Turgid weight
VPD	Vapor pressure deficit
WUE	Water use efficiency

1. Introduction

Water availability is the main limiting factor that affects the performance of plants in natural ecosystems (Santos et al., 2014; Chaves et al., 2016). Changes in global rainfall patterns have resulted in longer, more frequent droughts in semiarid environments, increasing the aridity of these environments worldwide (Arneth et al., 2019). In ecosystems with these rainfall irregularities, water acts as an environmental filter that determines the functional characteristics of species within that ecosystem (Falcão et al., 2017). Reducing water availability leads to a series of morphological, developmental / phenological, physiological, biochemical, and molecular changes in all plant organs, which negatively affect growth and productivity (Hessini et al., 2017; Xiao et al., 2018). These changes result primarily from a reduction in plant water status, which leads to the loss of cell turgor and stomatal closure, which in turn affects carbon acquisition by reducing photosynthesis. All of these functional disorders reduce growth and can result in the death of plants (Liao et al., 2019). Before death a progressive shedding of leaves is the most common behavior in semiarid species (Santos et al., 2014; Chaves et al., 2016). In seasonally dry tropical environments, prolonged drought events favor the proliferation of invasive species due to their high physiological performance when compared with native species under limited water availability (Oliveira et al., 2017). Furthermore, for some invasive species, performance is more efficient even under conditions without limited resources (Barros et al., 2020). A high tolerance to water deficit and efficient acquisition and use of resources can give invasive plants the ability to establish in different environments (Huan and Fenglan, 2017; Rivas et al., 2020). Some studies have revealed that invasion can be explained by several functional traits, such as high relative growth rate, increased efficiency in uptake and use of resources and phenotypic plasticity (Funk et al., 2016; Jo et al., 2017). To have a competitive advantage over other species, it is not enough to have high efficiency in the acquisition of resources, as invasive species have, but also a high capacity to use them (Falcão et al., 2017). The relationship between leaf functional attributes and the carbon balance is known as the leaf economics spectrum, and reflects the ability of plants to use their photosynthates (Wright et al., 2004; Edwards et al., 2014). Moreover, the cost of leaf construction associated with the time to compensate for expenses in the production of leaves can provide interesting data about the efficiency of energy use in plants. Thus, different strategies for the uptake and use of available resources can allow species to be classified as either acquisitive or conservative (Tecco et al., 2010; Dyderski and Jagodzin´ski, 2019). Previous studies have investigated the performance of invasive and native species. Until now, different functional traits have been shown as the key traits to support the success of one species over another. Thus, specific leaf area, biomass, gas exchange, and nutrient content are the most commonly measured traits compared between tree species (Oliveira et al., 2017; Dyderski and Jagodzinski, 2019; Barros et al., 2020) and different growth habits (Funk et al., 2016). However, little attention has focused on understanding how efficiency in the use of acquired resources influences the differences in performance between native and invasive species (Xiao et al., 2018; Barros et al., 2020). The aims of the present study were to investigate the different strategies adopted by a native and invasive species in Caatinga under water deficiency and after drought stress, as well as to identify the key traits of carbon metabolism that are essential for success under resource limitation. Caatinga is a seasonally dry tropical forest, located in northeastern Brazil, under a semi-arid climate, and its vegetation is threatened either by intense human disturbance or by increasing global climate change (Almeida et al., 2014; Santos et al., 2014). We hypothesized that the invasive species would present an acquisitive behavior, investing in growth and with greater tolerance to water deficit, thus preserving its relative water content and gas exchange, in relation to the native species. Presenting high rate of CO_2 assimilation in the leaves with low production cost when compared to the native species would allow a greater biomass gain in both water availability conditions. Native species would present a more conservative strategy, investing in expensive leaves with a low net rate photosynthetic, which would provide more time to recover the invested carbon.

2. Materials and methods

2.1. Plant material and growth conditions

The plant species were chosen because they belong to widely distributed families in semiarid regions (Giulietti et al., 2004). *Calotropis procera* (Aiton) W. T. Aiton (Apocynaceae) is an evergreen perennial shrub with C3 metabolism and is naturally distributed across continental Africa, Madagascar, the Arabian Peninsula, and Southwest Asia (Tezara et al., 2011; Rivas et al., 2020). This species has large leaves, succulent, arranged in opposite phyllotaxy and covered with abundant cuticular wax (Batool et al., 2020). In Brazil, it is widely found in the Northeast region, where it was introduced around 1900 as an ornamental species before becoming invasive and spreading to several states in this and other regions of the country (Sobrinho et al., 2013; Rivas et al., 2020). To make a comparison with the native flora, we chose *Cenostigma microphyllum* (Mart. ex G. Don) Gagnon & G. P. Lewis as a deciduous shrub species endemic to Caatinga, which has economic and ecological importance, being considered as a facilitating plant and presenting potential for the recovery of degraded areas (Gahem, 2020). It is easily recognized by multi-leaves and numerous small leaflets (Fig. S1). Most of the Caatinga woody species are deciduous (about 98%) as this is the main mechanism of tolerance to long dry seasons that occur every year (7 to 8 months without rain). The studied species *Cenostigma microphyllum* belongs to one of the most abundant families in Caatinga (Fabaceae) alongside Euphorbiaceae. It is widespread in this biome, which is why it was chosen. As the invader is an exotic species in Latin America that has become invasive throughout the South American territory, from the coast to semi-arid regions (see Tezara et al., 2011 and Rivas et al., 2020 for more details), it has an immense capacity to occupy devastated areas with strong limitation of resources such as water and nutrients. Seeds of the native species *Cenostigma microphyllum* were donated by the Núcleo de Ecologia e Monitoramento Ambiental (NEMA), while seeds of the invasive species *Calotropis procera* were collected in the semiarid region of Brazil. The seeds were disinfected with sodium hypochlorite (0.5%) and germinated in trays containing vermiculite. When the seedlings presented the first leaf pair, they were transferred to pots containing approximately 6 kg of soil and kept under pot capacity hydration. The experiment was carried out in a greenhouse in northeast Brazil (8◦ 08′ 58″ S, 34◦ 56′ 55″ W). The average temperature was 28 ± 2 ◦C, the relative humidity was 55–60% and photosynthetic photon flux density under greenhouse reached around 1500 µmol m − 2 s − 1 at midday. Plants were maintained under hydration (pot capacity of 350 ml) until the application of the water deficit conditions. The experimental design was completely randomized, with a factorial arrangement of 2 × 2 corresponding to the different species studied (one native and one invasive) and to the water deficit conditions (irrigated and suspended irrigation), with eight replicates used for each treatment. From these eight replicates, four were used to evaluate the biomass, cost of foliar construction, and nutrients, while the other four were used to evaluate the foliar relative water content and gas exchange. To determine the maximum stress, the water content, gas exchange and soil moisture were measured every two days after the start of the water deficit treatment; however, we only present data on the maximum stress and recovery due to the leaf construction cost measurements carried out at these times. The soil used in the experiment was a mixture of 2:1 organic horizon (rich in humus) and washed sand, respectively, and had the following characteristics: nitrogen (N): 23 mg dm− 3 (Kjeldahl); phosphorus (P): 25 mg dm− 3 (Mehlich); pH (H2O): 7.1; total concentrations of calcium (Ca): 5.40 cmolc dm− 3 ; magnesium (Mg): 0.7 cmolc dm− 3 ; sodium (Na): 0.38 cmolc dm− 3 ; potassium (K): 0.69 cmolc dm− 3 .

