UNIVERSIDADE FEDERAL DE ALAGOAS
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Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos

JAYNE SILVA SANTOS

INFLUÊNCIA DO TIPO DE SOLO EM RESPOSTAS ECOFISIOLÓGICAS VINCULADAS À ESCASSEZ HÍDRICA E À REIDRATAÇÃO EM *Schinus terebinthifolia* Raddi, UMA ESPÉCIE ARBÓREA TROPICAL

MACEIÓ - ALAGOAS
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Dissertação apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde da Universidade Federal de Alagoas, como requisito para obtenção do título de Mestre em CIÊNCIAS BIOLÓGICAS, área de concentração em CONSERVAÇÃO DA BIODIVERSIDADE TROPICAL.

Orientador: Prof Dr. Gilberto Costa Justino

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“Pra me reconhecer de volta, pra me reaprender e me apreender de novo”

Ana Caetano / Tiago Iorc

RESUMO

Schinus terebinthifolia Raddi (Anacardiaceae) é uma espécie arbórea tropical recomendada para a restauração florestal e que pode ser encontrada em várias localidades do litoral, principalmente em formações florestais da restinga, floresta semidecídua e floresta tropical aberta. Por ser encontrada em ambientes tão diversos, e apresentar grande potencial invasivo, acredita-se que esta espécie apresente grande capacidade de adaptação ao estresse hídrico e diferentes tipos de solo, podendo colonizar ambientes degradados e o semiárido brasileiro. Diante disso, o objetivo deste trabalho foi verificar o comportamento ecofisiológico de *Schinus terebinthifolia* Raddi sob condições de seca seguida de reidratação em três tipos de solo, oriundos de três diferentes tipologias da Mata Atlântica do nordeste do Brasil. O estudo foi dividido em dois experimentos. No experimento 1, foi utilizado em apenas um tipo de solo, oriundo da zona da mata alagoana. Já no experimento 2, foram usados 2 tipos de solo: (i) restinga e (ii) e semiárido para submeter as plantas ao déficit hídrico e a reidratação. Os experimentos foram conduzidos em casa de vegetação com distribuição completamente aleatória em dois tratamentos, sendo: (a) controle e (b) irrigação suspensa. As plantas do tratamento “irrigação suspensa” tiveram a hidratação interrompida até que a média dos valores de fotossíntese chegassem a valores próximos ou iguais a zero, e, após isso, as plantas deste tratamento foram reidratadas. Todos os tipos de solos passaram por análises em densímetro, peneiramento, grau de floculação e análise de fertilidade. No dia de maior estresse e após a reidratação foram realizadas análises de trocas gasosas, fluorescência da clorofila e quantificação de compostos osmorreguladores. Dados microclimáticos da casa de vegetação foram acompanhados durante todo o experimento. A primeira reação ao estresse foi a diminuição da condutância estomática que reduziu gradativamente conforme o déficit hídrico se instalava independentemente do tipo solo, indo de 0,4 a 0,01 (mmol H_2O $m^{-2}s^{-1}$) em média. A aroeira também conservou a integridade dos pigmentos cloroplastídicos importantíssimos na captura de energia luminosa, e regulou seu potencial osmótico principalmente com o aumento de aminoácidos e prolina. Com isso, plantas jovens de *S. terebinthifolia* foram resistentes à seca severa com rápida capacidade de recuperação nos três tipos de solo, tendo respostas mais severas em solo com feições argilosas, provavelmente, devido a maior compactação do solo seco e de características de disponibilidade hídrica neste tipo de solo.

Palavras-chave: estresse hídrico, plasticidade fisiológica, aroeira.

ABSTRACT

Schinus terebinthifolia Raddi (Anacardiaceae) is a neotropical tree species recommended for forest restoration that can be found in several coastal locations, mainly in ‘restinga’, semideciduous forest and open tropical forest. The ability to grow in diverse environments may be related to its capacity to adapt to water stress and different soil types, allowing it to colonize degraded environments and even the Brazilian semi-arid (caatinga) region. The objective of this work was therefore to verify the ecophysiological behavior of *Schinus terebinthifolia* Raddi under dry conditions followed by rehydration in three types of soil, from two different types of Atlantic Forest in northeastern Brazil, more one from the Caatinga. The study was divided into two experiments. In experiment 1, only soil from an area of Atlantic forest forest was used. In experiment 2, two types of soil were used: (i) restinga soil, and; (ii) soil from the semi-arid biome. The experiments were conducted in a greenhouse with completely random distribution in two treatments: (i) control, and; (ii) water stress (‘suspended irrigation’). Irrigation was suspended until average photosynthesis values reached levels near or equal to zero. Plants of this treatment were then rehydrated. All soil types were analyzed for density, screening, flocculation and fertility. Gas exchange, chlorophyll fluorescence and osmoregulatory compounds were quantified on the day of greatest stress and after rehydration. Microclimatic data from the greenhouse were collected throughout the experiment. The first reaction to stress was a decrease in stomatal conductance, which reduced gradually as water deficit settled (independent of soil type) from 0.4 to 0.01 (mmol H_2O $m^{-2}s^{-1}$). Chloroplastíd pigments retained their integrity throughout the treatment, and osmotic potential was regulated mainly through an increase in amino acids and proline. Young *S. terebinthifolia* were thus resistant to severe drought and had the capacity for rapid recovery in all three soil types. Physiological responses were more severe in the clay soil, probably due to root damage associated with soil compaction during drying.

Key words: water stress, physiological plasticity, aroeira.

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1 APRESENTAÇÃO

Schinus terebinthifolia Raddi é uma espécie arbórea tropical da família Anacardiaceae que tem grande importância farmacêutica, ambiental, ecológica e para projetos de restauração. É especialmente estudada na etnobotânica há algumas décadas por conta de suas propriedades médicas. Conhecida popularmente como aroeira-da-praia ou pimenta-rosa (Brazilian pepper tree - *inglês*), esta espécie é nativa da América do Sul (CORRÊA, 1974) e se tornou uma espécie considerada invasora em alguns países da América do Norte por conta de sua alta plasticidade e adaptabilidade (EWEL et al. 1982). No Brasil está presente em diversas localidades do litoral (ÁLVARES-CARVALHO et al. 2016), sendo encontrada principalmente em formações florestais de restinga, floresta semidecidual (CESÁRIO, 2008) e formações ombrófilas abertas, entretanto, em áreas semiáridas ainda não há registro de ocorrência dessa espécie (SpeciesLink, 2019).

Na Restinga, o período de baixa precipitação pode induzir restrição hídrica (JÚNIOR BOEGER, 2016), acompanhado de salinidade, alta radiação solar e de ventos constantes, fatores importantes quando se trata de manutenção de água na planta (MANTOVANI et al. 2010), fatores estes, que na floresta semidecidual e formações ombrófilas abertas estão amenizados, e englobam um limiar climático ótimo para esta espécie. Dessa forma, o potencial de sobrevivência de *S. terebinthifolia* ao estresse hídrico associado a outras adversidades encontradas em seu habitat natural de restinga ainda não foi totalmente descrito, e deve estar ligada a uma ampla plasticidade de respostas fisiológicas e ecológicas provavelmente presentes nesta espécie, e que poderia ser um ponto crucial para que a aroeira se propagasse por outras regiões sazonalmente secas e com diferentes tipos de solo, como o semiárido brasileiro onde a espécie ainda não é encontrada.

Ademais, o arranjo das espécies no ambiente é determinado, dentre outros fatores, pelas condições de estrutura e de nutrição do solo (CARVALHO et al. 2007; HARIDASAN, 2000). A água presente nesse substrato é um dos fatores abióticos mais limitantes, e juntamente com os nutrientes do solo, e suas características físicas, parecem ser decisivos na distribuição das espécies em seus ambientes (DUARTE et al. 2012; CARVALHO et al. 2017; BOTREL et al. 2002). Nesta dissertação são descritas respostas fisiológicas de *Schinus terebinthifolia* Raddi à restrição hídrica, juntamente com a dissolução dessas respostas frente a três tipos diferentes de solos oriundos de diferentes tipologias da floresta atlântica neotropical.

2 REVISÃO DE LITERATURA

2.1 Escassez hídrica e as respostas fisiológicas dos vegetais

Para o sucesso na colonização do ambiente terrestre, as plantas precisaram se ajustar à alguns fatores cruciais como a luz, absorção do dióxido de carbono, oxigênio, nutrição mineral do solo e principalmente à quantidade de água. Destes, a disponibilidade de água é um dos fatores ambientais que exerce a maior influência sobre as taxas fotossintéticas em espécies vegetais (SOUZA et al. 2010). Com isso, a restrição hídrica leva ao desenvolvimento de estratégias fisiológicas para a manutenção do metabolismo e, consequentemente, à sobrevivência das espécies nestas condições. Neste sentido, podemos então dizer que, as espécies que consigam ajustar o seu metabolismo em diferentes situações de disponibilidade de água, serão as mesmas com aptidão necessária para enfrentar períodos de escassez e/ou abundância hídrica previstas para o clima na terra em um futuro próximo, que indicam drásticas mudanças nas distribuições de chuva em todo o mundo (BOISVENUE et al. 2006).

Como já mencionado, a água é classificada como um fator vital que limita a distribuição das espécies no planeta, e sua disponibilidade no ambiente irá depender de vários fatores climáticos que influenciam a distribuição das chuvas, temperatura e da radiação solar, como também das correntes marítimas e atmosféricas, além de questões geológicas e atividades antrópicas (TRENBERTH et al. 2015). Ou seja, a presença de água no ambiente natural vem acompanhada de várias outras variáveis ambientais muito importantes na fisiologia das espécies vegetais (POREMBSKI, 2007), o que consequentemente coordena as estrátegias de controle da quantidade de água presente no próprio corpo vegetal. A regulação da abertura e do fechamento estomático é o que controla a transpiração através das folhas das plantas, sendo bastante eficiênte para este fim (DOMBROSKI et al. 2011). Com a abertura dos estômatos, as plantas absorvem o CO_2, realizam fotossíntese e fazem da transpiração o melhor mecanismo para dissipar o excesso de calor. Mas, por outro lado, perdem bastante água para a atmosfera (SILVA et al. 2004).

O ajuste adequado da abertura e fechamento dos estômatos, nestes casos, promove maior eficiência no uso da água, o que maximiza a entrada de CO_2 e reduz a perda de água por transpiração (GONÇALVES et al. 2009). Assim, esta capacidade de controle estomático pode ter se aperfeiçoado em algumas espécies, principalmente naquelas de ambientes tropicais de clima quente e úmido, por horas quente e seco, e, acredita-se que o nível de eficiciência no uso da água de cada espécie seja o diferencial para genótipos mais adaptados.

A disponibilidade hídrica está frequentemente associada a altas temperaturas e excesso de irradiância, e todas estas situações combinadas além de influenciar na traspiração vegetal, levam à fotoinibição devido a danos ao fotossistema II (HUANG et al. 2012). Caso haja restrição hídrica e fechamento estomático, este dano pode ser acentuado, o que irá depender também das características adaptativas da espécie em questão, envolvendo a capacidade da mesma em reparar os danos causados aos fotossistemas (MURATA et al. 2007) através de dissipação de energia e atividades de enzimas antioxidantes, por exemplo.

A água, além de ser necessária para fotossintese, é matéria prima primordial para o crescimento das plantas, levando a reprodução das células, mantendo a turgescência, saúde e crescimento das mesmas. A manutenção do turgor é importante para permitir a continuidade dos processos internos da célula, incluindo o funcionamento dos fotossistemas citados acima, e por fim, para o crescimento do vegetal em biomassa, ou seja, o déficit hídrico pode afetar a manutenção de todos os processos de produção vegetal (SANTOS, 1998; LÜTTGE, 2007).

Para auxiliar na manutenção da turgência, os vegetais regulam osmoticamente os tecidos, acumulando solutos compatíveis, não tóxicos e reaproveitáveis ao seu metabolismo como aminoácidos livres, prolina, açúcares solúveis e ureídeos, esses últimos, recentemente sugeridos como participantes em mecanismos de resistência ao déficit hídrico em plantas da família Fabaceae (SILVA et al. 2008), sendo necessários estudos em outras famílas botânicas não-nodulantes. Este ajuste osmótico se dá pelo efeito do soluto dissolvido sobre o potencial hídrico, auxiliando na translocação da água por osmose (HUANG et al. 2018; LUO e LUO, 2017). Um dos solutos mais estudados é a prolina, que é produzida à medida que o período de estresse hídrico se prolonga, demonstrando a significativa influência do déficit hídrico na produção e na formação de compostos, para redução do potencial osmótico na planta e, consequetemente, na manutenção de água nas células (ALVARENGA et al. 2011).

O acúmulo de prolina livre também pode ser causado por altas temperaturas e variações de salinidade (NOGUEIRA et al. 2000). Mas, em situações de baixa disponibilidade de água no solo, esse mecanismo adaptativo se faz necessário em todas as espécies e o auxilio deste processo para a manutenção do turgor celular é situação constante em ambientes áridos (SANTOS, 1998). Essas mudanças são vistas na expressão de genes relacionados ao estresse hídrico (SINGH-SANGWAN et al. 1994; SILVA, 2000; KRASENSKY e JONAK, 2012), genes que irão proporcionar as mudanças e alterações na síntese das clorofilas, por exemplo, que estão relacionadas com a eficiência fotossintética das plantas e, consequentemente, com seu crescimento e adaptabilidade aos diferentes ambientes (JESUS, 2008).

Diante de tudo isso, verifica-se que as variações ambientais induzem a expressão de genes que ao primeiro passo codificam sinais bioquímicos, que impulsionam mudanças fisiológicas e que ajustam o metabolismo vegetal de tal forma que resultam em mudanças morfológicas, caracterizando especies mais adaptadas. Algumas dessas respostas já podem ser classificadas como caracteristicas intrínsecas de muitas espécies, e abastecem a lista de caracteres que às idenficam. Dessa forma, respostas fisiológicas e morfológicas apontam que as plantas, quando são submetidas ao déficit hídrico, regulam seu metabolismo para a conservação da água disponível no solo e no corpo vegetal, otimizando seu uso para processos mais importantes do seu desenvolvimento e buscando a continuidade de sua sobrevivência (SHARMA et al. 2012; MARTINS et al. 2018).

