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MESTRADO EM BOTÂNICA TROPICAL**

ALAENE TEIXEIRA RIBEIRO

**24-EPIBRASSINOLÍDEO ALIVIA OS EFEITOS DA SECA EM PLANTAS JOVENS
DE *Carapa guianensis*, MELHORANDO A MARGEM DE SEGURANÇA
HIDRÁULICA, TROCAS GASOSAS E DEFESA ANTIOXIDANTE**

**BELÉM
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Dissertação apresentada ao Programa de Pós-graduação em Botânica Tropical da Universidade Federal Rural da Amazônia em parceria com o Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do grau de Mestre em Botânica Tropical.

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Orientadora: Prof. Dr^a. Grazielle Sales Teodoro
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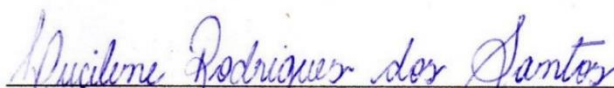
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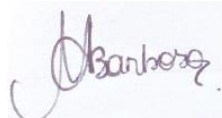
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RESUMO

As mudanças climáticas estão aumentando a frequência de eventos extremos, como secas, causando limitações no crescimento e produtividade das plantas. Tendo em vista os efeitos deletérios gerados pelo déficit hídrico no metabolismo vegetal, a aplicação exógena de reguladores vegetais, como o 24-epibrassinolídeo (EBR), surge como uma possível solução, pois esta molécula é orgânica, ecologicamente correta e biodegradável. Esta pesquisa é o primeiro resultado na literatura sobre possíveis papéis do EBR na margem de segurança hidráulica, comportamento fisiológico e metabolismo em plantas de *Carapa guianensis* expostas à seca. *C. guianensis* é uma árvore amplamente distribuída nas florestas tropicais da Amazônia. O objetivo desta pesquisa é responder se o EBR pode melhorar a tolerância à deficiência hídrica em plantas jovens de *C. guianensis*, medindo atributos hidráulicos, respostas nutricionais, bioquímicas e fisiológicas e biomassa. O experimento foi randomizado com quatro tratamentos, incluindo duas condições hídricas (controle e déficit hídrico) e duas concentrações de brassinosteróides (0 e 100 nM EBR). Este esteroide aumentou os valores do potencial hídrico e da margem de segurança hidráulica. Resultados positivos foram encontrados nas trocas gasosas, em que o EBR aumentou a fixação de CO₂ e estimulou o desempenho estomático. Além disso, este regulador de crescimento vegetal estimulou a defesa antioxidante (superóxido dismutase, catalase, ascorbato peroxidase e peroxidase). Portanto, nossos resultados comprovam que o pré-tratamento com EBR melhorou a tolerância à seca em plantas jovens de *C. guianensis*.

Palavras-chave: Árvore amazônica; brassinosteróides; potencial hídrico foliar; fotossíntese; déficit hídrico

ABSTRACT

Climate change is increasing the frequency of extreme events, such as droughts, causing limitations on growth and productivity in plants. Thus, in view of the deleterious effects generated by water deficit in plant metabolism, the exogenous application of plant growth regulators, such as 24-epibrassinolide (EBR) appears as a possible solution, because this molecule is organic, eco-friendly and biodegradable. This research is first result in the literature on possible EBR roles on hydraulic safety margin, physiological behavior and metabolism in *Carapa guianensis* plants exposed to drought. *C. guianensis* is a tree widely distributed in the tropical forests of the Amazon. The objective of this research is to answer if EBR can improve tolerance to water deficiency in young *C. guianensis* plants, measuring hydraulic traits, nutritional, biochemical and physiological responses and biomass. The experiment was randomized with four treatments, including two water conditions (control and water deficit) and two concentrations of brassinosteroids (0 and 100 nM EBR). This steroid increased the values of water potential and the hydraulic safety margin. Positive results were found in gas exchange, in which EBR increased CO₂ fixation and stimulated stomatal performance. Additionally, this plant growth regulator stimulated antioxidant defense (superoxide dismutase, catalase, ascorbate peroxidase and peroxidase). Therefore, our results prove that pre-treatment with EBR improved drought tolerance in young *C. guianensis* plants.

Keywords Amazon tree; brassinosteroids; leaf water potential; photosynthesis; water deficit

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LISTA DE ABREVIACOES

APX	Ascorbato peroxidase
BRs	Brassinosterides
Ca	Clcio
Car	Carotenides
CAT	Catalase
Chl <i>a</i>	Clorofila <i>a</i>
Chl <i>b</i>	Clorofila <i>b</i>
C_i	Concentrao intercelular de CO ₂
<i>E</i>	Taxa de transpirao
EBR	24-epibrassinoldeo
EL	Extravasamento de eletrlitos
ETR	Taxa de transporte de eltrons
ETR/ P_N	Relao entre a taxa de transporte de eltrons e taxa fotossinttica lquida
EXC	Excesso de energia relativa no nvel PSII
Fe	Ferro
F_0	Rendimento mnimo de fluorescncia do estado adaptado ao escuro
F_m	Rendimento mximo de fluorescncia do estado adaptado ao escuro
F_v	Fluorescncia varivel
F_v/F_m	Rendimento quntico mximo da fotoqumica PSII
H ₂ O ₂	Perxido de hidrognio
LDM	Matria seca da folha
Mg	Magnsio
Mn	Mangans
MDA	Malonaldedo
NPQ	Extino no fotoqumica
O ₂ ⁻	Superxido
P	Fsforo
PAD	Descarga de ar percentual

P_N	Taxa fotossintética líquida
P_N/C_i	Eficiência de carboxilação instantânea
POX	Peroxidase
q_P	Extinção fotoquímica
RDM	Matéria seca da raiz
SDM	Matéria seca do caule
SOD	Superoxido dismutase
TDM	Matéria seca total
Total Chl	Clorofila total
WUE	Eficiência no uso da água
Zn	Zinco
Φ_{PSII}	Rendimento quântico efetivo da fotoquímica PSII
ψ_w	Potencial hídrico foliar

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1. CONTEXTUALIZAÇÃO

As mudanças climáticas em curso estão aumentando a frequência de eventos extremos, como secas e ondas de calor em várias áreas do globo, limitando o crescimento das plantas e produtividade em diversos ecossistemas (HE et al., 2014; ZHU; GONG, 2014). Um dos ecossistemas mais vulneráveis à tais mudanças são as florestas tropicais, uma vez que, além de abrigar uma grande parte da biodiversidade terrestre e fornecer uma gama de serviços ecossistêmicos, estas florestas, representam cerca de metade do sumidouro global de carbono terrestre, absorvendo cerca de 15% das emissões antropogênicas de carbono anualmente (GORDON, 2008; HUNTINGFORD et al., 2013; TREUHAFT et al., 2015; UMMENHOFER; MEEHL, 2017; YANG et al., 2018; KOUR et al., 2021)

A Amazônia é considerada a maior cobertura de floresta tropical do mundo e desempenha um papel significativo na regulação do clima por conter aproximadamente 10% do reservatório de carbono terrestre e por conta da evapotranspiração (AVISSAR, 2004; HOORN et al., 2010; WERTH). Por conta de sua grande área, diversidade de solos, flora e fauna, a Amazônia representa um dos reservatórios de biodiversidade mais crítico do planeta (HECKENBERGER et al., 2007). O número de árvores foi estimado em $3,9 \times 10^{11}$ com aproximadamente 6.000 a 16.000 espécies que se distribuem em florestas de terra firme, igapó e várzea (HAUGAASEN; PERES, 2006; TER STEEGE et al., 2013; MYSTER, 2016; CARDOSO et al., 2017). Por imperar o clima equatorial, a Amazônia apresenta ciclos sazonais com estações secas naturais (NOBRE et al., 2013; HASHIMOTO et al., 2021).

Embora as secas na Amazônia sejam de ocorrência natural influenciada pelos ciclos sazonais, como supramencionado, secas severas influenciadas por mudanças climáticas têm sido ocorrentes na região. Pesquisas recentes revelam que no início do século 21, a região sofreu dois eventos de seca sem precedentes em 2005 e 2010 (MARENGO et al., 2008; MARENGO et al., 2011; e, mais recentemente, em 2015 (JIMÉNEZ-MUÑOZ et al., 2016). Cenários futuros indicam que provavelmente esses eventos extremos serão mais frequentes na região amazônica (DAI, 2013; DUFFY et al., 2015; PANISSET et al., 2018). Além de afetar diretamente no balanço de carbono, eventos de seca podem interferir na composição de espécies da região devido redução na condutividade e falhas hidráulicas (GORDON, 2008; PHILLIPS et al. 2009; ENQUIST;ENQUIST, 2011).

Uma importante ferramenta no entendimento das respostas de plantas à eventos extremos, como a seca, é o uso de atributos funcionais, o qual tem sido usado para descrever a

variação nos caracteres morfofisiológicos de diferentes espécies de plantas (MAMMOLA et al., 2021; MASON et al., 2005; VILLÉGER; MASON; MOUILLOT, 2008). Dentre tais atributos, compreender os atributos hidráulicos é importante para prever os impactos das mudanças climáticas nas plantas (CHOAT et al., 2012a).

Particularmente os atributos relacionadas à resistência à embolia, são fundamentais para explicar fatores tão importantes como mortalidade de árvores, resistência à seca e distribuição de espécies, que depende de métodos para medição consistente e precisa das características do xilema relacionadas à falha hidráulica do sistema de transporte (ROWLAND et al. 2015). A embolia é um fenômeno que ocorre em plantas vasculares e se refere à obstrução de vasos condutores de seiva por ar ou vapor de água. Isso pode ocorrer em condições de estresse hídrico, como períodos de seca prolongada, e pode levar a danos e morte das células do xilema (SPERRY; HACKE, 2015).

Os parâmetros que são frequentemente para estes atributos são quantificados como P_{50} (ou P_{88}), o potencial hídrico no qual as plantas perdem 50% (ou 88%) da condutividade hidráulica do xilema durante um processo de desidratação (MEINZER et al., 2009; SPERRY, J. S. et al., 2002). P_{50} representa um ponto de dano incipiente à funcionalidade da planta (SKELTON et al., 2018) e P_{88} , o ponto de potencial hídrico associado à conclusão da embolia em angiospermas (URLI et al., 2013).