2.2. Experimental design

Water deficit was imposed when the plants completed five months of development. Plants were divided into two treatments: control (irrigated with 350 ml of water once a day) and drought (suspension of irrigation) for each species. Watering suspensions were kept until the maximum stress was observed [stomatal conductance (gs) close to zero] and plants were rehydrated soon afterwards. Rehydration was carried out by re-watering the plants of the water deficit treatment (with 350 ml of water) until the plants reached net photosynthetic rates similar to those of the control plants. All measurements were performed on the day of maximum stress (gs close to zero) and rehydration (A of the dry plants 90% near the control). The maximum stress of the invasive species occurred after 21 days of drought, and after 15 days for the native species. Rehydration occurred seven days after maximum stress in both species.

2.3. Relative leaf water content and soil moisture

Leaf discs of approximately 1 cm diameter were collected during maximum stress and rehydration at 06:15 a.m. and weighed immediately on a precision scale (AND H200, Tokyo, JP; precision = 0.0001 g) to obtain the fresh weight (FW). Then, the discs were soaked for 24 h 3 deionized water and weighed again to obtain the turgid weight (TW). Later, leaf discs were dried in a stove for 48 h at 60 ◦C and weighed to obtain the dry weight (DW). The leaf relative water content (RWC) was calculated according to Barrs and Weatherley (1962): RWC (%) = [(FW-DW)/(TW-DW)] × 100. The volumetric soil moisture content was obtained using a soil moisture meter (v/v) measuring approximately 20 cm of depth (HFM 2030 Falker, Porto Alegre, BR).

2.4. Gas exchange

Gas exchange was measured in expanded leaves using an infrared gas analyzer (IRGA, ADC, model LCi-Pro; Hoddesdon, UK) to obtain the stomatal conductance (gs) and net photosynthetic rate (A). The water use efficiency (WUE, derived from A/E) was also calculated, where E is the transpiration rate. The measurements were performed between 09:00 a. m. and 09:30 a.m., and the photosynthetic photon flux density (PPFD) was determined according to the global radiation incident at the time of the measurements, ranging from 800 to 950 μmol m − 2 s − 1 during the experiment. The vapor pressure deficit (VPD) was calculated together with the gas exchange measurements using the es-ea formula, where es is the saturating vapor pressure and ea is the ambient vapor pressure (Campbell and Norman, 1998), using temperature and air humidity obtained by a digital thermo-hygrometer (Thermo-Higro SH 122, J. Prolab, São José dos Pinhais, BR). The VPD ranged from 1.24 to 1.87 kPa, leaf temperature was 30 ± 2 ◦C and CO2 concentration 400 μmol mol− 1 during the experiment.

2.5. Biomass

Four individuals per treatment were collected during maximum stress and rehydration. The shoots and roots were separated and placed in a stove at 70°C for five days. Subsequently, the material was weighed on a precision scale (AND H200, Tokyo, JP) to obtain the dry weight of each part. The shoot/root ratio was also calculated.

2.6. Specific leaf area, nitrogen, and photosynthetic nitrogen-use efficiency

All leaves of four individuals per treatment were collected during maximum stress and rehydration. Leaves with petioles were scanned for the calculation of the leaf area using Image Pro-Plus 4.5 program (Media Cybernetics, Inc., Rockville, MD, USA). Afterwards, the leaves were dried at 60 ◦C for 72 h and weighed on a precision scale (HR-200, E, Tokyo, JP) to obtain the dry biomass. The specific leaf area (SLA) was determined by the ratio of the leaf area to the leaf dry biomass. To measure the leaf and root nitrogen (N) contents, 100 mg of dry tissue was collected from four plants of each treatment during the maximum stress and rehydration. The material was digested in a sulfuric acid solution in a digester block at 350 ◦C to obtain the sample extract (Thomas et al., 1967). The total N concentration was determined by extract titration using HCl after adding boric acid and a colorimetric indicator (Thomas et al., 1967). The photosynthetic nitrogen-use efficiency (PNUE) was determined by the ratio of the net photosynthetic rate and nitrogen content per leaf area.

2.7. Leaf construction cost, photosynthetic energy use efficiency, and payback time

Leaves of four individuals per treatment were collected during the maximum stress and rehydration. The ash content (g kg− 1) of 100 mg of dry matter was obtained using a muffle furnace at 500 ◦C for 6 h to calculate the cost of foliar construction. The ash content was calculated through the pre- and post-muffle weight difference (Li et al., 2011). The calorific value (ΔHC; kJ g − 1) was obtained by the combustion of 150 mg dry matter in a calorimeter (C200, IKA, Heiters-Heim, DE) according to Villar and Merino (2001) through the formula: ΔHC = calories/(1-Ash); Ash is the ash content (g•g − 1 leaf dry mass). The leaf construction cost per unit mass (CCmass) (g glucose g − 1 DW) was obtained through the results of ash, nitrogen concentration, and ΔHC according to Williams et al. (1987): CCmass = [(0.06968 ΔHC - 0.065) × (1 - Ash) + 7.5 (k × NM/14.0067) × 0.89, where ΔHC means the combustion heat without ash (kJ g − 1); NM is the total concentration of nitrogen (g − 1 dry mass); and k is the oxidation state of the nitrogen source (+5 for nitrate, − 3 for ammonium). We assumed k = − 3 because the main source of soil nitrogen is ammonium (De Vries et al., 1974). The leaf construction cost (CC) per unit area (CCarea) (g glucose m − 2) was obtained through the ratio between CCmass and SLA. Photosynthetic energy use efficiency (PEUE) was determined from the relationship between CO_2 assimilation (A) and CCmass (Nagel et al., 2005). In addition, the payback time (PBT) was calculated through CCmass/Amass after converting CCmass from g glucose g − 1 dry mass to nmol g − 1 dry mass and Amass from µmol CO_2 g − 1 dry mass s − 1 to nmol C g − 1 dry mass h − 1 (Karagatzides and Ellison, 2009). PBT was demonstrated by hour rather than day because the diurnal radiation period changed during the experiment period (Shipley, 2006).

2.8. Statistical analysis

Data were subjected to a factorial analysis of variance (ANOVA), where the different species and water deficit conditions and the interaction between them were considered as factors. Means were checked by the Student Newman Keuls test at 5% using the Statistica 8.0 program (StatSoft, Inc., Tulsa, OK 74,104, USA). Pearson's correlation coefficient was used to evaluate the degree of relationship between the traits.

3. Results

3.1. Relative leaf water content and soil moisture

The RWC at the maximum stress was lower by 32% and 18% (F1,15 = 14.4, P = 0.001) for native and invasive plants under drought conditions, respectively, compared to the controls (Fig. 1a). The soil moisture at maximum stress was lower by 76% and 63% (F1,15 = 14.4, P = 0.001) for pots of native and invasive plants under drought conditions, respectively, compared to controls. The soil moisture in pots of the invasive control plants was 30% higher compared to the control of native plants (Fig. 1c).

3.2. Gas exchange

At maximum stress, plants under drought showed a decrease in all gas exchange parameters in relation to the control (Fig. 2a, c, e). There was a decrease of 63% and 82% (F1,15 = 57.1, P < 0.001) in gs, 82% and 99% (F1,15 = 6.5, P < 0.05) in A, and 47% and 93% in WUE (F1,15 = 13.4, P < 0.01) of native and invasive plants under drought conditions, respectively, compared to controls. The invasive control plants showed the highest rates of A (11.2 µmol m − 2 s − 1) and WUE (7.70 µmol CO2/ mmol H2O) (Fig. 2c, e).

After rehydration, all plants subjected to drought showed strong increase of gs, which has not been achieved for the invasive plants in relation to the WUE (Fig. 2b, d, f). The invasive species in both treatments showed higher gs (F1,15 = 14.4, $P < 0.01$) and A in both treatments (F1,15 = 9.2, $P < 0.01$) in relation to native.