2.2 Os vegetais e sua relação com o solo

O solo, de maneitra geral, é formado por materiais minerais e orgânicos, e, por definição, é a coleção de corpos naturais que ocupa a parte superficial da terra (EMBRAPA, 2018). Este substrato se relaciona estritamente com as plantas, e por isso, é influenciador direto das alterações do metabolismo vegetal, ou seja, o que acontece no solo reflete e causa efeitos nas plantas e o que acontece com a planta causa efeito no solo (CARVALHO et al. 2006). Como exemplo disso, temos a presença de água, a estrutura física do solo e nutrientes presentes nele estreitando essa relação. Condições biológicas, quimicas e físicas podem estar vinculadas com a distribução da vegetação entre os ambientes, pois as necessidades nutricionais e da fixação do organismo do vegetal no solo através das raízes de cada indivíduo variam entre as espécies botânicas (HARIDASAN, 2000). Essa relação entre os organismos e o solo, em conjunto com a atmosfera, resulta em diferentes formações vegetais, e toda essa interação entre solo-planta-atmosfera, vai ao longo do tempo, modificando a paisagem, tornando esse sistema dinâmico e possibilitando adaptação por partes de todos os organismos e determinando a composição floristica das regiões do globo (KOTCHETKOFF-HENRIQUES et al. 2005).

Como dito anteriormente, as plantas têm uma relação particular com o solo, se relacionando com o mesmo, tanto de forma direta e indireta. A forma mais direta dessa relação se dá pela absorção dos nutrientes minerais e da água retirados diretamente do solo pelas raízes das plantas, que por sua vez, liberam certas substâncias no solo e também se decompõem sobre ele (VIEIRA, 1988). Além da absorção, as plantas fazem do solo seu substrato de fixação, se “agarrando” em partículas e até mesmo rochas, resultando em um aumento na coesão aparente do solo que, indiretamente, evita o desenvolvimento de erosões e lixiviação de nutrientes exenciais para o desenvolvimento das próprias plantas (WANG et al. 2016).

A composição edáfica do Brasil engloba solos sedimentares do quaternário, onde a vegetação e todas as suas interfases se estabeleceu (GOMES et al. 1998), isso significa que o substrato brasileiro é fruto de transformações ambientais geologicamente recentes. A região nordeste do Brasil engloba três tipologias ambientais de maior evidência: (1) o litoral, (2) a região de transição entre o litoral e o interior do estado, também chamado de zona da mata (3) e o semiárido. Destes, a restinga presente no litoral (ASSUMPÇÃO et al, 2000) e a caatinga presente no semiárido (TROVÃO et al, 2007) são ecologicamente classificados como ambientes naturalmente estressantes (ZAMITH, et al 2006).

Alguns estudos classificam os solos da região litorânea como podzóis hidromórficos ou Espodossolos, ou, areias quartzosas marinhas (CAMARGO et al. 1987; OLIVEIRA et al. 1992), que normalmente têm textura arenosa e é pobre em nutrientes (GOMES et al. 2004). A zona costeira tem uma vegetação característica arbustivo-arbórea, variando desde formações herbáceas, até árvores que chegam a 20 m de altura (ALMEIDA-JR et al. 2011). Essa composição vegetal é resultado da interação das especificações de um solo arenoso, com uma vegetação adaptada a este tipo de substrato e clima específico dessa região, que inclue maior radição e ventos constantes (MANTOVANI et al. 2010).

A segunda região mais importante do Nordeste é usualmente chamada de zona da mata e compreende o domínio da mata atlântica, sendo uma área acobertada por um regime regular de chuvas, e, por ser relativamente próxima a zona litorânea, chega a receber influencia da dinâmica dos oceanos em seu ciclo de chuvas. Essa dinâmica resulta em uma estabilidade de clima e influência diretamente na disponibilidade de água no solo , garantindo o sucesso da colonização vegetal e animal. É uma região de solo francoargilo-arenoso fértil de amplo desenvilvimento agronômico e favorável a habitação humana (SANTOS, et al. 2019).

Já o solo do semiárido é convencionalmente classificado como um tipo de solo com horizonte mineral superficial fracamente desenvolvido, resultado de um reduzido teor de colóides minerais ou orgânicos e pelas condições externas de clima que esta região se encontra. A maioria das regiões do semiárido do Nordeste do Brasil apresenta uma estrutura física pedregosa em sua maior parte, e argilosa em algumas regiões, em geral, o solo da caatinga não retêm água em abundância (ASAAD, et al 2001) e com isso pode influenciar na ocorrência e frequência de algumas espécies especialmente adaptadas a estas condições (SILVA et al. 2009). É conhecida por ter um mosaico de florestas secas e vegetação arbustiva, com enclaves de floresta tropical montanhosa, com predominância de vegetação xerófila, aclimatadas a climas secos (LEAL et al. 2003).

Contudo, dentro de uma mesma família botânica, como Anacardeaceae, os vegetais são capazes de sobreviver em diferentes zonas climáticas como também em diferentes tipos de solo, podendo colonizar tanto regiões de restinga como regiões de zona da mata, e em caso raros, também o semiárido, ou ambientes equivalentes em todo o globo, fato que só é possivel graças aos ajustes genéticos, fisiológicos e morfológicos que as plantas apresentam em cada situção, mecanismos diversos que ainda necessitam ser descritos.

2.3 Schinus terebinthifolia Raddi

S. terebinthifolia, pertencente à família Anacardiaceae, é conhecida popularmente como aroeira-da-praia e por suas propriedades culinárias também é chamada de pimenta-rosa ou pimenta-vermelha em algumas regiões brasileiras. Esta espécie é natural da América do Sul, especificamente da Argentina, Paraguai e Brasil, utilizada como erva medicinal desde os ancestrais indígenas (JONES et al. 1997) e é amplamente explorada até os dias de hoje pela população. A pressão do extrativismo sobre esta espécie é preocupante, a colheita exagerada dos frutos causa redução no banco de sementes disponíveis na natureza, e está dificultando a distribuição e propagação natural da espécie no Brasil, levando as populações de plantas a entrar em declínio e impedindo a colonização em novos ambientes (ÁLVARES-CARVALHO et al. 2016).

Além de ter grande importância etnobotânica como erva medicinal, apresenta comprovação cientifica de propriedades anti-inflamatória (ROSAS et al. 2015), antialérgica (CAVALHER-MACHADO et al. 2008), antibiótica (COLE et al. 2014) e antifúngica (MOURA et al. 2010; JOHANN et al. 2008). Sua importância médica-farmacológica é imprescindível para a saúde humana, em especial no combate de doenças que acometem órgãos do sistema reprodutivo e trato urinário da mulher, sendo amplamente usada em cosméticos e fármacos relacionados a esses problemas.

Dentre os ambientes que a aroeira-da-praia é encontrada, a zona litorânea brasileira é o mais estressante deles. Comumente, a vegetação de restinga é caracterizada por um mosaico de habitats, indo da praia até uma formação de vegetação florestal densa, e entre esses extremos encontra-se uma organização vegetal em aglomerados com vários espaços abertos de areia nua (MANTOVANI et al. 2010). As espécies vegetais presentes na restinga são submetidas a combinações ambientais extremas, como alta salinidade, baixa disponibilidade de nutrientes, inundações, seca severa e irradiância elevada (MANTUANO et al. 2006). Por ocorrer neste ambiente, a plasticidade ecológica de *S. terebinthifolia* pode ser a justificativa de esta espécie poder habitar facilmente toda faixa litorânea do Brasil, próxima a rios, córregos e várzeas úmidas de formações secundárias, como também nas dunas existentes na restinga (SILVA et al. 2008) e, mesmo enfrentando tantas adversidades ambientais, não se conhece a distribuição dessa espécie em ambientes semiáridos (SpeciesLink, 2019).

S. terebinthifolia se tornou uma espécie invasora em muitos países, incluindo partes da América Central, Bermudas, nas Ilhas Bahamas, as Índias Ocidentais, Flórida, Arizona do Sul, Califórnia, Havaí, Norte da África, sul da Ásia e África do Sul e Europa Mediterrânea, compreendendo regiões de clima semiárido frio (BESTELMEYER et al, 2015), onde é internacionalmente conhecida como “Brazilian pepper tree”, (BARBOSA, et al. 2009; SHETTY et al. 2010). Por ser uma espécie pioneira (SILVA et al. 2008), se estabeleceu facilmente nestes locais e acredita-se que sua alta plasticidade ambiental contribuiu para o sucesso de suas colonizações.

Estudos com esta espécie comumente trazem a descrição das respostas de algumas variáveis fisiológicas sob consequência de um determinado ambiente, clima ou situação de estresse. A maioria desses estudos justificam seus resultados com o fato de a aroeira ser pioneira, heliófita e por possuir uma grande capacidade de invasão de novos ambientes (EWE et al, 2004; EWE et al, 2007; ESTEVES et al, 2010; DOS ANJOS, et al 2014). Estudando *S. terebinthifolia* e outras espécies arbóreas pioneiras e não-pioneiras, Coutin (2016) constatou a capacidade fotoprotetora e antioxidante dessas espécies frente a exposição solar e concluiu que plantas pioneiras de pleno sol acumulam vitamina E para evitar a peroxidação lipídica, ou seja, apenas um dos mecanismos bioquímicos fisiológicos que essa espécie possa ter para atingir sucesso em ambiente tropicais estressantes.

Estudos de comportamento silvicultural de árvores nativas após o plantio e suas respostas às condições ambientais também podem ser vistos na literatura. Rorato (2018) por exemplo, estudou o comportamento de seis espécies arbóreas frente variações de clima no inverno (geada) e, dentre estas espécies, estava *S. terebinthifolia* que juntamente com *Eugenia involucrata* foram consideradas espécies resistentes à geada, conclusão tirada pela medida de área foliar, altura e diâmetro do caule dessas plantas sob estas condições. Ou seja, *S. terebinthifolia*, é uma espécie de grande interesse científico, sendo estudada pela genética (ÁLVARES-CARVALHO et al, 2016; CHIOCHETA et al, 2017), em estudos de composição florística (CESÁRIO et al 2007), de interesse em reflorestamento (RORATO et al, 2017), e o potencial invasivo dessa espécie (PRATT et al 2006) frente a salinidade (KOUALI et al, 2017), alagamento (MIELKE et al, 2005), radiação (SABBI et al, 2010) e escassez hídrica (SILVA et al, 2008; VASCONCELOS-SILVA et al, 2011; PIMIENTA-BARRIOS et al, 2012),. Estudos que envolvem o cultivo da espécie em solos da Caatinga ainda não foram verificados na literatura.

Este estudo foi proposto para investigar e descrever as respostas fisiológicas e metabólicas de *S. terebinthifolia* em condições de restrição hídrica e posterior reidratação, em três variações de solo típicos das principais tipologias da Floresta Atlântica da região neotropical, considerando as previsões de mudanças na precipitação e nas variáveis climáticas juntamente com a natureza do ambiente que a espécie foco desse estudo está presente, e a possível colonização do ambiente semiárido brasileiro pela mesma, juntamente com o sucesso de invasão já constatado para esta espécie em outros ambientes. Adicionalmente, estes dados podem servir de base para futuras descrições fisiológicas de espécies com as mesmas características. E por fim, ressaltar a conservação dessa espécie, com o conhecimento de sua importância ecológica e das consequências do efeito da escassez hídrica sobre a mesma.

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CAPÍTULO 1: A reidratação imediata restaura o aparelho fotossintético de *Schinus terebinthifolia* (Raddi) após seca severa no solo?

Can rehydration restore the photosynthetic apparatus of *Schinus terebinthifolia* (Raddi) after severe soil drought?

Abstract

Schinus terebinthifolia Raddi is a pioneer tree species that is native to the Atlantic forest of South America, but which is considered invasive in some places. Information on the tolerance of this species to stress conditions, in particular low water availability, is still limited. Therefore, the aim of this study was to evaluate the physiological and enzymatic metabolism adjustments in response to water deficit in *S. terebinthifolia*. The experiment was conducted in a greenhouse in a completely randomized distribution with two water treatments: [a] a control, and; [b] a suspended irrigation treatment, which continued until photosynthesis values approached zero after which the plants were rehydrated. We analyzed gas exchange, chlorophyll fluorescence and osmoregulatory compounds such as carbohydrates, amino acids, proline, ureids, nitrate. After seven days without irrigation photosynthesis was close to zero. At this time there was an increase in amino acid and proline content in the leaves, which prevented the carbohydrates and photosynthetic apparatus from being directly affected by the lack of water. We also observed stomatal closure and preservation of chloroplast pigments. The plants recovered gas exchange capabilities five days after rehydration. Young plants of this species tolerated severe drought with a fast recovery capacity, further supporting the claim that this species is very suitable for restoring forests and colonizing new environments.

Key words: Intrinsic water use efficiency. Leaf gas exchange. Stomatal conductance. Forest restoration. Antioxidant enzyme. Water deficit.

Introduction

The Atlantic Forest is one of the most degraded biomes in Brazil, having been heavily exploited since the arrival of the Portuguese in the mid 1500’s (Zamith *et al.* 2006). One of the first steps to ensure a successful restoration of the remaining forest fragments is to identify suitable species for this purpose. The vegetation of the Atlantic forest has been classified into various sub-types, including dense ombrophylous forest, open ombrophylous forest, semideciduous seasonal forest, among others. Of these, the open forest is probably the most degraded by human actions (IBGE 2006) and is in urgent need of restoration. However, such initiatives require highly resilient species that are able to establish in stressful environments characterized by poor soil quality and variable precipitation. Such resistant species are especially valuable for restoration since their establishment can create valuable microhabitats for more sensitive species to establish (Mielke *et al.* 2005).

Degraded habitats are often limited in water and soil nutrients, both of which are essential for plant growth (Cabral *et al.* 2004), osmotic, physiological regulation and photosynthesis (Caron *et al.* 2014). The main effects of water stress on plant metabolism is loss of cellular turgor and decreasing in stomatal opening. These changes, although contributing to water use efficiency, end up limiting the assimilation of carbon and, consequently, the growth of the plant (Trovão *et al.* 2007). Water deficit also causes a decrease in transpiration, which is largely responsible for the absorption and transport of essential nutrients present in the soil as nitrate. The activity of the nitrate reductase enzyme, regulated by the presence of nitrate, is also quite sensitive to water deficiency. Nitrates are required for the synthesis of biomolecules such as nucleic acids, amino acids, and proteins (Kóvacs 2005; Firmano *et al.* 2009), meaning that all plant metabolism is compromised when water is scarce in the soil. Effective species for restoration should therefore be resilient to the adverse conditions is found in degraded environments (Volpato *et al.* 2013; Rorato *et al.* 2018; Chiochetta *et al.* 2017).