Por sua vez, as margens de segurança hidráulica para P_{50} , que é dada como a diferença entre o potencial mínimo da água medido em condições de campo e P_{50} é um índice frequentemente usado de resistência da planta à seca (MEINZER et al., 2009). Vale ressaltar que a resistência à seca é uma estratégia chave que afeta a distribuição de espécies ao longo de gradientes de disponibilidade de água, que atuam como filtros ambientais, incluindo ou excluindo espécies com base em suas características (ENGELBRECHT; KURSAR; TYREE, 2005; ESQUIVEL-MUELBERT et al., 2017).

A tolerância à seca também pode ser explicada por meio de mecanismos bioquímicos, incluindo defesa antioxidante, que são constituintes enzimáticos e não enzimáticos essenciais para manter o metabolismo da planta em níveis normais mesmo sob condições adversas (ASLAM et al. 2015; ILYAS et al. 2021). A maquinaria antioxidante da célula vegetal pode mitigar o estresse oxidativo, muitas vezes gerado devido à superprodução e consequente desequilíbrio de espécies reativas de oxigênio (ROS), que são moléculas tóxicas que induzem a oxidação de proteínas, lipídios de membrana e outros componentes celulares (FAROOQ et al. 2009). Para enzimas antioxidantes, superóxido dismutase (SOD), catalase (CAT),

peroxidase (POX) e ascorbato peroxidase (POX) são componentes orgânicos chave com papéis relevantes na manutenção da homeostase do estado redox intracelular (FANG; XIONG, 2015; GOBU et al. 2017; IRATO; SANTOVITO, 2021).

Diante dos efeitos tóxicos e os sintomas gerados pelo estresse hídrico em plantas, a aplicação exógena de brassinosteróides (BRs) se apresenta como um importante mecanismo de regulação (KRISHNA, 2003; JAGER et al., 2008). Brassinosteróides (BRs) são hormônios esteróides naturais envolvido em vários processos de crescimento e desenvolvimento de plantas (CLOUSE; SASSE, 1998). Entre os BRs, o 24-epibrassinolídeo (EBR) é usado com sucesso sob condições de campo (KHAMSUK et al., 2018). Estudos tem comprovado que, em condição de estresse hídrico, estes esteróides atuam na melhoria da eficiência do uso da água, taxa fotossintética e condutância estomática (LONE et al., 2022), aumento de atividades enzimáticas (JANGID; DWIVEDI, 2017) e regulação de trocas gasosase crescimento (BARROS JUNIOR et al., 2021). No entanto, não foram encontrados trabalhos na literatura que relatem a relação de Brassinosteróides com os atributos hidráulicos (P_{50} , P_{88} e margem de segurança hidráulica).

Nesse contexto, o entendimento de como as espécies arbóreas se comportam em condição de seca é fundamental para modelagens realistas da suscetibilidade dessas florestas frente às possíveis mudanças no clima. Isso é de extrema relevância considerando os inúmeros serviços ecossistêmicos prestados pela floresta e que podem ser comprometidos devido a eventos extremos de seca e enchentes (BRODRICK; ANDEREGG; ASNER, 2019; GAO et al., 2019). Entretanto, ainda existem muitas lacunas no conhecimento sobre o funcionamento das plantas frente à condição de seca e substâncias que podem mitigar os efeitos da seca no metabolismo.

Dentre as várias espécies sujeitas à seca na floresta Amazônica têm-se a *Carapa guianensis* (Andiroba, Meliaceae), uma planta amplamente distribuída nas florestas tropicais da Amazônia e outras regiões do Brasil, encontrada em florestas de terras altas e várzeas com porte de até 90 m de altura (GUARINO et al., 2014; FIRMINO et al., 2019). De alto valor econômico, esta espécie tem múltiplos usos e sua madeira tem alto valor para produtos sólidos, incluindo fabricação de móveis, construção, folheados e compensados, além de importância medicinal (VIEIRA et al., 2018; TSUKAMOTO et al., 2019; SOARES et al., 2021). Estudos com esta espécie sob condições de déficit hídrico vêm sendo desenvolvidos a fim de aprimorar o conhecimento sobre respostas desta importante espécie para o manejo florestal de grandes áreas na região amazônica (GONÇALVES et al. 2009; LIMA et al. 2015; SILVA et al., 2021).

Sendo assim, o objetivo desta pesquisa é responder se o EBR (24-epibrassinolídeo) pode melhorar a tolerância à deficiência hídrica em plantas jovens de *C. guianensis*, medindo atributos hidráulicos, respostas nutricionais, bioquímicas e fisiológicas e biomassa.

Testamos as hipóteses de que EBR: 1) melhora o estado hídrico da espécie, aumentando a margem de segurança hidráulica; 2) alivia os efeitos deletérios da seca no aparelho fotossintético; 3) estimula a defesa antioxidante em plantas sob déficit hídrico; 4) contribui para o incremento de biomassa em plantas submetidas à seca.

2. REVISÃO DE LITERATURA

2.1. Mudanças climáticas no contexto da Floresta Amazônica

Mudanças na biodiversidade atribuídas às mudanças climáticas já foram documentadas em uma ampla variedade de ecossistemas, incluindo os tropicais (DONEY et al., 2012; PALOMO, 2017; BARLOW et al., 2018). Os impactos dessas mudanças são inúmeros, e, na composição dos ecossistemas tropicais se dá principalmente ao fato de as temperaturas relativamente altas e a alta pluviosidade nessas regiões serem regidas primordialmente pelo clima, o qual permite utilizar e armazenar grandes quantidades de CO₂ por meio da produtividade das plantas (COX et al., 2013; TAYLOR et al., 2017). Dentre os ambientes tropicais mais vulneráveis nesse processo destaca-se a Floresta Amazônica, uma vez que detém a maior formação de floresta tropical no mundo, desempenhando um papel estratégico no sequestro de carbono (NUMATA et al., 2017; TORRES et al., 2020).

A floresta amazônica hospeda a maior floresta tropical e bacia de drenagem do planeta, sendo caracterizada por diferentes tipos de vegetação e elevada diversidade florística, e, portanto, é uma importante fonte de recursos naturais para o desenvolvimento socioeconômico (HOPKINS, 2007; CARDOSO et al., 2017; SORÍ et al., 2018). Além da grande riqueza de biodiversidade, presta uma ampla gama de bens e serviços ecossistêmicos em escalas locais e maiores (KUNZ et al., 2007), sendo fundamental para a ciclagem de nutrientes (LANUZA et al., 2018). A floresta amazônica funciona como reservatório global de carbono, com armazenamento de aproximadamente 120 bilhões de toneladas métricas de carbono na biomassa (TUNDISI et al., 2014), e, por conter em sua bacia importantes afluentes, conseqüentemente desempenha um importante papel no ciclo hidrológico e transporte de umidade local, regional e até mesmo continental (MARENGO, 2006; LOVEJOY; NOBRE, 2018).

A integridade da floresta amazônica é fundamental para o equilíbrio ambiental. No entanto, a região é vista como em grande risco por meio de interações sinérgicas com ameaças, como desmatamento, fragmentação de floresta, incêndios detectados, e, secas regionais que podem se intensificar e se tornar mais frequentes neste século como resultado da variabilidade e mudanças climáticas (BETTS; MALHI; ROBERTS, 2008; DAVIDSON et al., 2012; MARENGO et al., 2018).

2.2. Seca e estresse hídrico

A seca é definida pela disponibilidade insuficiente de água para as plantas, consequência do esgotamento da umidade do solo pela baixa precipitação e altas taxas de evapotranspiração (PAROLIN et al., 2010). Em condições naturais, a seca na Amazônia é ocorrente, uma vez que o clima da bacia é sazonal e desuniforme, ou seja, em geral, algumas áreas possuem menor precipitação anual e estações secas mais fortes do que outras áreas, sendo assim, as secas tropicais são frequentemente associadas a ciclos climáticos plurianuais e à sazonalidade (LAURANCE; BRUCE WILLIAMSON, 2001; CORLETT, 2016).

Embora seja natural, espera-se que essas secas tropicais aumentem em frequência, extensão e gravidade com as mudanças climáticas, aumentando a probabilidade de ocorrência de eventos extremos (WILLIAMS; JACKSON; KUTZBACH, 2007; MALHI et al., 2009). Muito tem se discutido sobre as causas de eventos extremos de seca na Floresta Amazônica e as mesmas são comumente atribuídas a eventos como o El Niño Oscilação Sul (ENSO) e a anomalias de temperatura no Atlântico Norte tropical (ZENG et al., 2008; MARENGO et al., 2011; TOMASELLA et al., 2011; JIMÉNEZ-MUÑOZ et al., 2016; PANISSET et al., 2018; ARAGÃO et al., 2018).

Os efeitos da seca sobre a estrutura e função do ecossistema na Amazônia são potencialmente grandes (METCALFE et al., 2010). Além de afetar diretamente a biodiversidade e os povos amazônicos (FENG et al., 2021), esses efeitos, em um macronível podem ser diversos, como: a diminuição da taxa de acúmulo de biomassa lenhosa acima do solo; alteração da composição de espécies com mortalidade de árvores e alteração do ciclo do carbono e hídrico (MALHI et al., 2009; CORLETT, 2016).

Apesar de existirem muitos estudos, como os supramencionados, à respeito dos efeitos da seca em nível ambiental, ainda há lacunas na compreensão dos efeitos da seca de plantas em nível funcional. Sabe-se que as plantas enfrentam o desafio de extrair água dos solos e transportá-las até as folhas para realizar seus processos metabólicos, no entanto, plantas sujeitas à estresse hídrico apresentam falhas na condutividade hidráulica e consequente disfunções temporárias ou permanentes (PASSIOURA, 1988; STEUDLE, 2000; TRIFILÒ et al., 2011).

O estresse hídrico é mensurável nas plantas por meio de medidas como o potencial hídrico do xilema, uma variável que é principalmente determinada por pressão no fluido do xilema e se torna cada vez mais negativa durante a seca. À medida que as plantas desidratam,

a perda do turgor celular causa poros na superfície da folha a fim de fechá-la, o que diminui acentuadamente as trocas gasosas, a taxa de diminuição do potencial hídrico do xilema e a desidratação da planta, tornando, dessa forma, a seiva do xilema vulnerável a formação de embolia por cavitação (TYREE, T.; DIXON, 1986; TYREE, M T; SPERRY, 1989; OLIVEIRA; DE GUALTIERI; BOCCHESI, 2011; CHOAT et al., 2018). Esta embolia induzida por cavitação reduz a condutividade hidráulica do xilema e leva a diminuição das taxas de assimilação de carbono pela fotossíntese, o que impacta negativamente a fotossíntese e a produtividade do ecossistema (TYREE, M T; SPERRY, 1989; HÖLTTÄ et al., 2009; NARDINI; LO GULLO; SALLES, 2011; TRIFILÒ et al., 2011; PALJAKKA et al., 2020).