3.3. Biomass

At the maximum stress, the invasive plants had more than twice the shoot biomass (F1,15 = 13.6, $P < 0.01$) compared to the native species of their respective treatments. Invasive plants under drought showed higher biomass of the underground part (F1,15 = 13, $P < 0.01$) and R/S (F1,15 = 5.7, $P < 0.05$) compared to the other treatments (Table 1). After rehydration, native plants showed a lower shoot biomass (F1,15 = 27.1, $P < 0.01$) in both treatments in relation to the invasive plants. On the other hand, the invader under drought had 44% less shoot biomass and three times more root biomass (F1,15 = 11.9, $P < 0.01$) in relation to the control (Table 1).

3.4. Specific leaf area, nitrogen, and photosynthetic nitrogen-use efficiency

At maximum stress, plants under drought showed a decrease in PNUE of 84% and 93% (F1,15 = 15.6, $P < 0.01$) compared with the controls for native and invasive plants, respectively (Fig. 3e). The SLA and leaf N content did not show any difference between species and treatments (Fig. 3a,c). The total leaf area, when compared between stress moment and treatments for each species, was different only between control and drought-stressed invasive plants for both measurement times (Table S1). After rehydration, for plants under drought SLA was lower by 78% and 56% (F1,15 = 10.8, $P < 0.01$) compared with the controls for native and invasive plants, respectively (Fig. 3b). There was an increase in N in invasive plants subjected to drought of more than 100% (F1,15 = 8.5, $P = 0.01$) compared with the control (Fig. 3d). However, in relation to PNUE, there was a decrease of 78% (F1,15 = 7.5, $P < 0.05$) in the invasive plants subjected to drought (Fig. 3f).

3.5. Leaf construction cost, photosynthetic energy use efficiency, and payback time

At maximum stress, native plants had the largest CCmass (F1,15 = 10.3, $P < 0.01$) compared to invasive plants (Fig. 4a). There was a decrease of 86% and 97% (F1,15 = 6.8, $P < 0.05$) of PEUE in native and invasive plants under drought, respectively, compared with the controls (Fig. 4c). The PBT increased by more than 30- and 20-fold (F1,15 = 41, $P < 0.001$) in native and invasive plants under drought, respectively, compared with the controls (Fig. 4e).

After rehydration, the CC of native plants was higher by 33% (F1,15 = 6.9, $P < 0.05$) in relation invasive plants subjected to drought (Fig. 4b). Invasive plants had two times higher PEUE in relation to the native species (F1,15 = 49.8, $P < 0.001$) (Fig. 4d). There was a decrease of 88% and 47% (F1,15 = 6.9, $P < 0.05$) of the PBT in native and invasive plants subjected to drought, respectively, compared with the controls (Fig. 4f).

4. Discussion

Our results suggest that both species, native and invasive, widely found in the semiarid region, although they have different leaf habits, the deciduous native and the evergreen invasive, present, at least under the work conditions, many similarities, such as: at maximum water deficiency, plants have the same rate of stomatal conductance, CO_2 assimilation and water use efficiency; both under drought and well hydrated, at maximum stress, the same values of specific leaf area, leaf nitrogen content and photosynthetic nitrogen use efficiency. Moreover, under drought and after rehydration, the invader has cheaper leaf and strong increase in the root/shoot ratio, which was not observed at both times measured in the native species. This rapid adaptation to the environmental conditions observed in the invader can support the ability to increase its presence in an environment with limited water resources. The containment of shoot growth at the expense of investment in the root system seems to be the basis for the higher leaf water content of the invader, at maximum stress, even with similar rates of gas exchange when compared to the native species.

Several previous studies have discussed the performance of invasive plants, sometimes comparing them with native species and measuring diverse functional traits, such as, gas exchange (Tezara et al., 2011; Naidoo and Naidoo, 2018; Rivas et al., 2020), biomass reallocation (Liao et al., 2019), carbon balance (Funk et al., 2016) and root water uptake capacity (Coêlho et al., 2021). Environments with limited resources, such as semiarid, with low water availability, tend to favor the establishment of invasive species (Oliveira et al., 2017; Barros et al., 2020; Rivas et al., 2020). *Calotropis procera* is an invasive species in Latin America, with wide dispersion throughout the continent today. Its performance under field conditions is supported by intense gas exchange, even in periods of water deficiency (Tezara et al., 2011; Rivas et al., 2020). It is known that an intense regulation of aquaporins in roots of this invader occurs at the beginning of soil water potential decrease (Coêlho et al., 2021), which can guarantee the continuity of hydration of aerial parts and translocation of sugars to sinks, such as the root system. Other studies with different invasive species have pointed out that the success of invasion is based on several functional traits, such as robust plasticity to alter root/shoot ratio (Funk et al., 2016; Jo et al., 2017). The increase in the ability to acquire resources such as water and nutrients through a greater root system needs to be followed by a high efficiency in using such resources, increasing photosynthetic activity (Falcão et al., 2017).

Invasive species have the ability to invest in root biomass during water deficiency, which could increase water and nutrient uptake (Erskine-Ogden et al., 2016; Dyderski and Jagodzinski, 2019). Previous studies have argued that the success of invasive species over native species is dependent on the conditions of the environment and on the growth habit of the species (Funk et al., 2016). The invasive species, evergreen and originating in an arid environment, has growth stability and biomass gain throughout the year in different habitats, regardless of the climatic season (Rivas et al., 2020). In contrast, the native species is deciduous and invests in leaves with a high cost to be efficient throughout the rainy season, including chemical compounds that act as defenses against small herbivores (Falcão et al., 2017). Like other deciduous species in a seasonally dry tropical forest, C. microphyllum has not a long time to recover this investment.

The RWC and SM of both species decreased under water deficit conditions. The invasive species showed higher RWC at maximum stress, and this factor contributed to support it for six days more than the native species under water deficit. For keeping leaf RWC under water deficit a progressive stomatal closure is a common response in plants (Santos et al., 2014; Chaves et al., 2016). Moreover, under low water availability, investment in root biomass can support water uptake, an essential ability for drought tolerance that mitigates the effects of low water availability on gas exchange (Erskine-Ogden et al., 2016; Naidoo and Naidoo, 2018). In order to invest in root biomass under water deficiency, the plant needs to maintain the leaf water status, as this will support the translocation of photosynthates to the sinks, including the roots (Santos et al., 2021). Previous studies have also shown high investment in the roots of *C. procera* (Sharma, 1968), and ability to increase water uptake under stress drought conditions (Coêlho et al., 2021). This behavior has been seen in another invader with strong gas exchange under water deficit, *Chromolaena odorata* (Naidoo and Naidoo, 2018). The invasive species always had a higher rate of carbon gain when compared with the native species when well-watered. Thus, high net carbon assimilation rate led the invasive species to another adaptative advantage under high water availability conditions, since the higher growth rate improved the uptake of available resources in the soil by roots and light by leaves (Erskine-Ogden et al., 2016; Dyderski and Jagodzinski, 2019). Both species had the same amount of N in their leaves at maximum stress and the same efficiency in the use of this nutrient. Under drought, the PNUE decreased in both species. Previous studies have shown that stomatal closure decreases the photosynthetic rate by lowering the internal carbon concentration (Chaves et al., 2016), leading to a lower PNUE (Xiao et al., 2018).