Schinus terebinthifolia (the Brazilian pepper tree) is a good potential candidate for use n restoration projects. It is a pioneer species that is native to the Atlantic forest, but which has also become established in several regions of South America and most of the neotropical region of the globe (Jones *et al.* 1997; Silva *et al.*

2008). *S. terebinthifolia* thrives in anthopogenic environments (Pratt *et al.* 2006) and has already been identified as having great potential for the restoration of degraded areas (Coutin *et al.* 2017; Rorato *et al.* 2018). However, its ecophysiological response to these environments has not been fully investigated, and its mechanisms of drought tolerance are not well understood.

Current knowledge of this species indicates that its hydraulic characteristics make it more tolerant to water stress compared to native species of environments that it has invaded (Pratt *et al.* 2006). Moreover, it is known that the antioxidant and photoprotective apparatus of this type of pioneer species in tropical regions can be very efficient (Coutin *et al.* 2016). This suggests that its water and saline resistance may be linked to its photosynthetic and photochemical characteristics (Ewe *et al.* 2003; Ewe *et al.* 2005; Ewe *et al.* 2007; Mielke *et al.* 2005). The aim of the current study was to provide a detailed description of the adaptive response of *S. terebinthifolia* to water stress and rehydratation, including gas exchange, accumulation of organic compounds and photochemical efficiency. This information can be used to the identify the main adaptive mechanisms used by this species to overcome water stress, clarifying and complementing existing physiological knowledge of this species.

Material and methods

Plant material and experimental conditions

This study was carried out in the Agrarian Sciences Center of the Federal University of Alagoas (UFAL), Rio Largo - AL (9º 28' 00" S, 35º 49' 34" W, at 131 m elevation). The experiment was conducted in a greenhouse, using seedlings of *S. terebinthifolia* at approximately one year of age. The seedlings were transplanted to 20 L plastic pots filled with 20 kg of sieved soil, collected in a forested area (9°27'58.4 "S, 35°49' 31.7" W). The experimental design was completely randomized, consisting of two treatments with eight replicates each.

The treatments were composed of two water regimes: [1] control (irrigated), consisting of plants irrigated daily, and; [2] water stressed, composed of plants submitted to water deficit by total suspension of irrigation and subsequent rehydration. Irrigation was suspended until the photosynthetic rate reached values close to 0 µmol CO_2 m^{-2} s^{-1} (the “maximum stress”), later the plants were rehydrated until the photosynthetic rates were equal to those of the control treatment. Physiological and biochemical analyses were performed at the end of each period. The water deficit lasted seven days and rehydration lasted five days.

The sediment used in the experiment was classified according to the Brazilian Soil Classification System (SBCS). A 0.5 kg sample of sediment was used in the evaluation of physical and chemical properties using: (1) clay (densimeter); (2) fine and coarse sand (sieving); (3) clay dispersed in water (densimeter); (4) degree of flocculation (GF). Nutritional analyses were performed using: (1) Mehlich-1 extractor; (2) 1.0 M KCl extractor; (3) Calcium acetate extractor at pH 7.0; (4) Welkley-Black method; (5) Base saturation; (6) Aluminum saturation. The soil of the experiment was classified as sandy claim loam: fine sand (320 g / kg), coarse sand (150 g / kg), clay (300 g / kg) and silt (230 g / kg). The soil had pH in water of 4.8 and contained sodium 10 (mg / dm^3), phosphorus 39 (mg / dm^3), potassium 200 mg / dm^3), calcium 2.78 (mg / dm^3), magnesium 1.52 (mg / dm^3) and aluminum 0.38 (mg / dm^3).

At the end of each experimental period, the soil water potential (MPa) was measured using WP4C Water Potential Meters (Decagon Devices) and the humidity (%) with a portable moisture meter model SM200, coupled to a model HH2 sensor. Temperature (Fig. 1A), relative air humidity (Fig. 1B), solar radiation (Fig. 1C) were recorded every 30 minutes by a meteorological station (Weather Station model WS -

GP1 / AT DELTA - T Devices, Cambridge - England) located within the greenhouse. From this data, the Vapor Pressure Deficit (DPV) was calculated based on Allen (1998), resulting in a value corresponding to the evaporative pressure of the environment towards the atmosphere, expressed in KPa (Fig. 1D).

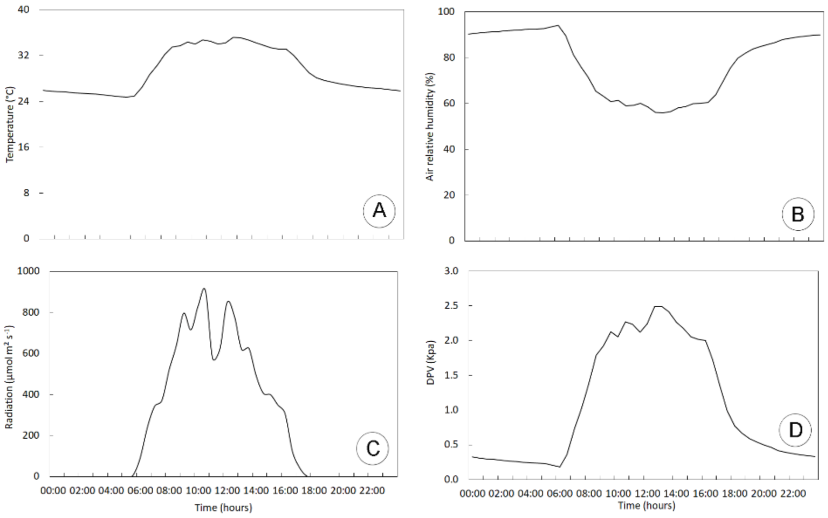

Fig. 1 Average hourly values of air temperature (° C), relative air humidity (%) and vapor pressure deficit (Kpa), recorded every thirty minutes and during twelve days of the experiment.

Leaf water potential

Leaf water potential (Ψw – MPa) was determined using a Scholander-type pressure chamber (Soil Moisture Equipment, Santa Barbara, CA, USA) (Scholander *et al.* 1965), in the periods of the pre-dawn (05:00 am) and midday (12:00 pm) on the third leaf from the apex. The pressure reading was performed according to the methodology proposed by Turner (1981).

Quantum Efficiency of Photosystem II

The quantum efficiency of PSII was performed with a portable fluorometer (PAM - 2500, Handy PEA, Hansatech, Norfolk, UK). The maximum quantum efficiency of the PSII represented by the Fv/Fm ratio was evaluated in leaves adapted to the dark for 20 minutes by means of leaf forceps, in the period of the pre-dawn (04:00 – 05:30 am) and at noon (12:00 – 12:30 pm) (Maxwell & Johnson 2000). The effective quantum efficiency of PSII (ΦPSII) was determined on the same leaves at noon (11:00 - 12:30 pm) (Baker 2008).

Gas exchange and water use efficiency

The rates of photosynthesis (*A* – μmol CO_2 m^{-2} s^{-1}), transpiration (*E* – mmol H_2O m^{-2} s^{-1}) and stomatal conductance to water vapor (*gs* – mol H_2O m^{-2} s^{-1}) were measured on mature leaves and completely expanded between 8:00 and 11:00 a.m. using an infrared gas analyzer (IRGA) (LI-6400 Li-color, USA) equipped with a 6400-02B Red Blue artificial light source, set at 1200 μmol m^{-2} s^{-1} of luminous intensity. The instantaneous water use efficiency (iWUE) and intrinsic water use efficiency (IWUE) were calculated by the A/E and A/gs ratios, respectively, and expressed in μmol CO_2 $mmol^{-1}$ H_2O.

Contents of photosynthetic pigments and SPAD Index

The extraction of the photosynthetic pigments was done according to the method of Arnon (1949). Approximately 50 mg of fresh leaves were placed into test tubes protected with aluminum foil containing 5 mL of 80% acetone. After 48 hours, the absorbance was quantified at wavelength of 663, 645 and 480 nm using a spectrophotometer. The values of chlorophyll *a*, *b*, total and carotenoids were calculated following Hendry & Grime (1993), and subsequently the chlorophyll *a / b* ratio was calculated. The SPAD index was determined by the non-destructive method using a portable chlorophyllometer (SPAD-502 - Minolta, Japan). Each sample was quantified using the average of 5 measurements performed on different leaves.

Biochemical analyses

Soluble carbohydrates were extracted and quantified according to the methodology of Dubois *et al.* (1956). The readings were performed in a spectrophotometer at 490 nm and the absorbance compared to the standard curve of glucose concentration (μg), values were expressed in mg g^{-1} FW. The free proline was extracted and quantified based on the methodology described by Bates *et al.* (1973). The reading was performed in a spectrophotometer at 520 nm and the absorbances compared to the standard proline curve, values were expressed in μmol g^{-1} FW.

Nitrogen compounds (nitrate, ureids and free amino acids) were extracted from 500 mg of fresh plant material in 5 mL of MCW (60% methanol: 25% chloroform: 15% H_2O) according to methodology of Bieleski & Turner (1966). The nitrate was quantified according to the methodology of Cataldo *et al.* (1975), the readings were performed in a spectrophotometer at 410 nm and the absorbance compared to the standard $NaNO_3$

curve. Ureids (total ureids, allantoin and alantoic Acid) were quantified according to the methodology of Vogels & Van Der Drift (1970). The readings were performed in a spectrophotometer at 535 nm and the absorbances compared to the standard allantoin curve. Total free amino acids were determined according to Yemm & Cocking (1995). The reading was performed in a spectrophotometer at 570 nm and the absorbance compared to the standard curve of amino acids (pool of amino acids - arginine, glycine, glutamic acid and phenylalanine), values were expressed in μmol g $^{-1}$ FW.

Statistical analyses

The data were submitted to analysis of variance (ANOVA) and the means were compared by the F test at 5% probability ($P<0.05$), using the statistical program SISVAR version 5.6 build 86.

Results

Soil of plants in the control treatment, retained an average of 30% of moisture and -0.5 MPa of water potential during the experiment (Fig. 2). At the day of maximum stress for the treatment group, soil moisture was approximately 5% and the water potential was -5.0 MPa. Both the moisture and the soil water potential increased after rehydration, reaching values close to the soil evaluated in the control plants. Plants reached maximum stress at the seventh day of experiment, and after rehydration, photosynthesis rates reached values close to irrigated (control) plants on the twelfth day.

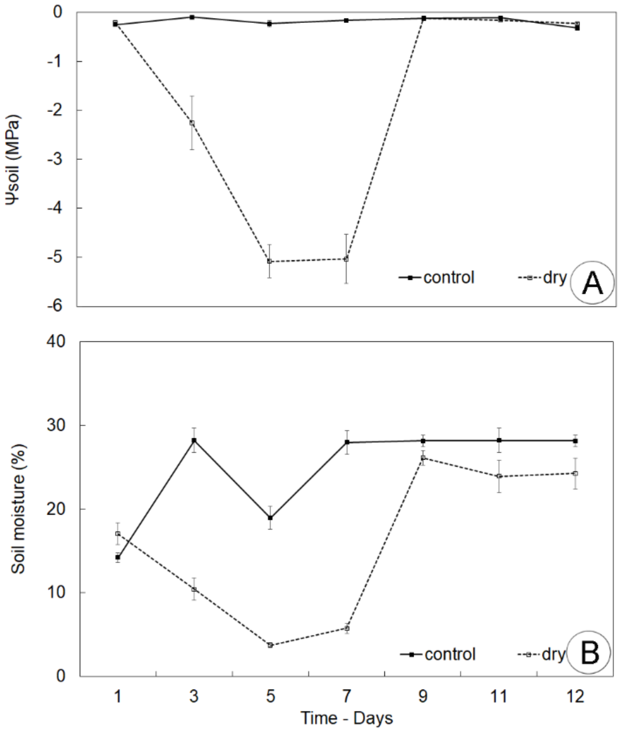

Fig. 2 (A) Soil water potential and (B) Soil moisture during the experiment.

When photosynthesis rates reached values close to zero (day of maximum stress) (Fig. 3A) we observed decreases in stomatal conductance (Fig. 3B), transpiration (Fig. 3C) and carboxylation efficiency (Fig. 3D) - direct consequences of the reduction in water availability. The values of these variables in the control treatment maintained a constant range throughout the experiment. After rehydration, stressed plants re-established pre-treatment photosynthetic rates of around 23 μmol CO_2 m^{-2} s^{-1}, indicating that this species can completely recover after a period of severe water stress.

The values of the instantaneous water-use efficiency (iWUE) (Fig. 3E) and the intrinsic water-use efficiency (IWUE) (Fig. 3F) were higher in control plants until the day of maximum stress, but after rehydration, stress treatment plants exceeded the values of the control treatment plants by optimizing water use soon after the severe water deficit.