O fechamento estomático parcial, ademais, é uma das primeiras respostas de plantas ao déficit hídrico e pode ocorrer em função da vulnerabilidade do xilema ao embolismo (NARDINI; SALLES, 2000; SANTOS et al., 2018) , uma vez que limita diminuições excessivas no potencial hídrico da planta, garantindo que a demanda de água das folhas não exceda a capacidade de abastecimento do sistema hidráulico. O controle estomático é uma estratégia para regular as trocas gasosas, reduzir as perdas de água e a absorção de dióxido de carbono a fim de reduzir os danos ocasionados pela limitação hídrica (BECKER; MEINZERT; WULLSCHLEGER, 2000; FAROOQ et al., 2009; MARTIN-STPAUL; DELZON; COCHARD, 2017).

2.3. Respostas funcionais de plantas

Sabe-se que para tolerar a seca, as plantas apresentam uma série de respostas que podem ser medidas por meio de atributos funcionais, os quais são caracterizados como são quaisquer características morfológicas, fisiológicas ou fenológicas mensuráveis no nível individual (VIOLLE et al., 2007). Essas características têm sido foco de estudo em diferentes grupos de organismos para responder questões ecológicas, desde o nível de indivíduo até o funcionamento ecossistêmico (MCGILL et al., 2006; DING et al., 2017). Nesse sentido, quando se estuda as respostas ecofisiológicas das espécies, é possível utilizar os atributos funcionais como bons elementos preditores de uso e aquisição de recursos, ou seja, refletem a eficiência adaptativa do comportamento dos indivíduos em resposta as condições do ambiente, como a seca (VIOLLE et al., 2007).

Dentre os atributos funcionais, os atributos hidráulicos, se mostram como importantes ferramentas para entender a resistência das espécies à seca. O potencial hídrico

em que ocorre perda de 50% da condutividade hidráulica do xilema (P_{50}) tem sido amplamente usado como atributo funcional hidráulico para estimar e comparar a vulnerabilidade das espécies vegetais. É o ponto de queda mais rápido, descrito como a parte mais íngreme da curva de vulnerabilidade à cavitação (CHOAT et al., 2012; ANDEREGG, 2016), enquanto que o P_{88} representa um ponto no qual as plantas não conseguem recuperar o seu funcionamento e parece ser o valor que reflete o risco inerente à falha hidráulica crítica para a maioria das angiospermas (CHOAT et al., 2012; SCHOLZ et al., 2014). Essas características funcionais capturam eixos de características hidráulicas importantes, como relações hídricas, resistência à embolia e margem de segurança hidráulica (LIU et al., 2020).

A margem de segurança hidráulica representa a diferença entre o potencial mínimo atingido pela espécie e o P_{50} e P_{88} (CHOAT et al., 2012a), no qual uma maior margem de segurança hidráulica pode estar relacionada a uma maior sobrevivência em condições mais extremas de seca. Outros parâmetros hidráulicos como a vulnerabilidade à cavitação estimados a partir do potencial hídrico são de suma importância para compreensão da adaptação da planta às variações das condições ambientais. Curvas de vulnerabilidade são tipicamente obtidas pela medição da condutividade hidráulica e do potencial hídrico do xilema para um tempo determinado de exposição dos ramos à desidratação. As curvas de vulnerabilidade das plantas, em conjunto com sua arquitetura hidráulica, podem fornecer uma visão considerável das suas relações hídricas e "estratégias" de tolerância à seca. A partir delas é possível extrair alguns parâmetros importantes na compreensão da resistência à cavitação pelas espécies, destes o P_{50} sem dúvida é o mais emblemático (ROWLAND et al., 2015; ANDEREGG et al., 2016) indicando o potencial hídrico em que a planta perde 50% da sua condutividade hidráulica. A cavitação um aspecto fundamental das relações hídricas das plantas e tem múltiplas implicações em sua anatomia, fisiologia e ecologia (COCHARD et al., 2002) uma vez que interfere na formação e desenvolvimento do xilema e conseqüentemente na formação e desenvolvimento de toda planta por sua interferência na assimilação de carbono.

Atributos que otimizam esses processos desempenham papel essencial na fotossíntese e crescimento, influenciando no transporte de água e conseqüentemente na sensibilidade da planta ao estresse hídrico, podendo ainda revelar diferenças ecológicas entre as espécies, apontando para os efeitos das condições ambientais no transporte de água

no xilema e indicando o grau em que a produtividade é limitada pelas propriedades do xilema (MELCHER et al., 2012).

2.4.Brassinosteróides

Estudos têm relatado que fitohormônios podem mitigar os efeitos de estresse hídrico em plantas (JAKAB et al., 2005; DASZKOWSKA-GOLEC; SZAREJKO, 2013; SHI et al., 2014; CHHAYA et al., 2021; JOGAWAT et al., 2021). Dentre tais fitohormônios, brassinosteróides têm ganhado destaque por se mostrar eficaz na modulação de uma série de respostas de plantas, como alívio de estresse oxidativo (BEHNAMNIA; KALANTARI; REZANEJAD, 2009), melhoria nas relações hídricas e trocas gasosas (FAROOQ; WAHID; BASRA; et al., 2009a) e aumento significativo no crescimento e biomassa (LI et al., 2012; KHAN et al., 2020).

Os brassinosteróides (BRs) formam um grupo de hormônios esteroides vegetais encontrados em diferentes concentrações em todos os órgãos vegetais, apresentando maiores teores em tecidos mais jovens (BAJGUZ; HAYAT, 2009; BORCIONI; NEGRELLE, 2012; FRIDMAN; SAVALDI-GOLDSTEIN, 2013). Pelo menos 69 BRs quimicamente diferentes foram encontrados em todo o reino vegetal, incluindo plantas terrestres e algas verdes. O BR mais bioativo do grupo é o Brassinolide (BL) e é frequentemente usado em experimentos de bioensaio em laboratório em uma escala experimental em baixas concentrações, na forma de 24-epibrassinolide (EBR) (VARDHINI; ANJUM, 2015).

Embora diversos trabalhos relatem a importância do papel de brassinosteróides na mitigação de efeitos deletérios em plantas, não encontramos estudos que relatassem sobre ações deste fitohormônio em mitigar os efeitos da seca e a relação com atributos funcionais, especificamente hidráulicos.

2.5. *Carapa guianensis* Aubl. (Andiroba)

Será utilizado para o presente estudo mudas de *Carapa guianensis* (Andiroba, Meliaceae). Vale ressaltar que mudas podem ser mais vulneráveis à mortalidade impulsionada por hidráulica do que os adultos, indicando que as características hidráulicas das mudas podem ser importantes na modelagem das mudanças na vegetação com as mudanças climáticas

(PRATT et al. 2014). Escolhemos trabalhar com esta espécie por ser uma das hiperdominantes na Amazônia (TER STEEGE et al., 2013; 2016) e, espécies de plantas com ampla distribuição geográfica e consideradas abundantes nas florestas tropicais são bons modelos de estudo, auxiliando na previsão de impactos causados pelas mudanças climáticas e subsidiando estratégias de conservação e uso sustentável (SILVA et al., 2018).

Carapa guianensis Aubl. (Meliaceae) é uma espécie de uso múltiplo e com potencial madeireiro, conhecida tradicionalmente na Amazônia como Andiroba, devido ao óleo extraído das sementes (FERRAZ et al., 2002). A espécie pode atingir até 30 metros de altura e possui uma copa ampla e arredondada, com folhas compostas e flores brancas ou amareladas, que surgem de inflorescências axilares. Suas sementes são recobertas por uma casca dura, de onde é extraído um óleo de cor amarelada e odor forte, utilizado na medicina popular e na indústria cosmética (LORENZI; MATOS, 2008).

A coleta das sementes da andiroba é realizada na época da frutificação, que ocorre entre janeiro e março. As sementes devem ser coletadas diretamente do chão, evitando a utilização de ferramentas, que podem danificar o fruto e prejudicar a germinação das sementes. As sementes devem ser beneficiadas imediatamente após a coleta, retirando-se a casca dura e deixando-as secar à sombra por alguns dias (EMBRAPA, 2016).

Além de sua utilização na medicina popular e na indústria cosmética, a andiroba é uma espécie de grande importância econômica e ecológica na Amazônia, sendo utilizada na produção de móveis, construção civil, combustível e como fonte de alimento para animais silvestres. No entanto, a exploração desordenada da espécie pode levar à sua extinção e ao desequilíbrio ambiental (PIRES et al., 2014).

Para garantir a sustentabilidade da exploração da andiroba, é fundamental que sejam adotadas práticas de manejo florestal que garantam a regeneração da espécie e a conservação da floresta. Além disso, é importante valorizar o conhecimento tradicional das comunidades locais, que têm um papel fundamental na conservação da biodiversidade e na preservação dos recursos naturais (FREITAS et al., 2009).

Estudos experimentais e de campo realizados com esta espécie mostram algumas respostas que a espécie apresenta em condições de seca (GONÇALVES et al., 2009; LIMA et al., 2015). No entanto, estes estudos costumam ser pontuais e quantificam apenas algumas características e nenhum aborda como ajustes hidráulicos podem influenciar no crescimento da espécie sob condição de déficit hídrico, tampouco a ação de hormônios vegetais, como os Brassinosteróides.

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MANUSCRITO

FORMATADO SEGUINDO AS NORMAS DA REVISTA *PHYSIOLOGIA PLANTARUM*

24-Epibrassinolide alleviates the drought effects in young *Carapa guianensis* plants, improving the hydraulic safety margin, gas exchange and antioxidant defence

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Author contribution statement

AKSL and GST were the advisors of this research, planned all phases of the research and critically revised the manuscript. ATR and YCPM conducted the experiment in the greenhouse and performed physiological, biochemical and morphological determinations, wrote and edited the manuscript, while BLB nutritional analysis, as well as ATR and KCS measured hydraulic traits. All authors read and approved the final version of the manuscript.

Data availability statement

Data are available upon request to the corresponding author.

Conflict of interest

The authors declare that they have no competing interests.