Under water deficiency, PEUE decreases in different species; however, in species with high CC, this lower efficiency results in long PBT (Xiao et al., 2018). This pattern of behavior did not occur in plants with the same traits as *Calotropis procera (*Penuelas et al., 2010; Xiao et al., 2018); thus, not reducing PEUE under semiarid conditions may be an advantage due to lower PBT (Gonzalez-Paleo and Ravetta, 2018). Species such as this invasive, with high carbon assimilation rate, have a fast return on investment in carbon. After stress, the invasive plant increased PEUE and maintained leaves with a low CC when compared with the native species. Thus, less time was required to recover the carbon invested in leaf construction, which could provide investment in root biomass (Karagatzides and Ellison, 2009; Xiao et al., 2018; Naidoo and Naidoo, 2018). Our hypothesis was partially confirmed. We hypothesized that this invasive species was more efficient in the use of photosynthetic energy regardless of water availability conditions than the native species, although only after stress (during the rehydration period) did the invasive species show greater PEUE.

On the other hand, regarding the native species, our expectation based on previous studies with Caatinga species was confirmed, where native species showed a more conservative strategy, investing in expensive leaves with a low rate of net photosynthesis, which led to more time to recover the invested carbon. The native stressed plants showed the lowest SLA after drought stress period, this trait in general is associated with semiarid species with high CC and low CO_2 assimilation rate (Falcão et al., 2017). In fact, this species also showed a lower PEUE and higher leaf construction cost. This behavior occurs in species that have higher carbon flow, with investments in more expensive leaf tissues, compensating for the higher construction cost for the leaf area units (Huan and Fenglan, 2017). Thus, leaves that are smaller, thicker and more drought tolerant would require high construction costs due to the synthesis of defense compounds such as tannins which are energy-expensive (Xiao et al., 2018). In a seasonally dry tropical forest, deciduous woody species need to invest in drought-tolerant leaves, which must withstand the irregularity of precipitation and also the attack of small herbivores; in this way, the photosynthetic area is preserved to survive during the short rainy season (Falcão et al., 2017). Thus, conservative species have specific leaf traits to increase the resilience of this organ after resources and energy have been invested (Gonzalez-Paleo and Ravetta, 2018). This behavior is considered a conservative strategy for plants from semiarid regions, such as

Caatinga, with irregular and short rainy seasons (Erskine-Ogden et al., 2016; Falcão et al., 2017; Dyderski and Jagodzinski, 2019).

As discussed in the paragraph above, the invasive plant, being evergreen, managed to keep its leaves for longer because it invested in physical structures (greater SLA) that allowed it to assimilate carbon more efficiently, thus decreasing CC and PBT. This species has large leaves, succulent and covered with abundant cuticular wax (Batool et al., 2020).

Both species studied here have a wide distribution under semiarid conditions, which allows us to imagine that leaf investment strategies is economically competitive (Wright et al., 2004). Previous studies show that there are several possibilities to increase the fitness of species under field conditions, such as, investment in components with similar effects, however, of lower cost (Falcão et al., 2017) or association with microorganisms such as mycorrhizas, which *C. microphyllum* has shown under semiarid conditions (Pereira et al., 2021). The evergreen species of C3 photosynthetic metabolism from arid environments with high performance during all seasons of the year (Rivas et al., 2020) would not have a strong worldwide dispersion if it did not invest in high return traits, while with low cost. Future studies that investigate these traits, in comparison to more native species, can make this behavior of the invader clearer.

5. Conclusions

The present study discussed key traits that support the tolerance of two shrub species to low water availability, the invasive species *Calotropis procera* and *Cenostigma microphyllum*, a species native to semiarid Brazil. Although both are found with high frequency in this environment, they have different strategies. Our work brought for the first time, as far as we know, the behavior of the leaf economics spectrum of an evergreen invasive species of extreme ability to occupy areas with limited resources. While the invasive species had high CO_2 assimilation rate in leaves with low production costs, the native species invested in expensive leaves with low photosynthetic net rate, which required more time to recover the invested carbon. Our results suggest that the more acquisitive strategy is fundamental for having enough carbon to invest in the root biomass in the invasive species under drought, which maintained higher leaf water status for longer time compared with the native species. Considering the climatic forecasts for the semiarid regions during this century, with shorter rainy season and longer drought period, we expect the prevalence of the invasive species will increase in habitats being occupied by native species before. Long-term studies under field conditions are necessary to better understand the strategies of both groups of species.

Author contribution

V. Barros conducted the experiment and performed the measurements. V. Barros and M. Oliveira analyzed the data and wrote the first version of the manuscript. M. Santos is an adviser of V. Barros and participated in the planning of the study, data analysis, and writing of the manuscript.

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Figures Legends

Figure 1. Foliar relative water content (RWC) (a,b) and soil moisture (SM) (c,d) in young plants of *Cenostigma microphyllum* (native) and *Calotropis procera* (invasive) subjected to drought stress and recovery (n = 4, ± S.E.). The letters in each column and time of treatment are comparing the averages through the Student Newman Keuls test ($p<0.05$). Not significative (NS).

Figure 2. Stomatal conductance (g_s) (a-b), CO_2 assimilation rate (*A*) (c-d) and water use efficiency (*WUE*) (e-f) in young plants of *Cenostigma microphyllum* (native) and *Calotropis procera* (invasive) subjected to drought stress and recovery (n = 4, ± S.E.). The letters in each column and time of treatment are comparing the averages through the Student Newman Keuls test ($p<0.05$).

Figure 3. Leaf specific area (SLA) **(**a-b); Nitrogen (N) (c-d) and photosynthetic nitrogen-use efficiency *(PNUE)* (e-f) in young plants of *Cenostigma microphyllum* (native) and *Calotropis procera* (invasive) subjected to drought stress (a, c, e) and recovery (b, d, f) (n = 4, ± S.E.). The letters in each column and time of treatment are comparing the averages through the Student Newman Keuls test ($p<0.05$). Not significative (NS).

Figure 4. Cost of foliar construction (CC) **(**a-b); photosynthetic efficiency of use energy (PEUE) (b-c) and Payback time (PBT) (e-f) in young plants of *Cenostigma microphyllum* (native) and *Calotropis procera* (invasive) subjected to drought stress and recovery (n = 4, ± S.E.). The letters in each column and time of treatment are comparing the averages through the Student Newman Keuls test ($p<0.05$).

Figure 5. Relationship between the leaf specific area (SLA), payback time (PBT), photosynthetic efficiency of use energy (PEUE), photosynthetic nitrogen-use efficiency (PNUE), Nitrogen (N) with leaf construction cost (CC) in young plants of *Cenostigma microphyllum* (native) and *Calotropis procera* (invasive) plants subjected submitted to drought stress in maximum stress.

Figure 6. Relationship between the leaf specific area (SLA), payback time (PBT), photosynthetic efficiency of use energy (PEUE), photosynthetic nitrogen-use efficiency

(PNUE), Nitrogen (N) with leaf construction cost (CC) in young plants of *Cenostigma microphyllum* (native) and *Calotropis procera* (invasive) plants subjected submitted to drought stress in rehydration.

Figure 7. Principal component analysis (PCA) based on the whole dataset of the study of young plants of *Cenostigma microphyllum* (native) and *Calotropis procera* (invasive) subjected to drought stress (a) and recovery (b) (n = 4). Throughout PC1, separation among species. During PC2, separation related to water regime.