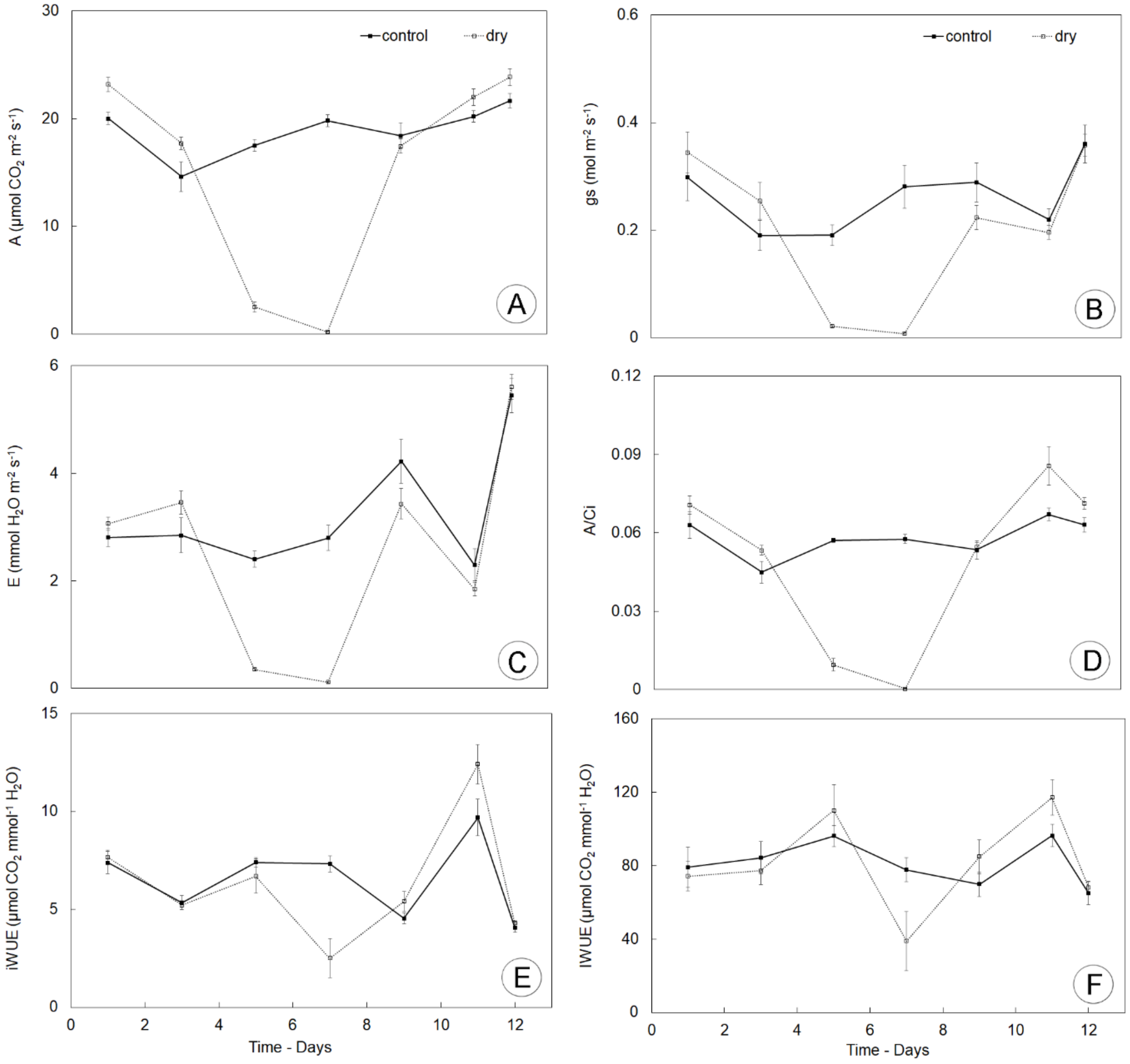

Fig. 3 Gaseous exchanges of *Schinus terebinthifolia* Raddi accompanied during twelve days of experiment: (A) photosynthesis, (B) stomatal conductance, (C) transpiration, (D) carboxylation efficiency, (E) instantaneous water use efficiency and (F) intrinsic water use efficiency.

Pre-treatment leaf water potential was around -0.3 MPa at pre-dawn and at midday (data not shown). After seven days without watering, verified leaf potentials were approximately -1.2 MPa in the stress treatment plants and -0.4 MPa in the control treatment at pre-dawn (Fig. 4A). However, at midday reduced air humidity and increased temperatures led to high values of DPV and a considerable decline in leaf water potential. The capacity of osmotic adjustment of *S. terebinthifolia* was approximately -3.6 MPa and -4.2 MPa for the stress and control treatments, respectively (Fig. 4B). After rehydration, irrigated plants had water potential of around -0.4 MPa, while stress treatment plants had values of -0.3 MPa at pre-dawn, and -1.2 MPa at midday (Fig. 4A-B).

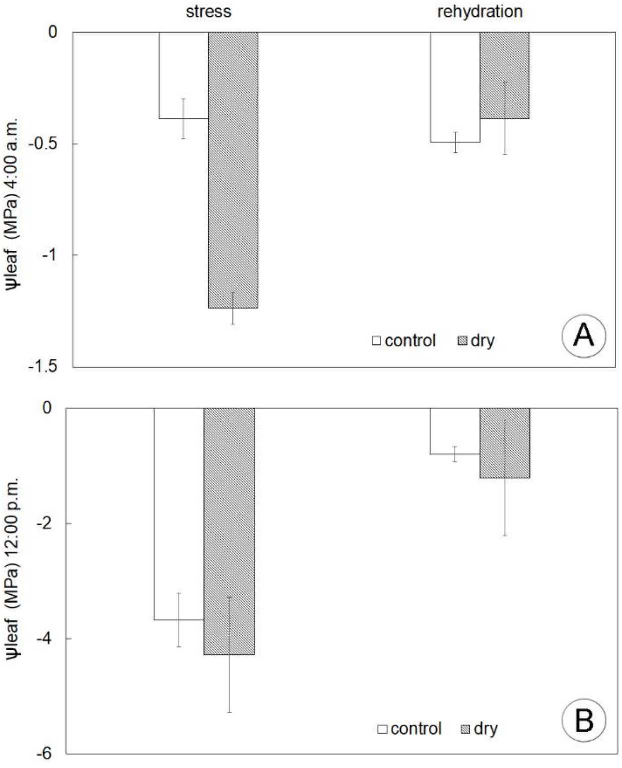

Fig. 4 Values of leaf water potential in *Schinus terebinthifolia* Raddi plants were verified seventh and twelfth day of the experiment at two times of day: (A) beforehand and (B) Midday.

Carbohydrate content was similar in leaves of both control and treatments plants (Fig. 5A). After rehydration a considerable increase in the carbohydrate content was observed on the twelfth day of the experiment. Amino acid levels increased in the drought stressed plants (24.4 µmol g^{-1} FW at maximum stress), while control plants had values of approximately 3.5 µmol g^{-1} FW (Fig. 5B). Amino acids accumulate in stress situations, acting as osmotic regulators of the cells and adjusting the water status of the plants. After rehydration the content of these compounds decreased in the stress treatment to approximately 14.7 µmol g^{-1} FW. The control plants had an amino acid content of approximately 11.7 µmol g^{-1} FW. This result suggest that they had an increase in amino acids after the seventh day of the experiment, which may be a consequence of atmospheric variables, since plants of the control treatment were kept hydrated throughout the experiment period. We observed a peak in proline in drought-stressed plants (202.3 µmol g^{-1} FW) and a drastic reduction of this value (9.1 µmol g^{-1} FW) in the same plants after rehydration. The control plants maintained a range between 22 and 28 µmol g^{-1} FW proline on the seventh day and twelfth day of the experiment, respectively (Fig. 5C).

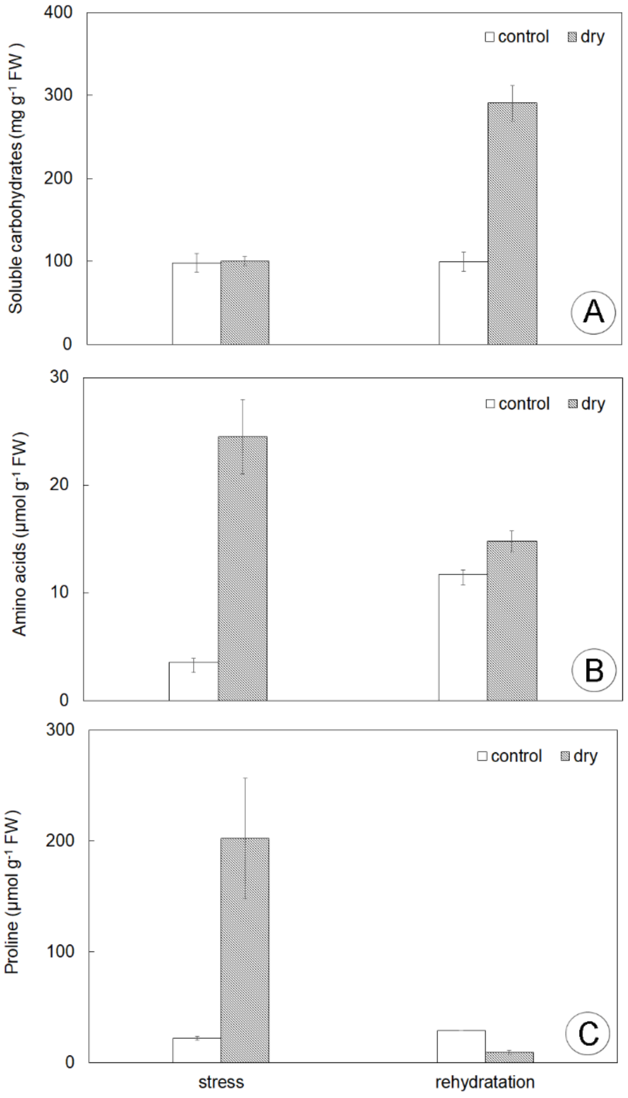

Fig. 5 (A) Quantification of soluble carbohydrates, (B) free amino acid content and (C) proline in leaves of *Schinus terebinthifolia* Raddi plants verified on the seventh and twelfth day of experiment.

Levels of allantoic acid did not change at the maximum stress point. After rehydration (on the twelfth day) we noticed a considerable increase in its levels in the stress treatment, from 1.9 to 2.7 µmol g^{-1} FW (Fig. 6A), whereas it remained at higher levels in control plants throughout the experiment (12 µmol g^{-1} FW in 7º day, and 9.2 µmol g^{-1} FW in the 12º day). Reductions in allantoin content were verified in stress treatment after rehydration, decreasing from 9.8 µmol g^{-1} FW, recorded on the maximum stress day to 5.7 µmol g^{-1} FW (Fig. 6B). This result suggests that water stress increases the nitrogen requirement during rehydration (Fig. 6C). Additionally, stressed plants had increased nitrate levels (0.11 µmol g^{-1} FW) on the day of maximum stress compared to control plats (0.09 µmol g^{-1} FW) on the same day (Fig. 6D). After rehydration, a decrease in nitrate levels (to 0.07 µmol g^{-1} FW) in stressed plants was observed, with as the control plants maintain the same levels observed on the day of maximum stress.

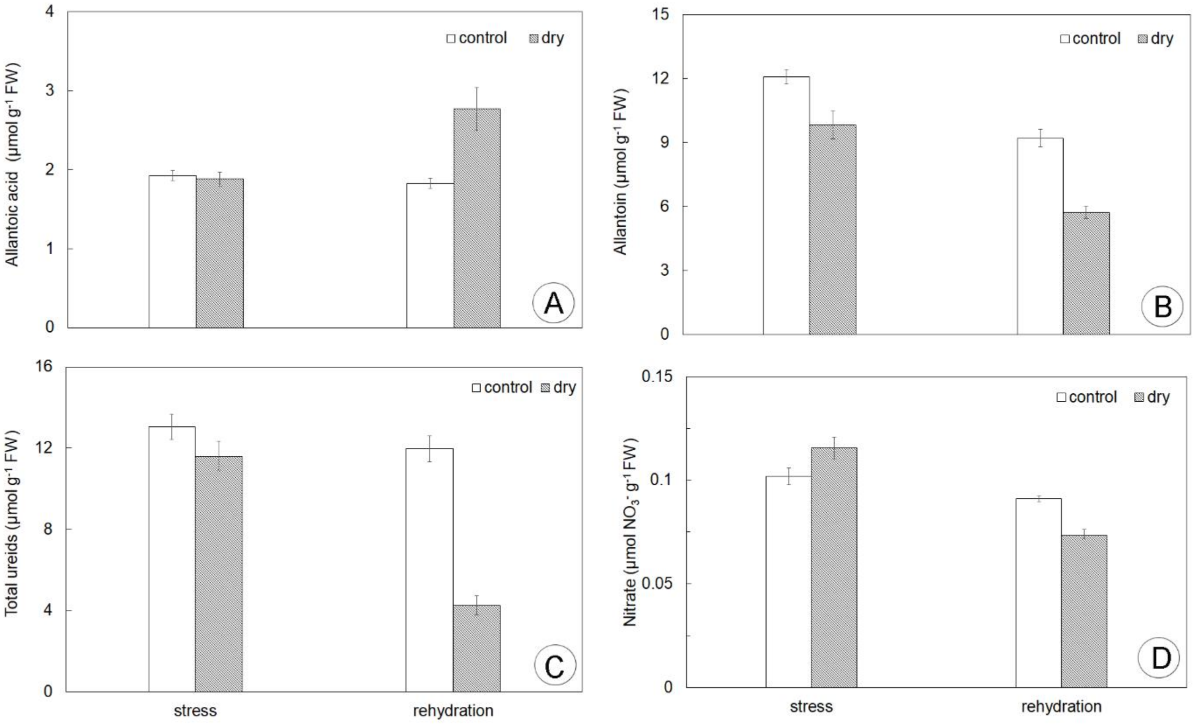

Fig. 6 Ureide content in leaves of *Schinus terebinthifolia* Raddi plants on the seventh and twelfth day of experiment: (A) allantoic acid, (B) allantoin and (C) total ureides and (D) nitrate.

Stressed plants had chlorophyll *a* at values close to those found in control, both during maximum stress and after rehydration (Tab. 1.). The SPAD index did not markedly change during the twelve days of the experiment, though there was a slight increase in the stress treatment after rehydration (Tab. 1.).

Table 1. Index SPAD, total chlorophyll (Chlo *T*), chlorophyll *a* (Chlo *a*), chlorophyll b (Chlo *b*), carotenoids (Carot) and Chlorophyll a/b (Chlo *a*/*b*) at maximum stress. Means followed by the same lowercase letter in the columns do not differ significantly from each other by the Tukey test ($P < 0.05$).

Treatment	SPAD	Chlo *T* μg/L	Chlo *a* μg/L	Chlo *b* μg/L	Carot μg/L	Chlo *a/b* μg/L
Control	53.1a	1.64a	1.72A	0.45a	0.72a	4.84a
Dry	50.1a	2.18a	1.38a	0.25a	0.91a	6.81A
CV	9.44	26.8	18.9	8.4	21.6	10.08

Apparently, chlorophyll was not severely impaired by the severe (but short duration) water stress. It has been observed that values below 0.725 F_v/F_m, may cause leaves to suffer photoinhibitory damage. Drought stress reduced quantum efficiency at pre-dawn and midday (Fig. 7). Specifically, on the day of maximum stress *Fv/Fm* decreased to 0.709 in stressed plants (Fig. 7A), but increased to 0.754 after rehydration (Fig. 7B). Control plants showed little variation in quantum efficiency during the experiment. After rehydration, stressed plants quickly restored the electron transport efficiency of their photochemical apparatus (Fig. 7C).