Abstract

Climate change is increasing the frequency of extreme events, such as droughts, causing limitations on growth and yield in plants. *Carapa guianensis* is a tree widely distributed in the tropical forests of the Amazon. In view of the deleterious effects generated by water deficit in plant metabolism, the exogenous application of plant growth regulators, such as 24-epibrassinolide (EBR) appears as a possible solution, because this molecule is organic, eco-friendly and biodegradable. This research is first result in the literature on possible EBR roles on hydraulic safety margin, physiological behavior and metabolism in *C. guianensis* plants exposed to drought. The objective of this research is to answer if EBR can improve tolerance to water deficiency in young *C. guianensis* plants, measuring hydraulic attributes, nutritional, biochemical and physiological responses and biomass. The experiment was randomized with four treatments, including two water conditions (control and water deficit) and two concentrations of brassinosteroids (0 and 100 nM EBR, described as – EBR and + EBR, respectively). This steroid increased the values of water potential and hydraulic safety margin. Positive results were found in gas exchange, in which EBR increased CO₂ fixation and stimulated stomatal performance. Additionally, this plant growth regulator stimulated antioxidant defense (superoxide dismutase, catalase, ascorbate peroxidase and peroxidase). Therefore, our results prove that pre-treatment with EBR improved drought tolerance in young *C. guianensis* plants.

Keywords Amazon tree; brassinosteroids; peroxidase; photosynthesis; water deficit

Abbreviations

APX	Ascorbate peroxidase
BRs	Brassinosteroids
Ca	Calcium
Car	Carotenoids
CAT	Catalase
Chl <i>a</i>	Chlorophyll <i>a</i>
Chl <i>b</i>	Chlorophyll <i>b</i>
C_i	Intercellular CO ₂ concentration
<i>E</i>	Transpiration rate
EBR	24-epibrassinolide
EL	Electrolyte leakage
ETR	Electron transport rate
ETR/ P_N	Ratio between the apparent electron transport rate and net photosynthetic rate
EXC	Relative energy excess at the PSII level
F_0	Minimal fluorescence yield of the dark-adapted state
Fe	Iron
F_m	Maximal fluorescence yield of the dark-adapted state
F_v	Variable fluorescence
F_v/F_m	Maximal quantum yield of PSII photochemistry
H ₂ O ₂	Hydrogen peroxide
LDM	Leaf dry matter
MDA	Malondialdehyde
Mg	Magnesium
Mn	Manganese
NPQ	Nonphotochemical quenching
O ₂ ⁻	Superoxide
P	Phosphorus
PAD	Percentage air discharge
P_N	Net photosynthetic rate
P_N/C_i	Instantaneous carboxylation efficiency
POX	Peroxidase
q _P	Photochemical quenching
RDM	Root dry matter
SDM	Stem dry matter
SOD	Superoxide dismutase
TDM	Total dry Matter
Total Chl	Total chlorophyll
WUE	Water-use efficiency

Zn	Zinc
Φ_{PSII}	Effective quantum yield of PSII photochemistry
Ψ_w	Leaf water potential

Introduction

Climate changes in recent years are increasing the frequency of extreme events, such as droughts and heat waves in many areas of the globe, limiting growth and productivity in many ecosystems (He et al. 2014; Zhu and Gong 2014). Tropical forests are one of the most vulnerable ecosystems, being necessary attention due to the harbor a large amount of terrestrial biodiversity and providing a range of ecosystem services, these forests represent about half of the global terrestrial carbon stock, absorbing about 15% of anthropogenic carbon emissions annually (Gordon 2008; Huntingford et al. 2013; Treuhaft et al. 2015; Ummenhofer and Meehl 2017; Yang et al. 2018; Kour et al. 2021).

The Amazon is considered the largest tropical forest cover in the world and plays a significant role in climate regulation by containing approximately 10% of the terrestrial carbon pool and through evapotranspiration (Hoorn et al. 2010). This ecosystem represents one of the most critical biodiversity reservoirs on the planet, due to its large area, diversity of soils, flora and fauna (Fearnside 2021). The number of trees was estimated at 3.9×10^{11} , with approximately 6,000 to 16,000 species that are distributed in upland, floodplain and flooded forests (Ter Steege et al. 2013; Myster 2016; Cardoso et al. 2017). Amazon has seasonal cycles with natural dry seasons, being explained by the equatorial climate (Nobre et al. 2013; Hashimoto et al. 2021). Although droughts in the Amazon are naturally occurring and influenced by seasonal cycles, severe droughts influenced by climate change have been recurring in this region. Recent research reveals that in the early 21st century, the region experienced two unprecedented drought events in 2005 and 2010 (Marengo et al. 2008, 2011) and more recently in 2015 (Jiménez-Muñoz et al. 2016). Future scenarios indicate that these extreme events are likely to be more frequent in the Amazon region (Dai 2013; Duffy et al. 2015; Panisset et al. 2018). Additionally, drought events often interfere the composition of plant species in the region, being related to limited water supply and hydraulic failures, affecting also the carbon balance (Gordon 2008; Phillips et al. 2009; Enquist and Enquist 2011).

Several plants are exposed to drought in the Amazon rainforest, including *Carapa guianensis*, a tree widely distributed in the tropical forests of the Amazon and other regions of Brazil, found in upland forests and floodplains, reaching height up to 40 meters (Sakamoto et al. 2013; Londres et al. 2017; Firmino et al. 2019). This tree have economic importance and multiple uses, with wood presenting high value for solid products, including furniture manufacturing, construction, veneer and plywood, as well as medicinal importance (Vieira et al. 2018; Tsukamoto et al. 2019). Studies with this species under conditions of water deficit have been developed in order to improve knowledge about responses of this important species for the forest management of large areas in the Amazon region (Costa et al. 2010; Carvalho et al. 2013; Cruz et al. 2013). Functional attributes are essential to understand the plant responses under extreme events, such as drought, which have been used to describe the variation in morphophysiological characters of different plant species (Mason et al. 2005; Villéger et al. 2008; Mammola et al. 2021). In other words, understanding

the hydraulic, biochemical and physiological attributes will be more efficient to predict the impacts of climate change on plants (Choat et al. 2012a).

Drought tolerance can be achieved through biochemical mechanisms, including antioxidant defense, which are enzymes and non-enzymatic constituents essential to maintain plant metabolism at normal levels even under adverse conditions (Aslam et al. 2015; Ilyas et al. 2021). The plant cell antioxidant machinery can mitigate oxidative stress, often generated due to overproduction and consequent imbalance of reactive oxygen species (ROS), which are toxic molecules that induce oxidation of proteins, membrane lipids and other cellular components (Farooq et al. 2009b). For antioxidant enzymes, superoxide dismutase (SOD), catalase (CAT), peroxidase (POX) and ascorbate peroxidase (POX) are organic components key with relevant roles in maintaining the homeostasis of the intracellular redox state (Fang and Xiong 2015; Gobu et al. 2017; Irato and Santovito 2021).

Lower susceptibility to cavitation in trees can be also associated with drought tolerance mechanisms. Cavitation is characterized by a reduction in water availability and an increase in tension in the xylem vessels, which causes embolism and limits the ability to replace the water lost during transpiration process, limiting the gas exchange and plant growth (Sorek et al. 2021). One of the most used parameters in determining vulnerability to embolism is the P_{50} , which consists of the water potential value where 50% of the hydraulic conductivity is lost and has been pointed out and generally used as one of the main mortality indices in plant species subjected to drought (Choat et al. 2012b; Hammond et al. 2019). In addition, the hydraulic safety margin has been identified as the best predictor to understand the vulnerability of a plant species to water restriction, because it indicates a range where the plants are how far away for a hydraulic failure to occur, and the closer to P_{50} , the more vulnerable the (Meinzer et al. 2009; Anderegg et al. 2016). Hydraulic attributes such as these allow the understanding of drought tolerance mechanisms, mainly because most forest communities operate within a narrow margin of hydraulic safety, being extremely vulnerable to climatic extremes (Choat et al. 2012a).

Brassinosteroids (BRs) are steroids involved in various plant growth and development processes (Manghwar et al. 2022). Among BRs, 24-epibrassinolide (EBR) is natural molecule and ecologically viable, being successfully used under field conditions (Khamsuk et al. 2018). Studies have shown that, under water deficit conditions, these steroids work to improve water use efficiency, photosynthetic rate and stomatal conductance (Lone et al. 2022), increase enzymatic activities (Jangid and Dwivedi 2017) and regulate exchange gas and growth (Barros Junior et al. 2021).

Based in this overview, the exogenous application of brassinosteroids (BRs) appears as relevant molecule with capacity to improve metabolism (Jager et al. 2008), aiming to mitigate the deleterious effects and symptoms generated by the water deficiency in plants. However, this research is first result in the literature on possible BRs roles on hydraulic safety margin, physiological behavior and metabolism in *C. guianensis* plants exposed to drought. Therefore, the objective of this research is to answer if EBR can improve tolerance to water deficiency in young *C. guianensis* plants, measuring hydraulic attributes, nutritional, biochemical and physiological responses and biomass.

Materials and Methods

Location and growth conditions

The experiment was performed at the Campus of Paragominas of the Universidade Federal Rural da Amazônia, Paragominas, Brazil (2°55' S, 47°34' W). The study was conducted in a greenhouse with the temperature and humidity controlled. The minimum, maximum, and median temperatures were 28, 33 and 26.9 °C, respectively. The relative humidity during the experimental period varied between 60% and 80%. Average maximum photosynthetic photon flux density was 755 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (plant canopy), and photoperiod of 12 h.

Plant material, containers, substrate and fertilization

Young *Carapa guianensis* plants with 6 months old were selected and placed in 5.0 L containers filled with Plantmax™ substrate. These containers with holes in the bottom for draining excess water were used, with one plant per container. Substrate Plantmax™ presents pH 5.8, electrical conductivity 1.3 dS cm^{-1} , density 0.65 kg L^{-1} , organic matter 4.5 %, cation exchange capacity 7.5 cmol (+) kg^{-1} , moisture 50 % of the total substrate dry weight and 35 % of water holding capacity. Fertilization was implemented in agreement with (Brasil et al. 2020), considering the previous chemical analysis of the substrate and nutritional requirements of the *C. guianensis* plants.

Experimental design

The experiment was randomized with four treatments, including two water conditions (control and water deficit) and two concentrations of brassinosteroids (0 and 100 nM EBR, described as – EBR and + EBR, respectively). The experiment comprised six replicate individuals per treatment.

Irrigation, 24-epibrassinolide (EBR) application and plant evaluation

All young plants were irrigated daily for 60 min at 07:30 to 08:00 h and 17:30 to 18:00 h. Irrigation within the greenhouse was performed by a microsprinkler system at a flow rate of 10 L h^{-1} . These plants were treated with 24-epibrassinolide (EBR) by six weeks (days 0-42 after the start of the experiment). This treatment was applied at 7-d intervals, being used EBR or Milli-Q water (containing a proportion of ethanol that was equal to that used to prepare the EBR solution). The 0 and 100 nM EBR (Sigma-Aldrich, USA) solutions were prepared by dissolving the solute in ethanol followed by dilution with Milli-Q water [ethanol:water (v/v) = 1:10,000] (Ahammed et al. 2013). The water deficit was induced by irrigation suspension for twenty-one days (21th to 42th day after experiment implementation). On day 42 of the experiment, physiological and morphological parameters were measured for all plants, and leaf tissues were harvested for biochemical and nutritional analysis.