Figures

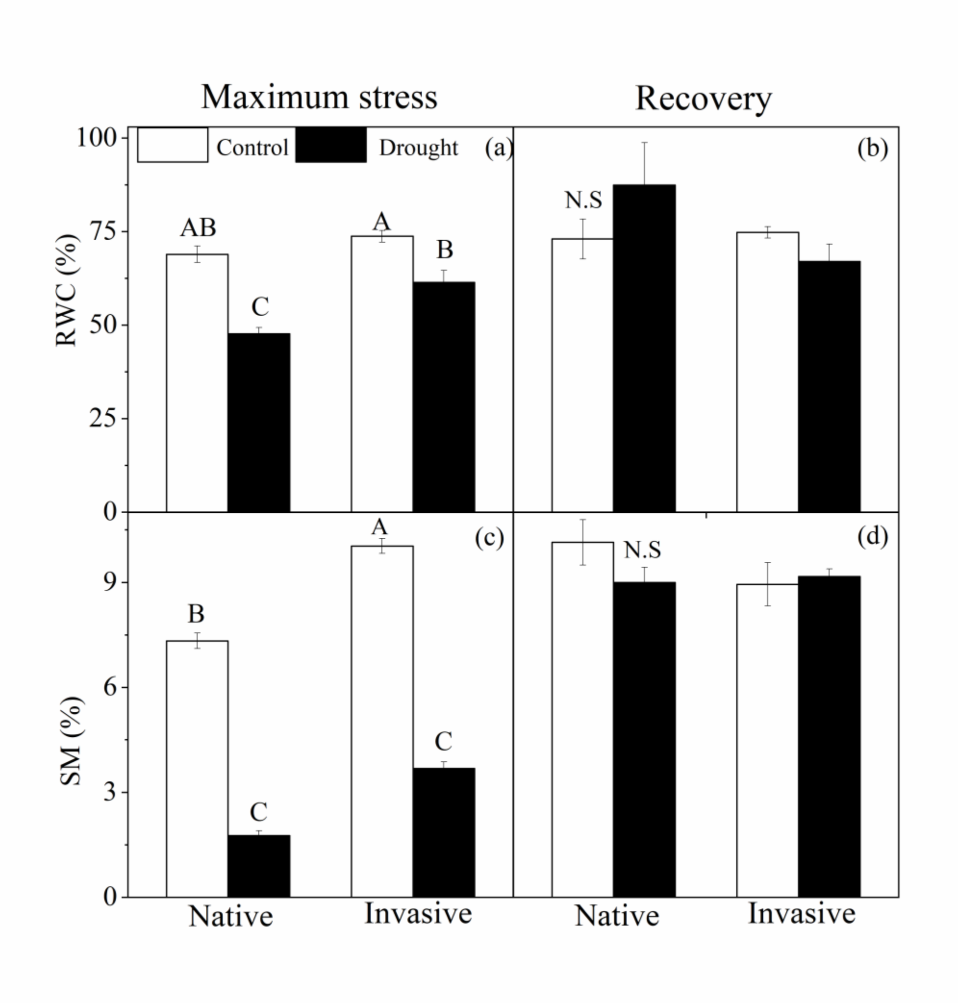

Fig.1

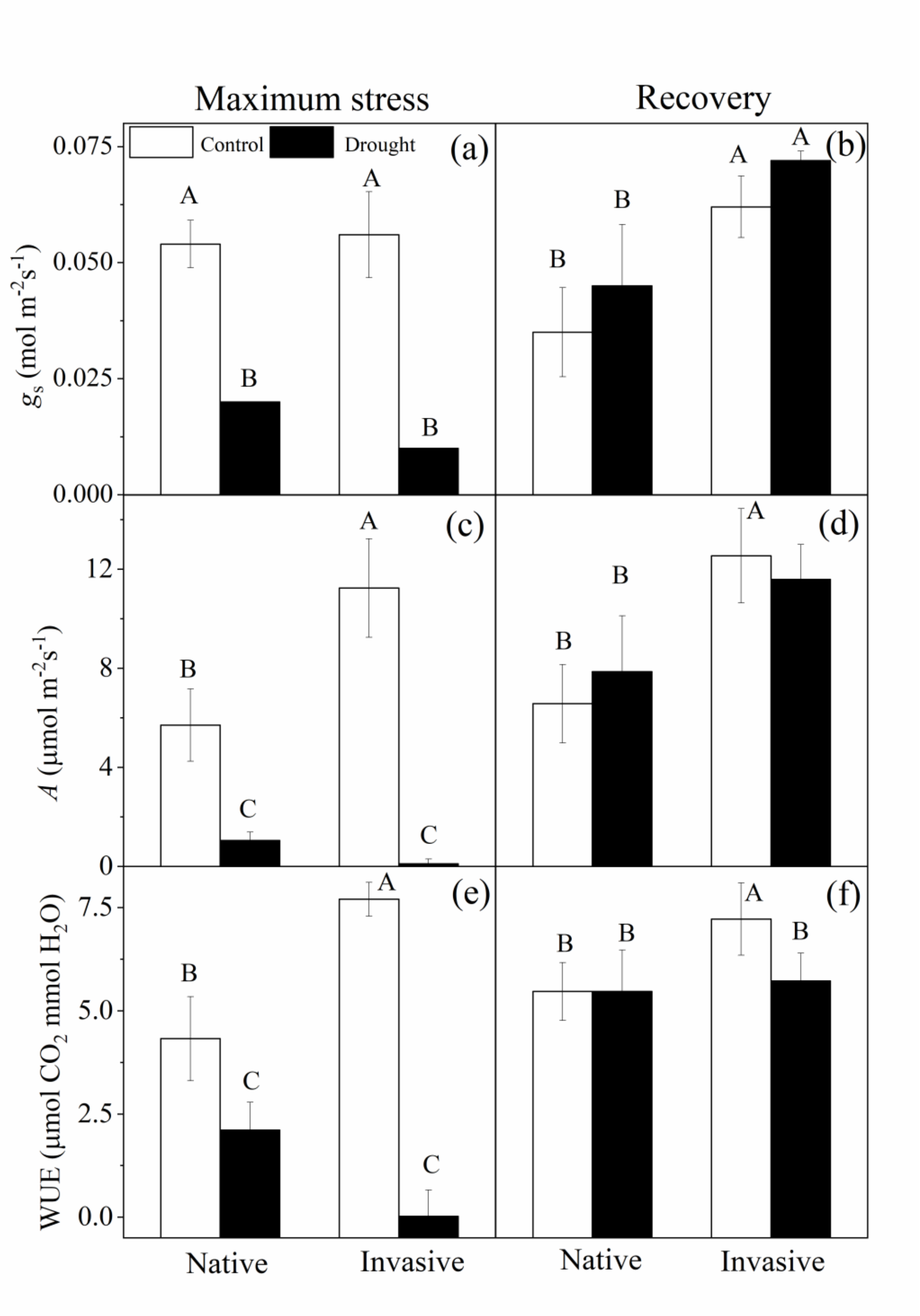
Maximum stress
Recovery
Control
Drought
(a)
(b)
(c)
(d)
(e)
(f)
g_s (mol m^{-2}s^{-1})
A (μmol m^{-2}s^{-1})
WUE (μmol CO$_2$ mmol H$_2$O)
0.000
0.025
0.050
0.075
0
4
8
12
0.0
2.5
5.0
7.5
A
B
A
B
B
B
A
A
B
C
A
C
B
B
A
B
B
C
A
C
B
B
A
B
Native
Invasive
Native
Invasive