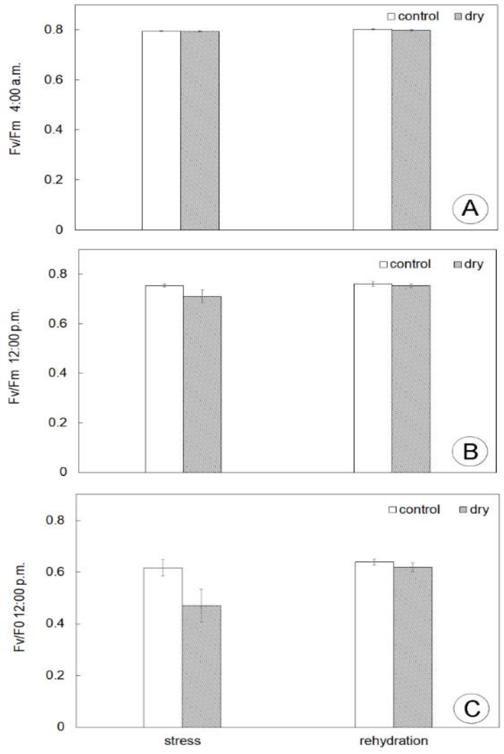

Fig. 7 Photochemical efficiency of *Schinus terebinthifolia* Raddi observed at the first, seventh and twelfth day of experiment: (A) Maximum quantum yield (F_v/F_m) evaluated at 4:00 am; (B) Maximum quantum production (F_v/F_m) evaluated at 12:00 o'clock; (C) Effective quantum efficiency of photosystem II.

Discussion

As expected, gas exchange was negatively affected in stressed plants. Studies using experimental drought or performed in the dry season usually have this type of result, with plants decreasing the water lost from transpiration mainly through reduction of the stomatal aperture (Mariano *et al.* 2009; Marenco *et al.* 2014; Albuquerque *et al.* 2013; Costa *et al.* 2015).These findings suggest that the photosynthetic apparatus of *S. terebinthifolia* may be the main reason for its observed success in invading multiple environments, showing characteristics similar to that of plants of seasonally dry environments. Ewe (2003) studied *S. terebinthifolia* on a plateau at different times of the year in South Florida, observing higher mesophilic conductivity, higher intrinsic water use efficiency and greater use of nitrogen than most native species. It also had the highest gas exchange rates, indicating that this species has an important physiological advantage for invading new environments.

Other variables directly affected by stomatal aperture reduction are photosynthetic and transpiratory rates, which commonly show decreases as stress becomes severe. This balance between stomatal opening and CO_2 capture directly reflects the amount of water used by plants for key physiological processes, since the reduction of stomatal openings prevents water loss, but also reduces CO_2 entry and assimilation (Ai *et al.* 1990). The instantaneous efficiency of water use and the intrinsic efficiency of water use evaluate the ability of a plant to perform photosynthesis in the face of water scarcity, which consequently impacts on biomass production (Souza *et al.* 2010). In our study, stressed plants showed higher values of instantaneous efficiency of water use than control plants in the days prior to maximum stress, when photosynthesis was being carried out with the minimum amount of water that could be lost.

Water deficit also negatively affected the electron transfer efficiency of the photosystems. As observed, the photoinhibitory damage caused to photosystem II during the stress period was reversible (Critcheley *et al.* 1995; Hasan *et al.* 2018; Maxwell *et al.* 2000; Araújo *et al.* 2004). This is typically seemed in species of seasonally dry forests that have photoprotective mechanisms (Trovão *et al.* 2007). These species have near-maximum quantum efficiency, even during periods of water stress, and can return to their maximum yield shortly after rehydration (Björkman *et al.* 1987). *S. terebinthifolia* has the plasticity of a pioneer species that grows on the edges of the forest (Rabelo 2013). The maximum photosystem II quantum yield (Fv/Fm) and the photosynthetic maximum photochemical yield of photosystem II (Fv/F0) also showed the same pattern of response to drought stress. This is also a consequence of the decreased in the amount of water in the plant organs, which could dissipate excess of heat through transpiration, and because of the stomatal closure. In addition, due to the inhibition of CO_2 entry (also caused by the stomatal closure) the electron transport chain of photosynthesis is disrupted and the contribution of NADP + to the photosystem I is impaired, producing the superoxide anion (O2•-) molecule that highly toxic to plant cells (Martins *et al.* 2018). This is caused by the reduction in the plant`s capacity to transport electrons through PSII, resulting from photoinhibition.

Our results suggest that *S. terebinthifolia* is highly resistant to periods of water scarcity and able to quickly overcome damages suffered due to lack of water in the metabolism. In this sense it belongs to a group of species that can successfully establish themselves in the midst of water scarcity (Sheil *et al.* 2018). The reduction of leaf Ψw verified in plants under stress reflect the effect of water restriction on their vegetable water status (Schimpl *et al.* 2019). The ability to reduce leaf Ψw in stressed plants indicates that this species has one of the main drought tolerant traits - a strategy to maintain the water potential gradients necessary for the plant to absorb water even in low humidity soils (Silva *et al.* 2016; Albrecht *et al.* 2006). These osmotic changes can be seen in the leaves, as has been observed in “aroeira” and also in leaves and fruits of other species in other studies (Fernandes *et al.* 2018; Falahi *et al.* 2018). Due to atmospheric variables, that are extremely different between the pre-dawn and midday hours, these responses may vary between species. Water deficit has been observed to induce lower leaf water potentials and has a significant effect on the gas exchange parameters (Sellin 2014; Silva-Braco 2017), which was also verified here.

Water stress can cause organic compounds that have nitrogen as feedstock to be degraded or for their synthesis to be drastically reduced (Golçalves *et al.* 2012). The increase in proline concentration is due to the reduction of protein synthesis and the action of proteases usually occurs in stressed plants (Stewart *et al.* 1973), which also explains the observed increase in amino acid content. Our results indicated that soluble carbohydrates remained stable during water stress. However, when rehydrated, there was a peak in sugar production, probably caused by the resumption of CO_2 assimilation and starch synthesis (Santos *et al.* 1988). The increase in soluble sugars concentration probably occurred due to the decrease in starch synthesis during stress, and also through hydrolysis of the starch reserves to generate ATP. Some researchers have noted an increase in carbohydrates during water stress, linking this to osmotic adjustment in the cells (Filho *et al.* 2001; Costa *et al.* 2015; Mendes *et al.* 2017).

Osmotic adjustment in *S. terebinthifolia* the may have been performed by other solutes, such as nitrate, total amino acids and especially proline, with a marked increase in stress and a decrease in rehydration. The products of protein lysis are proline, and other amino acids, which act as osmoprotectants and serve as substrate for the synthesis of more proline (Falahi *et al.* 2018; Nounjan *et al.* 2018; Lee *et al.* 2013). However, during rehydration the proline acts as a reservoir of nitrogen and a carbon source for post-stress growth, resulting in a pronounced drop in proline content and a marked increase in synthesized carbohydrates after the resumption of carboxylation using the haptonic skeleton of these compounds (Hossain *et al.* 2008).

Nitrate may have accumulated as a result of changes in nitrogen metabolism, since nitrate reductase enzyme is inhibited by drought stress (Shane *et al.* 1967; Marur *et al.* 2000; Omena-Garcia *et al.* 2015). As no nitrate toxicity in cells was observed in this study, the nitrate probably influenced the osmotic adjustment of the cells (Ariz *et al.* 2010; Beur *et al.* 1992; Beninni *et al.* 2002). Such responses activate the degradation pathways of biomolecules and cause the synthesis and accumulation of other organic solutes, such as nitrate, and compounds from the urea group. We observed that stressed plants had allantoic acid values close to the values found in well irrigated plants but that these ureids peaked after rehydration. This result does not support the hypothesis of accumulation of these compounds during water stress, as has been observed in legumes (King 2005). Allantoin and allantoic acid - considered the main forms of nitrogen reserve in tropical tree plants and better known in the family Fabeaceae (Kabbadj *et al.* 2017) - had a decreasing trend until the end of the experiment. This suggests that the decrease in the assimilation of these compounds is inversely proportional to water stress in *S. terebinthifolia.* It is well known that chlorophyll content responds to shading, soil fertility, nutritional status of the plant and to the water regime or with these factors in combination (Rego *et al.* 2006; Nogueira *et al.* 2001; Bayoumi *et al.* 2013), decreasing according to the level of stress. Salla (2007) demonstrated that total chlorophyll content is strongly correlated to SPAD index values using data from several tree species. Both these measures can estimate the loss of photosynthetic pigments in plants of *S. terebinthifolia* submitted to water deficit, with a significant decrease in total chlorophyll (Rabelo *et al.* 2013). One of the probable reasons for such variation is that the nitrogen metabolism, which is involved in the initial stages of chlorophyll production, is directly impaired by lack of water.

S. terebinthifolia is considered a resilient species in tropical environments. Our study suggests that young plants of this species are highly tolerant to water stress with a rapid and total recovery from short term severe stress. Water stress tolerance appears to be largely mediated through regulation of osmotic potential with associated increases amino acids and proline, ‘saving’ carbohydrates for the maintenance of biomass. *S. terebinthifolia* protects its photosynthetic apparatus by regulating stomatal closure, which also prevents the degradation of chloroplast pigments. Despite making a full physiological recovery after rehydration, there were many changes in its metabolism under water stress.

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Capítulo 2: Respostas fisiológicas *de Schinus terebinthifolia* Raddi (Anacardiaceae) submetida à deficiência hídrica seguida por reidratação em dois tipos de solos

Physiological responses of *Schinus terebinthifolia* Raddi (Anacardiaceae) submitted to water deficiency followed by rehydration in two types of soils

Abstract - In plant metabolism water and soil nutrients are involved in all physiological processes and the ability to adapt to variations and changes in soil and water conditions is a key factor in resilience to environmental change. The adaptability of ecologically important trees is major importance in restoration initiatives, since these often take place in degraded habitats under sub-optimal environmental conditions. Here, we evaluate the physiological responses of a putatively resilient and widespread native Brazilian tree, *Schinus terebinthifolia* Raddi, under conditions of water deficit and cultivated in two different soil types. Our aim is to investigate the capacity of the species to withstand drought stress in soil types from ecologically distinct biomes (coastal forest and savanna). The study was carried out in greenhouses at the Rio Largo Campus of the federal University of Alagoas (9 ° 28 'S, 35 ° 49' W, at 127 meters altitude) with one year old plants. We adopted a completely randomized design in a 2 x 2 factorial scheme (two types of soil x water management), with five replications of each treatment. The analyses were standardized at two time intervals: (1) maximum stress and (2) rehydration. Data were collected on soil moisture, gas exchange, nitrogen metabolism compounds and compatible metabolites (proline, amino acids and ureides). Photochemical efficiency variables also measured, as well as microclimate and physicochemical data of the soil. Differences between the interactions of soil types versus water treatments were verified in Ci, WUE, iWUE, Ψw12hs, chlorophyll *a*, *b*, total and carotenoids, proline index, proteins, total ureides, alanthine, nitrate and also in the activity of the enzyme nitrate reductase on the day of greatest stress. Gaseous exchange gradually decreased as the available water in the soil was depleted. In the dry treatment of soil type 2, photosynthesis zeroed eleven days after irrigation was suspended, while soil 1 it occurred after seventeen days. Water treatment was more important than soil type for promoting physiological changes. Soil type influenced the time needed to reach peak stress and the recovery trajectory after water stress.

Key words: invasive species, water stress, aroeira.

Introducion

The coastal region of Brazil is mainly composed of vast sedimentary plains and contains various ecologically distinct vegetation formations, including natural fields, restingas (coastal forest), mangroves and other types of vegetation such as seasonal forest, deciduous forest and savannas (Law 11.428). Of these, the coastal restingas and the semi-arid savannas represent the greatest abiotic challenges to native plants due to their climate, salinity, strong winds, and in many cases, soil types that make it even more difficult to absorb water (Gomes et al., 2007; Costa et al., 2006).

The edaphic composition of this region includes sedimentary soils of the quaternary where the coastal restinga vegetation was established (GOMES et al, 1998). Some studies have classified restinga soils as quartz sands (Camaro et al., 1987; Oliveira et al., 1992; EMBRAPA, 2006), which normally have a sandy texture and are poor in nutrients (GOMES et al., 2007). Thus, the shrub-tree vegetation that is characteristic of the restinga is a result of the interaction of the regional pool of vegetation with the sandy soil and the climate of that region. Nevertheless, there is a considerable diversity of vegetation occurring in Brazilian restingas including several botanical families varying from herbaceous formations to trees that reach 20m in height.

The soil of the savannahs of eastern Brazil has a poorly developed surface mineral horizon, resulting from a reduced content of mineral or organic colloids or from the external climatic and vegetation conditions of this region (EMBRAPA, 2006). It has a clayey physical structure with the presence of boulders, being able to retain abundant water – though this is not necessarily available to the savannah vegetation due to both physical barriers and high osmotic potential. Soil types with higher water retention capacity or that are more fertile can influence the occurrence and frequency of some plant species (SILVA et al, 2009).

Water and soil nutrients are key factors in all plant growth processes (CABRAL et al, 2004), osmotic regulation, physiological regulation and photosynthetic processes (CARON et al, 2014). Thus, in order to thrive native tree species need to be able to adapt to changes in soil and water conditions caused by abiotic variations and anthropogenic degradation in natural environments. The ecological resilience and adaptability of ecologically important trees in their habitats is therefore of great interest to plant physiologists, ecologists and conservationists, since information on these characteristics is of enormous value for sustainable management and the restoration programs of anthropically degraded areas (TRENBERTH et al. 2015).