Measurement of chloroplastic pigments, chlorophyll fluorescence and gas exchange

Pigments were quantified using a spectrophotometer (model UV-M51; Bel Photonics), according to the methodology of Lichtenthaler and Buschmann (2001). Chlorophyll fluorescence was measured using a modulated chlorophyll fluorometer (model OS5p; Opti-Sciences) in fully expanded leaves under light. Preliminary tests determined the location of the leaf, the part of the leaf and the time required to obtain the

greatest Fv/Fm ratio; therefore, the acropetal third of leaves that were in the middle third of the plant and adapted to the dark for 30 min was used in the evaluation. The intensity and duration of the saturation light pulse were 7,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 0.7 s, respectively. The gas exchange was evaluated using an infrared gas analyser (model LCPro+; ADC BioScientific) in all plants under constant conditions of CO₂ concentration, photosynthetically active radiation, air-flow rate and temperature in a chamber at 460 $\mu\text{mol mol}^{-1}$ CO₂, 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, 300 $\mu\text{mol s}^{-1}$ and 28 °C, respectively, between 10:00 and 12:00 h.

Leaf water potential

The water potential (Ψ_w) was measured on 42th day after experiment implementation, using a leaf that was totally expanded and was located in the middle region of the plant and exposed to light, during a period between 11:30 and 12:00 h and corresponding to the midday potential. One leaf per plant and five plants per treatment were measured with a pressure chamber (PMS Instrument Company, model 600). It is based on the technical aspects of the pressure chamber (Scholander et al. 1964), according to the procedure of Turner (1988).

Cavitation vulnerability curve and hydraulic safety margin

For the construction of the cavitation vulnerability curve, five young *C. guianensis* plants were selected. These individuals were used for this physiological characteristic were not accounted for in the experimental design, as this characteristic was quantified only at the beginning of the experiment (before submission to water deficit). Embolism vulnerability curves relate the water potential of the xylem to degree of embolism in the xylem, determining the percentage loss of conductivity (in relation to the maximum hydraulic conductivity) (Sperry et al. 1988). The potential at which the plant loses 50% (P_{50}) and 88% (P_{88}) of its conductivity was used as a descriptor of resistance to embolism (Choat et al. 2012a). Embolism vulnerability curves were measured by percentage loss of xylem conductivity (PLC) and xylem water potential. The PLC was estimated from the percentage of air discharge (PAD) by the pneumatic method (Pereira et al. 2016). To induce cavitation, we used the bench dehydration method (Sperry et al. 1988). To obtain water potential values, a branch leaf was cut and its water potential was measured with a pressure chamber (PMS Instrument Company, model 1505D). To prevent air from entering the branch where the petiole was cut, sealing instruments were used, such as white glue and parafilm. The hydraulic safety margin was based on the difference between the P_{50} , potential in which the plant loses 50% of the hydraulic conductivity, and P_{min} , minimum water potential (more negative) measured in treatments submitted to water deficit with EBR and water deficit without EBR (Choat et al. 2012a).

Determining of nutrients

Samples with 100 mg of milled samples were weighed in 50-mL conical tubes (Falcon^R, Corning, Mexico) and pre-digested (48 h) with 2 ml of sub boiled HNO₃ (DST 1000, Savillex, USA). After, 8 ml of a solution containing 4 ml of H₂O₂ (30% v/v, Synth, Brasil) and 4 ml of ultra-pure water (Milli-Q System, Millipore, USA) were added, and the mixture was transferred to a Teflon digestion vessel (Paniz et al. 2018), closed and heated in a block digester (EasyDigest®, Analab, France) (Paniz et al. 2018). The determinations of

Ca, P, Mg, Mn, Fe and Zn. were carried out using an inductively coupled plasma mass spectrometer (ICP-MS 7900, Agilent, USA).

Extraction of antioxidant enzymes, superoxide and soluble proteins

Antioxidant enzymes (SOD, CAT, APX and POX), superoxide and soluble proteins were extracted from leaf tissues according to the method of (Badawi et al. 2004). Quantification of the total soluble proteins was performed using the method described by (Bradford 1976). Absorbance was measured at 595 nm, using bovine albumin as a standard. SOD assay (EC 1.15.1.1) was measured at 560 nm (Giannopolitis and Ries 1977). One SOD unit was defined as the amount of enzyme required to inhibit 50% of the NBT photoreduction. The SOD activity was expressed in unit mg^{-1} protein. CAT assay (EC 1.11.1.6) was measured at 240 nm (Havir and McHale 1987). The CAT activity was expressed in $\mu\text{mol H}_2\text{O}_2 \text{mg}^{-1}$ protein min^{-1} . APX assay (EC 1.11.1.11) was measured at 290 nm (Nakano and Asada 1981). The APX activity was expressed in $\mu\text{mol AsA mg}^{-1}$ protein min^{-1} . POX assay (EC 1.11.1.7) measured at 470 nm (Cakmak and Marschner 1992). The POX activity was expressed in $\mu\text{mol tetraguaiacol mg}^{-1}$ protein min^{-1} .

Determination of superoxide concentration

To determine O_2^- , 1 ml of extract was incubated with 30 mM phosphate buffer [pH 7.6] and 0.51 mM hydroxylamine hydrochloride for 20 min at 25 °C. Then, 17 mM sulphanilamide and 7 mM α -naphthylamine were added to the incubation mixture for 20 min at 25 °C. After the reaction, ethyl ether was added in the identical volume and centrifuged at $3,000 \times g$ for 5 min. The absorbance was measured at 530 nm (Elstner and Heupel 1976).

Nonenzymatic compounds and electrolyte leakage

Nonenzymatic compounds (H_2O_2 and MDA) were extracted as described by Wu et al. (2006). Briefly, a mixture for extraction of H_2O_2 and MDA was prepared by homogenizing 500 mg of fresh leaf materials in 5 mL of 5% (w/v) trichloroacetic acid. To measure H_2O_2 was measured at 390 nm (Velikova et al. 2000). MDA was determined by the method of Cakmak and Horst (1991), with minor modifications and using an extinction coefficient of $155 \text{ mM}^{-1} \text{ cm}^{-1}$. Electrolyte leakage was measured according to the method of Gong et al. (1998) with minor modifications.

Measurements of biomass

The biomass of root, stem and leaf was measured based on constant dry weight (g), after drying in a forced-air ventilation oven at 65 °C.

Data analysis

The data had the homogeneity of variances tested and subsequently were submitted to one-way ANOVA and applied Scott–Knott test at a probability level of 5% (Steel et al. 2006). All statistical procedures used the AgrostatTM software.

Results

24-Epibrassinolide improves the hydraulic safety margin

Stress caused by water deficit led to reductions in Ψ_w (Fig. 1). Treatment submitted to drought without EBR presented value of -4.5 MPa. However, spray EBR in plants under water deficit treatment induced a significant increase of 29% in Ψ_w , when compared to the same treatment without EBR. The P_{50} and P_{88} obtained in young *C. guianensis* plants used this experiment were -2.3 MPa and -3.4 MPa, respectively. To hydraulic safety margin, individuals submitted to the water deficit without EBR presented P_{min} -4.5 \pm 0.30 MPa, while that the treatment sprayed with EBR and exposed to water limitation presented P_{min} of -3.2 \pm 0.04 MPa (Fig. 2). The hydraulic safety margin was negative in both treatments, however, being higher for plants treated with EBR.

Exogenous EBR increased the nutrient contents in plants exposed to water deficit

Water deficit caused reductions in nutrient contents of all tissues evaluated (root, stem and leaf) (Table 1). However, plants exposed to deficit and treated with EBR had increased the Ca, P, Mg, Mn, Fe and Zn contents by 6%, 6%, 9%, 35%, 98% and 5% in the root; of 13%, 10%, 4%, 17%, 8% and 14% in stem and 10%, 11%, 8%, 11%, 44% and 19% in leaf, respectively, when compared to equal water deficit without EBR.

EBR application alleviates the deleterious effects on photosynthetic apparatus

Water deficit provoked significant decreases photosynthetic pigments (Table 2). Plants exposed to deficit + EBR had increases in Chl *a* (14%), Chl *b* (20%), Car (20%) and total Chl (15%), and a decrease in Chl *a*/Chl *b* (4%) and Chl total/Car (4%), when compared to the same treatment without EBR. To chlorophyll fluorescence, water deficit increased F_0 and reduced F_v , F_m , F_v/F_m (Fig. 3). However, the application of EBR exogenous promoted significant increases in F_v , F_m , F_v/F_m of 22%, 8% and 13%, respectively, and in F_0 , reduction of 10%, in relation to water deficit without EBR. Plants subject to water deficit and sprayed with EBR presented positive repercussions (Table 2). Φ_{PSII} had an increase of 24%, q_p of 12% and ETR of 24%, while there were reductions in NPQ (41%), EXC (9%) and ETR/ P_N (10%), when compared to the same treatment without EBR. In gas exchange, water deficit induced negative impacts (Table 2). Plants subjected to water deficit and EBR spray resulted in increases of 37%, 27%, 53%, 8% and 46% in the values of P_N , E , g_s , WUE and P_N/C_i , however, reduction in C_i (6%), when compared to water deficit without EBR.

Steroid stimulates the antioxidant defense in plants under water deficit

Plants subjected to water deficit presented increases in studied antioxidant enzymes (Fig. 4). Plants treated with EBR and subjected to water deficit presented significant increases in SOD (19%), CAT (15%), APX (23%) and POX (78%), when compared to equal water deficit without EBR. Plants exposed to water deficit suffered increases in oxidative compounds (Fig. 4). Plants under water deficit and sprayed with EBR had reductions of 15%, 29%, 16% and 26% in O_2^- , H_2O_2 , MDA and EL, respectively, compared to the same treatment without EBR.

Drought impacts on biomass were partially reversed in plants pre-treated with EBR

The stress caused by the water deficit resulted in significant decreases in the variables related to growth (Fig. 5). However, plants sprayed with EBR showed significant increases of 21% and 8% in LDM and TDM, respectively, and an increase of 1% and 3% in SDM and RDM, compared to the same treatment without EBR.