Fig.2

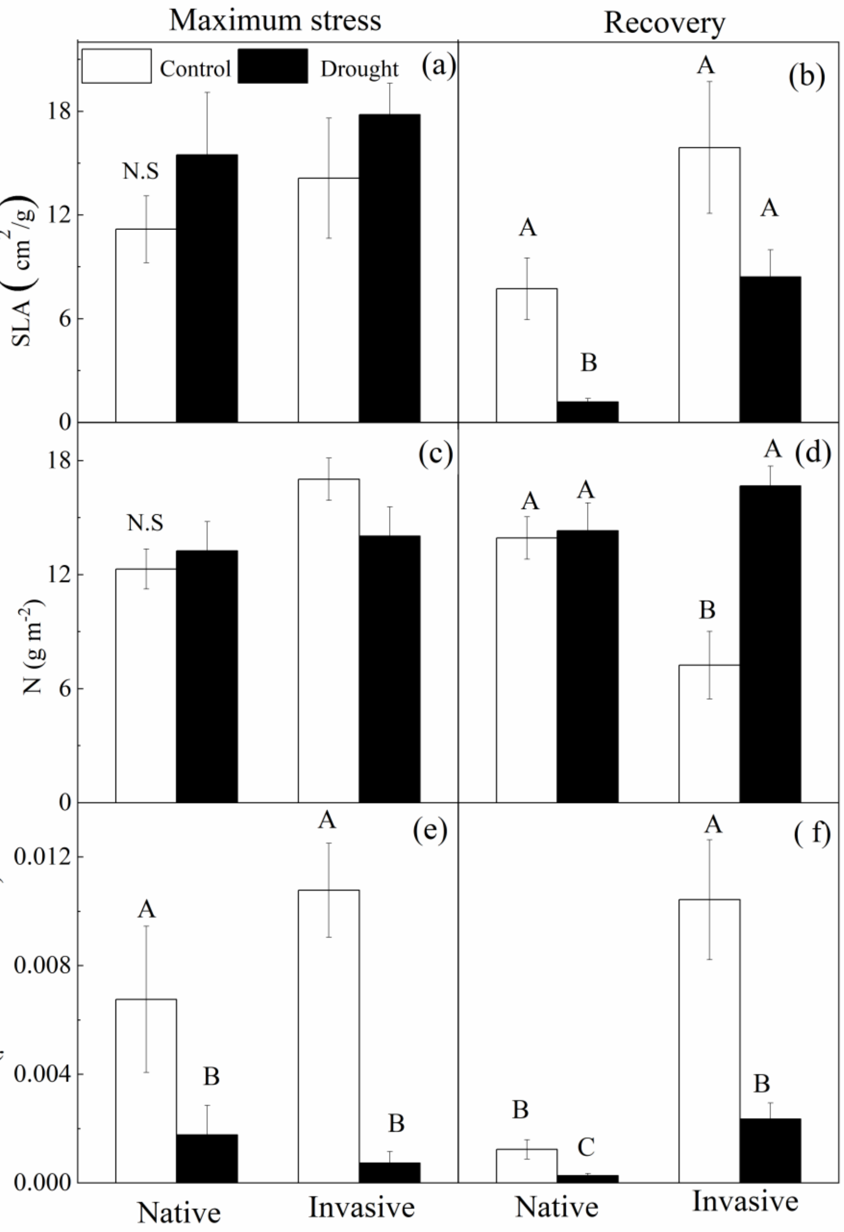
Maximum stress
Recovery
Control
Drought
(a)
(b)
(c)
(d)
(e)
(f)
SLA (cm^2/g)
N $(g\ m^{-2})$
PNUE $(\mu mol\ mol^{-1}\ N\ s^{-1})$
N.S
A
B
0
6
12
18
0.000
0.004
0.008
0.012
C
Native
Invasive

Fig. 3

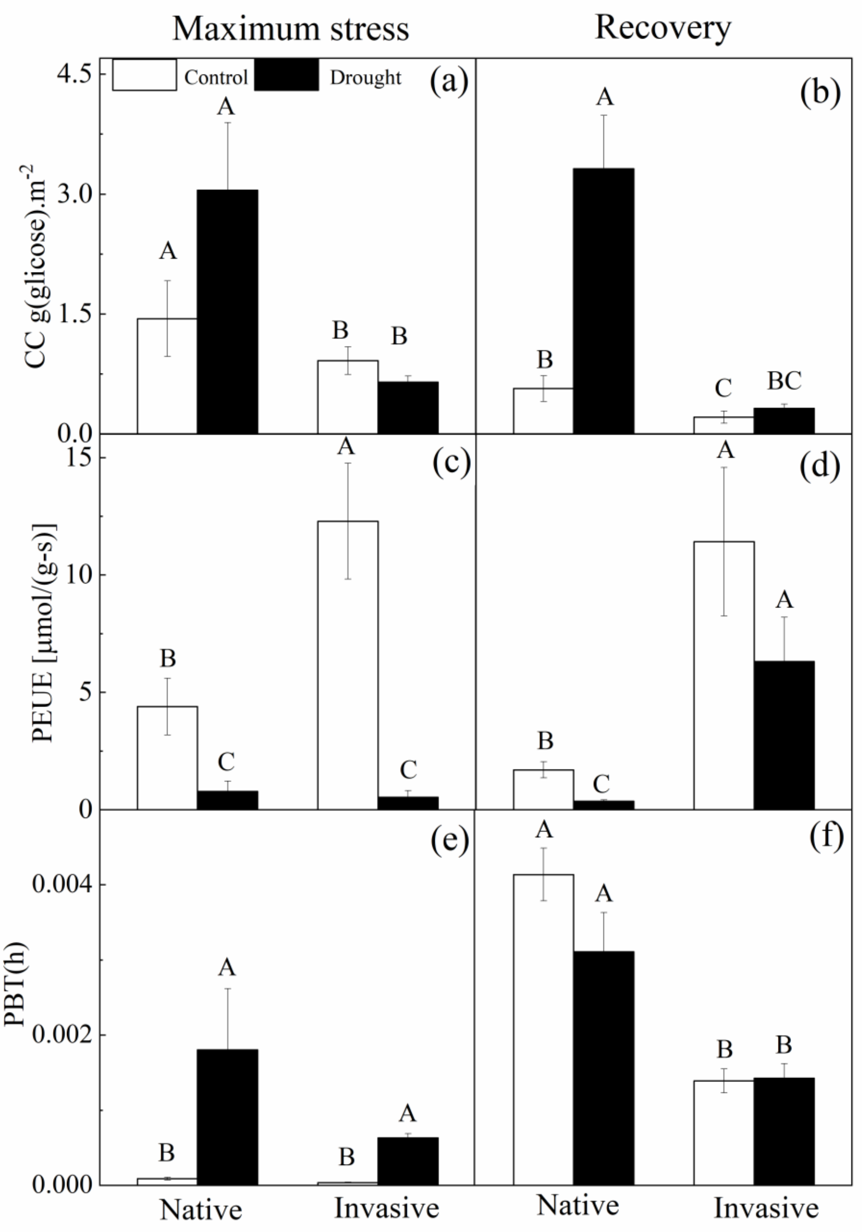
Maximum stress
Recovery
Control
Drought
(a)
(b)
(c)
(d)
(e)
(f)
CC g(glicose).m^{-2}
4.5
3.0
1.5
0.0
PEUE [µmol/(g-s)]
15
10
5
0
PBT(h)
0.004
0.002
0.000
A
A
B
B
A
B
C
BC
B
C
A
C
B
C
A
A
A
A
B
B
B
B
A
A
Native
Invasive
Native
Invasive