One of the most resilient native Brazilian tree species is the Brazilian pepper tree, *Schinus terebinthifolia* Raddi, a wide-ranging and adaptable species that can be found in the Atlantic forest, restinga, and in transition areas between these two biomes (SILVA et al, 2008). It`s great adaptability is reflected in the fact that it has become established in several extralimital neotropical regions (JONES et al, 1997), and has even invaded several countries from outside the neotropics (EWE, 2008). The Brazilian pepper tree is highly cited in the literature as an appropriate species for the restoration of degraded environments in the tropics (LIMA et al, 2018) due to its seemingly high plasticity and ability to withstand periods of drought stress (VOLPATO; MARTINS, 2013). Here, we try to uncover the mechanisms underlying the high resilience of *S. terebinthifolia*, experimentally exposing individual plants to conditions of high water deficit while cultivated on two types of soil (restinga and savannah).

Material and methods

Experimental design and physical-chemical analysis of soil

One-year-old plants of *Schinus terebinthifolia* were transplanted to pots with 20 kg of soil collected in two sites. Soil 1 was collected at 9°47'52.7"S 35°51'57.0"W, in a restinga native area in the city of Barra de São Miguel. Soil 2 was collected at 9°23'28.1"S 37°12'38.9"W, in a caatinga area native in the city of Santana do Ipanema. Samples soils a sent for physical and chemical analysis in the Laboratory of Soil, Water and Plant of the Federal University of Alagoas (UFAL). From which sample, a portion of approximately 0.5 kg was separated and classified according to the Brazilian Soil Classification System (SBCS) using: (1) clay (densimeter); (2) fine and coarse sand (sieving); (3) clay dispersed in water (densimeter); (4) degree of flocculation (GF). As well as nutritional analyzes were performed using: (1) Mehlich-1 extractor; (2) 1.0 M KCl extractor; (3) Calcium acetate extractor at pH 7.0; (4) Welkley-Black method; (5) Base Saturation; (6) Saturation by aluminum.

Soil 1 from a restinga area and soil 2 from native savannah area of a semi-arid region was collected in the state of Alagoas. Restinga soil comes from the natural habitat of the Pepper tree while the savannah soil comes from a region (and biome) where this species does not naturally occur. The two types of soil have, as expected, very different physical and nutritional characteristics (Table 1. and Table 2.). Specifically, the soil of the semiarid region belongs to the loam clay sandy category according to SBCS’s textural classification. Restinga soil is categorized as sandy, according to the same determinations and methodologies. Among the nutritional characteristics evaluated, the main difference between the two types of soil was the amount of potassium, which together with the other nutritional quantifications indicated that the savannah soil 2 was more fertile than the restinga soil.

Table 1. Physical soil analysis using (1) clay (densimeter); (2) fine and coarse sand (sieving); (3) clay dispersed in water (densimeter); (4) degree of flocculation (GF).

Determinations	*Coast (%)*	*Semiarid (%)*
Thick sand (g / kg)	940	410
Fine sand (g / kg)	20	180
Silt (g/kg)	20	190
Clay (g/kg)	20	220
Silt / clay ratio	1.00	0.86
Textural Classification (SBCS)	sand	Franco-Argiloarenosa

Biophysical data were monitored during two experimental periods. Period 1 lasted twelve days and included the maximum stress period and period 2 included the rehydration period (Figure 1.). The mean values of the air temperature, relative air humidity and the DPV are shown in the Figure 1. As can be seen, between 11:00 am and 14:00 pm there is an increase in DPV and air temperature, the opposite occurring with the relative humidity of the air, which at the same time has a considerable decrease, corresponding to the hottest and driest period of the day. These microclimatic variations have a great influence on the physiological responses of the plants to drought, as we will see later.

Table 2. Soil fertility analysis using (1) Mehlich-1 extractor; (2) 1.0 M KCl extractor; (3) Calcium acetate extractor at pH 7.0; (4) Welkley-Black method; (5) Base Saturation; (6) Saturation by aluminum.

Determinations	*Coast (%)*	*Semiarid (%)*
pH em água (1:2,5)	5.3	5.7
Na (mg/dm^3)$^{(1)}$	15	20
P (mg/dm^3)$^{(1)}$	3	14
K (mg/dm^3)$^{(1)}$	15	90
Ca (cmol$_c$/dm^3)$^{(2)}$	1.08	3.48
Mg (cmol$_c$/dm^3)$^{(2)}$	0.87	1.67
Al (cmolc/dm^3)$^{(2)}$	0.16	0.09
H + Al (cmol$_c$/dm^3)$_{(3)}$	3.48	2.28
CTCefetiva (cmol$_c$/dm^3)	2.22	5.56
CTC total (cmol$_c$/dm^3)	5.54	7.75
MO (g/kg)$^{(4)}$	18.5	11.8
V (%)$^{(5)}$	37	71
m (%)$^{(6)}$	7	2
Sat.de Ca (%)	19.5	44.9
Sat.de Mg (%)	15.7	21.5
Sat.de K (%)	0.7	3.0
Sat.de Na (%)	1.3	1.2

Seedlings of adequate phytosanitary status were standardized in a uniform phytosanitary state and transferred to a greenhouse in the Laboratory of Plant Physiology of the Center of Agricultural Sciences (CECA / UFAL). The plants were divided in four treatments, with five plants in each treatment: (a) irrigated plants in soil 1; (b) irrigated plants in soil 2; (c) plants with suspended irrigation in soil 1 and (d) plants with suspended irrigation in soil 2. When the photosynthesis of the plants with suspended irrigation reached zero, all plants were rehydrated. The treatments were arranged in a completely randomized distribution. The analyses were performed at two time periods: (1) the period of maximum stress and (2) the period of rehydration.

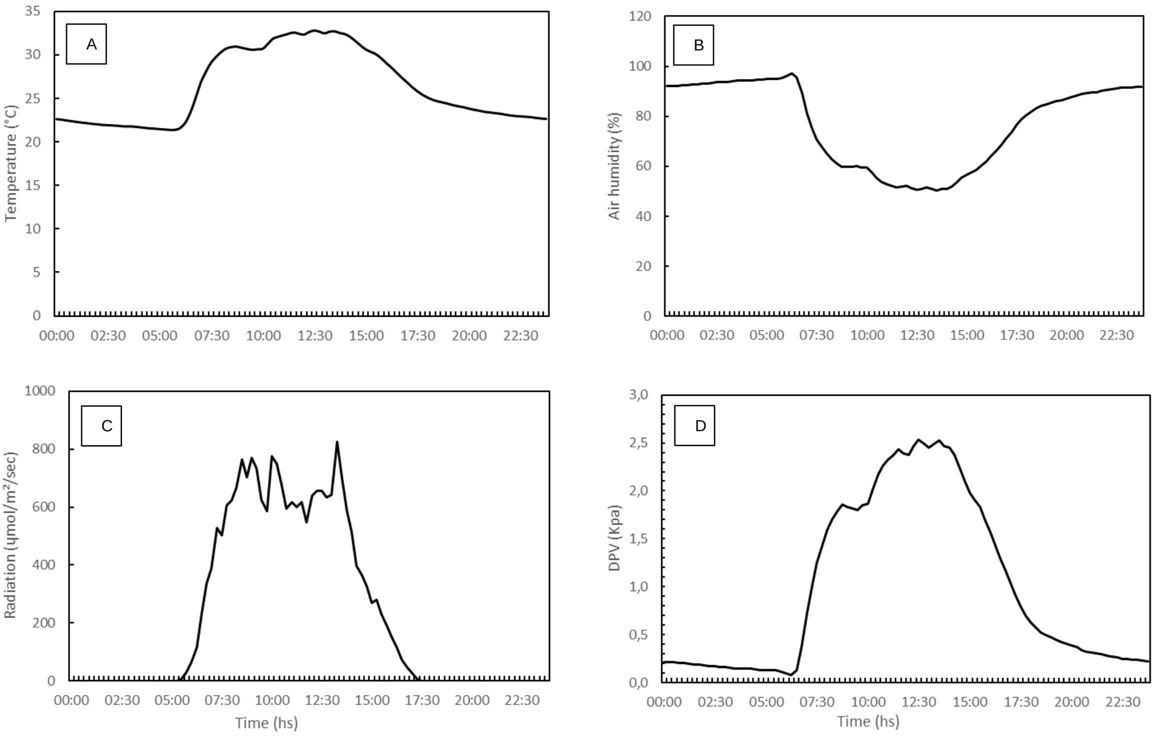


Fig 1. Average hourly values of air temperature (°C), relative humidity (%), radiation (μmol/m^2/sec) and vapor pressure deficit (Kpa), recorded every fifteen minutes and during the experiment in the greenhouse.

Determination of soil moisture

Measurements were taken on the first day of the experiment, on the day of maximum stress and after complete rehydration. Soil moisture was recorded with a portable humidity meter model SM200, coupled to a model HH2 sensor.

Determination of gas exchange; instantaneous water-use (iWUE) and intrinsic water-use efficiency (IWUE)

Gas exchange by fully expanded leaves was measured between 8:00 AM and 11:00 AM using an infrared gas analyzer (IRGA) model LI-6400 (Li-color, USA) equipped with a 6400-02B Red Blue artificial light source. The IRGA chamber (Li-cor 6400) was set to work with a flow of 1200 μmol/s $^{-1}$. With IRGA, photosynthesis, stomatal conductance and transpiration data were collected. From these variables, the values of instantaneous water-use efficiency (iWUE) and the intrinsic water-use efficiency (IWUE) were calculated as: iWUE (μmol CO_2 $mmol^{-1}$ H_2O = photosynthesis / transpiration) and IWUE (μmol CO_2 $mmol^{-1}$ H_2O) = photosynthesis / stomatal conductance).

Determination of the water potential of the leaf

Leaf water potential was verified through the pressure chamber (SCHOLANDER et al. 1965) in the predawn and at midday, using the third leaf from the apex, showing good phytosanitary status, according to Turner`s (1981) methodology.

Extraction of compounds

The extraction of the nitrogen compounds followed Bieleski and Turner (1966), where 500 mg of fresh material were macerated together with 5 ml of MCW solution (60% ml methanol, 25% ml chloroform, 15% ml H_2O). The material was centrifuged with 1 ml of chloroform and 1.5 ml of H2 O was added to each 4 ml of supernatant. After separation of the reaction phases, the supernatant (water soluble) was used to determine the compounds described below.

Quantification of nitrate

Nitrate was quantified following Cataldo (1975), where 0.2 ml of MCW extraction solution was added with 0.8 ml of 5% salicylic acid and concentrated sulfuric acid. After cooling the samples, 19 ml of 2N sodium hydroxide were added and read in a spectrophotometer at 410 nm.

Quantification of ureides (Allantoin and Alantoic Acid)

Was performed according to the method of Vogels and Van Der Drift (1970). A drop of phenylhydrazine was placed in test tubes with 250 μl of MCW extraction supernatant, 500 μl of distilled H_2O and 250 μl of 0.5 M NaOH and the assay was heated at 100 ° C in a 20% water bath. minutes and then cooled to room temperature. Once cooled, 250 μl of 0.65 N HCl is added and heated at 100 ° C again in a water bath for 4 minutes. After that time, the assay was cooled to room temperature and 250 μl of 0.4 M phosphate buffer pH 7.0 of 250 μl of 0.33% phenylhydrazine solution were added to this reaction and then, the assay was cooled in an ice bath for 5 minutes.

After cooling, 1.25 ml of pre-cooled, concentrated HCl and 250 µl of 1.65% Potassium Ferrocyanide solution were added. After another ice bath, the assay was brought to room temperature and after 15 minutes a spectrophotometer reading was performed at 535 nm. The concentration of ureides was estimated based on the standard curve of the allantoin solution; compared to the standard proline curve (0 to 100 µg mL -1).

Quantification of the proline content

Was performed based on the methodology described by Bates (1973) where 50µL of the MCW extraction solution were collected and added to 2 mL of ninhydrin acid solution (1.25 g nihidrine, 30 mL glacial acetic acid , 20 mL of 6 M phosphoric acid) and 2 mL of glacial acetic acid in 15 mL microcentrifuge tubes. Samples were incubated at 100°C for about one hour, when the test reached purple color were placed on ice to paralyze the reaction. The samples were then added with 4 mL of toluene and constantly stirred for 20 seconds on the tube shaker for complete extraction of proline. The supernatant was used for 520 nm reading spectrophotometry and absorbance.

Quantification of soluble carbohydrates

Was performed according to Dubois (1956), where 50 µL of the MCW extraction solution was added with 5% phenol and 250 µL of concentrated sulfuric acid. Thereafter, the assay was shaken and cooled in an ice bath and then the spectrophotometer read at 490 nm. Carbohydrate concentration values were determined by the standard curve of glucose concentration (µg).

Quantification of free amino acids

Using 1 ml of the supernatant (water soluble) from the MCW extraction was performed where 500 ul of citrate buffer + 200 ul of 5% of ninhydrin solution in methylglycol + 1 ml of KCN solution 0.0002M and this assay was heated at 100 ° C for 20 minutes and, after being cooled for 10 minutes, 1 ml of 60% ethyl alcohol was added according to Yemm and Cocking (1995), followed by spectrophotometer reading at 570 nm . The concentration of amino acids was estimated according to the standard curve of the Leucine solution.

Activity of the nitrate reductase enzyme

The enzymatic activity of nitrate reductase was determined following Stewart (1986), with 0.2 g leaf discs packed in 10 mL syringes and 5 mL of reaction medium (0.05 M K_2HPO_4, pH 7,5 0.1 M KNO_3, + 1% propanol). After insertion of the plunger, the syringe will be reversed to expel the air from the syringe. The technique of infiltration of the buffer during the determination of nitrate retune enzyme activity will be performed according to Majerowics et al. (2003). The exit of the syringe was closed with the finger and the plunger will be pulled 5 times in order to make the vacuum to totally submerge plant material. The syringes will be conditioned in the dark for 1 hour at room temperature (30 °C). After that time, the reaction was stopped and the samples used for the dosing of the enzymatic activity that was expressed in μmol of NO_2^- h^{-1} g MF^{-1}.

Quantification of the spectrometric content of chlorophyll

The procedure was carried out by minimizing the luminosity to avoid degradation of the pigments following Arnon (1949) methodology. Samples of 50 mg of fresh leaf were minced and placed into the threaded test tube containing 5 ml of acetone (80%), for 48 hours. After this, determination was made spectrophotometrically with optical densities obtained in three wavelengths of (664, 665 and 750 nm). The method provides data on chlorophyll *a*, chlorophyll *b* and carotenoids in unit volume (μg/L).