Discussion

The higher Ψ_w observed for plants pretreated with EBR and exposed to water deficit, comparing with individuals without EBR spray, revealed that this steroid improved the water status in leaf tissue, being these results explained by the synergic actions on root biomass and stomatal regulation in leaves, contributing to alleviate the stress simulated on gas exchange and growth. This research detected that the EBR maximized the RDM, being this organ intrinsically connected to uptake and maintenance of the water supply to essential processes, including photosynthesis and respiration and transpiration. Associating the P_{50} and the water potential obtained in each treatment, we observed a higher margin of hydraulic safety for individuals sprayed with EBR, suggesting that plants pretreated with EBR tend to regulate their water potential within a narrow range, reducing the risk of xylem cavitation caused by excessive tension on hydraulic system (Choat et al. 2012a). The hydraulic safety margin can be defined by the difference between P_{min} and P_{50} , revealing the proximity between the hydraulic functioning of a species and the steepest point of its vulnerability curve to xylem cavitation. In other words, the point of potentially catastrophic embolism for the plant hydraulic system (Johnson et al. 2012). Simultaneously, plants sprayed with EBR improved the water efficiency with clear beneficial repercussion on gas exchange, being found higher values in WUE and P_N , proved in this research. Other point relevant, antioxidant defense was stimulated after pretreatment with EBR, being these biochemical responses regulated by the SOD, CAT, APX and POX enzymes, representing an efficient mechanism against species reactive oxygen overproduced during water deficit. Vieira et al. (2022) evaluating the effect of BRs application on *Handroanthus serratifolius* under conditions of water restriction reported that this molecule increased the Ψ_w .

EBR spray improved the photosynthetic pigments (Chl *a*, Chl *b*, Car and total Chl). This fact suggests that this steroid probably increased the biosynthesis of enzymes responsible for the formation of chlorophyll combined with higher protection of the photosynthetic machinery against the harmful effects of the reactive oxygen species (ROS) (Prasad et al. 2005; Janeczko et al. 2007; Niu et al. 2016; Wang et al. 2016), being corroborated by the increases in antioxidant enzymes (CAT and APX) and photoprotective pigments, including Car, and a decrease in MDA, results also detected in this study. Additionally, higher values verified in chloroplastic pigments after EBR treatment is associated with increases in Mg contents found in this research, being an essential element during chlorophyll molecule formation (Siddiqui et al. 2018a). Li et al. (2012) studying the effects of 0.1 μM of EBR on *Chorispora bungeana* in drought condition showed significant improvement in Chl *a* and Chl *b* contents. Perez-Borroto et al. (2022) investigating the effects of DI-31, a EBR analogue, in *Glycine max* plants observed an increase in Car content in plants treated with the phytohormone.

Water deficit caused negative impacts on chlorophyll fluorescence, including an increase in the F_0 value, suggesting that the PSII reaction centers were compromised or the transfer of excitation energy from

the antenna to the reaction centers was impaired (Hu et al. 2018). The decrease in F_v , F_m , F_v/F_m corroborates this damage to the PSII, indicating that secondary injuries to the photosynthetic apparatus occurred mainly caused by photoinhibition (Murchie and Lawson 2013; Macedo et al. 2019). However, the results showed that plants treated with EBR showed benefits in these variables, reinforcing that EBR plays an important role in maintaining PSII efficiency and protecting the photosynthetic apparatus in plants subjected to water deficit (Siddiqui et al. 2018b; Barros Junior et al. 2021). Hu et al. (2019) studying the application of 0.1 μM of EBR on *Capsicum annuum* leaves under water restriction observed a significant increase in F_v/F_m , clearly alleviating the deleterious effects on the photosynthetic apparatus. Pereira et al. (2019) evaluating the mechanisms of action of EBR (0, 50, and 100 nM) on electron transport and photosynthesis in *Glycine max* plants affected by water deficit reported that the application of 100 nM of EBR induced a significant reduction in F_0 (29%) when compared to water deficit without EBR.

Plants treated with EBR had increases in Φ_{PSII} , q_p and ETR and decreases in NPQ, EXC and ETR/P_N . Φ_{PSII} is often used to measure the proportion of light absorbed by the PSII for the photochemical reaction (Khan et al. 2019). Increase stimulated by EBR spray on Φ_{PSII} is directly related to the intensification of the electron transfer capacity of the photosynthetic structure and the greater proportion of absorbed light energy used for the photochemical reaction, consequently provoking the increase in ETR (Su et al. 2021; Thussagunpanit et al. 2015). For q_p , increment after EBR treatment indicates that this molecule promoted a decrease in the reduced fraction of quinone A (Q_A) of the PSII, inducing the lower susceptibility to photoinhibition (Baker 2008). Reduction in NPQ in plants sprayed with EBR are related to results found in F_0 and F_m , being explained by the maintenance of excitation energy transfer from PSII antennas to PSII reaction centers, maintaining q_p values under stress conditions (Olvera-González et al. 2013). This variable reflects the proportion of light energy absorbed by the PSII antenna pigment that dissipates in the form of heat (Calatayud and Barreno 2004; Guo et al. 2006; Huang et al. 2006; Wilson and Ruban 2020; Shi et al. 2022).

EXC is positively correlated with ETR/P_N , as well as with the activities of SOD and APX enzymes (Silva et al. 2012), being highly influenced by the drought stress. In general, water deficit provokes photochemical damages in photosynthetic apparatus, causing a prominent increase in EXC (Chagas et al. 2008). Our study demonstrated that EBR decreased EXC, evidencing an effective role of EBR, controlling the excess of electrons linked to carbon fixation process and consequent oxidative protection against reactive oxygen species in chloroplast (Silva et al. 2015, 2018; Maia Júnior et al. 2020; Castillejo-Morales et al. 2021; Waqas et al. 2021). Hu et al. (2013) investigating the role of EBR (0.01 mg L^{-1}) in *Capsicum annuum* submitted to drought for 10 days, observed that treatment with this steroid mitigated the deleterious effects on Φ_{PSII} and q_p . (Lima and Lobato 2017) evaluating the drought responses of *Vigna unguiculata* treated with three EBR concentrations (0, 50 and 100 nM) found that the application of 100 nM EBR resulted in reductions of 30% in NPQ (30%), EXC (19%) and ETR/P_N (12%), compared to water deficit treatment + 0 nM EBR.

The EBR application mitigated the deleterious effects on gas exchange. The increases described in P_N , E , g_s , and WUE are related to probable fact that EBR increases CO_2 uptake and improves stomatal performance with consequent photosynthetic efficiency (Shu et al. 2016; Barros Junior et al. 2017), whereas the reduction in C_i and increase in P_N/C_i suggests that there was an increase in activity of Ribulose-1,5-

bisphosphate carboxylase/oxygenase (RuBisCO), with subsequent increase in CO₂ uptake into Calvin-Benson cycle (Cascaes et al. 2022). Khamsuk et al. (2018) studying *Capsicum annum* plants treated with 1 µM EBR applied under drought found increases in P_N , E and g_s , compared to plants without EBR. Farooq et al. (2009) working with *Oryza sativa* plants and BRs exogenously applied in conditions of drought stress observed that BRs application improved WUE.

Plants sprayed with EBR and submitted to water deficit presented increases in macronutrients (Ca, P and Mg) and micronutrients (Mn, Fe and Zn) content. These results demonstrate that exogenous application of EBR can mitigate the negative impacts on nutrient uptake under water stress, being explained by the better ionic balance and osmotic adjustment (Wu et al. 2017). Additionally, this restricted absorption of essential elements combined with oxidative stress are the main reasons for the decreases in growth, development and biomass production, as proven in this study (Ahanger et al. 2016; Alam et al. 2019). Kaya et al. (2019) evaluating the EBR roles on *Capsicum annum* plants under water deficit detected a significant increase in Ca content in plants treated with EBR, in relation to plants only under water stress. Ribeiro et al. (2020) observing the effects of Ni excess on young *Eucalyptus urophylla* plants treated with 100 nM of EBR detected increases in P, Ca and Mn contents in the root, stem and leaf, comparing with equal treatment without EBR. Santos et al. (2018) investigating the impact of exogenous application of EBR on *Vigna unguiculata* plants under Cd toxicity found significant increases in Mg, Fe and Zn.

EBR stimulated the activities of SOD, CAT, APX and POX enzymes, being intrinsically associated with the modulation of the antioxidant defense system in plants, indicating that EBR minimizes the oxidative stress triggered by the accumulation of free radicals and the intoxication caused by reactive species of oxygen (Hasheminasab et al. 2012; Verma et al. 2012; Zulfiqar and Ashraf 2021). The results obtained in this research suggest that EBR benefits SOD activity, being an enzyme capable of rapidly converting O₂⁻ into H₂O₂ (Li et al. 2016), with H₂O₂ being catalyzed by antioxidant enzymes (CAT, APX and POX). Our study confirmed this fact by increasing the activities of CAT, APX and POX, which convert H₂O₂ into unreactive compounds, such as H₂O and O₂ (Rajput et al. 2021; Fujita and Hasanuzzaman 2022). Behnamnia et al. (2009) submitting *Lycopersicon esculentum* plants pre-treated with three concentrations of EBR (0, 0.01 and 1 µM) and exposed to water deficit showed an increase in CAT and APX activities after the application of 1 µM EBR. Lone et al. (2022) studying the drought effects on *Brassica rapa* plants treated with EBR detected significant increases in SOD, CAT, APX and POX, revealing a better performance of the antioxidant system of plants treated with EBR, compared to plants subjected to water deficit.

The EBR spray mitigated the effects on accumulation of oxidant compounds in plants under water deficit. Reductions detected in O₂⁻, H₂O₂, MDA and EL are clearly related to EBR actions on activities of antioxidant enzymes, observed in this study, increasing the ROS elimination, minimizing oxidative stress and membrane damages caused by water stress (Cui et al. 2011). ROS damage proteins and lipids, main components of the membrane, impairing the plant cell functions (Gill and Tuteja 2010). However, EBR minimizes this damages, causing stability of the leaf tissue membranes (Talaat and Shawky 2013), which can be proven by the decreases in EL, MDA, TDM, proven in this research. Farooq et al. (2010) investigating the exogenous application of 0.01 µM EBR in *Oryza sativa* under water deficit found significant decreases in MDA and H₂O₂, comparing with water deficit without EBR. Ribeiro et al. (2019)

studying the effects of 0, 50 and 100 nM of EBR in *Glycine max* seedlings subjected to water deficit resulted in reductions in O_2^- (38%), H_2O_2 (24%), MDA (22%) and EL (22%) in seedlings treated with 100 nM of EBR under water deficit, if compared with treatment without steroid.