Fig. 4

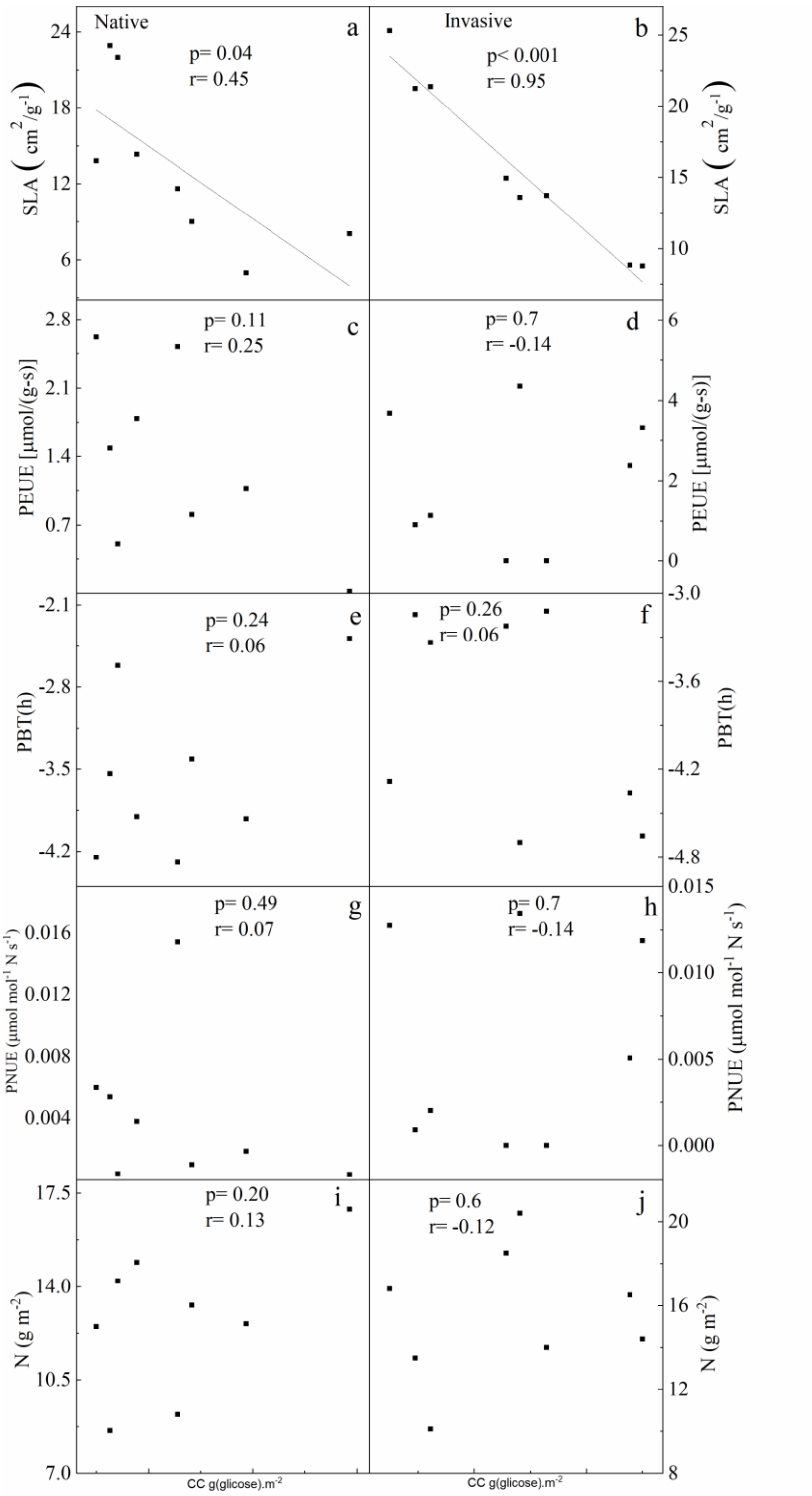
Native
a
p= 0.04
r= 0.45
Invasive
b
p< 0.001
r= 0.95
SLA (cm²/g⁻¹)
24
18
12
6
25
20
15
10
c
p= 0.11
r= 0.25
d
p= 0.7
r= -0.14
PEUE [µmol/(g-s)]
2.8
2.1
1.4
0.7
6
4
2
0
e
p= 0.24
r= 0.06
f
p= 0.26
r= 0.06
PBT(h)
-2.1
-2.8
-3.5
-4.2
-3.0
-3.6
-4.2
-4.8
g
p= 0.49
r= 0.07
h
p= 0.7
r= -0.14
PNUE (µmol mol⁻¹ N s⁻¹)
0.016
0.012
0.008
0.004
0.015
0.010
0.005
0.000
i
p= 0.20
r= 0.13
j
p= 0.6
r= -0.12
N (g m⁻²)
17.5
14.0
10.5
7.0
20
16
12
8
CC g(glicose).m⁻²
CC g(glicose).m⁻²

Fig. 5

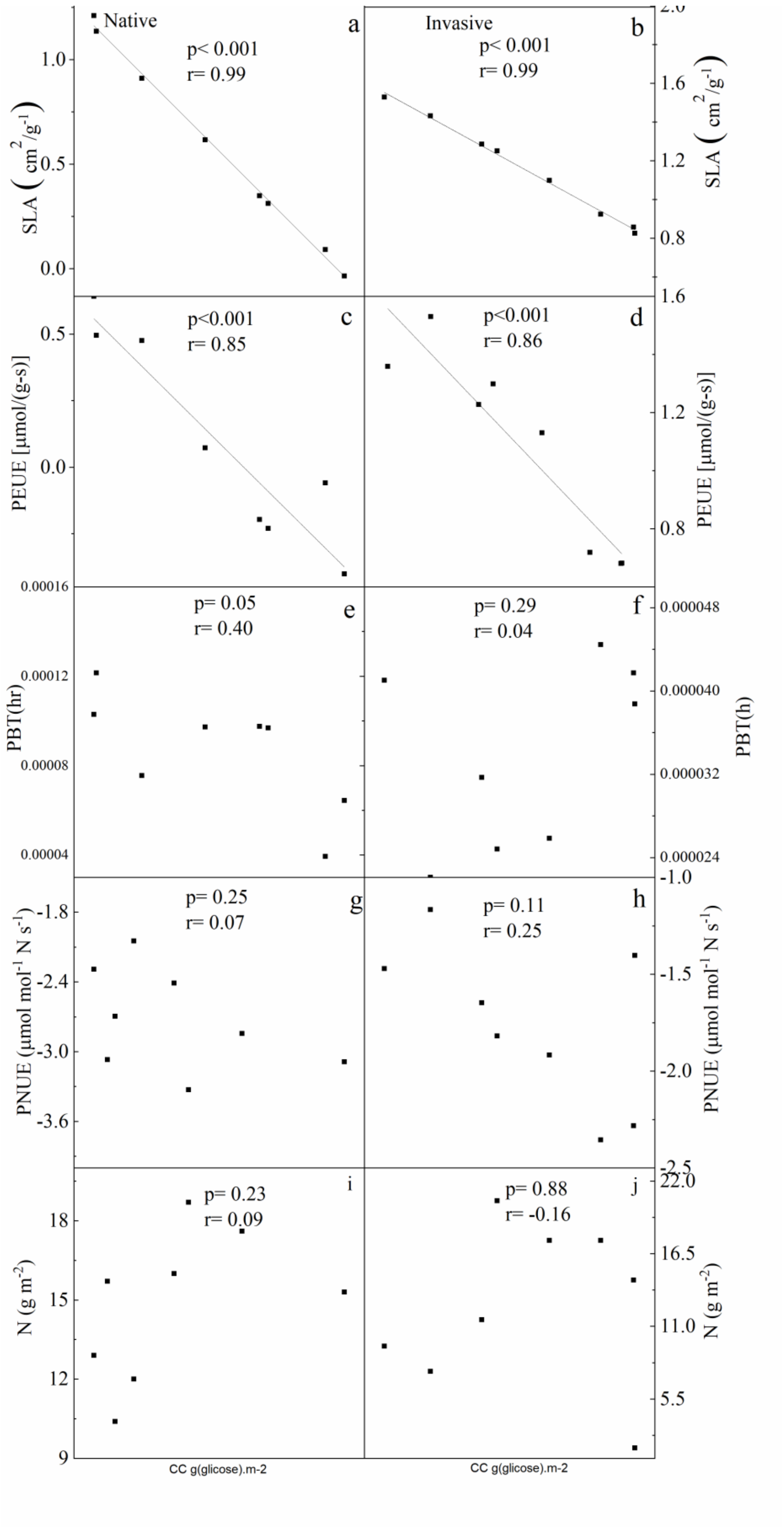
Native
a
p< 0.001
r= 0.99
SLA (cm²/g⁻¹)
1.0
0.5
0.0
Invasive
b
p< 0.001
r= 0.99
1.6
1.2
0.8
c
p<0.001
r= 0.85
PEUE [µmol/(g-s)]
0.5
0.0
d
p<0.001
r= 0.86
1.6
1.2
0.8
e
p= 0.05
r= 0.40
PBT(hr)
0.00016
0.00012
0.00008
0.00004
f
p= 0.29
r= 0.04
PBT(h)
0.000048
0.000040
0.000032
0.000024
g
p= 0.25
r= 0.07
PNUE (µmol mol⁻¹ N s⁻¹)
-1.8
-2.4
-3.0
-3.6
h
p= 0.11
r= 0.25
-1.0
-1.5
-2.0
-2.5
i
p= 0.23
r= 0.09
N (g m⁻²)
18
15
12
9
j
p= 0.88
r= -0.16
22.0
16.5
11.0
5.5
CC g(glicose).m-2
CC g(glicose).m-2