Quantification of colorimetric chlorophyll content (SPAD index)

The index of chlorophyll content was determined by non-destructive method using chlorophyll meter (SPAD-502 - Minolta, Japan). Five readings were performed on randomly chosen leaflets from each plant, and with the mean we obtained the final value of the SPAD index.

Determination of chlorophyll a fluorescence, determination of the maximum and effective quantum yield of photosystem II

Chlorophyll *a* fluorescence was determined using a portable fluorometer (Handy PEA, Hansatech, Norfolk, UK) between 4:00 and 5:30 hours and between 11:00 and 12:30 hours on mature, healthy and fully expanded leaves. The leaves were subjected to 20 minutes of darkness by leaf tweezers and after that time, subjected to a pulse of saturating light of 3000 (μmol $m^{-2}s^{-1}$) and the wavelength of 650 nm for 1 second. At midday the determination of the maximum and effective quantum yield of photosystem II with the same equipment was also performed.

Statistical analyzes

Significant differences between the two treatments and the two soils type were assessed with the Tukey Test (significant difference at 5% probability, $P<0.05$).

Results

Soil humidity

The control treatment plants of the two soil types were always maintained with the soil at field capacity. Soil moisture clearly reflected the water regimes. Soil 1 of the control treatment had values around 15 to 20% (Figure 3), values relatively lower than those found in pots with soil 2 in the same treatment (around 20 to 30%). A clear result of the granulometry of the two types of soil, since the sandy soil (soil 1) retains less water than the loam clay soil (soil 2).

The loam clay soil (soil 2), which theoretically retains more water than sandy soils, lost almost 20% of its moisture in 11 days (Figure 3), reaching the maximum stress for plant at this point. In contrast, the pots containing sandy soil (soil 1) maintained soil moisture (with a minimum of 7%) until the seventeenth day of the experiment (Figure 3), the day of maximum stress for plants in this soil (Figure 3).

We monitored physiological variables when photosynthesis reached values near or equal to zero in plants of the dry treatment of the two types of soil. Plants in soil 2 took ten to eleven days to zero their photosynthetic rates. Plants in soil 1 took seventeen days (Figure 3b). Thus, data collection at the point of maximum stress were carried out on different days, but were compared to each other, taking into account the stress level of the plant.

Photosynthesis was also used to determine the level of recovery after rehydration, that is, for dry treatment plants of the two types of soil that reached values close to zero and were rehydrated. Physiological monitoring data were therefore collected when photosynthesis reached values close to the values in control plants after rehydration. For plants in soil 2 this collection was performed on the seventeenth day and for plants in soil 1, on the nineteenth day of experiment (Figure 3b). For the control treatment plants the time of the data collections were carried out according to the corresponding soil type.

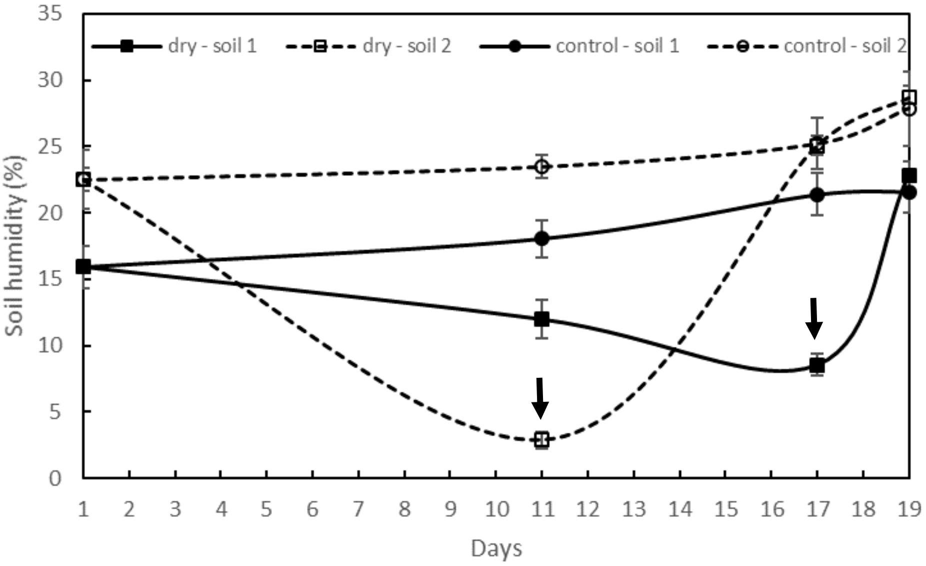
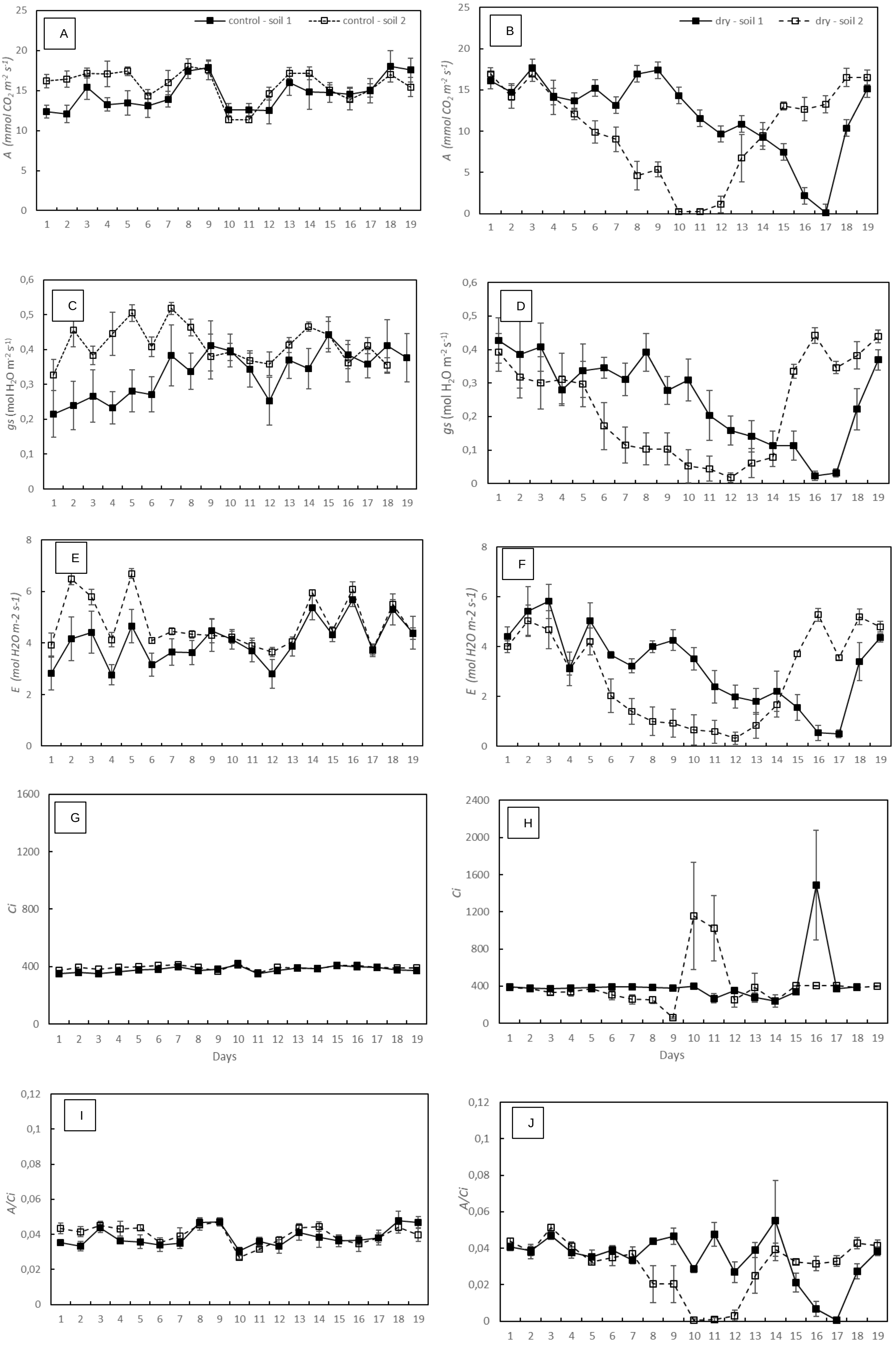


Fig 2. Temporal monitoring of soil moisture in both soil types (soil 1 and soil 2) and in both water treatments (control and drought). The arrow indicates the day of greatest stress (maximum stress).

Gas exchange

Rates of CO_2 assimilation reduced while the soil water was depleting in plants in the dry treatment. The peak of water stress for plants in soil type 2 occurred eleven days after the watering and after seventeen days for plants in soil type 1. At this time stomatal conductance was around zero. In this situation, stomata generally closed to avoid water loss by transpiration, which could consequently reduce photosynthesis, A/Ci, WUE and iWUE (Figure 4). Initially, plants cultivated in soil 1 under control conditions had higher photosynthesis rates. This is understandable considering that the restinga (Soil 1) is a natural habitat of the aroeira. However, by the eighth day the plants of this treatment matched their photosynthetic rates by dribbling the soil factor in their development (Figure 4a). Control and rehydrated plants maintained their photosynthetic rates between 13 and 17 μmol CO_2 m^{-2} s^{-1}. The initial stomatal conductance, even under hydration conditions, was lower in soil 2. After 9 days this had equaled the rates verified in control plants in the soil 1. The internal CO_2 concentration of the control treatment remained around 400 μmol CO_2 m^{-2} s^{-1} throughout the experiment regardless of soil type (Figure 4g), and consequently it maintained a stable A/Ci ratio (Figure 4i).


A
control - soil 1
control - soil 2
A (mmol CO$_2$ m^{-2} s^{-1})
B
dry - soil 1
dry - soil 2
C
gs (mol H$_2$O m^{-2} s^{-1})
D
E
E (mol H2O m-2 s-1)
F
G
Ci
H
I
A/Ci
J
Days
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19

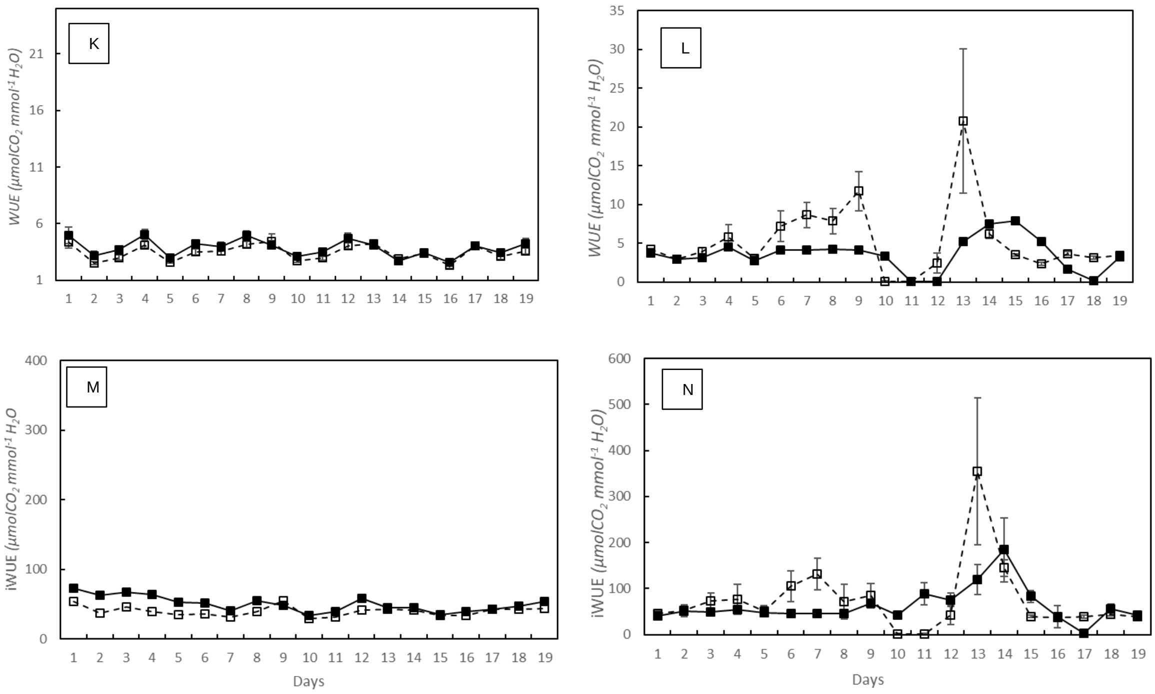


Fig 3. Gaseous exchanges of young plants of *Schinus terebinthifolia* Raddi for 19 days. *A* Control 1 and 2 (A); *A* Dry only 1 and 2 (B); *gs* control soil 1 and 2 (C); *gs* dry soil 1 and 2 (D); *E* control solo 1 and 2 (E); *E* dry only 1 and 2 (F); *Ci* control soil 1 and 2 (G); *Ci* Dry 1 and 2 (H); *A/Ci* controls only 1 and 2 (I); *A/Ci* Dry 1 and 2 (J); *EUA* control soil 1 and 2 (K); *EUA* dry soil 1 and 2 (L); *EIUA* control only 1 and 2 (M); *EIUA* dry soil 1 and 2 (N).

In the dry treatments, the variables Ci and A/Ci had considerable peaks in the days preceding the maximum stress, regardless the type of soil, that is, when the stomata closed and photosynthesis reached levels close to zero. The same happened with effective water use efficiency (WUE) and the intrinsic water use efficiency (iWUE), that both had their highest values in the days before the maximum stress (Figure 4l and 4n.). This occurred when the capacity of photosynthesize and decrease of water loss by transpiration was optimized in dry treatment plants. WUE and iWUE values almost tripled after rehydration of soil 2, a much more pronounced effect than that seen in soil 1 (Figure 4l and 4n).

Variables affected by water stress and soil type

Differences in the interaction of soil types and water treatments were verified for Ci, WUE, iWUE, Ψw12hs, chlorophyll *a*, *b*, total and carotenoids, proline, protein, total ureides, and allantoin and nitrate content and also in the nitrate reductase activity at the maximum stress (Table 3). When we compare the "water regime" factor alone, almost all variables are higher in the control treatment reflecting the loss of water from the metabolism under drought conditions. The exceptions were the green index SPAD and chlorophyll *a/b* ratio that were not measurably affected by stress (Table 4). We also observed substances that increased with increasing water stress, such as proline, proteins, amino acids, total ureides and allantoin (Table 6).