After exogenous EBR application, plants subjected to water deficit had increases in variables related to growth (LDM, RDM, SDM and TDM). This benefits on growth parameters are associated with responses related to Φ_{PSII} , ETR, and P_N , as previously observed in this study after the EBR utilization. Parallely, EBR-induced growth promotion is directly related to cell elongation and division (Castorina and Consonni 2020; Nolan et al. 2020), probably by the EBR mechanism activating the ATPases enzymes in plasma membrane, improving the mitosis process (Oh et al. 2020). Aghaee and Rahmani (2019) studying the application of 10^{-8} M EBR in plants of *Linum usitatissimum* under water deficiency described a significant increases in RDM and shoot dry matter, compared to plants subjected only to water deficit. Pereira et al. (2019) working with *Glycine max* plants treated with EBR (100 nM) and exposed to water deficit found increases of 13%, 11% and 8% in LDM, SDM and TDM, respectively.

Conclusion

This research clearly demonstrated that the exogenous application of EBR attenuated the deleterious effects caused by water deficit in *C. guianensis* plants, which was confirmed by improvements in hydraulic attributes, in biochemical, physiological, nutritional behaviors and biomass. This steroid increased the values of water potential and hydraulic safety margin, reducing the risks of the species to embolism. The application of EBR promoted beneficial effects on the effective quantum efficiency of PSII, with a consequent increase in electron transport and reduction of damage caused by photoinhibition. Positive results were found in gas exchange, in which EBR increased CO_2 fixation and stimulated stomatal performance, resulting from direct effects related to hydraulic maintenance and indirectly linked to increases in macro and micronutrients. Additionally, this plant growth regulator stimulated the enzyme activities linked to the antioxidant system (SOD, CAT, APX and POX), improving the redox balance, corroborated by the reduction of stress indicators (H_2O_2 and O_2^-), maintenance of photosynthetic pigments and growth. Therefore, our results prove that pre-treatment with EBR improved drought tolerance in young *C. guianensis* plants.

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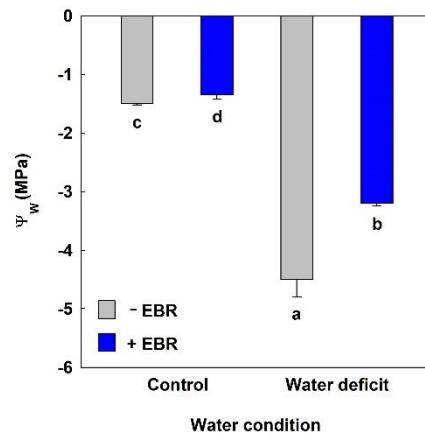
Figures

Fig 1. Leaf water potential in young *Carapa guianensis* plants pretreated with EBR and exposed to water deficit. Columns with different letters indicate significant differences from the Scott-Knott test ($P < 0.05$). Columns corresponding to means from six

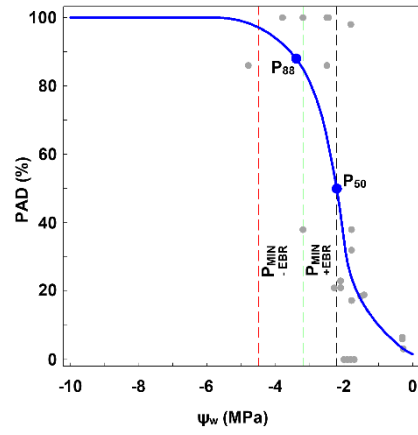


Fig 2. Cavitation vulnerability curve and minimum water potential in leaf of young *Carapa guianensis* plants pretreated with EBR and exposed to water deficit.

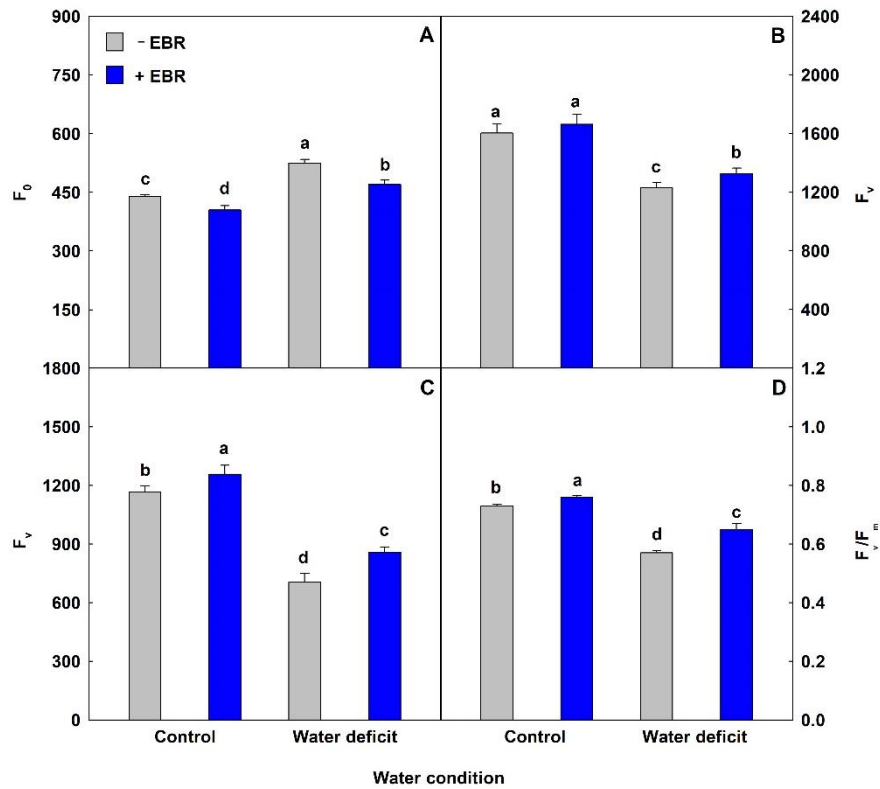


Fig 3. Minimal fluorescence yield of the dark-adapted state (F_0 ; A), maximal fluorescence yield of the dark adapted state (F_m ; B), variable fluorescence (F_v ; C) and maximal quantum yield of PSII photochemistry (F_v/F_m ; D) in young *Carapa guianensis* plants pretreated with EBR and exposed to water deficit. Columns with different letters indicate significant differences from the Scott-Knott test ($P < 0.05$). Columns corresponding to means from six repetitions and standard deviations.

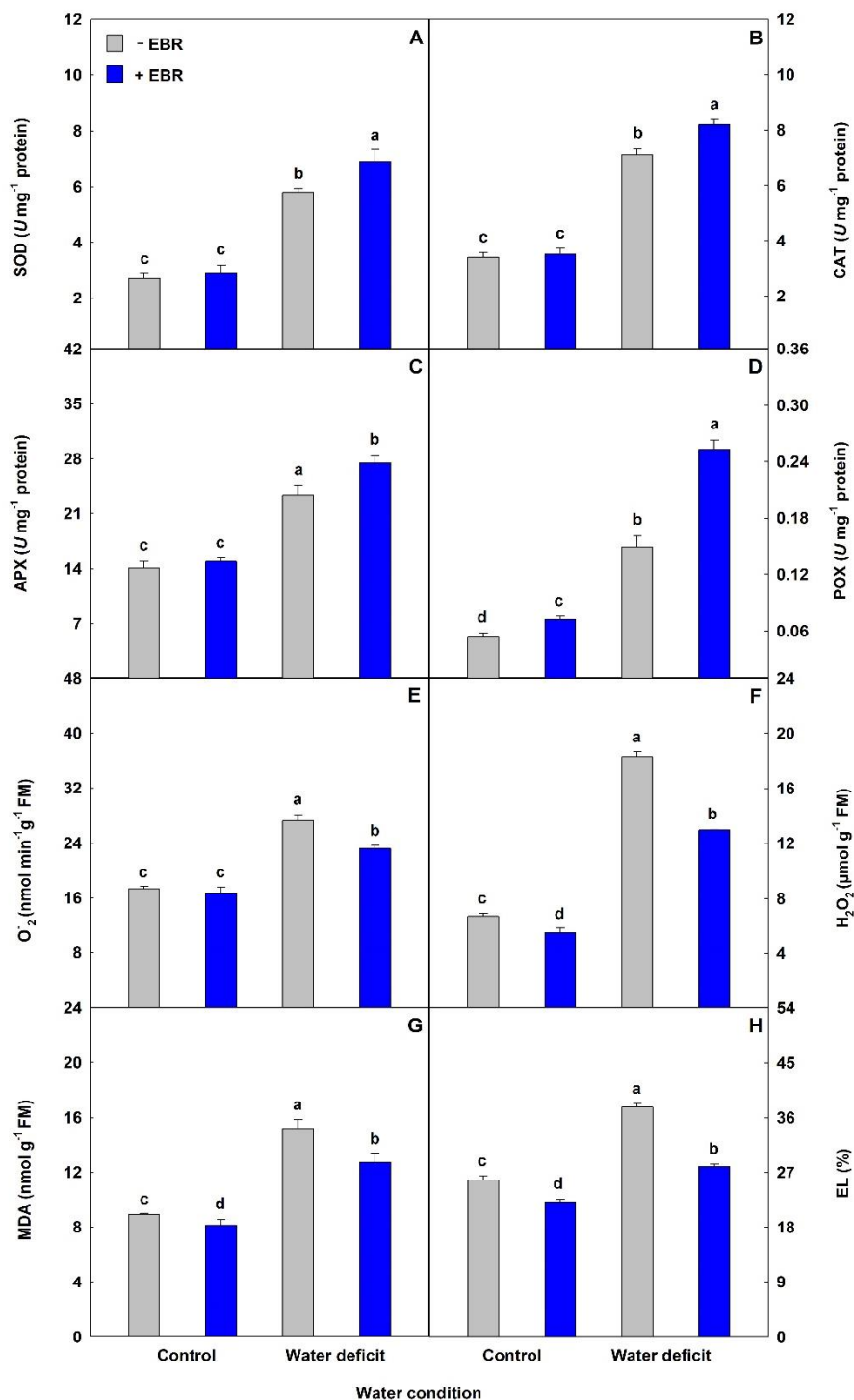


Fig 4. Superoxide dismutase (SOD; A), catalase (CAT; B), ascorbate peroxidase (APX; C), peroxidase (POX; D), Superoxide (O_2^- ; E), hydrogen peroxide (H_2O_2 ; F), malondialdehyde (MDA; G) and electrolyte leakage (EL; H) in young *Carapa guianensis* plants pretreated with EBR and exposed to water deficit. Columns with different letters indicate significant differences from the Scott-Knott test ($P < 0.05$). Columns corresponding to means from six repetitions and standard deviations.