Fig. 6

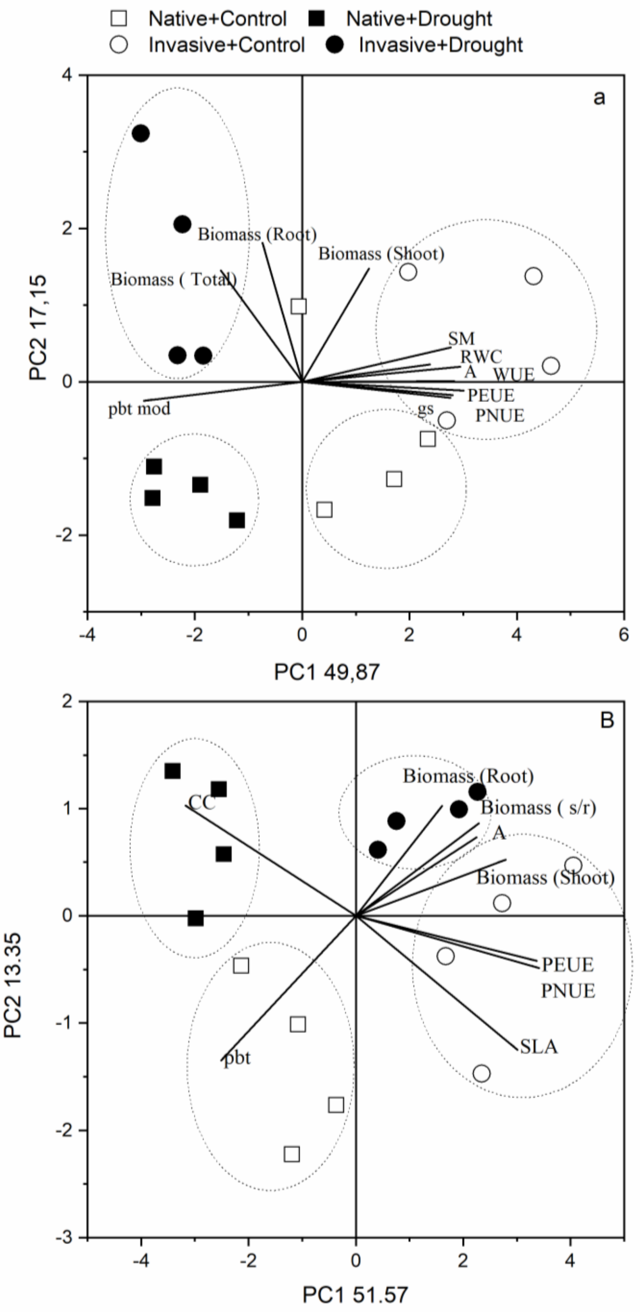
□ Native+Control
■ Native+Drought
○ Invasive+Control
● Invasive+Drought
a
Biomass (Root)
Biomass (Shoot)
Biomass (Total)
SM
RWC
A
WUE
PEUE
PNUE
gs
pbt mod
PC2 17,15
PC1 49,87
4
2
0
-2
-4
-2
0
2
4
6
B
Biomass (Root)
Biomass (s/r)
A
Biomass (Shoot)
CC
PEUE
PNUE
SLA
pbt
PC2 13.35
PC1 51.57
2
1
0
-1
-2
-3
-4
-2
0
2
4

Fig. 7

Table 1. Biomass (Root, Shoot and Root/Shoot) in young plants *Caesalpinia microphylla* (Native) and *Calotropis procera* (Invasive) submitted to water deficit under controlled conditions (*n* = 5 ± S.E). The letters in each column and time of treatment are comparing the averages through the Student Newman Keuls test (p<0.05).

Treatments	Plants	Biomass (g)		
		Maximum stress		
		Shoot	Root	Root/Shoot
Control	Native	1.85±0.98^{B}	2.66±2.16^{B}	0.92±0.35^{B}
Drought	Native	1.11±0.36^{B}	1.30±0.58^{B}	1.00±0.20^{B}
Control	Invasive	4.86±1.33^{A}	5.67±1.65^{B}	1.28±0.22^{B}
Drought	Invasive	3.99±0.32 ^{A}	11.47±2.7^{A}	2.79±0.48^{A}
		Recovery		
Control	Native	1.17±0.13^{C}	0.99±0.28^{B}	0.84±0.16^{ns}
Drought	Native	1.43±0.42^{C}	1.24±0.27^{B}	0.96±0.12
Control	Invasive	6.83±0.67^{A}	4.11±1.55^{B}	1.99±0.57
Drought	Invasive	3.87±0.27^{B}	13.06±3.0^{A}	1.29±0.54

5 CONCLUSÃO GERAL

O presente estudo discutiu as principais características que suportam a tolerância de espécies invasoras e nativas da Caatinga de porte arbóreo e arbustivo à baixa disponibilidade de água. De forma geral, as espécies de ambos portes apresentaram características semelhantes. As espécies invasoras apresentaram um comportamento mais aquisitivo, investindo mais em crescimento, e uma maior tolerância ao déficit hídrico em relação as nativas. Apresentando alta taxa de assimilação de CO_2 nas folhas com baixo custo de produção, altos teores de fósforo e nitrogênio, redução da perda instantânea de eficiência no uso de energia quando comparadas às espécies nativas. Essas estratégias levaram a um maior ganho de biomassa em ambos os tratamentos de água. As espécies nativas investiram em folhas caras e com baixa taxa líquida fotossintética, o que proporcionou mais tempo para recuperação do carbono investido. Esse comportamento ocorre em espécies que possuem maior fluxo de carbono com investimentos em tecidos foliares mais duráveis, compensando assim seu maior custo de construção por área foliar.

Considerando as previsões climáticas para a região semiárida da América do Sul durante este século (com estações chuvosas mais baixas e mais irregularidades previstas, juntamente com estações secas mais longas do que as experimentadas atualmente), esperamos que a prevalência das espécies invasoras aumente nos habitats em relação as espécies nativas. Estudos de longo prazo e com mais espécies em condições de campo são necessários para melhor compreender as estratégias de ambos os grupos de espécies.

ANEXO A

Manuscrito I: Manuscrito publicado ao periódico Plant Physiology and Biochemistry:

https://www.elsevier.com/journals/plant-physiology-and-biochemistry/0981-9428/guide-for-authors

Manuscrito II: Manuscrito publicado ao periódico Flora:

https://www.elsevier.com/journals/flora/0367-2530/guide-for-authors