However, isolating "soil type" we can see that within the same treatment there were some differences. For example, in the dry treatment of soil 2 Ci was 253% higher than in soil 1 of the same treatment , indicating that soil type directly influences the physiological responses of the plants (Table 4). The same pattern was observed with some variables in the control treatment; for example, chloro was lower in soil 1 than in soil 2 in control treatment plants (Table 5). In summary, few variables were directly influenced by the interaction between soil type and water treatment. Thus, we will focus on those variables sensitive to the set of changes: "soil + water regime". Similarly, rehydration appeared to be total and reversible in both types of soil.

Table 3. Summary of the analysis of variance of the interaction between two soil types (soil 1 and soli 2) and water regime (control and dry) with the gas exchange variables (A, gs, E, Ci, A/Ci, WUE, iWUE), photochemical (PSII, F_v/F_ma.m. and *Fv/Fm*p.m.), water potential (Ψ_wa.m. and Ψ_wp.m.), green intensity (chlorophyll a, chlorophyll b, carotenoids, total chlorophyll, ratio clor a/b and SPAD), water potential (Ψ_wa.m and Ψ_wp.m.), osmoregulators (proline, protein, amino acid, total sugars, total ureides, allantoin, allantoic acid) and compounds of nitrate metabolism (nitrate reductase, nitrate) in the four days of data collection.

				F value	
SV	d.f.	Variables	initial day	maximum stress	rehydration
S vs Wr	1	*A*	11.005^{ns}	2.87^{ns}	0.55^{ns}
Residue	16	*gs*	0.027^{ns}	2.16^{ns}	0.0001^{ns}
		E	2.83^{ns}	0.04^{ns}	0.021^{ns}
		Ci	1446.71^{ns}	742615.69*	239.43^{ns}
		A/Ci	0.00003^{ns}	0.0003^{ns}	0.00002^{ns}
		WUE	1.63^{ns}	1253.73**	0.21^{ns}
		iWUE	709.4^{ns}	405276.14**	78.76^{ns}
		F_v/F_0*12hs*	0,0058^{ns}	0.0042^{ns}	0.0009^{ns}
		F_v/F_m*4hs*	0,00046^{ns}	0.000045^{ns}	0.00002^{ns}
		F_v/F_m*12hs*	0,00035^{ns}	0.00050^{ns}	0.0004^{ns}
		Ψ_w*4hs*	0,048^{ns}	0.038^{ns}	0.009^{ns}
		Ψ_w*12hs*	0,00045^{ns}	0.75*	0.00002^{ns}
		Clor *a*	0.00033^{ns}	1.14**	0.00002^{ns}
		Clor *b*	0.055^{ns}	0.19*	0.00002^{ns}
		Clor *T*	0.046^{ns}	0.11*	0.0001^{ns}
		Carotenoids	0.0049^{ns}	2.29**	0.08*
		Clor *a/b*	12.85^{ns}	0.11^{ns}	0.02^{ns}
		SPAD	58,82^{ns}	39.48^{ns}	29.04^{ns}
		Proline	0.0015^{ns}	4.61*	0.09^{ns}
		Protein	0.091^{ns}	8.24*	2.92^{ns}
		Amino acid	0.31**	0.80^{ns}	5.48**
		Total sugars	1.52**	0.18^{ns}	0.78*
		Total ureides	0.024^{ns}	256.68*	883.78**
		Allantoin	0.050^{ns}	247.45*	883.12**
		Allantoic acid	0.14^{ns}	0.08^{ns}	0.00012^{ns}
		Nitrate reductase	0.069**	0.16**	2.92*
		Nitrate	0.15^{ns}	0.40*	0.09^{ns}

SV: Sources of variation; soils (s); water regime (wr); d.f.:Degrees of freedom; * and ** significant at 5 and 1% probability, respectively; ns: not significant.

Table 4. Unfolding the interaction between two type soil (soli 1 and soil 2.) and water regime (control and dry) with the variables of gas exchanges (Ci, WUE, iWUE) and water potencial (Ψ_w 12hs) in stress maximum.

Water regime	Ci		WUE		iWUE		Ψ_w12hrs.	
	Soils							
	S1	*S2*	*S1*	*S2*	*S1*	*S2*	*S1*	*S2*
Control	395.35aA	357.0bA	4.01aA	5.65bA	42.6aA	59.5bA	-0.66aA	-0.40bA
Dry	289.01aB	1021.4aA	3.07aB	6.3aA	44.9aB	631.3aA	-0.94aB	-1.46aA
CV	6.37		9.06		6.72		-38.39	

Means followed by the same lowercase letter, in the columns, and upper case, in the lines, do not differ significantly from each other by the Tukey test (p<0,05).

Chlorophylls were one of the variables least affected by water stress or soil type. Chlorophyll *a* increased with the water stress in plants in soil 2, starting at 1.83 µg/L on the first day of experiment (data not shown) and rising to 2.13 µg/L on the day of maximum stress. Chlorophyll b and carotenoid content remained stable throughout the experiment (Table 5), contributing to the stability of total chlorophylls even under stress condition when grown in soil 2. In relation to Fv/Fm 4hs, there was a decrease at the maximum stress in the two soil types, which coincidentally had values of 0.788 µmol m^{-2} s^{-1}. In the control treatments these values were 0.805 and 0.792 µmol m^{-2} s^{-1} (soil 1 and 2 respectively). At midday, even under the atmospheric influence, there were no significant changes in values (0.738 µmol m^{-2} s^{-1} for the dry treatment plants in soil 2, and 0.733 µmol m^{-2} s^{-1} for dry treatment plants in soil 1).

Table 5. Unfolding the interaction between two type soil (soli 1 and soil 2.) and water regime (control and dry) with the variables of chloroplastic pigments (Cloro a, b, total, carotenoids) in stress maximum.

Water regime	Clor a		Clor b		Clor T		Carot	
	Soils							
	S1	*S2*	*S1*	*S2*	*S1*	*S2*	*S1*	*S2*
Control	2.29bA	1.91aB	0.89aA	0.71aA	3.19aA	2.63aB	0.76aA	0.69aA
Dry	1.55aB	2.13aA	0.62bA	0.83aA	2.17bB	2.97aA	0.55bA	0.79aA
CV	13.02		24.12		11.40		16.08	

Means followed by the same lowercase letter, in the columns, and upper case, in the lines, do not differ significantly from each other by the Tukey test (p<0,05).

Based on predawn measurements of Fv/F0, water stress and atmospheric factors induced a decrease in the effective quantum efficiency of photosystem II, which reached levels of 0.457 and 0.420 in dry treatment plants in soil 2 and 1, respectively, at the time of maximum stress. Control treatment plants in both soil types had Fv/F0 of above 0.520.

As anticipated, nitrate reductase activity was affected by water stress. In dry treatment plants of soil 2, it reached values close to zero on the day of maximum stress (Table 6). This effect was milder in plant of the soil 1. The enzyme rapidly recovered after rehydration in plants of the two types of soil (Table 6). Control plants cultivated in soil 1 had higher values than control plants in soil 2. This result implies that the soil type influences nitrate assimilation. Consequently, it was verified that nitrate accumulates even after hydration. There was a negative effect of drought on the nitrate reductase activity and an accumulation of nitrate in leaves. In control plants, the accumulation of nitrate was not inversely proportional to enzyme activity (Table 6). Dry treatment plants accumulated higher levels of nitrate when grown on soil 2 (Figure 6b), where was enzymatic activity was lowest (Figure 5b).

Individuals decreased total sugar content at maximum stress, a probable consequence of the decrease in CO_2 assimilation verified in both types of soil. Conversely, there was an accumulation of total amino acids and proline at the maximum stress in both types of soil. Ureids and protein content were not significantly influenced by water regime or soil type (Table 6).

Table 6. Unfolding the interaction between two type soil (soli 1 and soil 2.) and water regime (control and dry) with the variables of osmoregulators (proline, protein, ureids, allantoin) and compounds of nitrogen metabolism (nitrate and RN) in stress maximum.

Water regime	Proline		protein		ureids		allantoin		nitrate		RN	
	Soils											
	S1	*S2*	*S1*	*S2*	*S1*	*S2*	*S1*	*S2*	*S1*	*S2*	*S1*	*S2*
Control	1.18b	0.88b	3.82bA	4.28aA	51.72aB	64.97bA	37.87bB	48.87aA	0.56aA	0.63bA	1.14bB	0.73aA
Dry	14.74a	16.37a	5.43aA	5.24aA	66.67aA	65.59aA	53.72aA	50.65aA	0.63aB	1.27aA	0.05aA	0.008bA
CV	11.41		25.05		8.96		12.77		18.92		11.16	

Means followed by the same lowercase letter, in the columns, and upper case, in the lines, do not differ significantly from each other by the Tukey test (p<0,05).

Discussion

Water stress conditions appear to cause more severe consequences for *S. terebinthifolia* when grown in clay soil (soil 2). In this soil the gas exchange reached zero in less time than in the sandy soil (soil 1), corroborating previous studies (AI et al, 2017). In contrast, the recovery of CO_2 assimilation after rehydration was considerably faster in soil 1. Sandy soils are the natural habitat of this species, and stress and recovery would seem to be related to a combination of water availability of the soil and the water absorption capacity of the plant (AI et al. 2017).

Previous studies have shown that the rates of liquid photosynthetic, stomatal conductance and photochemical efficiency (Fv/Fm) may differ significantly between soil types (AI et al, 2017). Soil 2 has better water retention, higher surface area of particles, higher amount of organic matter and greater presence of clay. It also has the greatest capacity to retain water, the scarcest for the plant to absorb, which involves physical and chemical issues (AI et al. 2017). The experimental plants tolerated a greater water shortage in the sandy soil, probably because greater water availability between the particles and dissolved solids (SAAD et al, 2009). In addition, when the water in the clay soil begins to evaporate, clefts form further increasing contact with the atmosphere leading to higher evaporation and damaging the roots by exposing them to the atmosphere.

The key value in our study was the level of soil moisture that could bring about changes in the species' metabolism. Indeed, Lopéz (2016) suggest that the effects of shade and soil type are less important than the effects of water deficit. Nevertheless, the level of water stress in the current study was insufficient to damage PSII functioning – corroborating the work of Bosque et al. (2018) on *Lithraea Caustica* (liters), an Anacardiaceae. This plant evolved in a typical mediterranean climate, characterized by summers of low soul water availability, high solar radiation and at high temperatures. This species probably has the capacity to minimize or delay the inactivation of photosystem proteins through a mechanism of more efficient dissipation of excess energy, as observed in cultivated plants (ZEGADA-LIZARAZU et al., 2015)..

Of the variables significantly influenced by water stress and soil type, Ci (along with WUE and iWUE) showed the greatest difference between dry soil 2 plants, probably due to the rapid stomatal closure response that occurred in dry plants during the days which preceded the maximum stress (CHIRICO et al. 2017; PEÑA-ROJAS et al., 2018). When the volume of transpired water exceeds the volume of water absorbed, the plant enters in a state of deficit and dehydrates, as observed in *Handroanthus impetiginosus* (Pessoa et al. 2017). The same process was observed in drought exposed *Myracrodruon urundeuva* (Anacardeaceae) and representatives of the family Arecaceae and Meliaceae (OLIVEIRA et al, 2002; MARIANO et al. 2009; MARENCO et al. 2014; ALBUQUERQUE et al., 2013; COSTA, et al 2015).

Proline accumulation has been reported to occur after certain external disturbances (VERBRUGGEN et al. 2008; HUANG et al. 2018). In our study, the increase of proline was considered as a sign of drought stress (SCHIMPL et al. 2019), together with the degradation of total soluble sugars (LUO and LUO, 2017) (SCHIMPL et al. 2019). As this increase was not verified among the same treatments in different soil types, we conclude that soil type did not contribute to stress in this species. Only lack of water affected the osmoprotective mechanism.

Ureides have also been implicated in resistance to water stress (KING et al. 2005). Their content was higher in dry treatment plants when compared to irrigated treatment in each soil type. The use of urea-derived compounds in tree species is very scarce, and is restricted to legumes or cultivated species (QUILES et al. 2019). Concentrations of these compounds are usually increased in stress conditions, corroborating our results (LAMBERT et al. 2016; LAMBERT et al. 2017; KABBADJ et al. 2017).

Nitrate is toxic in large quantities and was observed to accumulate in aroeira leaves under water stress condition (SHANER et al. 1967). This is because water stress inhibits the enzyme nitrate reductase in both soil types (CASTRO et al. 2007; OLIVEIRA et al. 2011; OMENA-GARCIA et al. 2015). As no leaf necrosis caused by nitrate toxicity was observed in this study, following BENINNI (2002) we believe that nitrate probably influences the osmotic adjustment of the cells in non-toxic amounts. We tried to relate this to the value of the water potential of the leaf and were able to verify that the soil interaction versus water treatment was significant at noon and stressed plants had lower values than control plants. Dry treatment plants in soil 2 decreased their soil water potential more than those in soil 1, probably due to the difficulty of absorbing water from the clay soil. This lead to changes in the osmotic adjustment of leaves (FERNANDES et al. 2018), photosynthetic responses, and photochemical responses, mainly during the day (SELLIN et al. 2014; SILVA-BRANCO et al. 2017). It is important to note that other factors, such as water, atmospheric variables, and soil, are extremely important to evaluate in this context (SILVA et al, 2006; TROVÃO et al. 2004; ALBUQUERQUE et al. 2013).

Plants grown in soil 2 increased their pigment content, including Clor *a* and Clor T. The opposite pattern was observed in plants cultivated in soil 1, which decreased their chlorophyll content under stress. This corroborates several previous studies in other species (REGO, et al. 2006; NOGUEIRA et al 2001; BAYOUMI et al. 2015; SILVA et al. 2003) *S. terebinthifolia* is halophytic and maintains chlorophyll content even under severe stress conditions (BRITO et al. 2018).

In conclusion, water stress most strongly stimulated the observed physiological changes with a more limited influence of soil type mediated through the time in which the species takes to reach its peak of stress and recovery. When hydrated, soil type did not appear to limit the growth and functioning of the plant.

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