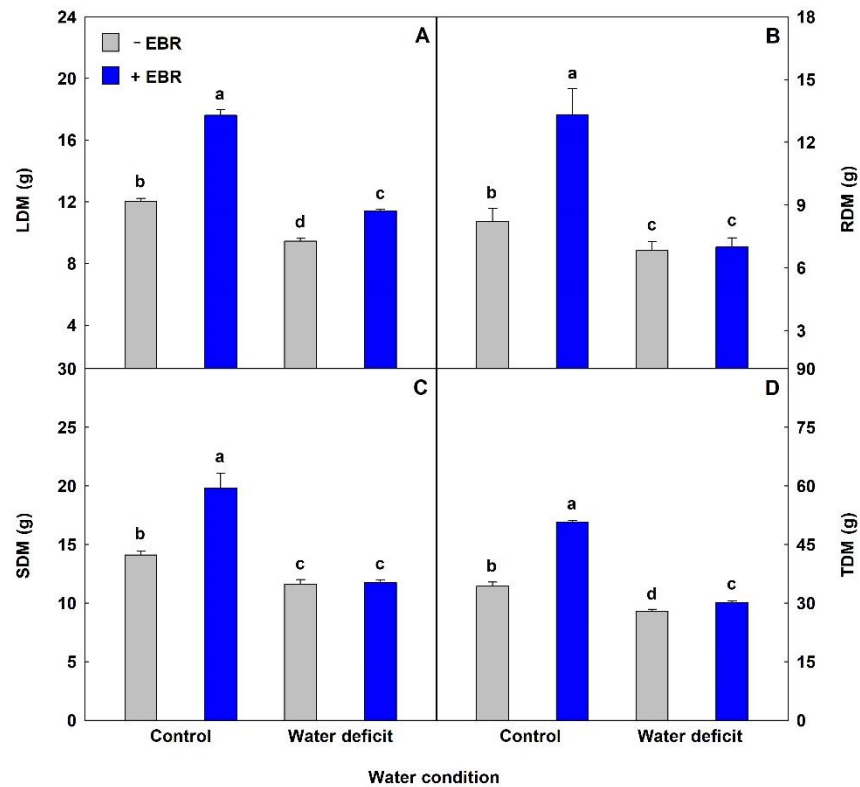


Fig 5. Leaf dry matter (LDM; A), root dry matter (RDM; B), stem dry matter (SDM; C) and total dry matter (TDM; D) in young *Carapa guianensis* plants pretreated with EBR and exposed to water deficit. Columns with different letters indicate significant differences from the Scott-Knott test ($P < 0.05$). Columns corresponding to means from six repetitions and standard deviations.

TablesTable 1. Nutrient contents in young *Carapa guianensis* plants pretreated with EBR and exposed to water deficit.

Contents in root							
Water condition	EBR	Ca (mg g DM ⁻¹)	P (mg g DM ⁻¹)	Mg (mg g DM ⁻¹)	Mn (µg g DM ⁻¹)	Fe (µg g DM ⁻¹)	Zn (µg g DM ⁻¹)
Control	-	6.47 ± 0.12b	2.60 ± 0.09a	4.10 ± 0.05b	589.20 ± 5.93b	11032.1 ± 361.4b	56.02 ± 3.57a
Control	+	6.82 ± 0.09a	2.65 ± 0.13a	4.26 ± 0.10a	638.28 ± 25.57a	12373.6 ± 216.6a	58.12 ± 2.17a
Water deficit	-	5.52 ± 0.11d	2.12 ± 0.09b	3.26 ± 0.11d	435.48 ± 13.67c	2524.2 ± 53.6d	50.39 ± 1.76b
Water deficit	+	5.86 ± 0.09c	2.24 ± 0.07b	3.55 ± 0.05c	586.21 ± 15.65b	4997.3 ± 86.4c	53.04 ± 0.84b
Contents in stem							
Water condition	EBR	Ca (mg g DM ⁻¹)	P (mg g DM ⁻¹)	Mg (mg g DM ⁻¹)	Mn (µg g DM ⁻¹)	Fe (µg g DM ⁻¹)	Zn (µg g DM ⁻¹)
Control	-	19.79 ± 0.30b	4.18 ± 0.11b	6.45 ± 0.40b	72.56 ± 4.09a	78.94 ± 1.60b	54.00 ± 1.50b
Control	+	22.39 ± 0.76a	4.42 ± 0.10a	8.20 ± 0.07a	74.48 ± 2.43a	98.65 ± 2.72a	59.18 ± 2.52a
Water deficit	-	15.49 ± 0.20d	3.66 ± 0.10d	5.13 ± 0.02c	58.91 ± 3.21b	52.28 ± 1.50d	41.28 ± 2.91d
Water deficit	+	17.53 ± 0.89c	4.02 ± 0.10c	5.36 ± 0.09c	68.90 ± 2.44c	56.60 ± 2.43c	46.91 ± 1.98c
Contents in leaf							
Water condition	EBR	Ca (mg g DM ⁻¹)	P (mg g DM ⁻¹)	Mg (mg g DM ⁻¹)	Mn (µg g DM ⁻¹)	Fe (µg g DM ⁻¹)	Zn (µg g DM ⁻¹)
Control	-	20.54 ± 0.28b	2.72 ± 0.06b	4.41 ± 0.05b	124.55 ± 4.46b	247.12 ± 2.10b	41.72 ± 0.85b
Control	+	24.02 ± 0.25a	3.02 ± 0.05a	4.63 ± 0.09a	134.58 ± 1.99a	257.76 ± 7.27a	43.99 ± 0.58a
Water deficit	-	17.47 ± 0.18d	2.25 ± 0.06d	3.24 ± 0.09d	106.61 ± 3.31d	102.74 ± 1.91d	28.32 ± 1.75d
Water deficit	+	19.28 ± 0.6c	2.50 ± 0.04c	3.49 ± 0.11c	118.57 ± 2.30c	147.50 ± 4.04c	33.70 ± 0.95c

Ca = calcium; P = phosphorus; Mg = magnesium; Mn = manganese; Fe = iron; Zn = zinc. Columns with different letters indicate significant differences from the Scott-Knott test ($P < 0.05$). Values described corresponding to means from six repetitions and standard deviations.

Table 2. Photosynthetic pigments, chlorophyll fluorescence and gas exchange in young *Carapa guianensis* plants pretreated with EBR and exposed to water deficit.

Photosynthetic pigments							
Water condition	EBR	Chl <i>a</i> (mg g ⁻¹ FM)	Chl <i>b</i> (mg g ⁻¹ FM)	Total Chl (mg g ⁻¹ FM)	Car (mg g ⁻¹ FM)	Ratio Chl <i>a</i> /Chl <i>b</i>	Ratio Total Chl/Car
Control	-	6.60 ± 0.31b	5.08 ± 0.23b	11.68 ± 0.08b	1.21 ± 0.03b	1.30 ± 0.12b	9.69 ± 0.29c
Control	+	7.50 ± 0.13a	6.90 ± 0.09a	14.40 ± 0.04a	1.55 ± 0.04a	1.09 ± 0.03b	9.29 ± 0.19d
Water deficit	-	4.31 ± 0.05d	1.48 ± 0.11d	5.79 ± 0.07d	0.55 ± 0.01d	2.93 ± 0.25a	10.45 ± 0.15a
Water deficit	+	4.90 ± 0.06c	1.77 ± 0.21c	6.67 ± 0.16c	0.67 ± 0.02c	2.80 ± 0.40a	10.03 ± 0.22b
Chlorophyll fluorescence							
Water condition	EBR	Φ _{PSII}	q _P	NPQ	ETR (μmol m ⁻² s ⁻¹)	EXC (μmol m ⁻² s ⁻¹)	ETR/P _N
Control	-	0.278 ± 0.010a	0.186 ± 0.005b	0.74 ± 0.03c	40.92 ± 1.45a	0.616 ± 0.008c	8.42 ± 0.48c
Control	+	0.280 ± 0.009a	0.219 ± 0.011a	0.59 ± 0.01d	41.16 ± 1.31a	0.605 ± 0.012c	5.56 ± 0.36d
Water deficit	-	0.177 ± 0.015c	0.125 ± 0.011d	2.35 ± 0.10a	25.97 ± 2.21c	0.714 ± 0.021a	15.33 ± 1.52a
Water deficit	+	0.220 ± 0.013b	0.140 ± 0.006c	1.38 ± 0.13b	32.30 ± 1.95b	0.653 ± 0.012b	13.87 ± 0.09b
Gas exchange							
Water condition	EBR	P _N (μmol m ⁻² s ⁻¹)	E (mmol m ⁻² s ⁻¹)	g _s (mol m ⁻² s ⁻¹)	C _i (μmol mol ⁻¹)	WUE (μmol mmol ⁻¹)	P _N /C _i (μmol m ⁻² s ⁻¹ Pa ⁻¹)
Control	-	4.87 ± 0.21b	1.43 ± 0.08b	0.133 ± 0.012b	314 ± 6c	3.42 ± 0.24b	0.015 ± 0.001b
Control	+	7.43 ± 0.55a	1.74 ± 0.11a	0.160 ± 0.011a	300 ± 5d	4.29 ± 0.31a	0.025 ± 0.002a
Water deficit	-	1.70 ± 0.11d	0.78 ± 0.04d	0.050 ± 0.006d	387 ± 4a	2.19 ± 0.17c	0.004 ± 0.000d
Water deficit	+	2.33 ± 0.10c	0.99 ± 0.03c	0.077 ± 0.005c	363 ± 5b	2.37 ± 0.08c	0.006 ± 0.000c

Chl *a* = chlorophyll *a*; Chl *b* = chlorophyll *b*; Total chl = total chlorophyll; Car = carotenoids; Φ_{PSII} = effective quantum yield of PSII photochemistry; q_P = photochemical quenching coefficient; NPQ = nonphotochemical quenching; ETR = electron transport rate; EXC = relative energy excess at the PSII level; ETR/P_N = ratio between the electron transport rate and net photosynthetic rate; P_N = net photosynthetic rate; E = transpiration rate; g_s = stomatal conductance; C_i = intercellular CO₂ concentration; WUE = water-use efficiency; P_N/C_i = carboxylation instantaneous efficiency. Columns with different letters indicate significant differences from the Scott-Knott test ($P < 0.05$). Values described corresponding to means from six repetitions and standard deviations.